# Consequences of climate change and land-use intensification for decomposer communities and decomposition processes

## Folgen von Klimawandel und intensiver Landnutzung für Zersetzergemeinschaften und Abbauprozesse

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*“In nature, nothing is wasted – not even waste”*

– Richard Jones

# Zusammenfassung

Die Zunahme intensiv genutzter Landschaften und der Klimawandel sind direkte und indirekte Folgen menschlichen Handelns, verursacht durch eine wachsende Weltbevölkerung und zunehmende Mengen an Treibhausgasen. Die Zahl der wissenschaftlichen Studien, die sich mit den Veränderungen der Umwelt und den Konsequenzen für Ökosysteme, einschließlich Flora, Fauna und Ökosystemleistungen auseinandersetzen, steigt stetig. Mit dieser Thesis möchte ich meinen Beitrag zu diesem wichtigen und aktuellen Forschungsgebiet leisten. Dazu untersuche ich die Auswirkungen von Landnutzung und Klima auf die Ökosystemleistung „Zersetzung toten organischen Materials“ (Nekromasse) und die Auswirkungen auf die daran beteiligten Arthropoden- und Mikrobengemeinschaften.

Kapitel II dieser Thesis setzt sich mit den Konsequenzen von intensiver Landnutzung und Klimawandel für die Ökosystemleistung „Zersetzung toten Materials“ auseinander. Unter Anbetracht des globalen Insektenrückgangs, wurde dieser Aspekt anhand eines Insektenausschluss-Experimentes zusätzlich simuliert. Es stellt sich heraus, dass sowohl der Abbau von Dung als auch von Aas sehr robust gegenüber landschaftlicher Nutzung war. Zudem blieb der Abbau von Dung unberührt von Temperaturänderungen und dem Ausschluss von Insekten. Entlang eines Höhengradienten wurde hingegen ein Trend zu einem unimodalen Muster mit maximaler Zersetzung bei ca. 600-700 m ü.M. beobachtet. Dieser Trend lässt vermuten, dass in dieser Höhe das Verhältnis von Niederschlag und Temperatur ideal für Dung zersetzende Gemeinschaften ist. Aas hingegen wurde in zunehmender Höhe und unter der Beteiligung von Insekten schneller zersetzt, was verdeutlich, dass Klimaänderungen und ein ansteigender Insektenrückgang starke Auswirkungen auf die Zersetzung von Aas und somit auf Nährstoffkreisläufe haben können. Hierbei wurde zudem ersichtlich, dass verschiedene Typen von Nekromasse unterschiedlich auf Umweltparameter reagieren und daher in künftigen Studien und Auswertungen separat betrachtet werden sollten.

Kapitel III behandelt die Auswirkungen von Landnutzung und Klima auf die Biodiversität und Spezialisierung von Käfergemeinschaften an Dung. Hierbei wurden sämtliche Käfer berücksichtigt, welche vor allem an Dung, Aas oder sonstigem faulenden Material gefunden werden können. Sowohl α- als auch γ-Diversität von diesen Käfern wurde durch Agrarlandschaften und urbane Gebiete stark reduziert. Hohe Niederschlagsmengen wirkten sich negativ auf die Abundanz von Dungkäfern aus, wohingegen die γ-Diversität in warmen Regionen am niedrigsten war. Der Grad der Spezialisierung von Käfergemeinschaften auf verschiedene Dungressourcen nahm mit abnehmenden Temperaturen zu. Aus den Ergebnissen geht hervor, dass sowohl intensive Landnutzung als auch Klimaveränderungen Auswirkungen auf die Diversität und den Spezialisierungsgrad von Käfergemeinschaften an Dung haben können und somit das ökologische Gleichgewicht der Dungkäfergemeinschaften und ihren Ökosystemfunktionen beeinflussen können.

Das darauffolgende Kapitel IV stellt eine Ergänzung zu Kapitel II dar. Hier wird die Zersetzung von Aas nicht nur anhand von Landnutzung und Klima erklärt, sondern auch anhand der α-Diversität und der Artenzusammensetzung von Käfern und Bakterien an Aas diskutiert. Es zeigte sich, dass Abundanz und Artenzusammensetzung der Bakteriengemeinschaft an Aas vor allem von der Temperatur abhingen. Außerdem wurde die Zersetzungsgeschwindigkeit maßgeblich von der Bakteriengemeinschaft und der Niederschlagsmenge bestimmt. Mit dieser Studie konnte ich zeigen, dass Bakterien trotz ihrer mikroskopischen Größe maßgeblich an der Zersetzung von Aas beteiligt sind und diese in Zersetzungsversuchen nicht vernachlässigt werden sollten.

Das letzte Kapitel, Kapitel V, befasst sich mit den Konsequenzen von intensiver Landnutzung und Klimawandel auf mikrobielle Gemeinschaften in Totholz. Untersucht wurden hier sowohl Bakterien- als auch Pilzgemeinschaften. Haupttreiber der Artenvielfalt für beide Gruppen (gemessen als Anzahl an OTUs) war das Klima (Niederschlag und Temperatur). Ein wärmeres Klima kam der Vielfalt von Bakterien zugute, wohingegen die Pilzvielfalt nicht tangiert wurde. Außerdem reagierten Pilze negativ auf urbane Landnutzung, Bakterienvielfalt in Totholz war auf Wiesen jedoch höher als im Wald. Vor allem Pilze zeigten eine sehr starke Bindung zu ihrem Wirtsbaum, welche auch von äußeren Einflüssen wie Landnutzung und Klima nicht beeinflusst werden konnte. Die Spezialisierung von Bakterien hingegen wurde stark von Landnutzung und Klima beeinflusst. Diese Ergebnisse untermauern frühere Studien, die besagen, dass Pilze hoch spezialisiert sind und geben neue Erkenntnisse zur Robustheit der Spezialisierung gegenüber Landnutzungsintensität und Klima.

Zusammenfassend kann ich sagen, dass sowohl Klima als auch Landnutzung Auswirkungen auf die Biodiversität haben. Während Temperatur und Niederschlag jedoch positive so wie negative Effekte hatten, wirkte sich anthropogene Landnutzung überwiegend negativ auf die Diversität von Zersetzergemeinschaften aus.

# Summary

The increase in intensively used areas and climate change are direct and indirect consequences of anthropogenic actions, caused by a growing population and increasing greenhouse gas emissions. The number of research studies, investigating the effects of land use and climate change on ecosystems, including flora, fauna, and ecosystem services, is steadily growing. This thesis contributes to this research area by investigating land-use and climate effects on decomposer communities (arthropods and microbes) and the ecosystem service ‘decomposition of dead material’.

Chapter II deals with consequences of intensified land use and climate change for the ecosystem service ‘decomposition of dead organic material’ (necromass). Considering the severe decline in insects, we experimentally excluded insects from half of the study objects. The decomposition of both dung and carrion was robust to land-use changes. Dung decomposition, moreover, was unaffected by temperature and the presence/ absence of insects. Along the altitudinal gradient, however, highest dung decomposition was observed at medium elevation between 600 and 700 m above sea level (although insignificant). As a consequence, we assume that at this elevation there is an ideal precipitation:temperature ratio for decomposing organisms, such as earthworms or collembolans. Carrion decomposition was accelerated by increasing elevation and by the presence of insects, indicating that increasing variability in climate and an ongoing decline in insects could modify decomposition processes and consequently natural nutrient cycles. Moreover, we show that different types of dead organic material respond differently to environmental factors and should be treated separately in future studies.

In Chapter III, we investigated land-use and climate effects on dung-visiting beetles and their resource specialization. Here, all beetles that are preferentially found on dung, carrion or other rotten material were included. Both α- and γ-diversity were strongly reduced in agricultural and urban areas. High precipitation reduced dung-visiting beetle abundance, whereas γ-diversity was lowest in the warmest regions. Resource specialization decreased with increasing temperatures. The results give evidence that land use as well as climate can alter dung-visiting beetle diversity and resource specialization and may hence influence the natural balance of beetle communities and their contribution to the ecosystem service ‘decomposition of dead material’.

The following chapter, Chapter IV, contributes to the findings in Chapter II. Here, carrion decomposition is not only explained by land-use intensity and climate but also by diversity and community composition of two taxonomic groups found on carrion, beetles and bacteria. The results revealed a strong correlation between bacteria diversity and community composition with temperature. Carrion decomposition was to a great extent directed by bacterial community composition and precipitation. The role of beetles was neglectable in carrion decomposition. With this study, I show that microbes, despite their microscopic size, direct carrion decomposition and may not be neglected in future decomposition studies.

In Chapter V a third necromass type is investigated, namely deadwood. The aim was to assess climate and land-use effects on deadwood-inhabiting fungi and bacteria. Main driver for microbial richness (measured as number of OTUs) was climate, including temperature and precipitation. Warmer climates promoted the diversity of bacteria, whereas fungi richness was unaffected by temperature. In turn, fungi richness was lower in urban landscapes compared to near-natural landscapes and bacteria richness was higher on meadows than on forest sites. Fungi were extremely specialized on their host tree, independent of land use and climate. Bacteria specialization, however, was strongly directed by land use and climate. These results underpin previous studies showing that fungi are highly specialized in contrast to bacteria and add new insights into the robustness of fungi specialization to climate and land use.

I summarize that climate as well as intensive land use influence biodiversity. Temperature and precipitation, however, had positive and negative effects on decomposer diversity, while anthropogenic land use had mostly negative effects on the diversity of decomposers.

# Chapter I

## Introduction

# Introduction

How does global change affect biodiversity and the stability of ecosystems? To answer this question, it is important to unravel global change into its major components – land-use intensification and climate change.

In the Brundtland Report, sustainable development is defined as "development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (World Commission on Environment and Development 1987). Ecologically, this implies a conscious use of resources provided by nature. Land-use intensification, however, is named the biggest threat to biodiversity (Díaz et al. 2019) and, hence, to a sustainable world. Within the last half-century, the biodiversity of terrestrial communities has decreased by more than 20 % and more than 60 % of the services provided by nature have been negatively impacted by human activities. Alarmingly, this impact is accelerating (Millennium Ecosystem Assessment 2005; Díaz et al. 2019). The transformation from natural to anthropogenic land use is often a result of deforestation, habitat fragmentation and increased use of pesticides (Dudley and Alexander 2017; Tittensor et al. 2014). These disturbances have severe consequences for the quality of habitats and entire ecosystems (Lauber et al. 2008; Polasky et al. 2011; Ipcc 2021).

Within the last decades, global agricultural landscapes have increased by 12 %, mainly originating from near-natural landscapes. More than 10 % of anthropogenic greenhouse gases are produced by livestock, making agriculture one of the major contributors to climate change (Dudley and Alexander 2017). Climate change is characterized by increasing temperatures, an increased frequency and intensity of extreme weather events, drought, or shifts in precipitation rates (Ipcc 2021). For about 20 years we are aware that these modifications of the abiotic environment affect biodiversity through numerous shifts in species abundance and distributions as stated by Parmesan and Yohe (2003). Affected organisms are, for instance, amphibians (Hof et al. 2011), insects (Halsch et al. 2021), birds (Jetz et al. 2007; Mantyka-Pringle et al. 2015), mammals (Mantyka-Pringle et al. 2015), and microbes (Tiedje et al. 2022).

Global warming and the destruction of natural habitats are assumed to be additive threats to biodiversity (Hof et al. 2011) and the interaction of these stressors might exacerbate the risk of biodiversity loss (Mantyka-Pringle et al. 2015; Jetz et al. 2007; Sala et al. 2000; Visconti et al. 2016). Further, climate change modifies habitat characteristics and, thus, can enhance habitat conversion effects on biodiversity (Mantyka-Pringle et al. 2015).

There is a serious conflict between the global demand for food, water, and energy and the urgent need to protect biodiversity and ecosystems. The fact that consequences for biodiversity are often accompanied by consequences for human beings is often overlooked. Biodiversity is the foundation for many ecosystem functions, which maintain the balance of ecosystems. These functions often directly result in ecosystem services. Ecosystem services are defined as benefits people obtain from nature and can be distinguished into cultural services (e.g. spiritual places), provisioning services (e.g. food production), and regulating services (e.g. flood control by forests) (Haines-Young and Potschin 2018). As the name suggests, regulating services are particularly relevant for the regulation and maintenance of ecosystems. This includes, among others, the control of erosion rates, wind protection or pest and disease control (Haines-Young and Potschin 2018). One crucial but often neglected regulating service is the natural ‘waste removal’: the decomposition of dead organic matter (necromass), such as dung, carrion, and deadwood. In the following, I will explain the importance of decomposition processes and introduce two major actors in this process, namely microbes and beetles.

## Importance of decomposition processes

Considering that solely deadwood already harbours about 8 % of the global carbon stock (Pan et al. 2011), the decomposition of these massive amounts of dead organic matter, including deadwood, dung, and carrion, is an essential function for the self-regulation of ecosystems and an ecosystem service to human beings by maintaining nutrient cycles and fertilizing soils (Thompson et al. 2014). In contrast to deadwood, dung and carrion are quickly colonized by various organisms that disintegrate the necromass in a minimum of time (Holter 2016; Benbow et al. 2015). Deadwood, however, may last for several decades and serves as a food resource for many organisms over a long period (Bobiec et al. 2005). Nutrients such as nitrogen, phosphorous or carbon are released into the soil through decomposers, where they serve as new nutrients for other soil-inhabiting organisms and plants (Bobiec et al. 2005; Moore et al. 2004).

### Decomposer communities

Necromass, in this study comprising dung, carrion, and deadwood, is an almost ubiquitous resource, which not only serves as a food resource for various organisms but also as a temporary habitat (Stokland et al. 2012; Hanski and Cambefort 1991; Benbow et al. 2015). As mentioned above, necromass is an important source of nutrients and is decomposed by a complex multispecies community, including microbes and insects amongst others (Hanski and Cambefort 1991; Moore et al. 2004; 2019; Benbow et al. 2015; Newsome et al. 2021).

Although they are physically the smallest contributors, 90% of all organic matter is decomposed by microbes (Swift et al. 1979). During decomposition, microbes emit odours, so-called volatile organic compounds. Volatile profiles, a bouquet of different volatile organic compounds, can vary among microbial succession, decomposition stages, substrates, and environmental conditions (Cammack et al. 2015; Dekeirsschieter et al. 2009; Pascual et al. 2017). Variations in volatile profiles are expected to determine the assemblage of necromass-feeding insects (von Hoermann et al. 2011; Crippen et al. 2015; Dormont et al. 2007; Sladecek et al. 2021; Weisskopf et al. 2021; Benbow et al. 2015; Leather et al. 2014). Thus, changes in microbial community composition potentially caused by climate change or intensified land use might lead to modified volatile profiles, which in turn might determine attracted insects (Benbow et al. 2015; Frank et al. 2017a). Alterations in decomposition rates and nutrient cycles might be the final product of these changes in necromass communities. Despite their importance in decomposition processes, only little attention has been paid to the responses of necromass-inhabiting microbes to climate change and land-use intensification. Furthermore, potential consequences from these responses for ecosystems remain unclear (Wilson et al. 2007; Barton and Bump 2019).

Insect decline, as observed in recent studies (e.g., Seibold et al. 2019; Hallmann et al. 2017; Wang et al. 2017), is a great threat not only to ecosystems but also to ecosystem services. A reduction in functional diversity of dung beetles, for instance, results in lower decomposition rates (Beynon et al. 2012). Retardation or malfunction of the decomposition of cattle faeces through a decline in dung beetles could lead to fouling of rangeland (seen already e.g. in Australia) and attract pest species, which leads to drastic economic losses (Castle and MacDaid 1972; Losey and Vaughan 2006). Decomposers, such as dung- and carrion-decomposing beetles, hence, represent an important functional group. Still, it remains an open question how climate and land use affect decomposer communities, insects, and microbes, on different necromass types.

## Knowledge gap

Even though there exist several studies about climate and land-use effects on single decomposer communities and decomposition processes across all necromass types (e.g. von Hoermann et al. 2018; Carpaneto et al. 2007; Bässler et al. 2010), the majority of the studies focusses on insects or only one taxonomic group. Thus, an integrative broad-scale approach considering climate and land-use effects on different necromass types and multi-taxonomic decomposer groups is missing. With this thesis, I aim to shed light onto this knowledge gap. In addition, this thesis is among the first that seeks to answer the question to what extent beetle and microbial communities in concert contribute to decomposition processes in times of global change.

## Aim of this dissertation

In this thesis, I evaluate the impact of direct and indirect anthropogenic threats, i.e. land-use intensification and climate change on the diversity of arthropod and microbial decomposer communities on necromass and the ecosystem service ‘decomposition’ they provide. For this, decomposition processes and decomposer communities were assessed on 179 study sites across Bavaria, Germany, along a climate and land-use gradient. These study sites were established in Bavaria, Germany, as part of the LandKlif project.

To disentangle local and regional land-use effects on decomposer communities and decomposition processes, a nested design was used in which habitats (forest, grassland, arable sites, settlements as local land-use types) were embedded in different landscapes (near-natural, agricultural, urban as regional land-use types). First, I examined how climate and land use affect the decomposition of dung and carrion and whether the decomposition processes among necromass types differ (Chapter II). Second, I investigated the impact of land use and climate on the diversity of coprophilous beetles and their specialization on dung resources (Chapter III). In addition to climate and land-use effects on decomposition processes, I assessed arthropod and microbial communities on carrion and their contribution to decomposition processes in Chapter IV. As a third necromass type, I assessed whether land use and climate affect deadwood-inhabiting microbial richness and their host-tree specialization (Chapter V). In Chapter VI all results were summarized and set into the context of global change.

# Chapter II

## Diverse effects of climate, land use, and insects on dung and carrion decomposition

with

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## Summary

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 bison dung, on 179 study sites in Central Europe across an elevational climate gradient of 168 to 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 – 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 temperature. 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.

## Introduction

The decomposition of organic matter (detritus or necromass) is a crucial process for nutrient cycling (Cardinale et al. 2012), influences trophic networks, and stabilizes ecosystem structure and function (Moore et al. 2004; Nichols et al. 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, i.e. climate change and intensified land use, exacerbates the risk of biodiversity loss (Jetz et al. 2007; Mantyka-Pringle et al. 2015; Sala et al. 2000; Visconti et al.

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 (Hanski and Cambefort 1991; Moore et al. 2004; 2019; Benbow et al. 2015). Over the past several decades, however, there have been documented reductions in terrestrial insect biomass by more than two-thirds in Germany (Hallmann et al. 2017; Seibold et al. 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 et al. 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 et al. 2012). Without the ecosystem service provided by dung beetles, however, slowly decomposing cattle feces would lead to fouling of rangeland (e.g. 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 et al. 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 et al. 2020; von Hoermann et al. 2018; 2020), and soil-inhabiting fungi in temperate regions, whereas soil-inhabiting bacterial abundance decreases with increasing temperatures (Castro et al. 2010). Higher microbial respiration rates were also observed at higher elevations despite cooler temperatures, suggesting moisture as another important determinant of microbial activity (Murphy et al. 1998). Yet, high microbial species richness, e.g. in deadwood, can also negatively correlate with decay rate due to competition among saprophytic species (Fukami et al. 2010; Hagge et al. 2019).

Land-use intensification leads to changes in soil properties, habitat loss, and habitat fragmentation (Dudley and Alexander 2017; Lauber et al. 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 et al. 2018). For dung beetles Frank et al. (2017b) 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 et al. 2008; Sánchez-Bayo and Wyckhuys 2019). Similarly, carrion-feeding insects are influenced by forest structure (Heidrich et al. 2020), soil properties (von Hoermann et al. 2018), and land-use type (Babcock et al. 2020; Dekeirsschieter et al. 2011). Furthermore, an increasing use of fertilizers, as a consequence of intensified land use, leads to a decrease in soil microbial diversity (French et al. 2017). Soil microbes, however, substantially contribute to nutrient cycling and accelerate decomposition processes (Dubey et al. 2019; Lauber et al. 2014). During decomposition microbes emit volatile organic compounds that can vary among habitats and substrates, and mediate carrion decomposition by attracting necrophagous insects (Cammack et al. 2015; Dekeirsschieter et al. 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 influences 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.

## Methods

### *Study sites*

This study was conducted in southeast Germany within the federal state Bavaria. We selected 60 study regions (~5.8 km x 5.8 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 m x 30 m) in the three most dominant local land-use types (habitats) out of four possible (i.e. 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 et al. (2021).

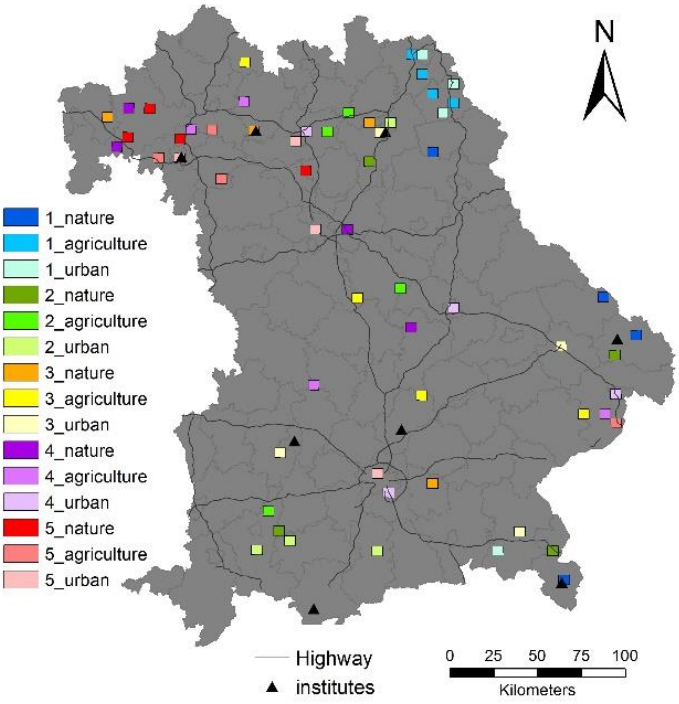

**Figure 1:** Location of study regions across Bavaria. Numbers (1-5) indicate climate zones; landscapes are defined as nature (near-natural), agriculture, and urban.

### *Study design and data collection*

In May 2019, two pats of European bison dung (á 450 g) and two rat carcasses (á 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 20th century (Kuemmerle et al. 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 et al. 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 ± 2 (mean ± SD) days and each pile was dried for five days at 100°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 II A). Temperature data loggers failed on four study sites, leaving 349 data points for the final statistical analysis.

Representing a functional 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 et al. 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. Photos 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 et al. (2012), and early and late active decay stages and mummification and unexpected disappearance as additional categories (Table 1). Due to our bi-weekly 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, 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).

**Table 1:** Description of carrion decomposition stages (adapted from Dekeirsschieter and others 2012)

| 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 |

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 et al. (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®, 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 modelled 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 non-linear relationships. To account for each response variable, 'final dry weight' and 'time until final decomposition', we used the families Gaussian and Cox.ph, respectively, the latter implying a Cox proportional hazards model (Cox 1972). Since local temperature measured by the datalogger 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 ± 0.01 g (mean ± SD)) and days of dung exposure (29 ± 2 days (mean ± 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.

While 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 temperature 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 II 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 II C).

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 II D).

Coefficients in the Cox model represent the linear effect of the corresponding predictors on the hazard rate, i.e., 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 II 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 2 A, 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 non-linear effect of elevation (Fig. 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 II E).

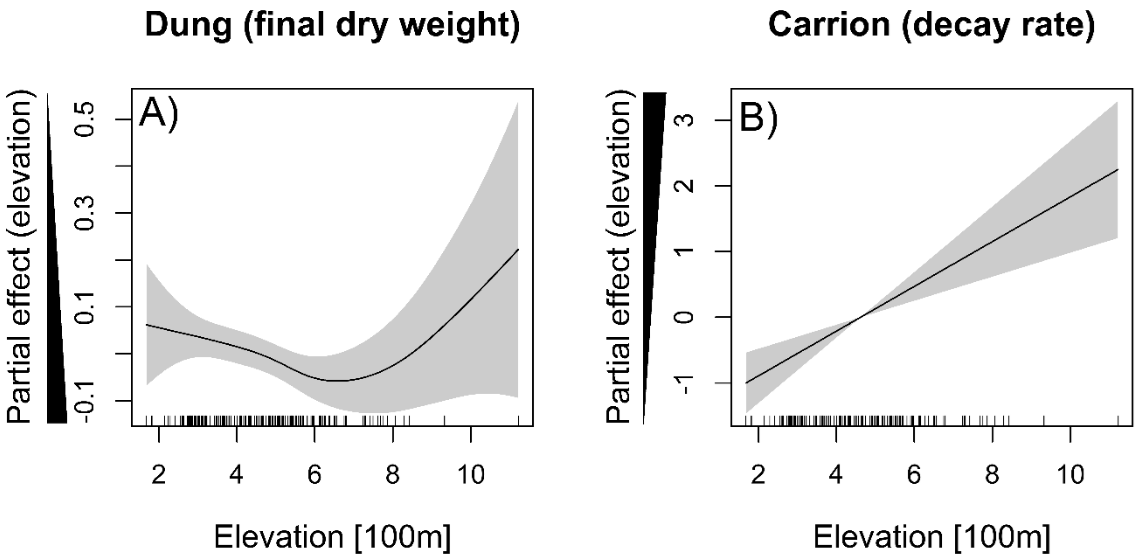

**Figure 2***:* Partial plots for the smooth term *s(elevation100)* for both GAMs with confidence intervals indicated by the grey shaded areas. A) unimodal relationship for the final dry weight of dung along elevation with a minimum dry weight at about 700 m. B) linear relationship for the decomposition 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.

**Table 2:** Summary statistics for generalized additive Gauss and Cox.ph models. 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.

| | **Dung weight loss (family = Gauss)** | | | **Day of final carrion decomposition (family = Cox.ph)** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *std. Error* | *p* | *Estimates* | *std. Error* | *p* |
| (Intercept) | 0.71 | 0.23 | **0.002** | | | |
| Insects [yes] | -0.01 | 0.01 | 0.664 | 0.56 | 0.15 | **<0.001** |
| Habitat grassland vs. forest | 0.07 | 0.05 | 0.155 | -0.16 | 0.30 | 0.589 |
| Habitat arable field vs. forest | -0.01 | 0.05 | 0.903 | -0.50 | 0.31 | 0.102 |
| Habitat settlement vs. forest | 0.04 | 0.05 | 0.490 | -0.52 | 0.36 | 0.146 |
| Landscp. agric. vs. near-natural | -0.06 | 0.04 | 0.165 | -0.33 | 0.27 | 0.229 |
| Landscp. urban vs. 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 | **<0.001** |
| Smooth term (elevation100) | | | 0.097 | | | **<0.001** |
| Random effect (study site) | | | **<0.001** | | | **<0.001** |
| Observations | 349 | | | 253 | | |
| $R^2$ | 0.606 | | | 0.564 | | |

*Carrion decomposition*

Higher carrion decomposition was associated with higher elevation (Figure 2 B). 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 II 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 access, local temperature, and elevation on carrion decomposition (Appendix II 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).

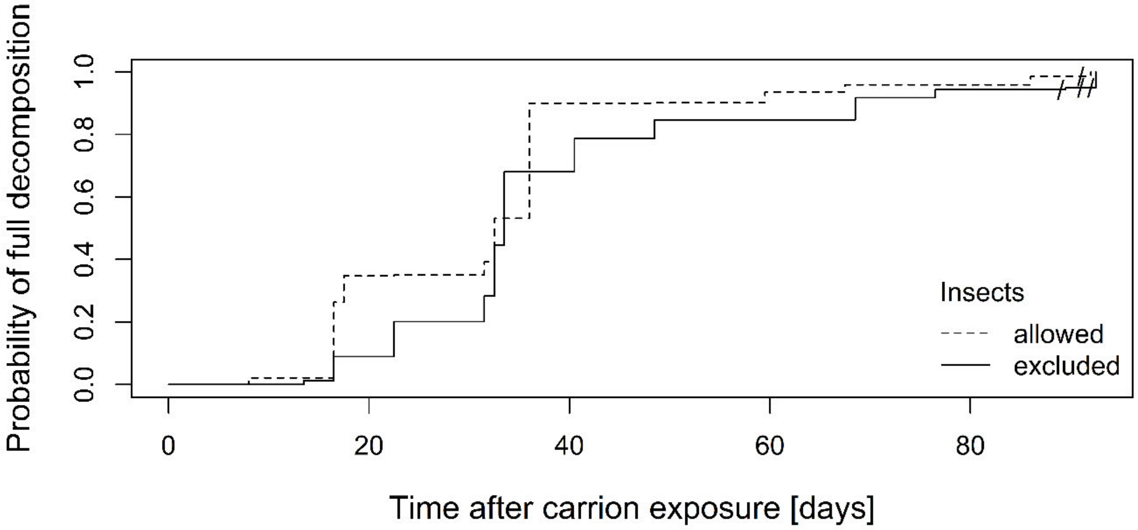

**Figure 3:** Survival curve for the probability of full carrion decomposition (onset of mummification or dry remains) with and without insect access over time. The dashed line indicates insect access, while the solid line displays no insect access.

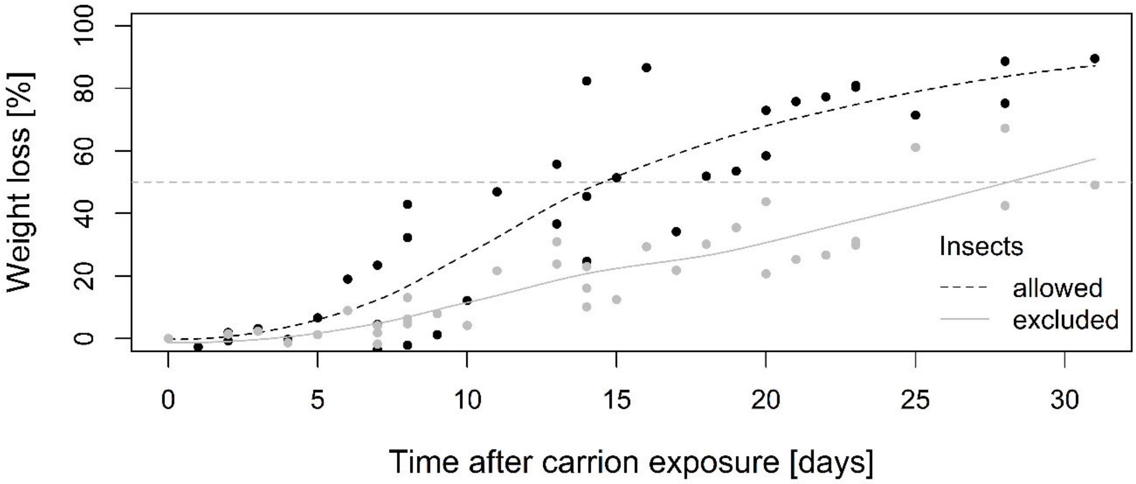

**Figure 4:** Weight loss of rat carrion with and without insect access (n = 5 for each treatment) measured in weight loss in percentage over time. Grey and black dots indicate individual measurements, curves represent the associated regression lines. Rats with allowed insect access are depicted in black,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

## 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 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 et al. 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 et al. 2017; Lauber et al. 2008; Lumini et al. 2010; Minor and Cianciolo 2007; Nichols et al. 2008; Polasky et al. 2011; von Hoermann et al. 2018; 2020).

Land-use change and new agricultural practices, e.g. the use of anthelmintics, can negatively affect dung beetles (Carpaneto et al. 2007), whereas grazing-continuity of grasslands and a low habitat complexity positively affect dung beetle abundance and richness (Buse et al. 2015; Romero-Alcaraz and Ávila 2000). Moreover, dung beetle functional diversity is highly variable among different regions, resulting in varying dung decomposition rates (Milotić et al. 2019). Although 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), e.g. 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 et al. 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 et al. (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 et al. 2015; Weatherbee et al. 2017), and microbial counts increase from woodland to pasture sites, accompanied by faster decomposition rates of carrion (Wilson et al. 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 et al. (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, e.g. by microbial decomposers and fly larvae (Carter et al. 2007).

As expected, carrion decomposed faster with increasing local temperatures. This might be an indirect effect of increased microbial activity (Pechal et al. 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 et al. 2021), and higher necrophagous insect abundances and feeding rates at carcasses (Barton and Bump 2019; von Hoermann et al. 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 et al. 2008; Shean et al. 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 et al. (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 et al. 2020) and richness (Herzog et al. 2013). Furthermore, soil microbial diversity (Shen et al. 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 et al. 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 et al. 2019). Furthermore, Collembolans (springtails) contribute considerably to the decomposition processes (Wang et al. 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 et al. 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 et al. 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 et al. 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 et al. 2014; Herzog et al. 2013), which might influence the decomposition process as reported by Farwig et al. (2014). Lower temperature (and associated slowing microbial activity; Pechal et al. 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, are more prone to negative desiccation effects on associated microbes (Crippen et al. 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 (e.g., 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 lead to substantial reduction in decay and the subsequent insect population size and community composition (Lee and Wall 2006; Pechal et al. 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 et al. 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 et al. 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 (Richards and Goff 1997; Benbow et al. 2015). 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 et al. 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 (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.

## Appendix II

### Appendix II A: Dung control samples

To calculate the initial dry weight of dung samples, in order to get the overall dry weight loss of samples, wet weight of 14 dung control samples was measured before drying them at 100°C for five days. Dry weight was then measured and used to model dry weight from wet weight using a linear regression function (Figure A1).

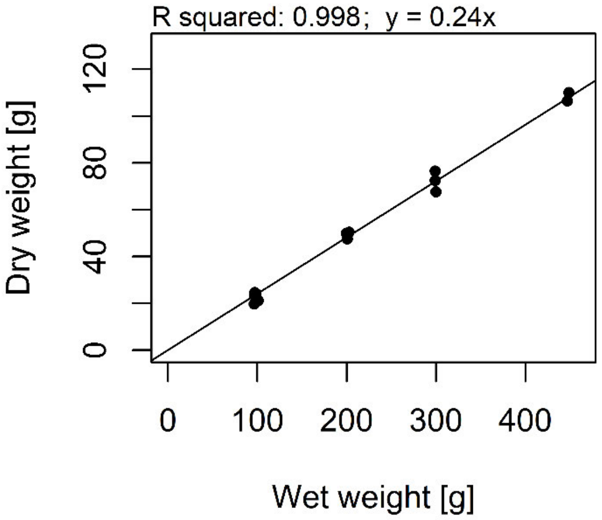

**Figure II A1:** Regression function (y = 0.24x) describing the relation between wet weight and dry weight of the control samples (n = 14).

### Appendix II B: Results of the generalized additive models with long-term temperature and precipitation data

To account for long-term temperature and precipitation data as surrogates for macroclimate, we additionally calculated both generalized additive models (dung and carrion) including mean annual temperature and precipitation over the past 30 years on our study sites instead of elevation (Table B1). Akaike's information criterion (AIC) was then calculated for each model:

$AIC_{dung\_elevation} = 2714.38 < AIC_{dung\_temp+prec} = 2775.37$

$AIC_{carrion\_elevation} = 2208.31 < AIC_{carrion\_temp+prec} = 2279.51$

**Table II B1:** Results of generalized additive gauss and cox models respectively for dung and carrion decomposition including mean multi-annual temperature and precipitation as surrogates for macroclimate. Insects, habitat, landscape, local temperature, and mean multi-annual temperature and precipitation were included as predictors, and study site as a random effect. 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.

| | **Dung weight loss (family = Gauss)** | | | **Day of final carrion decomposition (family = cox.ph)** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *std. Error* | *p* | *Estimates* | *std. Error* | *p* |
| (Intercept) | 0.42 | 0.26 | 0.107 | | | |
| Insects [yes] | -0.00 | 0.01 | 0.783 | 0.54 | 0.14 | **<0.001** |
| Habitat grassland vs. forest | 0.06 | 0.05 | 0.188 | -0.20 | 0.28 | 0.479 |
| Habitat arable field vs. forest | 0.00 | 0.05 | 0.986 | -0.19 | 0.28 | 0.502 |
| Habitat settlement vs. forest | 0.04 | 0.05 | 0.497 | -0.24 | 0.32 | 0.452 |
| Landscape agriculture vs. near-natural | -0.04 | 0.04 | 0.357 | 0.08 | 0.27 | 0.779 |
| Landscape urban vs. near-natural | 0.04 | 0.04 | 0.337 | 0.01 | 0.26 | 0.963 |
| Annual temp. long-term | -0.02 | 0.02 | 0.350 | 0.53 | 0.15 | **0.001** |
| Annual precipitation long-term | 0.00 | 0.00 | 0.087 | 0.00 | 0.00 | **<0.001** |
| Random effect (study site) | | | **<0.001** | | | **<0.001** |
| Observations | 357 | | | 260 | | |
| $R^2$ | 0.616 | | | 0.542 | | |

## Appendix II C: Results of the cox survival model for carrion decomposition rate

The mixed effect cox survival model based on interval-censored data estimated faster decomposition with insect access by a factor of 2.9. With every 100 m increase in altitude the decay is accelerated by 1.7 and every 1°C increase in local temperature leads to faster decay by a factor of 2.17. Carrion on arable fields tended to decay slower by a factor of 0.4 (Table C1).

**Table II C1:** Mixed effect cox survival model for carrion decomposition (time~ insects + landscape + habitat + temperature + elevation100 + (1|study site)); only (marginal) significant parameters and exponentiation of coefficients (exp(Estimate)) are displayed.

| **Summary** | **Estimate** | **Std. Error** | **Z value** | **Pr(>\|z\|)** |
|---|---|---|---|---|
| Insects | 1.07 | 0.25 | 4.22 | 2.49e-05*** |
| Local temperature | 0.77 | 0.23 | 3.40 | 0.00067*** |
| Habitat arable | -0.91 | 0.51 | -1.79 | 0.07· |
| Elevation | 0.53 | 0.15 | 3.48 | 0.0005*** |
|  | **Exp(Estimate)** | **Lwr** | **Upr** |  |
| Insects1 | 2.92 | 1.78 | 4.81 |  |
| Local temperature | 2.17 | 1.39 | 3.39 |  |
| Habitat arable | 0.40 | 0.15 | 1.09 |  |
| Elevation | 1.7 | 1.26 | 2.29 |  |

## Appendix II D: Illustrating effects on decomposition of dung and carrion

### Dung

To demonstrate the effects of insects, landscape, habitat, local temperature, and elevation on the weight loss of dung the estimates of the GAM model (Table 2) can simply be interpreted as relative effects on weight. As we utilized a logarithmic link function, the multiplicative effect of each coefficient x is calculated by exponentiation exp(x) which can be approximated by exp(x) ~ 1 + x when x << 1 as shown to be the case in Table 2. Thus, estimates of -0.01 and -0.02 for e.g., predictors insects and local temperature result in a decrease of 1 % and 2 %, respectively, when insects are not excluded and temperature is increased by 1°C.

Carrion

For illustrating the effect size on rat carcass decomposition, we estimated the joint cumulative distribution function for the duration of decomposition by evaluating the conditional distribution of covariates multiplied by the probability distribution function of the random effects of study sites. Integration over random effects yielded the marginal distribution providing the average impact of fixed effect predictors on duration of decomposition as predicted by the statistical model. To visualize the effect of changing predictors we referred to a standard scenario of mean local temperature (17.5°C), mean elevation (465 m), insects included, landscape type "agriculture", and habitat type "arable field". Figure D1 shows the expected shift in the marginal cumulative distribution function (MCDF), when insects exclusion status, local temperature, mean elevation, landscape, and habitat deviate from the reference scenario, leading e.g., to a prolongation of decomposition of c. six and four days at the 50 % MCDF level, when insects are excluded and temperature is reduced by 1°C, respectively.

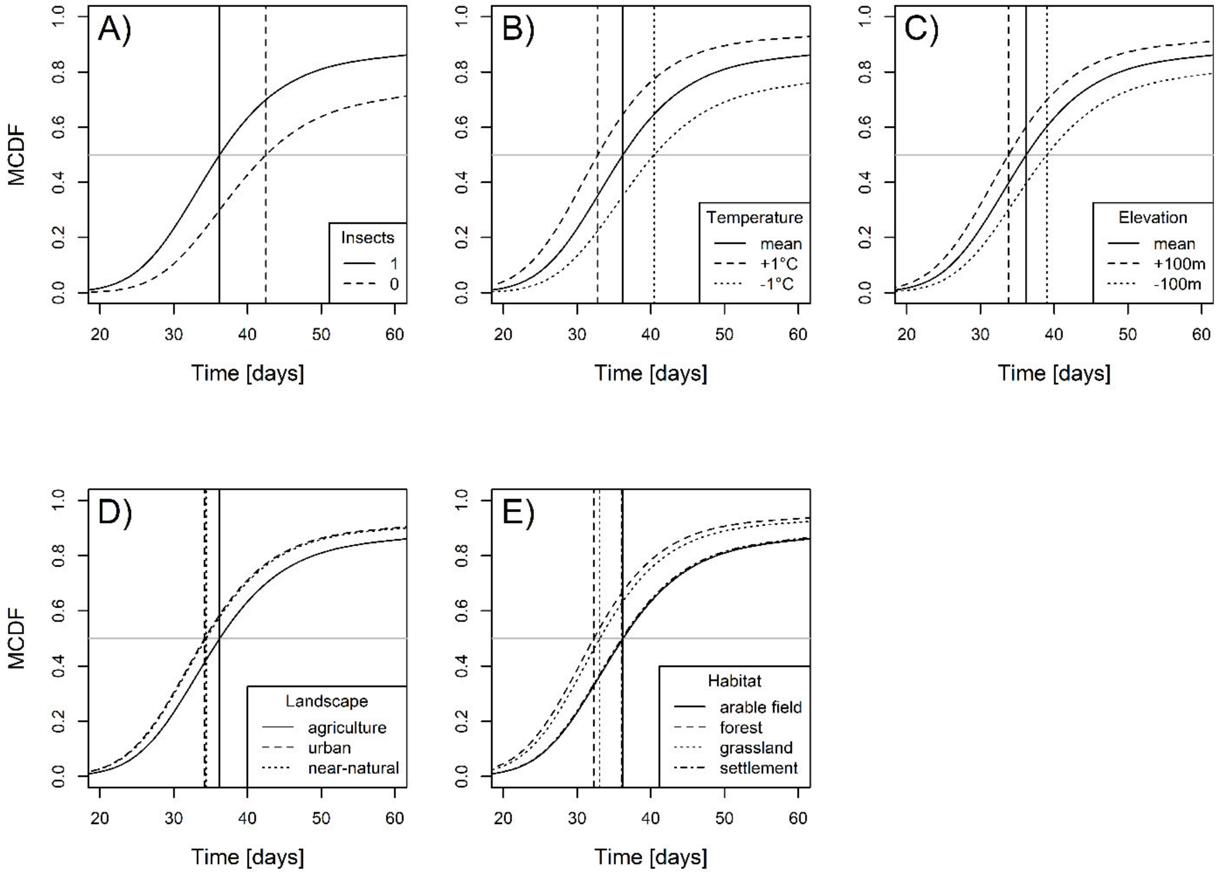

**Figure II D1:** Marginal cumulative distribution function (MCDF) indicating the probability of decomposition of carcasses until the end of the time span given on the x-axis for different scenarios. Solid lines represent the reference scenario with insects included, local temperature fixed at mean temperature, elevation fixed at mean elevation, habitat “arable field”, and landscape “agriculture” in contrast to situations with A) insects excluded, B) temperature reduced and increased by 1°C, C) elevation reduced and increased by 100 m, D) landscape type changed, and E) habitat type changed. Gray horizontal lines indicate 50 % level and vertical lines the intersections of the corresponding curves with 50 % level.

## Appendix II E: Interaction effect between elevation and insect access on dung decomposition

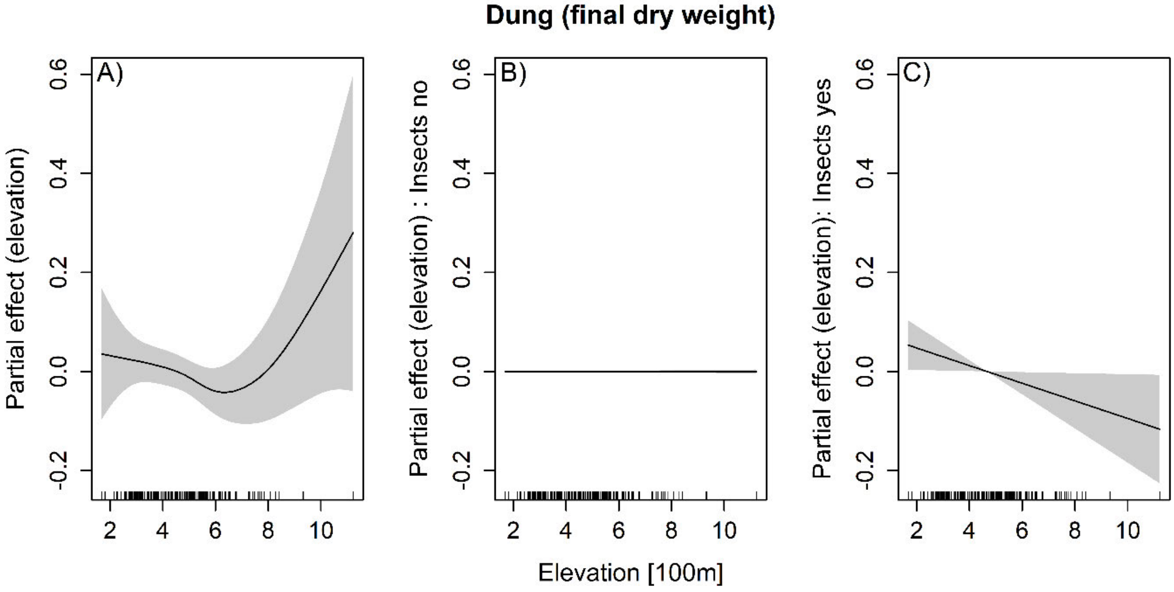

Figure II E1: Partial plots for the smooth term *s(elevation100)* (A) and the interactions between presence/absence of insects and elevation (B and C) for the dung GAM with confidence intervals indicated by the grey shaded area. AIC value of the dung GAM decreased from 2714 for the model without interaction to 2706 with interaction between elevation and insects added. High y-values for dung decomposition indicate high final dry weights and consequently slower decomposition rates. A) unimodal relationship for the decomposition of dung along elevation with highest decomposition at about 700 m. B) horizontal line at y = 0, indicating no change in decomposition along an elevational gradient with the absence of insects and C) presence of insects reveals an increase in decomposition with increasing elevation (reduction of decomposition at low altitudes, enhancing decomposition at high altitudes).

# Chapter III

## Dung-visiting beetle diversity is mainly affected by land use, while community specialization is driven by climate

with

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## Summary

Dung beetles are important actors in the self-regulation of ecosystems by driving nutrient cycling, bioturbation, and pest suppression. Urbanization and the sprawl of agricultural areas, however, destroy natural habitats and may threaten dung beetle diversity. In addition, climate change may cause shifts in geographical distribution and community composition. We used a space-for-time approach to test the effects of land use and climate on α-diversity, local community specialization ($H_2'$) on dung resources, and γ-diversity of dung-visiting beetles. For this, we used pitfall traps baited with four different dung types at 115 study sites, distributed over a spatial extent of 300 km x 300 km and 1000 m in elevation. Study sites were established in four local land-use types: forests, grasslands, arable sites, and settlements, embedded in near-natural, agricultural, or urban landscapes. Our results show that abundance and species density of dung-visiting beetles were negatively affected by agricultural land use at both spatial scales, whereas γ-diversity at the local scale was negatively affected by settlements and on a landscape scale equally by agricultural and urban land use. Increasing precipitation diminished dung-visiting beetle abundance, and higher temperatures reduced community specialization on dung types and γ-diversity. These results indicate that intensive land use and high temperatures may cause a loss in dung-visiting beetle diversity and alter community networks. A decrease in dung-visiting beetle diversity may disturb decomposition processes at both local and landscape scales and alter ecosystem functioning, which may lead to drastic ecological and economic damage.

**Keywords:** coleoptera; coprophagous beetles; decomposition; global change; hill numbers; network analysis

## Introduction

One fundamental yet often overlooked process for terrestrial ecosystem functions is the decomposition of vertebrate dung by beetles (Hanski and Cambefort 1991; Pecenka and Lundgren 2018). This functional group is frequently used as a bioindicator for habitat quality and conversion (McGeoch et al. 2002) and is particularly sensitive to land-use intensity and climate (Carpaneto et al. 2007; Gardner et al. 2008; Menéndez et al. 2014; Sánchez-Bayo and Wyckhuys 2019).

Land-use intensification, as a consequence of the constantly growing global human population (Seto et al. 2011), comes along with more intensive management techniques and the transformation of natural habitats to agricultural and urban areas, which may negatively affect dung beetle abundances (Carpaneto et al. 2007; Gardner et al. 2008; Sánchez-Bayo and Wyckhuys 2019). Additionally, dung beetles are faced with climate change. Beetles are poikilothermic, and their feeding activities and population dynamics, e.g. population growth, are sensitive to temperature (Frazier et al. 2006). Increasing temperatures may contribute to thermal stress that can affect their phenology, community structure, and ecosystem functions (Angilletta Jr. 2009; Barton and Bump 2019; Graham and Grimm 1990; Warren et al. 2013). Even a change in the geographical distribution of dung beetles, e.g. to higher elevational ranges, has been suggested as a consequence of long-term climate change (Menéndez et al. 2014). Since climate change is often associated with rising temperatures and changes in precipitation patterns (Collins et al. 2013), it is vital to investigate the effects of both temperature and precipitation on dung beetle assemblages.

In general, a decline in dung beetles not only results in lower decomposition rates of dead organic material (necromass) (Frank et al. 2017b). It potentially leads to shifts in the self-regulation of ecosystems, since dung beetles contribute to nutrient cycling, soil aeration, secondary seed dispersion, and parasite suppression (Evans et al. 2019; Nichols et al. 2008). For example, a decline in dung beetles is likely to cause fouling of grasslands and an increase in livestock parasite and pest species, which may have drastic economic consequences (Castle and MacDaid 1972; Losey and Vaughan 2006).

Changes in abundance, number of species, and community composition, e.g. by habitat loss, may affect community networks and stability (Neff et al. 2021; Spiesman and Inouye 2013). Climate, moreover, might also moderate the structure and dynamics of networks (Classen et al. 2020). Community networks can be described by the structure and density of interaction links, and allow, inter alia, drawing conclusions about the specialization of individual species or communities (Neff et al. 2021; Newman and Girvan 2004; Spiesman and Inouye 2013), for instance about the specialization of dung beetles on dung types. Network stability depends on the connectivity, the number of interactions in a network, and the network size. Therefore, species-rich networks can enhance community stability (Neff et al. 2021; Spiesman and Inouye 2013) and resilience to the loss of single species through climate or land-use change.

Although dung beetles are known to be good bioindicators of ecosystem health (McGeoch et al. 2002), most studies on insect networks focus on plant-pollinator interactions and neglect dung beetle networks (but see Frank et al. 2018). In addition, most research on dung beetles has hitherto focused on forest and agricultural systems (Carpaneto et al. 2007; Frank et al. 2017b; von Hoermann et al. 2020; Weithmann et al. 2020).

This study is among the first to investigate dung beetle assemblages across a large range of typical land-use types in temperate regions, ranging from near-natural landscapes to highly disturbed agricultural and urban landscapes and along a large climate gradient.

Using a space-for-time approach with independent climate and land-use gradients, we investigated α-diversity as abundance of dung-visiting beetles, species density (*sensu* Gotelli and Colwell 2001), and species richness (*sensu* Gotelli and Colwell 2001), local community specialization on dung resources, and γ-diversity as an indicator for community homogenization. We used a fully crossed design along both land-use and climate gradients at local (habitat) and regional (landscape) scales. Specifically, we addressed the following research questions:

1) Do local habitat and regional landscape types affect α-diversity, local community specialization on dung types, and γ-diversity of dung-visiting beetles?
2) Do temperature and precipitation affect α-diversity, local community specialization on dung types, and γ-diversity of dung-visiting beetles?

## Methods

### *Study sites*

This space-for-time study was conducted on 115 study sites, embedded in 44 study regions and along two independent gradients of land-use intensity and climate in southeast Germany (Bavaria) (Redlich et al. 2021) (Fig. III A1 and Fig. III A2). Each of the 44 study regions (à 5.8 km x 5.8 km) was assigned to the dominant regional landscape type (near-natural, agricultural, urban). The regional landscape types consisted of 16 near-natural landscapes (defined as >85% near-natural vegetation including a minimum of 50% forest), 15 agricultural landscapes (>40% arable land and managed grassland), and 13 urban landscapes (>14% housing, industry, and traffic infrastructure). Within the 44 study regions, 115 study sites were embedded and distinguished in four habitat types (forest, grassland, arable field, and settlement). Within each study region, the three most dominant local land-use types (habitats) out of forest, grassland, arable field, and settlements were selected for establishing study sites (3 m x 30 m). Habitats were represented as 36 forest sites (forest clearings), 28 grassland sites (meadows), 27 arable fields (crop field margins), and 24 settlements (green spaces within settlements or cities).

Study regions covered five climatic zones (from 1- cool to 5- warm) based on multi-annual mean air temperatures (1981-2010) ranging between 4.5-10°C. The final selection of study sites covered a spatial extent of 300 km x 300 km and 1000 m in elevation.

### *Study design and data collection*

In May 2019, we established four baited pitfall traps on each of the 115 study sites. We sampled in May because highest dung beetle diversity was expected (according to Šlachta 2013, who sampled in April, May, June, July, and August in a similar geographic region). To attract a broad range of beetle species, we covered a trophic gradient using dung from a carnivore (Eurasian lynx, *Lynx lynx*) as the highest trophic level, an omnivore (wild boar, *Sus scrofa*) as intermediate trophic level, and two types of herbivores (red deer, *Cervus elaphus* as browser-grazer and European bison, *Bos bonasus,* as grazer) as the lowest trophic level. We chose European bison dung because it functionally represents the current dominant domestic animal in agriculture, which is cattle. At the same time, bison is evolutionarily close to domesticated cattle. The advantage of using bison is that this species was widely distributed across Europe until the 20th century (Kuemmerle et al. 2011; Svenning 2002) and organisms like insects could adapt to its dung. Contrary to domesticated cattle, bison prefer forests as well as herbaceous vegetation (Kuemmerle et al. 2011), which makes them a suitable study organism for land-use studies like this.

The dung for the experiment was collected in March 2019 from animal enclosures; none of the defecating animals was treated with antibiotics or anthelmintics. Each dung type was thoroughly mixed to ensure uniform constituency and texture before weighing. Due to different natural appearances of dung types, dung was weighed as follows: 35 g (Eurasian lynx), 90 g (wild boar), 25 g (red deer), and 450 g (European bison).

Dung of red deer, wild boar, and lynx was put in elastic sausage nets (mesh size *c.* 1.5 cm) to avoid unintended dung dispersal on the study sites (bison heaps were heavy enough not to be removed by animals that passed through the study sites). All dung pats were stored frozen and only thawed one day before the beginning of the experiment. On the study sites, baited pitfall traps were established 5 m apart from each other. Pitfall traps (400 mL plastic cups) were filled with 200 mL liquid (70 mL propylene glycol and 130 mL water) and emptied after 14 days. Small holes beneath the rim of the cup prevented overspill in case of rain. We placed the bait on the center of a coarse mesh wire (mesh size 2 cm x 2 cm) that was placed half on the pitfall trap and half on the ground. The mesh wire and dung nets were then fixated to the ground with tent pegs. To empty the traps in the field, the coarse mesh wire with the dung was carefully removed from the pitfall traps, and the content of the pitfall traps was sifted through a tea bag paper. The tea bag containing any specimens was then put in a sampling container with 70% Ethanol. Beetles were then identified to species level by the experts and co-authors TL, J-AS, and DS.

Aim of this experiment was to sample all beetles that are attracted by dung, which comprises coprophagous, coprophilous, necrophilous, as well as copronecrophilous species (hereafter collectively referred to as dung-visiting beetles). Necrophilous beetles were included since dung and carrion emit similar volatile organic compounds (Sladecek et al. 2021; von Hoermann et al. 2016; Weithmann et al. 2020) and attract necro- as well as coprophilous beetles. Hence, all species associated with this lifestyle (according to Böhme and Lucht 2005 and Assing and Schülke 2012) were incorporated in this study (Table III A1).

### *Climate variables*

As climate variables, we used long-term averages (1991 to 2020) of air temperature and precipitation amounts. The data for individual study plots were derived from monthly gridded observational datasets with a horizontal resolution of 1 km, from which 30-year averages were subsequently calculated. Temperature and precipitation were only moderately correlated (spearman's rho = -0.54, $p < 0.05$). The raw input datasets were provided by the German Meteorological Service (Deutscher Wetterdienst, DWD) and are described in Kaspar et al. (2013). Additionally, local temperature was measured by dataloggers on each study site to account for small-scale variations. However, since local temperature and multi-annual mean temperature were highly correlated (spearman's rho = 0.71, $p < 0.05$), we only included long-term temperature data in our analysis.

### *Statistical Analysis*

We tested the effects of land use and climate on dung-visiting beetle α- diversity and local community specialization on study-site level, and γ-diversity among habitat and landscape types and climate zones using the software R, version 4.0.5 (R Core Team 2021).

Alpha-diversity on study sites was described using three metrics (data of individual traps per study site were pooled): abundance (number of individuals), species density (number of species, *sensu* Gotelli and Colwell 2001) and species richness (number of species, accounting for abundance, *sensu* Gotelli and Colwell 2001) (package 'vegan' by Oksanen et al. 2020). We fitted a negative-binomial generalized linear model (glm.nb) using the package 'MASS' (Venables and Ripley 2007) to provide estimates of the effects of habitat and landscape types, and temperature and precipitation data on the response variables 'abundance', 'species density', and 'species richness'. Since the number of species and individuals in some samples was low, we decided against a resampling approach, such as chao1 or ACE, to calculate species richness. Instead, we accounted for abundance by including $\log_e$ (abundance) as a predictor in the species richness model.

Additionally, a TukeyHSD post-hoc test was conducted to explore differences in abundance, species density, and species richness among habitat and landscape types (package 'multcomp' by Hothorn et al. 2008). To check for potential spatial autocorrelation of the model residuals, we used cross-correlograms (package 'ncf' by Bjornstad and Falck 2001) based on Moran's I and found no spatial autocorrelation among study sites (Fig. III A3).

As a measure of community specialization on dung resources at study-site level, the standardized two-dimensional Shannon entropy ($H_2'$) – ranging between 0 (no resource preference) and 1 (total specialization) (Blüthgen et al. 2006a) – was calculated based on the abundance of beetle species per dung type (package 'bipartite' by Dormann et al. 2009). In this framework, higher specialization translates into more exclusive use of interaction partners by the existing species, i.e., higher niche differentiation (Blüthgen 2010). Total specialization would thus imply that each species uses only one resource. Further, H2' calculates the interaction frequencies of two groups of different trophic levels in relation to all possible interactions, hence being network-size independent. This makes comparisons across networks along ecological gradients possible, e.g. if species shift to a more specialized or generalized resource use with a temperature shift. In addition to $H_2'$, the Kulback-Leibler distance d' is used as an index for specialization on species level (Blüthgen et al. 2006a), which allows to identify specialization on specific dung types (lynx, boar, deer or bison). By analogy to $H_2'$, d' ranges between 0 (no specialization) and 1 (high specialization).

After calculating $H_2'$ (we only included study sites where at least three samples revealed dung-visiting beetles, n = 94 study sites), we compared the observed $H_2'$ values with a null model with full randomization that kept species frequencies and species richness constant ('r2dtable', 1000 simulations). A linear model was then fitted to calculate the effects of habitat and landscape type, temperature, and precipitation on $H_2'$ of dung-visiting beetle communities.

In cases where one of the predictors led to a significant change in resource specialization of the dung-visiting beetle community ($H_2'$), we calculated the degree of specialization on individual dung types d' (package 'bipartite', Dormann et al. 2009) to determine whether the community specialization $H_2$' resulted from specialization on a specific dung type (d'). Then, we fitted a linear mixed effect model to test for correlations between d' and the predictor variables 'dung type' and 'temperature', including 'study site' as random factor, followed by a pair-wise comparison (TukeyHSD) of the specialization d' between individual dung types. Consequently, we fitted a linear model including d' for each dung type as response variable and 'temperature' as predictor variable and plotted the results in a linear regression curve.

To test for differences in the total γ-diversity among habitats, landscapes, and climate zones, we performed separated sample-based rarefaction-extrapolations (package 'iNEXT', Hsieh et al. 2020) along the Hill numbers ($q$ = 0, 1, and 2) (Hill 1973). Because Hill numbers imply mathematical properties that allow drawing conclusions about diversity across different diversity indices (Chao et al. 2014a; Jost 2006), there seems to be broad agreement on the use of Hill numbers to quantify species diversity (Ellison 2010). In this approach, $q$ determines the measures' sensitivity to species relative abundance, with $q = 0$ focusing on rare species (species richness), $q = 1$ focusing on common species (Shannon diversity) and the order $q = 2$ focusing on dominant species (Simpson diversity) (Chao et al. 2014b). Having multiple assemblages, this framework can be used to partition the Hill numbers of a pooled assemblage (γ-diversity) into its within-assemblage component (α-diversity) and between-assemblage component (β-diversity) (Chiu et al. 2014). Allowing to weigh from rare to dominant species, this methodology seems particularly relevant in functional ecosystem engineer groups as dung beetles, where dominant species are often the major actors in the removal process (Frank et al. 2017b).

This approach is based on predictor categories, which works for our habitat and landscape types. To include climate in the Hill analysis, we used the five climate zones (1 – cool, 5 – warm) as described in the section *Study sites* and more detailed in Redlich et al. (2021). For each $q$ and predictor variable (habitat, landscape, climate), we plotted species diversity against the number of sampling units, non-overlapping confidence intervals indicating significant differences in γ-diversity.

## Results

In total, 12,948 dung-visiting beetles from 37 genera and 87 species were collected in our 385 traps. The species *Onthophagus ovatus* (Linnaeus, 1767) (Scarabaeidae) was most abundant and recorded in 62 study sites (151 traps), followed by *Onthophagus joannae* (Goljan, 1953) (Scarabaeidae) in 65 study sites (156 traps) and *Anoplotrupes stercorosus* (Hartmann in L. G. in Scriba, 1791) (Geotrupidae) in 47 study sites (113 traps) (Fig. 1).

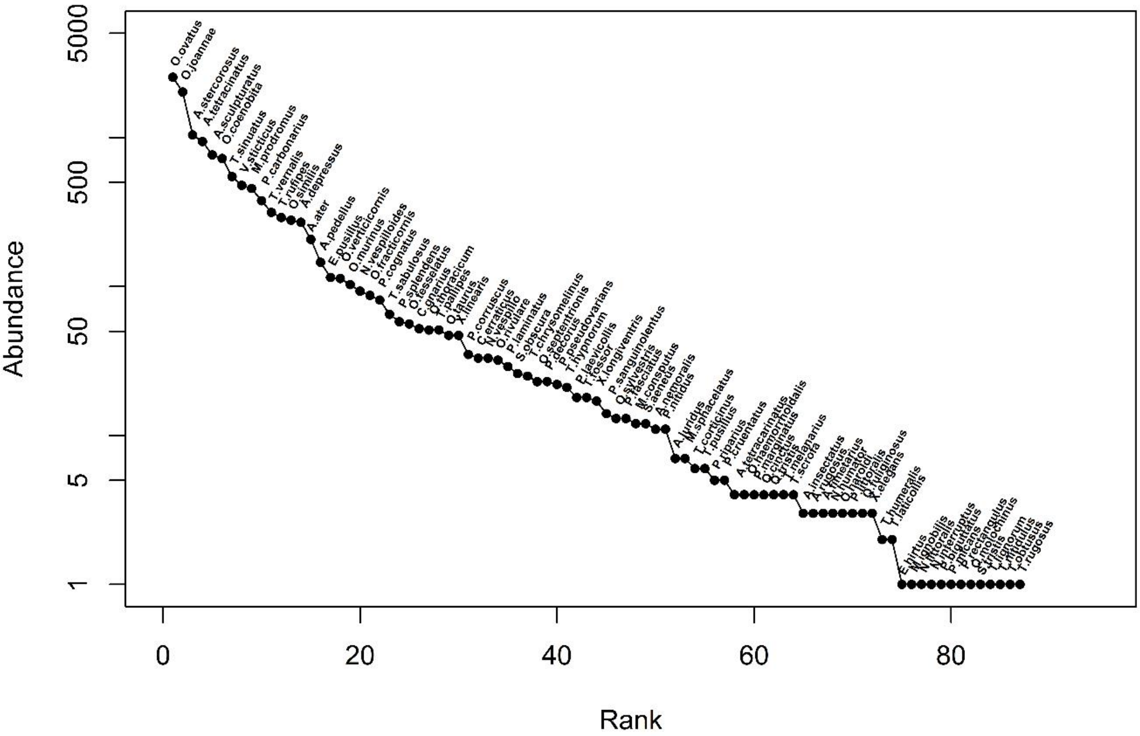

**Figure1**: Rank abundance curve depicting the number of individuals of all recorded beetle species on a logarithmic scale.

### *Alpha diversity*

Land-use intensity affected the abundance and species density of dung-visiting beetles at both habitat and landscape scale (Table 1, all comparisons from post-hoc test in Table III A2). On the habitat scale, dung-visiting beetle abundance was lower on arable fields compared to forest habitats (Table 1, Table III A2). Species density and richness, however, were rather robust to local land use (Table III A2).

**Table 1**: Results of the negative-binomial generalized linear model including abundance, species density, and species richness as responses to habitat type, landscape type, and temperature and precipitation. Significant *p*-values in bold. For complete pairwise level comparison within the categorical predictors *p*-values were adjusted in Table III A2.

| | **Abundance** | | | **Species density** | | | **Species richness** | | |
|---|---|---|---|---|---|---|---|---|---|
| *Predictors* | *Estimate* | *std. Error* | *p* | *Estimate* | *std. Error* | *p* | *Estimate* | *std. Error* | *p* |
| (Intercept) | 6.844 | 1.520 | **<0.001** | 3.121 | 0.660 | **<0.001** | 1.184 | 0.498 | **0.017** |
| Habitat grassland vs. forest | -0.046 | 0.247 | 0.851 | 0.042 | 0.107 | 0.693 | 0.057 | 0.070 | 0.416 |
| Habitat arable vs. forest | -0.651 | 0.254 | **0.010** | -0.070 | 0.111 | 0.528 | 0.099 | 0.077 | 0.199 |
| Habitat settlement vs. forest | 0.037 | 0.268 | 0.891 | -0.186 | 0.120 | 0.122 | -0.113 | 0.083 | 0.176 |
| Landscp. agric.vs. near-natural | -0.429 | 0.241 | 0.075 | -0.223 | 0.106 | **0.035** | -0.093 | 0.073 | 0.206 |
| Landscp. urban vs. near-natural | 0.013 | 0.239 | 0.957 | -0.114 | 0.104 | 0.275 | -0.102 | 0.070 | 0.143 |
| Temperature in °C | -0.073 | 0.128 | 0.571 | -0.051 | 0.056 | 0.359 | -0.022 | 0.039 | 0.567 |
| Precipitation in mm | -0.002 | 0.001 | **0.013** | -0.000 | 0.000 | 0.929 | 0.000 | 0.000 | 0.107 |
| Log(abundance) | | | | | | | 0.305 | 0.026 | **<0.001** |
| Observations | 115 | | | 115 | | | 115 | | |
| $R^2$ Nagelkerke | 0.157 | | | 0.152 | | | 0.844 | | |

On the landscape scale, species density in agricultural landscapes was significantly lower than in near-natural landscapes (Table 1). As expected, extending the linear analysis by pairwise tests including p-value adjustment yielded a less distinctive pattern (Table III A2).

Alpha-diversity in terms of abundance, species density, and species richness was robust to temperature. Dung-visiting beetle abundance, though, decreased with increasing precipitation (Table 1). Species richness strongly increased with increasing beetle abundance (Table 1).

### *Local community specialization on dung resources*

Excluding study sites where dung-visiting beetles were found in less than three pitfall traps, 94 study sites (networks) were included in the analysis. The $H_2'$ value as an index for the specialization of dung-visiting beetle communities on dung resources did not significantly change among local habitat or regional landscape types (Table 2) and beetle assemblages in different habitats or landscapes were neither generalistic nor specialized (Fig. III A4). Dung-visiting beetle assemblages did not respond to changes in precipitation but were less specialized in warmer than in cooler regions (Table 2, Fig. 2).

**Table 2:** Results of the linear model showing the effects of habitat, landscape, temperature and precipitation on the degree of specialization ($H_2'$) of coprophilic beetle assemblages. Significant *p*-values in bold.

| | | **H2_obs** | |
|---|---|---|---|
| *Predictors* | *Estimates* | *std. Error* | *p* |
| (Intercept) | 0.765 | 0.237 | **0.002** |
| Habitat grassland vs. forest | 0.020 | 0.037 | 0.598 |
| Habitat arable vs. forest | -0.039 | 0.041 | 0.340 |
| Habitat settlement vs. forest | 0.012 | 0.040 | 0.776 |
| Landscape agriculture vs. near-natural | 0.009 | 0.039 | 0.821 |
| Landscape urban vs. near-natural | -0.002 | 0.036 | 0.953 |
| Temperature in °C | -0.046 | 0.020 | **0.023** |
| Precipitation in mm | -0.000 | 0.000 | 0.988 |
| Observations | | | 94 |
| $R^2$ / $R^2$ adjusted | | | 0.118 / 0.046 |

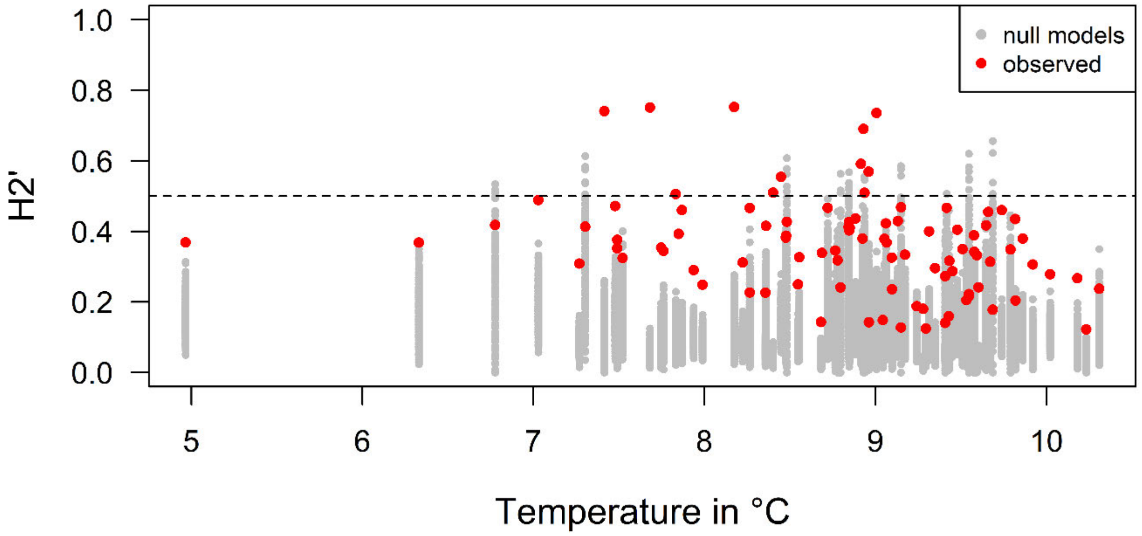

**Figure 2:** Scatterplot of observed $H_2$' (red dots) and randomized $H_2$' values (grey dots) along a mean multi-annual temperature gradient. Dashed horizontal line indicates $H_2$' = 0.5. A null-model calculated randomized H2' values with 1000 simulations (in 87 % of the networks, the observed $H_2$' was significantly higher than in random assemblages).

Specialization (d') of dung-visiting beetles was negatively correlated with temperature and was highest for bison dung along the entire temperature gradient (Fig. 3, Table 3). With cooler temperatures, specialization on bison, wild boar, and lynx dung significantly increased (Fig. 3, Table III A3).

**Table 3:** Results of the linear mixed effect model, testing d' against temperature and dung type (study site as random effect) and TukeyHSD post-hoc analysis to test for differences in specialization among dung types. Significant *p*-values in bold.

| **Linear mixed effect model** | | **d'_obs** | |
|---|---|---|---|
| *Predictors* | *Estimates* | *std. Error* | *p* |
| (Intercept) | 0.691 | 0.130 | **<0.001** |
| Deer vs. boar | 0.000 | 0.019 | 1.000 |
| Lynx vs. boar | 0.012 | 0.018 | 0.495 |
| Bison vs. boar | 0.057 | 0.018 | **0.002** |
| Multi-annual mean temperature in °C | -0.040 | 0.015 | **0.007** |
| *Random Effects* | | | |
| $\sigma^2$ | | | 0.01 |
| $\tau_{00\ \mathrm{plot}}$ | | | 0.01 |
| ICC | | | 0.46 |
| $N_{\mathrm{plot}}$ | | | 94 |
| Observations | | | 351 |
| Marginal $R^2$ / Conditional $R^2$ | | | 0.066 / 0.498 |

| **Post-hoc analysis** | | **d'** | |
|---|---|---|---|
| | *Estimate* | *z* | *p* |
| Deer – boar | 0.000 | 0.000 | 1.000 |
| Lynx – boar | 0.012 | 0.683 | 0.904 |
| Bison – boar | 0.057 | 3.101 | **0.011** |
| Lynx – deer | 0.012 | 0.658 | 0.913 |
| Bison – deer | 0.060 | 2.987 | **0.015** |
| Bison - lynx | 0.045 | 2.438 | 0.070 |

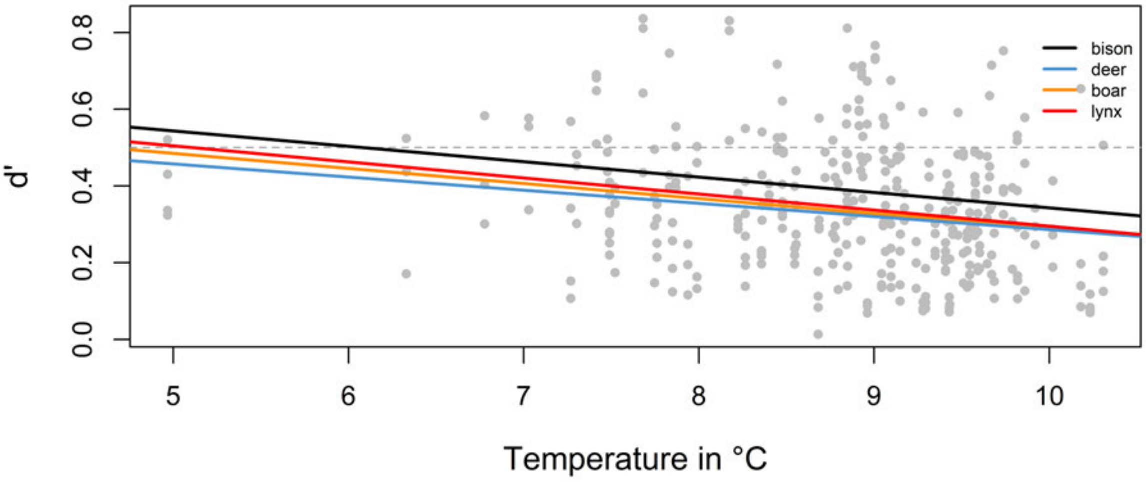

**Figure 3:** Linear regression showing the degree of specialization (d') on individual dung resources along the temperature gradient. Grey dots depict individual d' values, colored lines represent regression lines of each dung type. Dashed line indicates d' = 0.5.

### *Gamma-diversity*

The rarefaction interpolation curves for $q = 0$ on habitat scale showed no distinctive pattern for rare species diversity. At a landscape level, rare species diversity tended to be lower in agricultural and urban landscapes than in near-natural landscapes, but this difference was not significant (Fig. 4). With increasing sensitivity to common species ($q = 1$), species diversity on a habitat scale was significantly lower in settlements than in grasslands and arable fields (Fig. 4). Species diversity of common species also decreased on a landscape scale from near-natural to urban and agricultural landscapes, with a significant difference between near-natural and agricultural landscapes (Fig. 4). Diversity of dominant species ($q = 2$) on a habitat scale was significantly lower in settlements compared to other habitats. On a landscape scale, diversity was significantly higher in near-natural landscapes compared to agricultural and urban landscapes (Fig. 4).

The rarefaction interpolation curves showed for $q = 0$ no climate effect on rare species diversity (Fig. 4). Diversity of common species ($q = 1$) in the warmest climate zone (5) was lowest with significant differences to climate zones 1 and 4 (Fig. 4). Dominant species diversity ($q = 2$) was significantly lowest in the warmest climate zone compared to all other climate zones (Fig. 4).

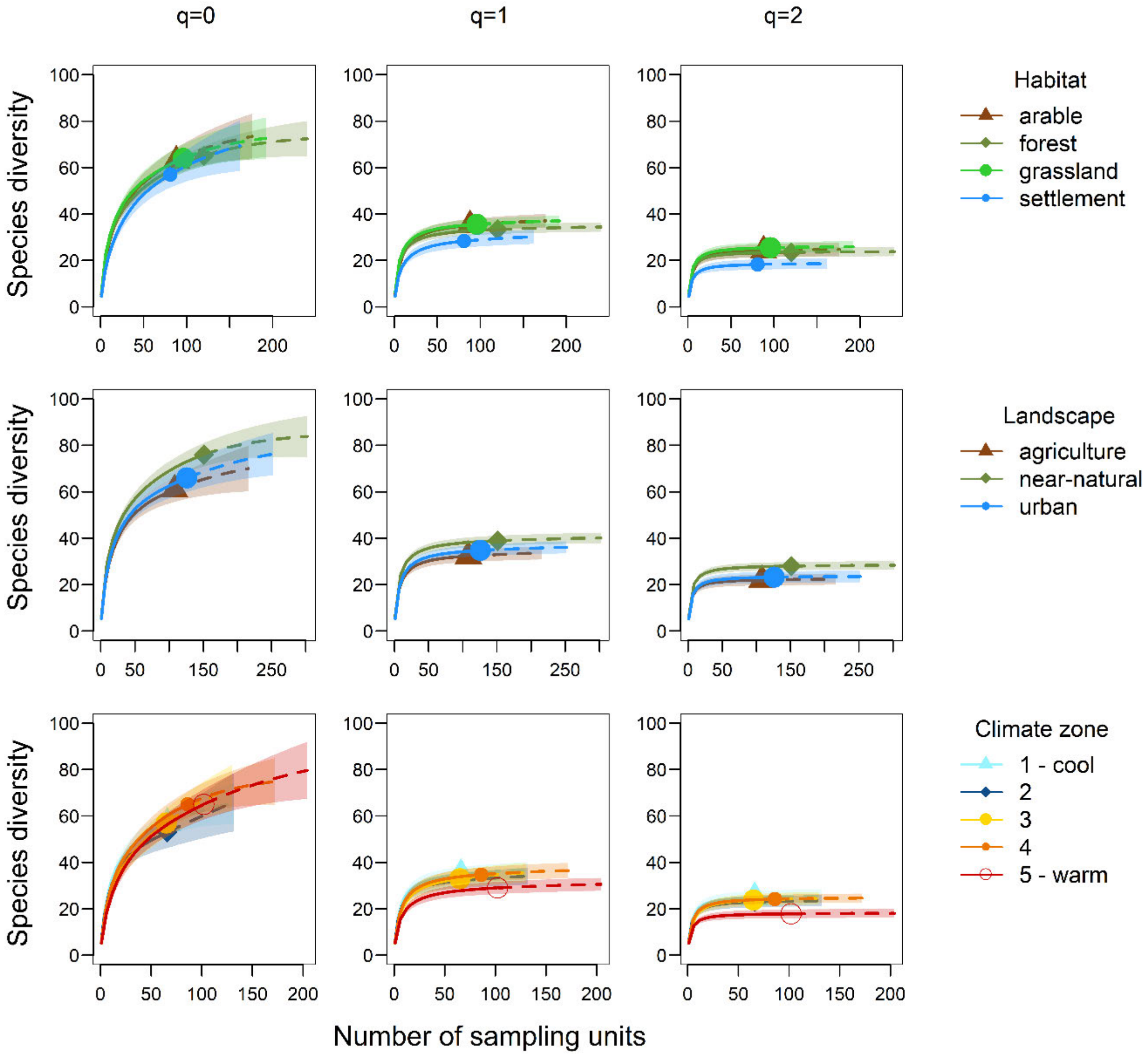

**Figure 4**: Sample-size based rarefaction curves of rare, common, and dominant dung beetles for Hill numbers (*q* = 0, 1, and 2) across habitats, landscapes, and climate zones. Solid lines depict the interpolated number of sampling units (rarefaction), while dashed lines depict the extrapolation of sampling units. Shaded areas indicate the 95% confidence interval. Non-overlapping confidence intervals indicate significant differences in γ-diversity between treatments

## Discussion

Our results provide new insights into the response of dung-visiting beetle diversity and community specialization on dung types to land-use intensity on local and regional scales and along a climate gradient, disentangling temperature and precipitation. We found significant negative effects of anthropogenically transformed environments (locally and regionally) on dung-visiting beetle abundance, species density, γ-diversity, but not on community specialization. Climate affected dung-visiting beetles through lower abundances associated with increasing precipitation and decreased local community specialization and γ-diversity with higher temperatures.

### *Land-use effects on dung beetle α-diversity, community specialization, and γ-diversity*

In agricultural habitats and landscapes, the reduced abundance, species density and γ-diversity of dung-visiting beetles might be explained by the negative effects of potentially intensified land use, including low grazing continuity, small pasture sizes, habitat fragmentation, the reduction of rangeland, and the use of pesticides that negatively impact dung beetle assemblages (Beynon et al. 2012; Buse et al. 2015; Carpaneto et al. 2007; Sánchez-Bayo and Wyckhuys 2019). Our findings are in line with Korasaki et al. (2013) and Carpaneto et al. (2007) and partly agree with Gebert et al. (2020), who reported land-use effects on dung beetle abundance but not on the number of species. In our study, however, species density was significantly dependent on abundance. Hence, the reduction in species density in agricultural landscapes compared to near-natural systems likely occurred because of lower dung-visiting beetle abundances. This does not imply that all agricultural land use is detrimental to dung-visiting beetles. In this case, management intensity (e.g. grazing continuity) and pasture area should be considered as important factors for the conservation of dung-visiting beetles (Buse et al. 2015).

In settlements and to a lesser extent in urban landscapes γ-diversity was drastically reduced. In settlements and cities, dog dung is often the only resource for dung beetles (Carpaneto et al. 2005) due to a lack of cattle or larger wild ungulates and carnivores. The reduced variety and amount of mammalian dung can directly affect dung beetles (Errouissi et al. 2004; Iida et al. 2016; Korasaki et al. 2013; Ramírez-Restrepo and Halffter 2016), which potentially makes urban areas less attractive. In addition, we suggest that the amount of sealed area in settlements and cities restricts dung burying by some dung beetle species, which may limit the amount and species richness of dung burying beetles in urban environments. Dung volatiles, moreover, which attract dung beetles and guide them towards their food source (Sladecek et al. 2021), might be masked by other odors typical for urban spaces, such as car exhausts and organic waste, and might be less detectable than dung volatiles in natural environments. There is first evidence that the dung beetle *Anoplotrupes stercorosus* responds to certain plant volatiles (alpha-pinene and camphor) (Weithmann et al. 2020), which should be lower in urban environments. If these plant volatiles are used by *A. stercorosus* for orientation or food location, however, is yet unknown (Weithmann et al. 2020) but could explain potential habitat preferences by dung beetles.

Although dung beetle species often have different habitat preferences (open versus closed habitats) (Romero-Alcaraz and Ávila 2000), we found no differences in α- and γ-diversity between forest and grassland habitats. Findings about habitat preferences are inconsistent, though. Damborsky et al. (2015) and Frank et al. (2017b) report significantly higher dung beetle richness and biomass in forests than grasslands, whereas Romero-Alcaraz and Ávila (2000), for instance, summarize that dung beetles are more likely to be found in open habitats. However, our forest study sites were placed within an area of tree clearing, which might be as attractive for beetles that prefer open habitats as for forest species. Moreover, study sites were not grazed during the sampling period. As a consequence, less dung was probably present, which decreases habitat quality for dung-visiting beetles specialized on grasslands. Nonetheless, the preference for less polluted and disturbed habitats and landscapes might explain the reduced dung-visiting beetle α- and γ-diversity in agricultural and urban environments.

Dung beetle biomass (Frank et al. 2017b) and multi-species communities significantly enhance dung decomposition, even in disturbed systems (Ambrožová et al. 2021; Beynon et al. 2012; Milotić et al. 2019). Consequently, the observed lower beetle abundance, density, and γ-diversity in urban and agricultural environments could reduce dung removal rates and disturb the balance of those ecosystems. This, in turn, might cause both ecological and economic damage (Beynon et al. 2012; Losey and Vaughan 2006).

### *Climatic effects on α-diversity, community specialization, and γ-diversity*

The limited occurrence of dung-visiting beetles in regions with high precipitation might be explained by restricted flight activities (Juillet 1964) and increased soil moisture that can be detrimental to the dung beetle larval development (Sowig 1995; von Hoermann et al. 2020).

Unlike previous large-scale studies by Frank et al. (2018) and Milotić et al. (2019), who report no latitudinal effect and a precipitation effect on resource specialization, respectively, we observed community specialization on dung resources with decreasing temperatures, although we only considered a temperature gradient from 5-10°C (mean annual temperature). It should be noted, though, that the networks in general were not highly specialized. The maximum $H_2$’ value was 0.75 and only ten out of 94 networks had a $H_2$’ bigger than 0.5, which should be considered when interpreting the results. In the large-scale studies mentioned above, variance in community specialization was rather high, and effects might be masked by other environmental parameters, such as land use. We can confirm the assumption by Milotić et al. (2019), though, that resource specialization is linked to spatial characteristics (in temperate zones). There may be two explanations for the increased degree of specialization in cooler climates of the studied gradient: One is that resource specialization of dung beetles is expected to increase with an increasing variety of dung resources (Frank et al. 2018). Study sites in the coolest climate zones were mainly located in, or close to, Nature and National Parks, where the density and functional diversity of larger mammals (lynx, wolf, red deer, chamois, capricorn) are higher than in other study regions, and specialization of dung-visiting beetles is more likely. Second, dung is a nutrient-rich but ephemeral resource that many organisms compete for. Competition is a premise for niche differentiation and specialization, both influencing community network structures and robustness (Frank et al. 2018; Frank et al. 2017a). Dung in cold and moist regions is less prone to desiccation and persists longer than in warmer climates (Milotić et al. 2019). Hence, dung beetle species in cold climates could co-exist by resource partitioning (McKane et al. 2002), allowing for high levels of species diversity and specialization. Since specialized communities are less robust and more prone to environmental changes and extinction (Davies et al. 2004; Neff et al. 2021), we should ensure that species in these areas will experience special consideration in conservation strategies.

We also evaluated trophic specialization of dung-visiting beetles among dung types. Beetles were most specialized on bison dung along the temperature gradient, although bison, as grazer, was at the bottom of our trophic gradient. Herbivorous dung (sheep dung), however, was already shown to be more attractive for dung beetles than dog dung (Carpaneto et al. 2005). Since in temperate regions more dung beetles are attracted by bigger dung heaps rather than smaller dung heaps (Errouissi et al. 2004) and dung that is available for a longer period (Buse et al. 2021), it is very likely that the high specialization on bison dung was due to its high weight, compared to the other dung types. In a global meta-analysis, considering 45 case studies, Frank et al. (2018) found low specialization on bison dung; yet their results might be limited by the number of studies including bison dung as a research subject (n = 3). Since nutrient content and composition are reported to be not relevant for the long-distance chemical attraction of dung beetles (Frank et al. 2017a), we support the interpretation by Frank et al. (2017a) that volatiles emitted by dung and not nutrient content might be primary determinants in dung beetles' attraction (see e.g., Weithmann et al. 2020) for what the large bison dung heaps, emitting more volatiles due to its size, were potentially more preferred despite lower nutrient content.

We show that γ-diversity for common and dominant species was lowest in the warmest climate zone, which was to a great extent represented in NW Bavaria. This is due to Bavaria’s topography with an increase in elevation from west to east and north to south which results in a temperature gradient from warm (NW Bavaria) to cold (SE Bavaria). Since the NW corner of Bavaria is not as densely populated as other parts of our study area, we believe that the low diversity in this particular climate zone was not caused by urbanization effects. Instead, we assume that in this area there are less favorable climatic conditions for dung decomposition (Milotić et al. 2019) due to a higher risk of dung desiccation at higher temperatures. When dung desiccates, microbial activities which are key for the emission of volatile organic compounds (Le et al. 2005) are slowed down (Anderson and Coe 1974) and consequently, insects' attraction is reduced (Davis et al. 2013). Moreover, in Harris et al. (2019) and Williams et al. (2014), increasing temperatures and low precipitation, respectively, were found to potentially decrease the abundance and diversity of some ground-dwelling beetles. In a previous study, Englmeier et al. (2022b) found a hump-shaped pattern of dung removal rates along an elevational gradient, indicating that environmental conditions at intermediate altitudes are more beneficial for dung beetles than in lowlands. Therefore, we assume that climate warming might exacerbate the access to and decomposition of dung by insects, which could explain the potential future emigration of coprophilic beetles to cooler regions as observed by Menéndez et al. (2014).

A limiting factor in the interpretation of our results is that our sampling probably does not mirror the full dung-visiting beetle diversity across the year, although Šlachta (2013) found highest diversity in May.

## Conclusion

Our study of land-use and climate effects on diversity and community specialization of dung-visiting beetles has shown that intensive land use (agriculture, urban areas) and climate affect dung-visiting beetle assemblages. Diversity decreased from near-natural to intensive land use, on a local and regional scale. Dung-visiting beetle assemblages were more specialized in cooler climates, and hence, are likely more vulnerable to environmental changes. Our approach of a simultaneous study of climate and land use shows that both parameters affect different aspects of dung beetle communities. Urbanization and agriculture threaten diversity, while climate influences the dung specialization of communities, which might affect dung decomposition processes.

## Appendix III

**Table III A1:** Full species list of necro-/coprophilic beetles (according to Böhme and Lucht 2005 Assing and Schülke 2012) trapped in our experiment and included in the analysis

| **Species** | **Family** | **No.** | **Diet** |
|---|---|---|---|
| *Acrossus depressus* (Kugel., 1792) | Scarabaeidae | 270 | c |
| *Acrossus luridus* (Fabricius, 1775) | Scarabaeidae | 7 | c |
| *Agoliinus nemoralis* (Erichson, 1848) | Scarabaeidae | 11 | c |
| *Agrilinus ater* (DeGeer, 1774) | Scarabaeidae | 207 | c |
| *Anoplotrupes stercorosus* (Hartmann in L. G. in Scriba, 1791) | Geotrupidae | 1042 | cn |
| *Anotylus insecatus* (Gravenhorst, 1806) | Staphylinidae | 3 | c/ phy |
| *Anotylus rugosus* (Fabricius, 1775) | Staphylinidae | 3 | c/ phy |
| *Anotylus sculpturatus* (Gravenhorst, 1806) | Staphylinidae | 763 | c/ phy |
| *Anotylus tetracarinatus* (Block, 1799) | Staphylinidae | 944 | c/ phy |
| *Aphodius fimetarius* (L., 1758) | Scarabaeidae | 3 | c |
| *Aphodius pedellus* (DeGeer, 1774) | Scarabaeidae | 145 | c |
| *Calamosternus granarius* (L., 1767) | Scarabaeidae | 52 | c |
| *Colobopterus erraticus* (L., 1758) | Scarabaeidae | 33 | c |
| *Emus hirtus* (L., 1758) | Staphylinidae | 1 | c |
| *Esymus pusillus* (Herbst, 1789) | Scarabaeidae | 115 | c |
| *Margarinotus ignobilis* (Marseul, 1854) | Histeridae | 1 | n/ ca |
| *Melinopterus consputus* (Creutzer, 1799) | Scarabaeidae | 12 | c |
| *Melinopterus prodromus* (Brahm, 1790) | Scarabaeidae | 455 | c/s |
| *Melinopterus sphacelatus* (Panzer, 1798) | Scarabaeidae | 7 | c/s |
| *Necrodes littoralis* (L., 1758) | Silphidae | 1 | n/ ca |
| *Nicrophorus humator* (Gled., 1767) | Silphidae | 3 | n/ ca |
| *Nicrophorus interruptus* (Stephens, 1830) | Silphidae | 1 | n/ ca |
| *Nicrophorus vespillo* (L., 1758) | Silphidae | 33 | n/ ca |
| *Nicrophorus vespilloides* (Herbst, 1783) | Silphidae | 93 | n/ ca |

| | | | |
|---|---|---|---|
| *Oiceoptoma thoracicum* (L., 1758) | Silphidae | 51 | n |
| *Omalium rivulare* (Paykull, 1789) | Staphylinidae | 32 | s |
| *Omalium septentrionis* (Thomson,1857) | Staphylinidae | 23 | s |
| *Ontholestes haroldi* (Eppelsheim, 1884) | Staphylinidae | 3 | c |
| *Ontholestes murinus* (L., 1758) | Staphylinidae | 103 | n/c |
| *Ontholestes tesselatus* (Geoffr., 1785) | Staphylinidae | 56 | c/n |
| *Onthophagus coenobita* (Herbst, 1783) | Scarabaeidae | 722 | c/ne |
| *Onthophagus fracticornis* (Preyssler, 1790) | Scarabaeidae | 87 | c/ne |
| *Onthophagus joannae* (Goljan, 1953) | Scarabaeidae | 2020 | c |
| *Onthophagus ovatus* (L., 1767) | Scarabaeidae | 2537 | c/ne |
| *Onthophagus similis* (L. G. Scriba, 1790) | Scarabaeidae | 279 | c/ne |
| *Onthophagus taurus* (Schreber, 1759) | Scarabaeidae | 47 | c |
| *Onthophagus verticicornis* (Laich., 1781) | Scarabaeidae | 113 | c |
| *Otophorus haemorrhoidalis* (L., 1758) | Scarabaeidae | 4 | c |
| *Oxyomus sylvestris* (Scopoli, 1763) | Scarabaeidae | 13 | c |
| *Paederus littoralis* (Gravenhorst, 1802) | Staphylinidae | 3 | ca/ phytophagous |
| *Paederus riparius* (L., 1758) | Staphylinidae | 5 | ca/ phytophagous |
| *Phalacronothus biguttatus* (Germar, 1824) | Scarabaeidae | 1 | c |
| *Philonthus carbonarius* (Gravenhorst, 1802) | Staphylinidae | 376 | ca |
| *Philonthus cognatus* (Stephens, 1832) | Staphylinidae | 81 | ca |
| *Philonthus corruscus* (Gravenhorst, 1802) | Staphylinidae | 35 | ca |
| *Philonthus cruentatus* (Gmelin, 1790) | Staphylinidae | 5 | ca |
| *Philonthus decorus* (Gravenhorst, 1802) | Staphylinidae | 23 | ca |
| *Philonthus laevicollis* (Lacordaire, 1835) | Staphylinidae | 18 | ca |
| *Philonthus laminatus* (Creutzer, 1799) | Staphylinidae | 29 | ca |
| *Philonthus marginatus* (O. F. Müller, 1764) | Staphylinidae | 4 | c/ca |
| *Philonthus micans* (Gravenhorst, 1802) | Staphylinidae | 1 | ca |
| *Philonthus nitidus* (F., 1787) | Staphylinidae | 11 | c/ca |
| *Philonthus pseudovarians* (A. Strand, 1941) | Staphylinidae | 22 | ca |

| | | | |
|---|---|---|---|
| *Philonthus rectangulus* (Sharp, 1874) | Staphylinidae | 1 | ca |
| *Philonthus sanguinolentus* (Gravenhorst, 1802) | Staphylinidae | 14 | ca |
| *Philonthus splendens* (F., 1792) | Staphylinidae | 58 | c/ca |
| *Planolinus fasciatus* (Olivier, 1789) | Scarabaeidae | 13 | c |
| *Quedius cinctus* (Payk., 1790) | Staphylinidae | 4 | c/ca |
| *Quedius fuliginosus* (Gravenhorst, 1802) | Staphylinidae | 3 | ca |
| *Quedius molochinus* (Gravenhorst, 1806) | Staphylinidae | 1 | ca |
| *Quedius tristis* (Gravenhorst, 1802) | Staphylinidae | 4 | ca |
| *Saprinus aeneus* (F., 1775) | Histeridae | 12 | n/ca |
| *Silpha obscura* (L., 1758) | Silphidae | 26 | n/e |
| *Silpha tristis* (Illiger, 1798) | Silphidae | 1 | n/e |
| *Tachinus corticinus* (Gravenhorst, 1802) | Staphylinidae | 6 | s (on dung, fungi and carrion) |
| *Tachinus humeralis* (Gravenhorst, 1802) | Staphylinidae | 2 | s (on dung, fungi and carrion) |
| *Tachinus laticollis* (Gravenhorst, 1802) | Staphylinidae | 2 | s (on dung, fungi and carrion) |
| *Tachinus lignorum* (L., 1758) | Staphylinidae | 1 | s (on dung, fungi and carrion) |
| *Tachinus pallipes* (Gravenhorst, 1806) | Staphylinidae | 51 | s (on dung, fungi and carrion) |
| *Tachinus rufipes* (L., 1758) | Staphylinidae | 290 | s (on dung, fungi and carrion) |
| *Tachyporus chrysomelinus* (L., 1758) | Staphylinidae | 25 | ca |
| *Tachyporus hypnorum* (F., 1775) | Staphylinidae | 21 | ca |
| *Tachyporus nitidulus* (F., 1781) | Staphylinidae | 1 | ca |
| *Tachyporus obtusus* (L., 1767) | Staphylinidae | 1 | ca |
| *Tachyporus pusillus* (Gravenhorst, 1806) | Staphylinidae | 6 | ca |
| *Tasgius melanarius melanarius* (Heer, 1839) | Staphylinidae | 4 | ca |
| *Teuchestes fossor* (L., 1758) | Scarabaeidae | 18 | c |
| *Thanatophilus rugosus* (L., 1758) | Silphidae | 1 | n |
| *Thanatophilus sinuatus* (F., 1775) | Silphidae | 546 | n |

| | | | |
|---|---|---|---|
| *Trichonotulus scrofa* (F., 1787) | Scarabaeidae | 4 | c |
| *Trox sabulosus* (L., 1758) | Trogidae | 65 | n |
| *Trypocopris vernalis* (L., 1758) | Geotrupidae | 314 | c/cn |
| *Volinus sticticus* (Panzer, 1798) | Scarabaeidae | 477 | c |
| *Xantholinus elegans* (Oliver, 1795) | Staphylinidae | 3 | ca |
| *Xantholinus linearis* (Oliver, 1795) | Staphylinidae | 47 | ca |
| *Xantholinus longiventris* (Heer, 1839) | Staphylinidae | 17 | ca |

c: coprophagous; ca: carnivorous; cn: copronecrophagous; e: entomophagous; n: necrophagous; ne: necrophilous; phy: phytosaprophagous; s: saprophagous

**Table III A2:** Post-hoc test comparing abundance, species density, and species richness among habitats and landscapes.

| **Post-hoc** | | **Abundance** | | | **Species density** | | | **Species richness** | |
|---|---|---|---|---|---|---|---|---|---|
| *Habitat* | *Estimate* | *z* | *p* | *Estimate* | *z* | *p* | *Estimate* | *z* | *p* |
| grassland- forest | -0.046 | -0.188 | 0.998 | 0.042 | 0.394 | 0.979 | 0.057 | 0.814 | 0.847 |
| arable – forest | -0.651 | -2.565 | 0.050 | -0.070 | -0.630 | 0.922 | 0.099 | 1.284 | 0.571 |
| settlement- forest | 0.034 | 0.138 | 0.999 | -0.186 | -1.547 | 0.408 | -0.113 | -1.354 | 0.526 |
| arable – grassland | -0.604 | -2.256 | 0.108 | -0.112 | -0.961 | 0.771 | 0.042 | 0.522 | 0.953 |
| settlement- grassland | 0.083 | 0.294 | 0.991 | -0.228 | -1.811 | 0.267 | -0.170 | -1.968 | 0.198 |
| settlement- arable | 0.688 | 2.431 | 0.071 | -0.116 | -0.909 | 0.799 | -0.211 | -2.379 | 0.080 |
| *Landscape* | | | | | | | | | |
| agriculture - near-natural | -0.430 | -1.780 | 0.176 | -0.223 | -2.105 | 0.089 | -0.093 | -1.264 | 0.415 |
| urban - near-natural | 0.013 | 0.054 | 0.998 | -0.114 | -1.092 | 0.519 | -0.102 | -1.464 | 0.308 |
| urban - agriculture | 0.442 | 1.858 | 0.151 | 0.109 | 1.022 | 0.563 | -0.009 | -0.126 | 0.991 |

**Table III A3:** Linear model output testing d' against temperature for individual dung types. Significant *p*-values in bold.

| | | **d' of bison** | | | **d' of deer** | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *std. Error* | *p* | *Estimates* | *std. Error* | *p* |
| (Intercept) | 0.804 | 0.170 | **<0.001** | 0.491 | 0.195 | **0.014** |
| Temperature in °C | -0.047 | 0.019 | **0.017** | -0.019 | 0.022 | 0.394 |
| Observations | 87 | | | 81 | | |
| $R^2$ / $R^2$ adjusted | 0.065 / 0.054 | | | 0.009 / -0.003 | | |

| | | **d' of boar** | | | **d’ of lynx** | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *std. Error* | *p* | *Estimates* | *std. Error* | *p* |
| (Intercept) | 0.663 | 0.161 | **<0.001** | 0.772 | 0.167 | **<0.001** |
| Temperature in °C | -0.037 | 0.018 | **0.044** | -0.048 | 0.019 | **0.012** |
| Observations | 91 | | | 92 | | |
| $R^2$ / $R^2$ adjusted | 0.045 / 0.034 | | | 0.068 / 0.058 | | |

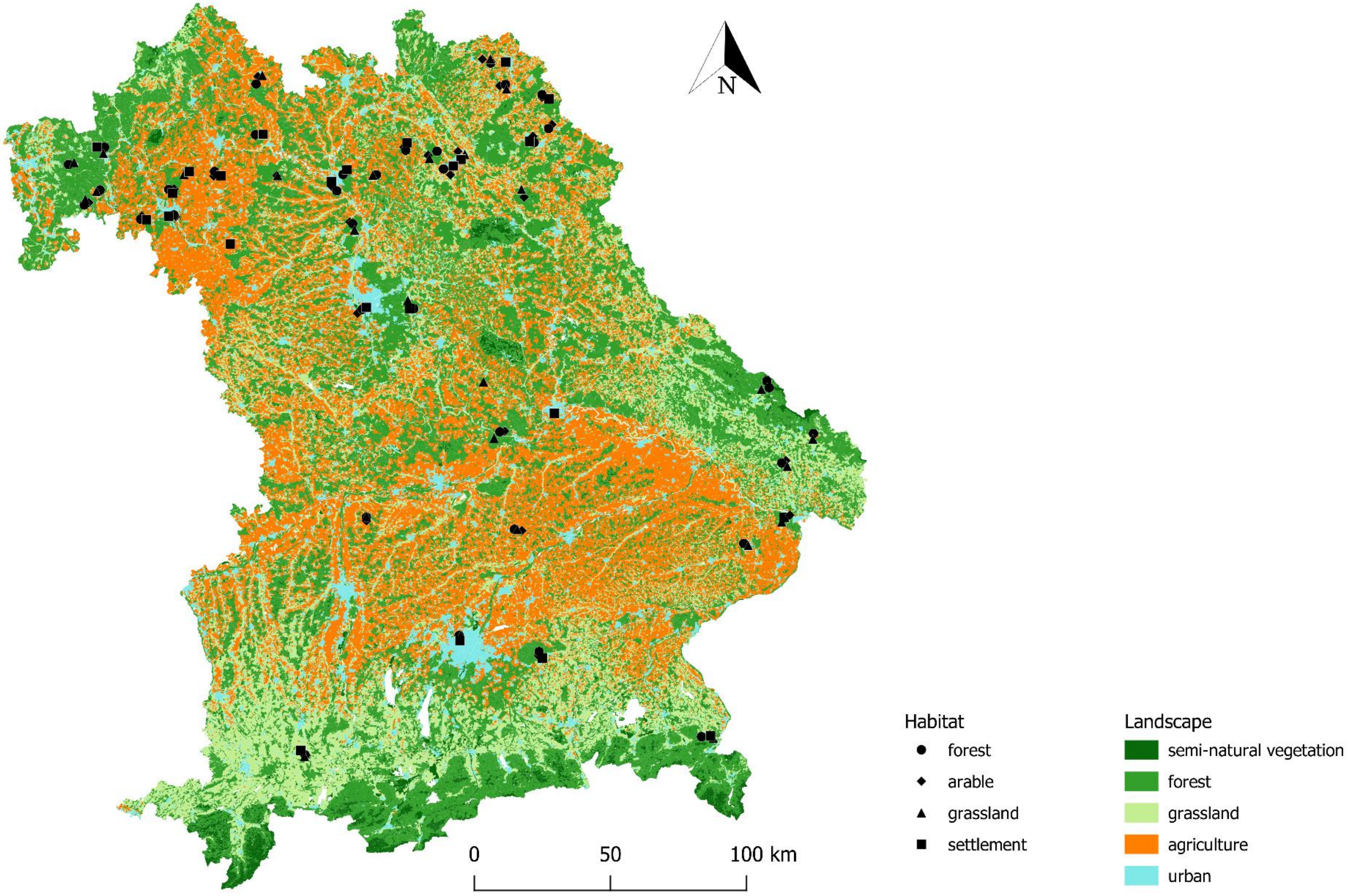

**Figure III A1:** Location of the 115 study sites within the land-use gradient (categories according to Corine 2012. Habitat types are depicted as black symbols.

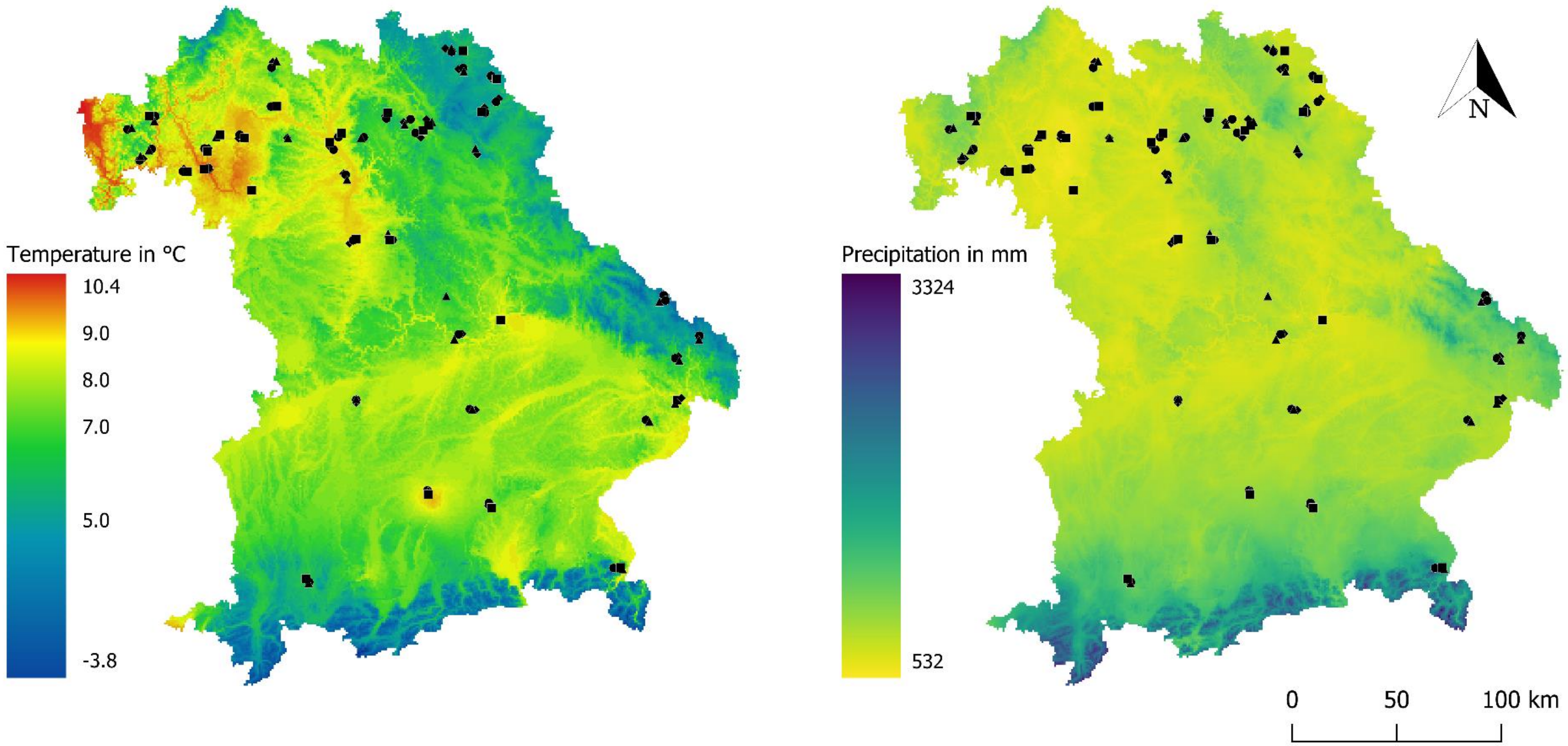

**Figure III A2:** Location of the 115 study sites along the temperature (left) and precipitation (right) gradients in Bavaria, Germany. The temperature- and precipitation-gradients comprise 30-year annual means (1981-2010).

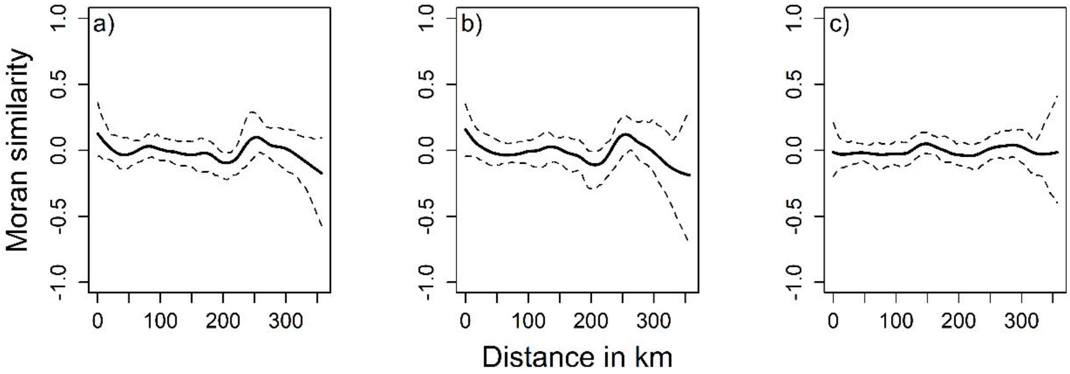

**Figure III A3:** Cross-correlogram of the negative-binomial generalized linear model residuals for a) abundance, b) species density, and c) species richness

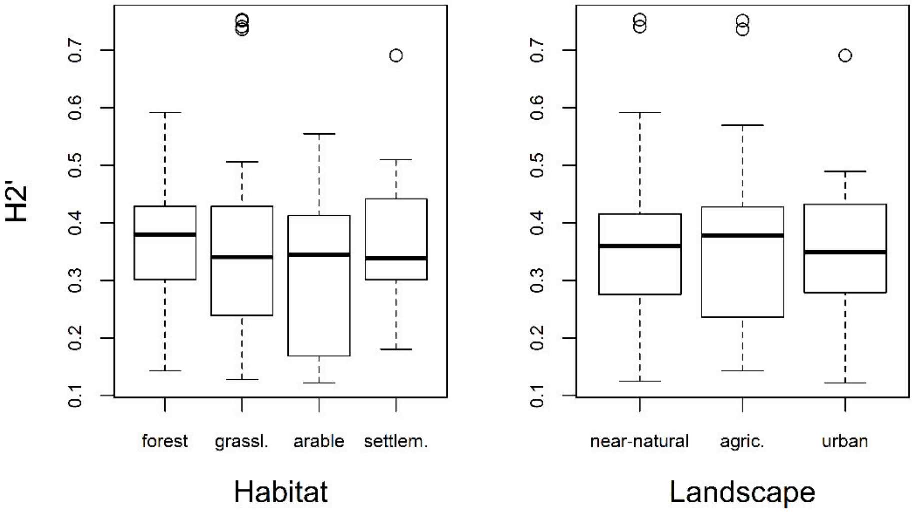

**Figure III A4:** Boxplots indicating the degree of specialization ($H_2$') in different habitats and landscapes

*“Life depends on little things we take for granted”*

- Anonymous

# Chapter IV

## Bacteria community composition and climate drive carrion decomposition – not beetles or land use

in preparation for publication

## Summary

Carrion is an important resource for many organisms that provide a critical ecosystem service, the decomposition of dead organic matter. Through decomposition, natural nutrient cycling is perpetuated, and ecosystems are stabilized. This process, however, could be threatened by global change. Climate change and land-use intensification modify biodiversity and ecosystem processes. In this study, I investigated climate and land-use effects on carrion decomposer communities, namely beetle and bacteria α-diversity, their community composition, and their role in decomposition processes. Beetles and bacteria were sampled on rat carrion exposed in 84 study sites across Bavaria, Germany using a full factorial design to distinguish climate and land-use effects. Study sites were established in four local land-use types: forests, grasslands, arable sites, and settlements, embedded in near-natural, agricultural, or urban landscapes. I found that the number of beetle species was reduced in settlements compared to forest sites. Bacteria richness, however, did not vary by land use but increased with higher temperatures. Interestingly, carrion decomposition was mainly directed by bacteria community composition and precipitation. In this study, I show the outstanding importance of bacteria, compared to insects and vertebrates, in carrion decomposition and that this microbial group of decomposers require more comprehensive research treatment in carrion ecology.

## Introduction

The functioning of an ecosystem depends on multiple processes that interact to regulate and maintain stability (Haines-Young and Potschin 2012). One fundamental ecosystem process is the decomposition of dead material from both plant- and animal-based sources, collectively known as necromass (Moore et al. 2004; Benbow et al. 2019). Necromass in the form of e.g., carcasses are reintroduced into nutrient cycling in both above-ground and below-ground nutrient pools (Cardinale et al. 2012). In this process, there is a community of organisms representing mammals, invertebrates, and microbes that are involved in decomposition (Olea et al. 2019; Benbow et al. 2019). Climate change, land use intensification and the decline in insects may threaten the interplay of ecosystem processes such as necromass decomposition. For instance, when the roles of land use, insects and local climate were evaluated for carrion decomposition, Englmeier et al. (2022b) (Chapter II) showed that temperature and the presence of insects were significant factors, while land use had no effect on decomposition rates.

To better understand the response of decomposition processes to climate and land-use intensification in more detail, it is necessary to evaluate the overall decomposition process into individual components. These components include but are not limited to insects and microbes that interact and change in relation to local and regional climatic and land-use conditions (Dubey et al. 2019; Lauber et al. 2014; Benbow et al. 2015).

Land-use intensity and climate were already found to have a significant influence on copronecrophilous beetle communities. In Englmeier et al. (2022a), for instance, agricultural land use and increasing precipitation were found to reduce copronecrophilous beetle abundance and species density on dung necromass. Carrion beetles have been observed to respond to increasing temperatures with higher abundances (von Hoermann et al. 2018; 2020) and are influenced by forest structure (Heidrich et al. 2020), soil properties (von Hoermann et al. 2018), and land-use type (Babcock et al. 2020; Dekeirsschieter et al. 2011). Further, the development of larvae, microbial metabolism, and hence decomposition rates are highly regulated by temperature (Barton and Bump 2019). Moisture, moreover, prevents the carrion from desiccation and enables microbial enzymatic activities and proliferation (Barton and Bump 2019). In the course of decomposition, bacteria produce volatiles that, in turn, attract decomposing insects, such as beetles or flies (Barton and Bump 2019; von Hoermann et al. 2022). Land use, temperature and precipitation all may influence bacterial communities, which in turn can determine arriving and remaining insect assemblages on carrion (through their volatiles emitted, von Hoermann et al. 2022). The interactions of microbes and beetles (and other insects), then, should influence the overall decomposition process.

However, there is a lack of large-scale studies that investigated beetle diversity and its contribution to decomposition processes in temperate zones. The same holds for that of microbial communities of carrion outside of research related to human forensics (Barton et al. 2013); however, recent studies are suggesting microbial importance to carrion decomposition and overall ecology

(Dangerfield et al. 2020; Crippen et al. 2015; Pechal et al. 2013). Hence, there is need to investigate mechanisms and interactions of microbes and beetle communities with climate and land use during decomposition processes.

Hence, this study aimed to evaluate variation of beetle- and microbial communities with climate change and land-use intensity using a large geographic scale factorial design. These results will contribute to a more comprehensive analysis on the influence and interplay of beetle- and microbial communities during the decomposition processes along large-scale climate and land-use gradients. To accomplish this, I analyzed the community diversity and composition of necro-, copro-, and copronecrophilous beetles and bacteria during rat carrion decomposition in relation to multiple land uses and climate zones covering a large geographic area of Bavaria, Germany.

## Methods

### *Study sites*

The study was conducted in 84 study sites across 36 study regions (à 5.8 x 5.8 km), with each region assigned to one regional landscape type (near-natural, agricultural, urban). Study sites (à 3 x 30 m) were then represented as one of four habitat types (forest, grassland, arable field, and settlement). The regional landscape types consisted of 13 near-natural landscapes (>85% near-natural vegetation including a minimum of 50% forest), 11 agricultural landscapes (>40% arable land and managed grassland), and 12 urban landscapes (>14% housing, industry, and traffic infrastructure). Within each study region, the three most dominant local land-use types (habitats) were represented as following: 30 forest sites, 17 grassland sites, 21 arable sites, and 16 settlement sites. At each site data from each carcass were collected in an open area with herbaceous vegetation, such as forest clearings, meadows, crop field margins, and green spaces within settlements or cities. A detailed description of the study-site selection process can be found in Redlich et al. (2021).

### *Study design and data collection*

**Insect sampling.** From May to June 2019, one pitfall trap baited with a rat carcass (200 – 250 g) was established on each of the 84 study sites. Carcasses were stored frozen and thawed one day before the beginning of the experiment.

Pitfall traps (400 mL plastic cups) were filled with 200 mL liquid (70 mL propylene glycol and 130 mL water) and emptied after 14 and 28 days after exposure. Small holes beneath the rim of the cup prevented overspill in case of rain. The bait was placed on the centre of a coarse mesh wire (mesh size 2 x 2 cm) that was placed half on the pitfall trap and half on the ground. The mesh wire was then fixated to the ground with tent pegs. To empty the traps in the field, the coarse mesh wire with the bait was carefully removed from the pitfall traps, and the content of the pitfall traps was sifted through a tea filter. The tea filter containing any specimens was then put in a sampling container and immediately covered with 70% Ethanol. Beetles were then identified to species level by the experts Tomáš Lakner, Jörg-Alfred Salamon, David Sommer, and Alexander Szallies. Since dung and carrion emit similar volatile organic compounds (Sladecek et al. 2021; von Hoermann et al. 2016; Weithmann et al. 2020), they attract necro- as well as coprophilous beetles. All species associated with this lifestyle (according to Böhme and Lucht 2005 and Assing and Schülke 2012) were incorporated in this study (Table IV A1). For further analysis, samples from the two sampling events per study site were pooled.

**Microbial sampling.** Additionally, microbial swabs of rat carrion were taken at 45 of the study sites. Carrion swabs were sampled after 14 days of decomposition by rotating a DNA-free cotton-tipped swab three times in the upper and lower oral cavity of the carcass head. The cotton applicator tip was then placed inside an Eppendorf tube filled with 200 µl of 96 % molecular grade ethanol and stored at -20°C. The subset of 45 samples was based on a balanced selection of habitat types, landscape types, and climate.

To determine the bacterial (16S rRNA gene) communities, DNA was extracted using DNeasy PowerSoil Kit (Qiagen, Germany) according to the manufacturer's instructions except an additional 5 ng/µL of lysozyme was added during the lysis step for reaction. The DNA was quantified by

Qubit 2.0 and the Quant-iT dsDNA HS Assay Kit (Thermo Fisher Scientific, Waltham, MA, USA). 16S rRNA gene amplicon library construction and DNA sequencing were performed at the Michigan State University Genomics Core Facility (East Lansing, MI, USA) using an Illumina MiSeq. The variable region 4 (V4) of the 16S rRNA gene was amplified using region specific primers (515 f [5' GTGCCAGCMGCCGCGGTAA] and 806 r [5' GGACTACHVGGGTWTCTAAT]).

Raw data were assembled, quality-filtered, demultiplexed and analyzed using the default settings in Qiime2 (Bolyen et al. 2019). Chimeric reads and artifacts were removed. For classification into taxonomic groups (16S rRNA region V4) I used the databases silva-138-99-515-806-nb-classifier.

### *Climate variables*

Long-term averages from 1991 to 2020 of air temperature (MAT) and precipitation amounts (MAP) were used as surrogates for climate. The data for individual study sites were derived from monthly gridded observational datasets with a horizontal resolution of 1 km, from which 30-year averages were subsequently calculated. Temperature and precipitation were only moderately correlated (spearman's rho = -0.61, $p < 0.05$). The raw input datasets were provided by the German Meteorological Service (Deutscher Wetterdienst, DWD) and are described in Kaspar et al. (2013).

### *Statistical Analysis*

I tested the effects of local (habitat) and regional (landscape) land use and climate (MAT and MAP) on the α-diversity of decomposer assemblages, including necro-, copro-, and copronecrophilous beetles and bacteria, and then modelled the effects of decomposer diversity (beetles and bacteria) on the decomposition processes of carrion. All analyses were conducted using the software R, version 4.0.5 (R Core Team 2021).

**Alpha-diversity** of beetles was described as species abundance, density (number of species), and richness (number of species corrected for abundance) per sample (*sensu* Gotelli and Colwell 2001). Bacterial diversity was measured as the rarefied number of OTUs (operational taxonomic units) detected in rat carrion. As predictors for α-diversity of beetles and bacteria, habitat type, landscape type, MAT, and MAP were used.

**Community composition.** To distinguish between diversity and composition effects on decomposition processes, an ordination for each decomposer group (beetles and bacteria) was created using Bray-Curtis dissimilarity matrices (package *vegan* by Oksanen et al. 2020). Based on these matrices, non-metric multidimensional scaling ordination plots (metaMDS) were used to visualize community dispersion. Environmental factors, i.e. habitat type, landscape type, MAT, and MAP were fitted onto the ordination with the function *envfit* (package *vegan* by Oksanen et al. 2020). For beetles, ‘abundance’ was also fitted onto the ordination. This step was not necessary for bacterial communities since the number of OTU reads was already rarefied.

**Decomposition.** Generalized additive models (GAMs) were used to model the effects of beetle and bacteria diversity and composition on decomposition processes (package *mgcv* by Wood 2006). To account for the response variable 'time until final decomposition', the family Cox.ph was used by implying a Cox proportional hazards model (Cox 1972). For further details see Englmeier et al. (2022b) or Chapter II.

## Results

### *Alpha diversity of beetles*

In total, 27,424 beetles from 75 species were collected (Table IV A1). The species *Thanatophilus sinuatus* (Fabricius, 1775) was most abundant with 17,005 individuals, then *Nicrophorus vespilloides* (Herbst, 1783) with 1,790 individuals and *Onthophagus ovatus* (Linnaeus, 1767) with 1,444 individuals. Alpha-diversity in terms of abundance, density, and species richness was robust to all environmental variables, i.e. MAT, MAP, local, and regional land use (Table 1). Marginally negative effects, though, were observed at a local scale with reduced abundance and density in settlements than forest habitat and a reduced richness in urban landscapes compared to near-natural landscapes.

**Table 1:** Results of the negative-binomial generalized linear model including beetle abundance, species density, and species richness as responses to habitat type, landscape type, mean annual temperature (MAT) and precipitation (MAP). Significant *p*-values in bold.

| | **Abundance** | | **Density** | | **Richness** | |
|---|---|---|---|---|---|---|
| *Predictors* | *z-value* | *p-value* | *z-value* | *p-value* | *z-value* | *p-value* |
| (Intercept) | 1.887 | 0.059 | 1.811 | 0.070 | 1.985 | **0.047** |
| Habitat grassland vs. forest | 0.930 | 0.353 | 1.111 | 0.266 | 0.839 | 0.401 |
| Habitat arable vs. forest | -0.274 | 0.784 | -0.336 | 0.737 | 0.079 | 0.937 |
| Habitat settlement vs. forest | -1.938 | 0.053 | -1.910 | 0.056 | -0.879 | 0.380 |
| Landscp. agric. vs. near-natural | -0.180 | 0.857 | -0.455 | 0.649 | -0.724 | 0.469 |
| Landscp. urban vs. near-natural | 0.024 | 0.981 | -1.068 | 0.286 | -1.750 | 0.080 |
| MAT in °C | 1.456 | 0.145 | 0.709 | 0.478 | -0.588 | 0.556 |
| MAP in mm | 0.620 | 0.535 | 1.309 | 0.191 | 0.697 | 0.486 |
| Abundance [log] | | | | | 9.669 | **<0.001** |
| Observations | 84 | | 84 | | 84 | |
| $R^2$ Nagelkerke | 0.182 | | 0.185 | | 0.864 | |

### *Alpha diversity of microbes*

Sufficient DNA was extracted for the analysis of 43 rat carrion samples, resulting in 11,815 OTUs identified. Carrion bacteria diversity was not significantly associated with either habitat and landscape type but it increased with greater MAT (Tab. 2).

**Table 2:** Results of the negative-binomial generalized linear model including the number of OTUs as responses to habitat type, landscape type, mean annual temperature (MAT) and precipitation (MAP). Significant *p*-values in bold.

| | **Bacteria diversity (No. of OTUs)** | |
|---|---|---|
| *Predictors* | *z-value* | *p-value* |
| (Intercept) | 2.907 | **0.004** |
| Habitat grassland vs. forest | -0.148 | 0.882 |
| Habitat arable vs. forest | 0.114 | 0.909 |
| Habitat settlement vs. forest | 0.068 | 0.946 |
| Landscape agriculture vs. near-natural | -0.893 | 0.372 |
| Landscape urban vs. near-natural | -1.825 | 0.068 |
| MAT in °C | 3.058 | **0.002** |
| MAP in mm | 1.214 | 0.225 |
| Observations | | 43 |
| $R^2$ Nagelkerke | | 0.353 |

### *Effects of land use and climate on decomposer community composition*

Beetle community composition was strongly correlated with the abundance of beetles (*envfit*, R2 = 0.564, p < 0.001) and strongly differed among habitat types (*envfit*, R2 = 0.192, p < 0.001) (Fig. 1). Beetle community composition was best described by the NMDS1-axis representing beetle abundance and NMDS2-axis representing habitat types (Fig. 1).

Bacteria communities, however, only responded to MAT (*envfit*, R2 = 0.182, p < 0.05) (Fig. 1). Bacteria community composition can be best described two-dimensionally by NMDS1- and NMDS2-axes, both representing MAT (Fig. 1).

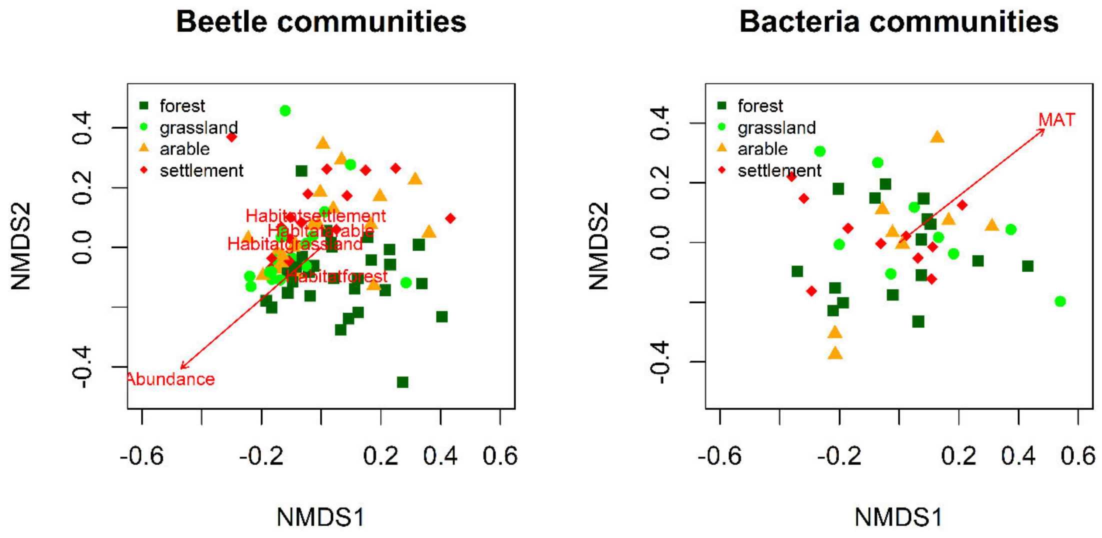

**Figure 1:** Ordination based on non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices (beetles: k=2, stress = 0.19; bacteria: k=3, stress=0.16). Dots are indicating communities in individual habitat types (forest: dark green, grassland: light green, arable field: orange, settlement: red). The closer the dots, the higher the proportion of species shared. Significant predictors are indicated by arrows and/ or red text.

### *Effects of land use, climate and decomposer communities on decomposition processes*

Carrion decomposition did not change among habitat and landscape types but was faster on study sites with high precipitation. While the number of beetle species and bacteria OTUs had no impact on decomposition, bacteria communities in warm regions accelerated decomposition processes.

**Table 3:** Summary statistics for the generalized additive Cox.ph model. Beetle diversity and composition, bacteria diversity and composition, habitat, landscape, mean annual temperature (MAT) and precipitation (MAP) were included as predictors in both models. Significant p-values in bold.

| | **Rat carrion (Cox.ph)** | |
|---|---|---|
| *Predictors* | *t-value* | *p-value* |
| (Intercept) | | |
| Beetle density | 0.384 | 0.700 |
| Beetle NMDS1 | 1.128 | 0.259 |
| Beetle NMDS2 | -1.609 | 0.108 |
| Bacteria density | 1.638 | 0.102 |
| Bacteria NMDS1 | 2.148 | **0.032*** |
| Bacteria NMDS2 | 2.534 | **0.011*** |
| Habitat grassland vs. forest | 0.897 | 0.370 |
| Habitat arable vs. forest | 1.642 | 0.101 |
| Habitat settlement vs. forest | 1.761 | 0.078 |
| Landscape agriculture vs. near-natural | -0.964 | 0.335 |
| Landscape urban vs. near-natural | -0.527 | 0.599 |
| MAT in °C | 1.303 | 0.193 |
| MAP in mm | 2.822 | **0.005**** |
| Observations | | 29 |
| $R^2$ adj. | | 12% |

## Discussion

This study is among the first that tests the effects of climate and land use on carrion-associated beetle and bacterial communities on decomposition rates at a large spatial scale.

Beetle α-diversity did not respond to either climate or land use, but community composition strongly changed among habitat types. Bacteria richness and community composition were unrelated to land use; however, bacteria richness was strongly and directly associated with increasing temperatures. Carrion decomposition was not affected by local and regional land use but responded to precipitation with accelerated decomposition and to bacteria community composition that was mainly directed by MAT.

### *Land-use effects on decomposer communities and decomposition processes*

Similar to the reported negative effects of anthropogenic land use (agriculture) on dung-visiting beetles (Englmeier et al. 2022a, Chapter III), urban land use (local and regional) was only marginally associated with reduced beetle α-diversity, whereas community composition significantly differed among habitat types. In Shizukuda and Saito (2021) they found canopy openness and the surrounding land-use type were the main drivers of carrion beetle community structure, explaining significantly different communities in forests compared to agricultural and urban areas. Although our study sites were established on open habitat patches (forest clearings, meadows, green spaces), forests offer a larger area with closed canopy than open habitats, such as arable fields and green spaces in urban environments, which might explain the tendentially higher species density in forests than settlements and different community compositions among habitat types.

Bacteria, in turn, did not respond to habitat and landscape types. Most carrion-decomposing bacteria are part of the living animal microbiome and initiate the decomposition process soon after death (Benbow et al. 2015), and particularly bacteria found in the gut of animals strongly contribute to the decomposition processes (Barton and Bump 2019). Hence, I assume that bacteria community structure is primarily defined by their host rather than by their surrounding environment. Since microbes contribute to inherent decomposition speed to a great extent (Barton and Bump 2019), it is likely that decomposition rates are constant among land-use types due to the robustness of bacteria to land-use intensity (von Hoermann et al. 2022)

### *Climate effects on decomposer communities and decomposition processes*

In contrast to Chapter III (Englmeier et al. 2022a), neither MAT nor MAP had a significant impact on beetle diversity. However, although significant, the effect size of the precipitation effect in the before mentioned study was relatively low and should not be overestimated. Other studies, e.g. von Hoermann et al. (2018) and (2020) found positive local temperature effects on carrion-visiting beetle abundance but negative effects on their community diversity (von Hoermann et al. 2018). In these studies, ambient temperature was measured during the experiment on-site to represent local conditions and no long-term data were used. Consequently, their temperature range was smaller as in this study, suggesting that beetles on carrion are more sensitive to short-term, local temperature changes than to long-term fluctuations.

Temperature was the main driver for bacterial community composition, which in turn had the strongest impact on carrion decomposition processes. Thus, warmer climates did not only increase bacterial diversity (higher number of OTUs), but it also indirectly accelerates decomposition processes by shaping bacterial community composition. Bacteria play a major role in overall decomposition processes and their presence can significantly enhance decomposition rates (Lauber et al. 2014). Von von Hoermann et al. (2022), for instance, found strong linkages among bacteria, their emitted volatiles, and insects (carrion-associated flies) attracted by these volatiles, suggesting that the presence and composition of bacterial communities is a premise for the attraction of insects that in turn can significantly accelerate decomposition processes (Englmeier et al. 2022b). Precipitation was another major factor influencing carrion decomposition. Carrion in warm regions with low precipitation would desiccate quickly and decomposer activities would be slowed (Barton and Bump 2019). It becomes apparent that carrion decomposition is indirectly mediated by higher temperatures through higher microbial diversity and activity (including high proliferation rates) and directly by precipitation, which prevents the carrion substrate from rapid desiccation and provides microbes a suitable environment (Barton and Bump 2019; Benbow et al. 2015).

### *Conclusion*

These results are consistent with Englmeier et al. (2022b) (Chapter II), where carrion decomposition was directly driven by MAT and MAP, whereas land use had no effect. In addition to Englmeier et al. (2022b), I found that when including microbial community data in the analysis, the direct temperature effect disappears but temperature indirectly influences decomposition by shaping bacteria community structures. Interestingly, bacteria community composition was more important than the number of OTUs, beetle abundance and beetle community composition, showing that despite of their microscopic size, more attention should be paid to the role of microbes in overall decomposition processes.

## Appendix IV

**Table IV A1:** Full species list of necro-/coprophilic beetles trapped in our experiment and included in the analysis

| Species | Family | Diet | No. |
|---|---|---|---|
| *Acrossus depressus* (Kugelann, 1792) | Scarabaeidae | c | 1 |
| *Agrilinus ater* (DeGeer, 1774) | Scarabaeidae | c | 1 |
| *Aleochara curtula* (Goeze, 1777) | Staphylinidae | n | 46 |
| *Anoplotrupes stercorosus* (Hartmann in L. G. in Scriba, 1791) | Geotrupidae | cn | 709 |
| *Anotylus sculpturatus* (Gravenhorst, 1806) | Staphylinidae | phy | 337 |
| *Anotylus tetracarinatus* (Block, 1799) | Staphylinidae | phy | 720 |
| *Aphodius pedellus* (DeGeer, 1774) | Scarabaeidae | c | 1 |
| *Bisnius fimetarius* (Gravenhorst, 1802) | Staphylinidae | partly nidicolous | 17 |
| *Calamosternus granarius* (Linnaeus, 1767) | Scarabaeidae | c | 1 |
| *Chilothorax distinctus* (Müller, 1776) | Scarabaeidae | c | 1 |
| *Colobopterus erraticus* (Linnaeus, 1758) | Scarabaeidae | c | 11 |
| *Creophilus maxillosus* (Linnaeus, 1758) | Staphylinidae | n | 31 |
| *Esymus pusillus* (Herbst, 1789) | Scarabaeidae | c | 6 |
| *Geotrupes stercorarius* (Linnaeus, 1758) | Geotrupidae | c | 1 |
| *Gyrohypnus angustatus* (Stephens, 1833) | Staphylinidae | on rotten material | 1 |
| *Margarinotus ignobilis* (Marseul, 1854) | Histeridae | n/ ca | 2 |
| *Melinopterus prodromus* (Brahm, 1790) | Scarabaeidae | c/s | 3 |
| *Necrobia violacea* (Linnaeus, 1758) | Cleridae | n | 1 |
| *Necrodes littoralis* (Linnaeus, 1758) | Silphidae | n/ ca | 162 |
| *Nicrophorus humator* (Gleditsch, 1767) | Silphidae | n/ ca | 181 |
| *Nicrophorus vespillo* (Linnaeus, 1758) | Silphidae | n/ ca | 668 |
| *Nicrophorus vespilloides* (Herbst, 1783) | Silphidae | n/ ca | 1790 |
| *Oiceoptoma thoracicum* (Linnaeus, 1758) | Silphidae | n | 1352 |
| *Omalium rivulare* (Paykull, 1789) | Staphylinidae | on rotten material | 25 |
| *Omalium septentrionis* (C.G. Thomson, 1857) | Staphylinidae | on rotten material | 3 |

| | | | |
|---|---|---|---|
| *Ontholestes haroldi* (Eppelsheim, 1884) | Staphylinidae | c | 29 |
| *Ontholestes murinus* (Linnaeus, 1758) | Staphylinidae | n | 108 |
| *Ontholestes tesselatus* (Geoffroy, 1758) | Staphylinidae | c/n | 9 |
| *Onthophagus coenobita* (Herbst, 1783) | Scarabaeidae | c/ne | 590 |
| *Onthophagus fracticornis* (Preyssler, 1790) | Scarabaeidae | c/ne | 55 |
| *Onthophagus illyricus* (Scolpoli, 1763) | Scarabaeidae | c | 45 |
| *Onthophagus joannae* (Goljan, 1953) | Scarabaeidae | c | 561 |
| *Onthophagus nuchicornis* (Linnaeus, 1758) | Scarabaeidae | c | 23 |
| *Onthophagus ovatus* (Heer, 1847) | Scarabaeidae | c/ne | 1444 |
| *Onthophagus similis* (Scriba, 1790) | Scarabaeidae | c/ne | 60 |
| *Onthophagus taurus* (Schreber, 1759) | Scarabaeidae | c | 43 |
| *Onthophagus verticicornis* (Laicharting, 1781) | Scarabaeidae | c | 44 |
| *Philonthus carbonarius* (Gravenhorst, 1802) | Staphylinidae | ca | 623 |
| *Philonthus cognatus* (Stephens, 1832) | Staphylinidae | ca | 80 |
| *Philonthus corruscus* (Gravenhorst, 1802) | Staphylinidae | ca | 9 |
| *Philonthus decorus* (Gravenhorst, 1802) | Staphylinidae | ca | 19 |
| *Philonthus laevicollis* (Lacordaire, 1835) | Staphylinidae | ca | 4 |
| *Philonthus laminatus* (Creutzer, 1799) | Staphylinidae | ca | 13 |
| *Philonthus marginatus* (O. F. Müller 1764) | Staphylinidae | c | 8 |
| *Philonthus nitidus* (Fabricius, 1787) | Staphylinidae | c | 2 |
| *Philonthus politus* (Linnaeus, 1758) | Staphylinidae | ca | 4 |
| *Philonthus pseudovarians* (A. Strand, 1941) | Staphylinidae | ca | 3 |
| *Philonthus quisquiliarius* (Gyllenhal, 1810) | Staphylinidae | ca | 6 |
| *Philonthus sanguinolentus* (Gravenhorst, 1802) | Staphylinidae | ca | 4 |
| *Philonthus splendens* (Fabricius, 1792) | Staphylinidae | c | 29 |
| *Philonthus succicola* (C. G. Thomson, 1860) | Staphylinidae | ca | 32 |
| *Philonthus tenuicornis* (Mulsant & Rey, 1853) | Staphylinidae | ca | 6 |
| *Proteinus brachypterus* (Fabricius, 1792) | Staphylinidae | dung/fungi/compost feeder | 7 |

| | | | |
|---|---|---|---|
| *Proteinus ovalis* (Stephens, 1834) | Staphylinidae | dung/ fungi/ compost feeder | 20 |
| *Quedius cinctus* (Paykull, 1790) | Staphylinidae | c | 2 |
| *Quedius fuliginosus* (Gravenhorst, 1802) | Staphylinidae | ca | 2 |
| *Saprinus aeneus* (Fabricius, 1775) | Histeridae | n/ca | 5 |
| *Saprinus lautus* (Erichson, 1839) | Histeridae | n/ca | 8 |
| *Silpha obscura obscura* (Linnaeus, 1758) | Silphidae | n/e | 46 |
| *Tachinus corticinus* (Gravenhorst, 1802) | Staphylinidae | on dung, fungi and carrion | 4 |
| *Tachinus humeralis* (Gravenhorst, 1802) | Staphylinidae | on dung, fungi and carrion | 1 |
| *Tachinus pallipes* (Gravenhorst, 1806) | Staphylinidae | on dung, fungi and carrion | 16 |
| *Tachinus proximus* (Kraatz, 1855) | Staphylinidae | on dung, fungi and carrion | 1 |
| *Tachinus rufipes* (Linnaeus, 1758) | Staphylinidae | on dung, fungi and carrion | 131 |
| *Tachyporus chrysomelinus* (Linnaeus, 1758) | Staphylinidae | ca | 3 |
| *Tachyporus hypnorum* (Linnaeus, 1755) | Staphylinidae | ca | 16 |
| *Tachyporus pusillus* (Gravenhorst, 1806) | Staphylinidae | ca | 1 |
| *Tasgius melanarius melanarius* (Heer, 1839) | Staphylinidae | ca | 1 |
| *Thanatophilus rugosus* (Linnaeus, 1758) | Silphidae | n | 158 |
| *Thanatophilus sinuatus* (Linnaeus, 1755) | Silphidae | n | 17005 |
| *Trox sabulosus* (Linnaeus, 1758) | Trogidae | n | 12 |
| *Trypocopris vernalis* (Linnaeus, 1758) | Geotrupidae | c/cn | 41 |
| *Volinus sticticus* (Panzer, 1798) | Scarabaeidae | c | 4 |
| *Xantholinus linearis* (Oliver, 1795) | Staphylinidae | ca | 14 |
| *Xantholinus longiventris* (Heer, 1839) | Staphylinidae | ca | 2 |

c: coprophagous; ca: carnivorous; cn: copronecrophagous; e: entomophagous; n: necrophagous; ne: necrophilous; phy: phytosaprophagous; s: saprophagous

# Chapter V

## Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria

with

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## Summary

**Aim:** Climate and land use are major drivers of species richness. Lower species richness in cold climates and anthropogenic landscapes can be caused by lower rates of biotic interactions. Deadwood fungi and bacteria interact strongly with their hosts due to long-lasting evolutionary trajectories. However, how rates of biotic interactions (specialization) change with temperature and land-use intensity is unknown. We hypothesize a decrease in species richness and specialization of communities with decreasing temperature and increasing land-use intensity. According to the literature, effects should be more pronounced for fungi than for bacteria.

**Location:** Germany, Bavaria

**Methods:** We used a full-factorial nested design to disentangle effects of temperature (mean annual temperatures (MAT) and local temperature) and land use at habitat and landscape scale on microbial diversity and specialization, spanning an area of 300 km x 300 km. We exposed four deadwood objects representing the dominant tree species in Central Europe (beech (*Fagus sylvatica*), oak (*Quercus sp.*), spruce (*Picea abies*), and pine (*Pinus sylvestris*)) on 179 study plots.

**Main Results:** While fungal richness did not respond to any temperature variable, bacterial richness increased with MAT and decreased with local temperature. We found higher fungal richness in near-natural than urban landscapes. Bacterial richness was higher in grassland than in forest habitats. Specialization of fungi showed no significant relationship with MAT and land use at landscape scale but a negative relationship with local temperature. Specialization of bacteria increased with MAT and was higher in agricultural than in near-natural landscapes. Fungal and bacterial community composition was mainly explained by host tree identity.

**Main Conclusions:** Host identity and hence specialization strongly exceeds effects of climate and land use on fungal but not bacterial communities. This suggests contrasting responses between microbial taxa to climate and land-use intensity with consequences on deadwood diversity interactions and hence decomposition processes.

**Keywords:** climate change, land-use intensification, microbes, network analysis, saproxylic, urbanization

## Introduction

Climate and land use are major drivers of species diversity at various spatial scales (Storch et al. 2007). In many taxonomic groups, species richness decreases with decreasing temperature (Lomolino 2001) and with increasing land-use intensity (Murphy and Romanuk 2014; Newbold et al. 2015). The mechanisms, however, are often not well understood (Urban et al. 2016). This limits our ability to predict how climate change and land-use intensification will affect species richness. In species groups characterized by strong interactions with a host (ecological specialization), the mechanism behind observed declines in species richness along climate and land use gradients can be lower rates of biotic processes (Pellissier et al. 2018).

Fungi and bacteria are tremendously species-rich and the main decomposers of deadwood (Boddy and Watkinson 1995; Johnston et al. 2016). They are thus particularly important for the global carbon and nutrient cycle (Bani et al. 2018), considering that the amount of carbon stored in deadwood is equivalent to about 8 % of the global forest carbon stocks (Pan et al. 2011). Fungi and bacteria depending on deadwood are highly specialized due to strong co-evolutionary trajectories with their host tree species (Moll et al. 2021; Floudas et al. 2012). However, fungi show a slightly stronger specialization than bacteria (Moll et al. 2021). Still, our knowledge of how temperature and land use affect fungal and bacterial species richness and how this is linked to changes in biotic interactions (specialization) is limited.

In this study, we used a full-factorial design to disentangle temperature and land-use effects on fungal and bacterial richness, and host tree specialization along climate and land-use gradients in southern Germany. We expect that specialization of both groups decreases with decreasing temperature and increasing land-use intensity caused by increasing environmental variability for the following reasons. First, theory predicts an increase of generalist species thereby reducing community specialization with decreasing mean temperature at different spatial scales (latitudinal and altitudinal niche breadth hypothesis, MacArthur 1972), caused by a higher temperature variability in cold environments (Rasmann et al. 2014). Second, land-use intensification causes environmental variability via disturbance and perturbation of habitats (Dudley and Alexander 2017; Tittensor et al. 2014; Polasky et al. 2011; Curtis et al. 2018) and hence, anthropogenic habitats should support generalist species, thereby decreasing specialization within communities. This assumption is supported by an empirical study suggesting that the observed decline in specialist species can be attributed to habitat destruction and degradation (Clavel et al. 2011). Variability of environmental conditions, e.g. in terms of temperature and land-use intensity, is crucial for niche evolution: The evolution of specialization has been attributed to stable environmental conditions, while generalist species are thought to have evolved under variable heterogeneous environmental conditions (van Tienderen 1991). Environmental unpredictability causes variability in species population sizes and hence supports the evolution of generalists (Whittaker 1975). Hence, if fungi species within a community are more specialized on hosts than bacteria, they should be characterized by narrower environmental niches and should respond more strongly to climate and land use (Pellissier et al. 2018; MacArthur 1972). This evolutionary mechanism should translate into the structuring of communities observed today (ecological mechanism) and can be tested via specialization measures of communities in a given environment.

To test these expectations, we experimentally exposed four deadwood objects representing the main tree species in Central Europe (beech, oak, spruce, pine) on 179 study plots across a large climate and land-use gradient. We characterized fungal and bacterial communities via high-throughput sequencing and determined species richness and specialization (H2’ index). We tested the following hypotheses: 1) Species richness and specialization decrease with decreasing temperature, and 2) decrease with increasing land-use intensity. We expected that the effects are more pronounced for fungi than for bacteria.

## Methods

### *Study design*

In April 2019, we placed deadwood objects along a climate and land-use gradient in Bavaria, Germany. To establish these gradients, five climate zones based on mean annual temperature from 1981 to 2010 (Deutscher Wetterdienst 2020) and three land-use categories (near-natural, agricultural and urban) were defined and assigned to a matrix of grid cells (5.8 km x 5.8 km) across

Bavaria. Grid cells were selected to represent all 15 possible combinations of climate and land-use categories with four replicates, resulting in 60 grid cells (following: 'study region').

Within each of the 60 study regions, three study plots (à 3 x 30 m) were embedded, representing the most dominant habitat types (out of forest, grassland, arable fields, and settlements), resulting in 179 study plots in total (one study region contained only two study plots). For reasons of standardization, study plots were established on an open area with herbaceous vegetation, such as forest clearings, meadows, crop field margins, and green spaces within settlements or cities. The study area covers an area of 300 km x 300 km and 1000 m in elevation. More details about the study design can be found in Redlich et al. (2021).

As deadwood, the four dominant tree genera in German forests were chosen, i.e. beech (*Fagus sylvatica*), oak (*Quercus sp.)*, spruce (*Picea abies)*, and pine (*Pinus sylvestris)*. All deadwood branches originated from the Steigerwald Forest, northern Bavaria, to ensure equal starting conditions in microbial communities. On each study plot, one branch (10 cm in diameter, 50 cm length) of each of the four tree genera was vertically leaned on a pole, with direct soil contact, for one growing season (April – September 2019).

### *Environmental parameters*

The information on mean annual temperature (MAT) for each study plot was extracted from gridded monthly datasets with a horizontal resolution of 1 km using the nearest source to destination approach. Subsequently, long-term averages were calculated for the period 1991 to 2020. The raw input datasets were provided free of charge by the German Meteorological Service (DWD) and are described in Kaspar et al. (2013). To characterize small-scale habitat-related variation in temperature, we used ibutton thermologgers (type DS1923, Hygrochron iButton, Whitewater, WI, USA) on each study plot (average temperature from April – September 2019). Each datalogger was mounted on a wooden pole at 1.10 m height, facing north and with a roof panel to protect against direct sun exposure. We define this temperature measure as ‘local temperature’ in the following. Furthermore, we used the co-variate mean annual sum of precipitation (MAP) to account for offset effects. MAP was assessed analogously to MAT, using data from the German Meteorological

Service (DWD), described in Kaspar et al. (2013). Land use variables considered were the four habitat types (forest, grassland, arable field, settlements) embedded within near-natural, agricultural or urban landscapes.

### *Microbial sample processing*

For the assessment of the microbiome in the deadwood, we removed the bark from each branch with a knife before drilling three holes (diameter *c.* 0.5 cm) horizontally into the middle of the branch. Five grams of the extracted powdery debris were pulverized using liquid nitrogen in a swing mill (Retsch, Haan, Germany). The knife and drill were sterilized after each sample using a bunsen burner and 99 % Ethanol. Total bacterial and fungal DNA was isolated from 0.25 g of each homogenized, powdery wood sample using the Quick-DNA Fecal/ Soil Microbe Miniprep kit (D6010) (Zymoresearch, Irvine, CA, USA) following the manufacturer's instructions. Bacteria DNA was amplified using the V4 region 16S gene amplicon and region-specific primers 515F-Y (*forward*) [GTGYCAGCMGCCGCGGTAA] and 806RB (*reverse*) [GGACTACNVGGGTWTCTAAT] modified by Caporaso et al. (2011; 2012). The fungal ITS region was amplified using the region-specific primers fITS7 (*forward*) [GTGARTCATCGAATCTTTG] and ITS4 (*reverse*) [TCCTCCGCTTATTGATATGC] described by Ihrmark et al. (2012). Samples were sequenced on an Illumina MiSeq system. Subsequently, data were demultiplexed allowing one or two mismatches or Ns in the barcode and sorted by amplicon inline barcodes (allowing for one mismatch per barcode). Reads with a final length of <100 bases were discarded. Forward and reverse reads were combined using BBMerge v34.48 (Bushnell et al. 2017). Sequencing and bioinformatics were done by LGC Genomics, Berlin (Germany). We removed all singletons (OTUs with only one sequence read) from the dataset prior to statistical analysis.

### *Response variables*

To determine fungal and bacterial species richness, we calculated the rarefied OTU (by minimum row sums) for each object using the function rarefy (package vegan by Oksanen et al. 2020). For the plot-level analyses, we summed up the rarefied species richness of all objects per study plot. We are aware of the fact that OTUs are not equivalent to species but for reasons of readability we chose the term species when talking about OTUs.

To compare community compositions among objects and plots, along MAT and local temperature gradients, and among habitat and landscape types, rarefied community matrices were used (function *rrarefy*, package *vegan* by Oksanen et al. 2020). Rarefaction depths were chosen based on histograms representing the distribution of the sum of reads per study plot.

Community specialization, based on the rarefied community matrix at plot level (the same as for community composition analysis), was calculated by a bipartite network analysis using the package *bipartite* (Dormann et al. 2009). Here, the standardized two-dimensional Shannon entropy ($H_2$’, Blüthgen et al. 2006b) serves as a measure of fungal and bacterial community specialization on host trees and ranges between 0 (no host tree preference) and 1 (total specialization). $H_2$’ calculates the interaction frequencies of two groups of different trophic levels (number of OTUs per host tree) in relation to all possible interactions, hence being network-size independent. By this, comparisons across networks and along ecological gradients are possible, i.e. whether community specialization shifts to a more specialized or generalistic resource use with a shift in MAT, local temperature, and land use. After calculating $H_2$’, we compared the observed $H_2$’ values with a null model with full randomization that kept frequencies and richness constant (‘r2dtable’, 1000 simulations).

### *Statistics*

All statistical analyses were performed using R 4.0.2 (R Core Team 2021).

To test the relationship between fungal and bacterial richness versus MAT, local temperature and land use at habitat and landscape scale, we used four separate negative-binomial generalized linear models (Venables and Ripley 2007), one for each microbial group and each resolution level (plot level and object level). As main predictors, we used MAT, local temperature, habitat type and landscape type. Since MAT and local temperature were only moderately correlated (spearman’s rho = 0.50 and $p < 0.05$), both variables were included in the models. As outlined above, we used MAP as a co-variate in our models. In the models on object level, we included ‘study plot’ as random factor. Finally, post-hoc tests were performed to assess effects among host tree identities, habitat types, and landscape types, respectively (package *multcomp* by Hothorn et al. 2008). We compared the effects between fungi and bacteria based on the models' effects sizes (z-values).

Effects of host tree identity, MAT, local temperature and land use at habitat and landscape scale on fungal and bacterial species composition were analyzed using Bray-Curtis dissimilarity matrices (package *vegan*, Oksanen et al. 2020). Based on these matrices (fungi and bacteria separately), non-metric multidimensional scaling ordination plots (metaMDS) were created. We applied a permutational multivariate analysis of variance (permanova, function *adonis*) with 999 permutations to test the relative importance of our set of predictors on the composition of fungal and bacterial communities. We compared the effects between fungi and bacteria based on the models' $R^2$-values.

To test the relationship between fungal and bacterial specialization versus MAT, local temperature and land use at habitat and landscape scale, we built a beta-regression model for both fungi and bacteria using $H_2$' as response variable. MAP, moreover, was included as co-variate as described above.

## Results

### *Microbial richness at study-plot level*

Fungal species richness showed a non-significant negative relationship with MAT (Table 1, Fig. 1a). In contrast, bacteria species richness was significantly positively related to MAT (Table 1, Fig. 1a). Fungal species richness was significantly higher in near-natural landscapes compared to urban landscapes (Table 1, Fig. 1b), whereas bacteria species richness showed no significant relationship with land-use intensity (Table 1, Fig. 1b). Post-hoc test results for land use at habitat and landscape scale can be found in Table V A1.

**Table 1:** Effects of the main predictors (MAT, local temperature and land use at habitat and landscape scale) and the co-variate mean annual sum of precipitation on the richness and degree of community specialization on host tree ($H_2$') of fungi and bacteria estimated by generalized linear models (negative binomial) and beta-regression models, respectively. Significant effects are indicated in bold and by asterisks.

| | | **Fungi** | | | **Bacteria** | | |
|---|---|---|---|---|---|---|---|
| | | **Richness** | | **$H_2$'** | **Richness** | | **$H_2$'** |
| *Predictors* | | *IRR* | *z-value* | *z-value* | *IRR* | *z-value* | *z-value* |
| | (Intercept) | 3285.55 | **5.70***** | 1.21 | 0.09 | -1.55 | **-4.60***** |
| **Main predictors** | | | | | | | |
| Temperature | Mean annual temperature (MAT) in °C | 0.96 | -0.84 | 0.08 | 1.25 | **3.79***** | **2.29*** |
| | Local temp. in °C | 1.04 | 1.34 | **-2.03*** | 0.93 | **-2.18*** | -0.59 |
| Habitat type | Grassland vs. forest | 1.06 | 0.72 | -1.26 | 1.29 | **2.76**** | 1.41 |
| | Arable vs. forest | 0.92 | -0.97 | -0.82 | 1.12 | 1.19 | 1.61 |
| | Settlement vs. forest | 1.02 | 0.21 | -0.17 | 1.09 | 0.86 | 0.37 |
| Landscape type | Agric. vs. near-natural | 0.88 | -1.52 | -0.62 | 1.00 | -0.03 | **2.89**** |
| | Urban vs. near-natural | 0.83 | **-2.26*** | -0.28 | 0.95 | -0.57 | 1.69 |
| **Co-variate** | | | | | | | |
| Precipitation | Mean annual sum of precipitation (MAP, log10) in mm | 0.35 | **-2.55*** | 0.69 | 6.58 | **4.28***** | **4.99***** |
| Observations | | | 160 | 172 | | 157 | 172 |
| $R^2$ Nagelkerke/ pseudo for $H_2$' | | | 0.12 | 0.04 | | 0.25 | 0.14 |

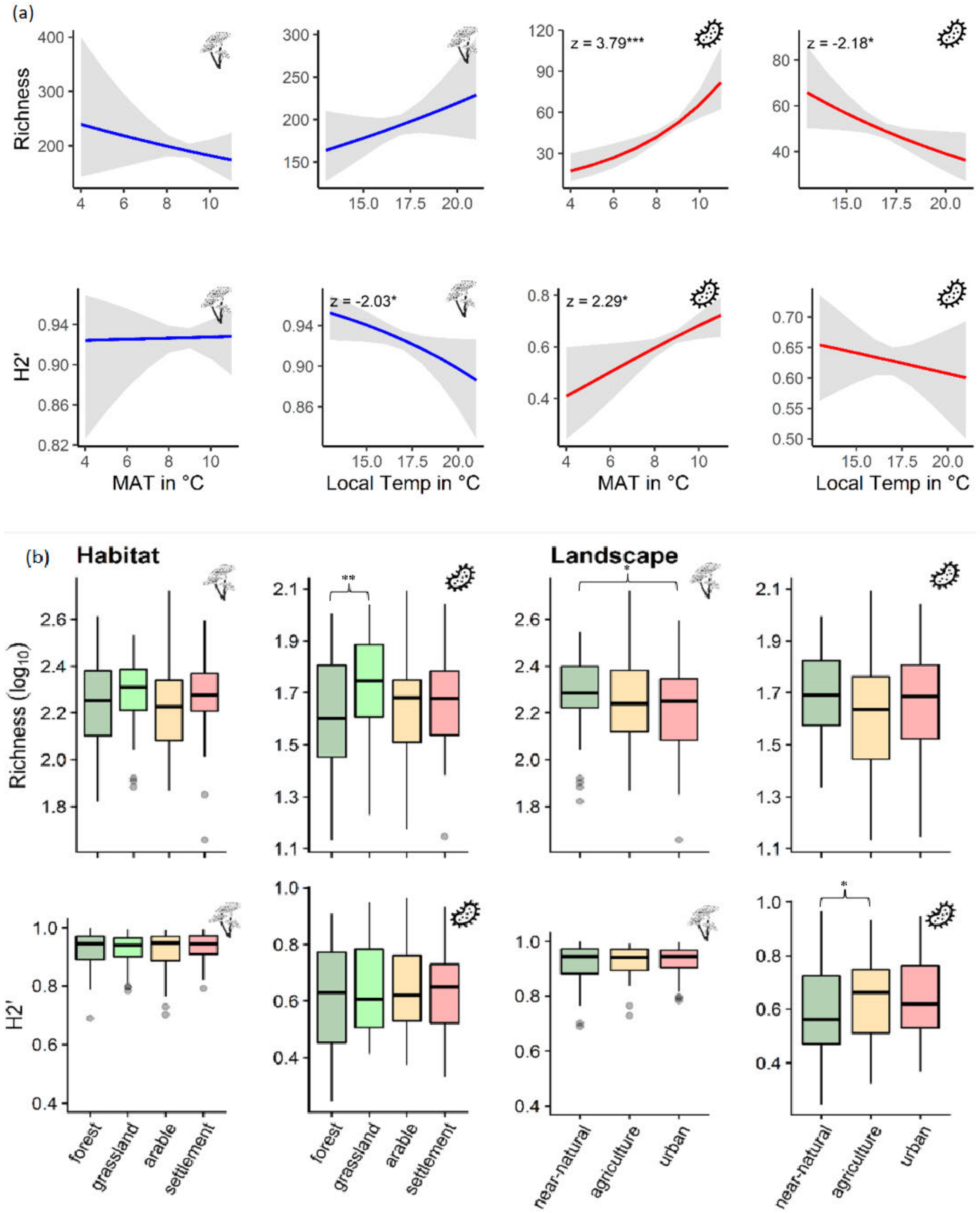

**Figure 1:** a) Regression curves of predicted microbial richness at plot level (fungi in blue, bacteria in red) and mean annual temperature (MAT) and local temperature. Significant changes in richness and specialization are indicated by z-values and asterisks. b) Boxplots showing microbial species richness and specialization among habitat and landscape types at plot level. Significant differences are indicated by asterisks. Detailed results can be found in Table 1.

### *Microbial richness at object level*

The results gained from the negative binomial generalized linear model on object level are in line with the results on study-site level. Additionally, we found strong significant differences in richness between tree genera for both fungi and bacteria (Table V A2.1). The post-hoc test revealed significant differences in fungal richness between each tree genera. For bacterial richness, only beech differed from all other tree genera with lower richness (Table V A2.2)

### *Community composition*

Permanova of fungal communities at object level revealed the host tree identity as the most significant factor followed by habitat type and MAT (Table 2, Fig. 2a, Table V A2.1). Local temperature had no effect on fungal community composition. Bacterial community composition strongly depended on host tree identity and MAT, followed by the other predictors (Table 2, Fig. 2b).

**Table 2:** Permanova results for the effects of host tree identity, MAT, local temperature, habitat, and landscape type on community composition of deadwood-inhabiting fungi and bacteria. We used mean annual sum of precipitation as a co-variate.

| ***Fungi*** | Df | SumOfSqs | R2 | F | Pr(>F) |
|---|---|---|---|---|---|
| **Main predictors** | | | | | |
| Host tree | 3 | 94.574 | 0.327 | 109.730 | **0.001***** |
| MAT | 1 | 0.584 | 0.002 | 2.034 | **0.025*** |
| Local temp. | 1 | 0.392 | 0.001 | 1.365 | 0.159 |
| Habitat type | 3 | 1.358 | 0.005 | 1.575 | **0.023*** |
| Landscape type | 2 | 0.706 | 0.002 | 1.229 | 0.173 |
| **Co-variate** | | | | | |
| MAP | 1 | 1.177 | 0.004 | 4.098 | **0.001***** |
| Residual | 662 | 190.188 | 0.658 | | |
| Total | 673 | 288.979 | 1.000 | | |

| ***Bacteria*** | Df | SumOfSqs | R2 | F | Pr(>F) |
|---|---|---|---|---|---|
| **Main predictors** | | | | | |
| Host tree | 3 | 15.970 | 0.071 | 18.491 | **0.001***** |
| MAT | 1 | 0.550 | 0.002 | 1.910 | **0.044*** |
| Local temp. | 1 | 0.521 | 0.002 | 1.809 | **0.045*** |
| Habitat type | 3 | 1.916 | 0.009 | 2.218 | **0.002**** |
| Landscape type | 2 | 1.063 | 0.005 | 1.847 | **0.018*** |
| **Co-variate** | | | | | |
| MAP | 1 | 13.956 | 0.062 | 48.478 | **0.001***** |
| Residual | 658 | 189.428 | 0.848 | | |
| Total | 669 | 223.404 | 1.000 | | |

### *Community specialization*

Fungal specialization showed no significant relationship with MAT and land use at habitat and landscape scale (Table 1, Fig. 1a and 1b). However, fungal specialization was significantly positively related to local temperature. In contrast, bacteria specialization showed a significant positive relationship with MAT. Further, bacteria specialization was higher in agricultural compared to near-natural landscapes (Table 1, Fig. 1).

The weak relationship of fungal specialization with MAT and land use is supported by the fact that the specialization level of fungal communities is generally high with most study plots characterized by a specialization index close to 1.0 ($H_2$' mean value of 0.93 (± 0.06 SD), Fig. 2c). The specialization index of bacteria showed a normal distribution (mean $H_2$' = 0.63 ± 0.12 SD), Fig. 2).

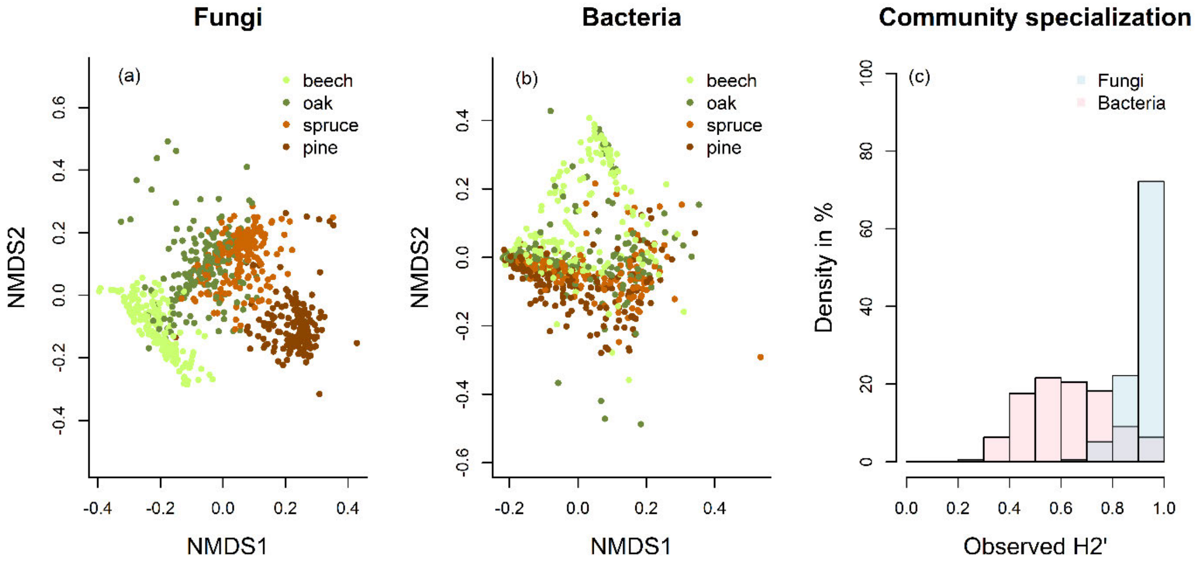

**Figure 2**: (a) and (b) Ordinations based on non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices (fungi: k=3, stress = 0.146; bacteria: k=3, stress=0.156). Dots indicate communities in individual deadwood objects (beech: light green, oak: dark green, spruce: light brown, pine: dark brown). The closer the dots, the higher the proportion of species shared. (c) Frequency of observed $H_2$' values (community specialization) in percent for fungi (blue) and bacteria communities (red).

## Discussion

We hypothesized that species richness and specialization decrease with decreasing temperature, and with increasing land-use intensity and that the effects are more pronounced for fungi than for bacteria.

In this study bacterial species richness and specialization were correlated with MAT, supporting our hypothesis that species richness and specialization decreased with decreasing MAT. This, however, did not hold true for fungi. Furthermore, species richness was lower in urban than in near-natural landscapes supporting our hypothesis only for fungi but not bacteria. Fungal specialization was independent of land use, but bacteria specialization increased with land-use intensity, both were not in line with our hypothesis. Overall, bacterial diversity and specialization were more sensitive to environmental variability (low temperatures and high land-use intensity) than fungi.

### *Species richness and temperature*

We found no significant relationship between fungal species richness and MAT. This is in contrast to studies showing a negative relationship between fungal species richness and temperature decrease within and across landscapes. For example, Bässler et al. (2010) found a decrease in fungal species richness on fine woody debris (similar to branches used in our study) with temperature at landscape scale. In another study, Thorn et al. (2018) found a decrease in fungal species richness on coarse and fine woody debris with elevation, representing a considerable temperature gradient across landscapes. However, both studies used species richness based on fruit body inventories. We, instead, used species richness based on metabarcoding from within the woody substrate. Rieker et al. (2022) suggested that the fruiting communities are more sensitive to environmental gradients than the within-substrate (mycelial) communities due to the stronger exposure of fruit bodies to environmental constraints. This might explain the discrepancy between these studies and our findings. Another explanation might be that the studies mentioned are based on an observational survey at plot level (deadwood originating from forest stands) while our study is based on an experiment (all deadwood types standardized exposed across landscapes). Hence, confounding effects cannot be excluded in observational studies which might explain the discrepancy (e.g., changes in temperature confounded with changes in host species).

In contrast, bacteria species richness showed a strong positive relationship with MAT, as expected. Studies of deadwood-inhabiting bacterial diversity at larger scale are scarce. However, at a larger scale than our study, Rieker et al. (2022) found that environmental conditions (e.g., macroclimate) among three study regions across Germany contributed only weak explanation to beta-diversity of deadwood bacteria. A low beta-diversity might indicate that differences in species richness among study plots are not very pronounced, which disagrees with our findings. However, our study used a considerably stronger macroclimate gradient (see Methods). The large extension of the climate gradient might explain this discrepancy and why we found lower species richness in cold environments. Moreover, we found a decrease in bacterial richness with increasing local temperature. Open habitats, as in our study, coincide with higher variability in temperature and probably with the prevalence of temperature extremes (De Frenne et al. 2019). Harsh microclimate conditions causing stress might restrain some bacteria species from assembling and hence decrease the species richness of communities. Loss of species across taxa under harsh environmental conditions was also described by Lomolino (2001).

### *Species richness and land use*

We show that fungal richness was only influenced by land-use intensity at landscape scale, although the effect was not pronounced, being lower in urban than in near-natural landscapes. Further, species richness was also lower in agricultural than in near-natural landscapes indicating a general decrease of species from near-natural to anthropogenically dominated landscapes, although this difference was not significant.

Availability of deadwood as a resource is a key determinant for fungal diversity (Thorn et al. 2018; Bässler et al. 2010). The amount and diversity of deadwood in intensively used landscapes are often reduced by anthropogenic interventions, e.g., due to forest fragmentation and deforestation for agricultural production (Dudley and Alexander 2017; Curtis et al. 2018) and within forests by management intensity (Gossner et al. 2013; Mazziotta et al. 2014). In agricultural areas, deadwood amount and heterogeneity are often drastically reduced, e.g. when only hedgerows and single trees serve as a habitat for deadwood dependent species (Clements and Alexander 2009; Stokland et al.

2012). Similarly, in urban areas the availability of deadwood is also reduced, and it further depends on the type of green space. Moreover, deadwood in urban areas is often removed for safety or aesthetic reasons (Fröhlich and Ciach 2020). Taken together, availability of diverse deadwood as a resource is expected to decrease from near-natural versus agricultural and urban dominated landscapes. Therefore, two possible mechanisms might explain our observed pattern. The first mechanism, although unlikely, is that fungi are constrained by environmental conditions preventing species from successful colonization and establishment on the exposed deadwood objects in urban and agricultural plots. One important factor in this respect might be microclimate harshness. As outlined above, forests buffer microclimate extremes even if there are small clearings (Thorn et al. 2020) in contrast to rather wide open habitats like agricultural areas. However, we suggest that this mechanism is less plausible for the following reasons. We considered a measure of local microclimate within our models (local temperature), and the habitat categories might serve as proxies for environmental conditions not directly measured in our project. As all these co-variates are not significantly related to fungal species richness, we do not expect that this mechanism can explain the observed pattern. A second mechanism that might explain the observed pattern is dispersal limitation. Komonen and Müller (2018) suggested that fungi are not dispersal limited at landscape scale. Studies focusing on dispersal limitation of fungi at larger scales are scarce. However, Abrego et al. (2017) found that airborne fungal communities differed if distances exceed 100 km. Our results therefore suggest that lower species richness in urban landscapes might be better explained by dispersal limitation. However, even though significant, the effects are not very pronounced (Fig. 1). An only weak role of dispersal limitation is also suggested through similar relationships of fungal communities with their hosts (specialization) irrespective of environmental and geographic variability. In contrast, bacteria species richness showed no relationship with land use at landscape scale but was significantly higher in grasslands than in forests. Even though speculative, the latter finding might be explained by the possibility that some grassland bacteria are able to colonize deadwood. The contrasting effects between the microbial taxa observed in our study suggest differences in assembly processes between bacteria and fungi depending on the land-use type. Finally, it is important to note that many more studies exist for deadwood fungi than for deadwood bacteria. More comparative studies are therefore needed to better understand assembly mechanisms at different spatial scales among deadwood microbial taxa.

*Specialization of communities along temperature and land-use gradients*

In contrast to our expectation, fungal specialization showed no significant relationship with MAT and land use at landscape scale. Previous studies showed that deadwood-inhabiting fungi are highly specialized on their hosts (Moll et al. 2021; Lee et al. 2020). However, no study focused on how specialization might change along such large environmental gradients. Our results support a high specialization level in fungi that remains unchanged across large environmental gradients. The results based on the specialization index ($H_2$') are supported by our community composition analysis at object level. Here we show highly distinct communities depending on host tree identity. These findings suggest that fungal species, despite their strong relationship to certain host tree species, are characterized by broad environmental niches (e.g. thermal niches). This additionally suggests a strong co-evolution of fungi with their hosts under various environmental conditions (Floudas et al. 2012). However, we found a weak negative but significant effect of fungal specialization with local temperature. As outlined above, on average, higher mean temperatures at small spatial scales might coincide with a higher level of temperature variability (Thorn et al. 2018). Higher local temperature variability should, according to theory, promote generalist species (Rasmann et al. 2014; MacArthur 1972). However, our local temperature measure spans a single season. Hence, this finding should be treated with care. Further studies are needed to explore the role of microclimate on fungal specialization at different spatial scales.

Our models revealed a weak positive but significant effect of bacteria specialization with MAT, which is in line with other biotic interaction systems e.g., plant-pollinator interactions (Classen et al. 2020; Rasmann et al. 2014). Further, bacteria seem less specialized than fungi even across strong environmental gradients supporting earlier findings (Moll et al. 2021). We are not able to explain why bacteria specialization is higher in agricultural than in near-natural landscapes. Therefore, further studies focusing on how strongly bacteria species are related to certain substrates (e.g. soil vs. wood) and how selection and preferences for specific substrates change with environmental factors are needed.

### *Conclusions*

Our results suggest that bacteria are more affected by climate than fungi. The latter sustain their high host specificity even in harsh climates and anthropogenically modified landscapes, despite some diversity reduction with land-use intensification at landscape scales. This underlines very different responses of both microbial communities to climate and land use in deadwood. The high robustness of the host species communities for fungi as main drivers of the deadwood decomposition suggests that even under global change, the wood decomposition process could be little affected in Central European landscapes. However, more studies are needed to illuminate the role of bacteria communities and their interaction with fungi on decomposition processes.

## Appendix V

**Table V A1:** Post-hoc comparison of fungal and bacterial OTU richness among habitat types and landscape types. Significant values are indicated by asterisks.

| | **Fungi richness** | **Bacteria richness** |
|---|---|---|
| | *z-value* | *z-value* |
| ***Habitat*** | | |
| grassland – forest | 0.718 | **2.759*** |
| arable – forest | -0.966 | 1.187 |
| settlement – forest | 0.213 | 0.861 |
| arable – grassland | -1.581 | -1.416 |
| settlement – grassland | -0.409 | -1.521 |
| settlement – arable | 1.092 | -0.222 |
| ***Landscape*** | | |
| agric. – near-natural | -1.521 | -0.025 |
| urban – near-natural | -2.259 | -0.569 |
| urban – agric. | -0.702 | -0.517 |

**Table V A2.1:** Results of the negative-binomial generalized linear mixed effect model estimating the effects of host-tree genera, local and regional land use, MAT, MAP, and local temperature on the richness of fungi and bacteria on host-tree level.

| | **Fungi richness** | | | **Bacteria richness** | | |
|---|---|---|---|---|---|---|
| *Predictors* | *IRR* | *z-value* | *p-value* | *IRR* | *z-value* | *p-value* |
| (Intercept) | 214.28 | 4.17*** | **<0.001** | 0.04 | -2.87** | **0.004** |
| oak vs. beech | 4.27 | 19.15*** | **<0.001** | 1.23 | 3.56*** | **<0.001** |
| spruce vs. beech | 8.46 | 28.68*** | **<0.001** | 1.36 | 5.33*** | **<0.001** |
| pine vs. beech | 1.80 | 7.65*** | **<0.001** | 1.20 | 3.08** | **0.002** |
| MAT in °C | 0.92 | -1.71 | 0.087 | 1.17 | 4.29*** | **<0.001** |
| Local temp in °C | 1.05 | 1.74 | 0.082 | 0.95 | -2.82** | **0.005** |
| Habitat grassland vs. forest | 1.04 | 0.53 | 0.593 | 1.14 | 2.50* | **0.013** |
| Habitat arable vs. forest | 0.91 | -1.15 | 0.252 | 1.11 | 1.83 | 0.068 |
| Habitat settlement vs. forest | 1.04 | 0.46 | 0.646 | 1.11 | 1.66 | 0.097 |
| Landscp. agric. vs. near-nature | 0.89 | -1.52 | 0.128 | 0.99 | -0.11 | 0.913 |
| Landscp. urban vs. near-nature | 0.83 | -2.55* | **0.011** | 0.98 | -0.47 | 0.642 |
| MAP [log10] in mm | 0.36 | -2.81** | **0.005** | 3.56 | 4.15*** | **<0.001** |
| **Random Effects** | | | | | | |
| $\sigma^2$ | | | 0.36 | | | 0.24 |
| $\tau_{00}$ | | | $0.02_{\text{PlotID}}$ | | | $0.00_{\text{PlotID}}$ |
| ICC | | | 0.06 | | | |
| N | | | $172_{\text{PlotID}}$ | | | $172_{\text{PlotID}}$ |
| Observations | | | 674 | | | 671 |
| Marginal $R^2$ / Conditional $R^2$ | | | 0.639 / 0.661 | | | 0.106 / NA |

**Table V A2.2:** Post-hoc comparison of fungal and bacterial richness among different tree genera

| | **Fungi** | | **Bacteria** | |
|---|---|---|---|---|
| | *z-value* | *p-value* | *z-value* | *p-value* |
| oak – beech | 19.154 | **<0.001** | 3.560 | **<0.01** |
| spruce – beech | 28.676 | **<0.001** | 5.334 | **<0.001** |
| pine – beech | 7.651 | **<0.001** | 3.083 | **<0.05** |
| spruce – oak | 9.382 | **<0.001** | 1.772 | 0.287 |
| pine – oak | -11.637 | **<0.001** | -0.501 | 0.959 |
| pine – spruce | -20.955 | **<0.001** | -2.286 | 0.101 |

# Chapter VI

## General Discussion

Evidence is increasing that land use and climate affect biodiversity and the associated ecosystem services. Still, large-scale studies investigating both effects in concert are missing. With this thesis, I shed light onto the impact of land-use intensity and climate change on multi-taxon decomposer communities and the consequences for decomposition processes of different necromass types.

## Summary of results

I show that decomposer communities and decomposition processes are sensitive to land use and climate. Anthropogenic land use significantly reduced dung-visiting beetle diversity at a local and regional scale (Chapter III), carrion-visiting beetle diversity at a local and regional scale (marginally, Chapter IV), and fungal diversity in deadwood at a regional scale (Chapter V) (Table 1). Grasslands, in turn, increased deadwood-inhabiting bacterial diversity, and agricultural landscapes increased their community specialization (Chapter V). Other networks were unrelated to land use (Table 1). Decomposition processes of dung and carrion did not respond to local and regional land use (Chapters II and IV) (Table 1).

Climate translated into equivocal effects on the diversity of decomposing organisms, their community specialization, and decomposition processes. Beetle communities on dung, for instance, were less diverse and less specialized in warmer regions (Chapter III) (Table 1). Bacterial richness in carrion and deadwood, however, was positively related to higher MAT (Chapters IV and V). Regions with high MAT and MAP, moreover, hosted more specialized deadwood-inhabiting bacterial communities (Chapter V) and carrion was decomposed faster (Chapters II and IV).

High precipitation was related to a reduced number of dung-visiting beetles (Chapter III) and deadwood-inhabiting fungi (Chapter V). The number of deadwood-inhabiting bacteria, however, responded positively to precipitation (Chapter V).

**Table 1:** Simplified summary of climate and land use effects on beetle and microbial diversity (*Div.*) and specialization (*H2'*) on dung, carrion, and deadwood and decomposition processes of dung and carrion. Colours are indicating significant positive effects (blue) and negative effects (orange). Symbols depict habitat/ landscape type (✿: grassland, 🌾: arable fields/ agricultural landscapes, and 🏠: settlements/ urban landscapes). Forest habitats and near-natural landscapes were used as references.

| | **Dung** | | **Carrion** | | **Deadwood** | | | | **Decomposition** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Insects** | | **Insects** | **Bacteria** | **Fungi** | | **Bacteria** | | **Dung** | **Carrion** |
| | *Div.* | *H2'* | *Div.* | *Div.* | *Div.* | *H2'* | *Div.* | *H2'* | | |
| **Climate** | | | | | | | | | | |
| MAT in °C | ⬇ | ⬇ | | ⬆ | | | ⬆ | ⬆ | | ⬆ |
| MAP in mm | ⬇ | | | | ⬇ | | ⬆ | ⬆ | | ⬆ |
| Local Temp. | NA | NA | | | | ⬇ | ⬇ | | | ⬆ |
| **Land use** | | | | | | | | | | |
| Habitat | 🏠 🌾 | | 🏠 1) | | | | ✿ | | | |
| Landscape | 🏠 🌾 | | 🏠 1) | 🏠 1) | 🏠 | | | 🌾 | | |
| **Decomposers** | | | | | | | | | | |
| Insects | | | | | | | | | | ⬆ |
| Bacteria | | | | | | | | | | community composition |

1) marginally ($p < 0.1$)

## Land-use and climate effects on biodiversity

### Land-use intensification

The results of this study indicate that urban, and to some extent agricultural, areas might not provide suitable habitats for decomposer communities (Chapters III – V) but suggest that meadows (at habitat scale) can promote diversity (Chapter V).

Land-use conversions from near-natural to anthropogenic landscapes often imply habitat loss and fragmentation (Díaz et al. 2019; Dudley and Alexander 2017). Habitat fragmentation, in turn, implies a reduction of habitat size, an increasing number of smaller habitats, and larger distances between them. This is often accompanied by habitat loss, which can have drastic consequences for species richness, population abundances and distributions, growth rates, genetic diversity, and dispersal ability (Fahrig 2003). However, it remains the question 'how much habitat is enough?'. The answer strongly depends on the species and the life cycle of individual species (Law and Dickman 1998). In this thesis, for instance, deadwood-inhabiting bacteria did not suffer from anthropogenic land use (Chapters IV and V), contrary to dung-visiting beetles and deadwood-inhabiting fungi (Chapters II and V). Ideally, a landscape consists of several habitat patches of different types spread across the landscape without reducing habitat amount (Law and Dickman 1998), highlighting the importance of refugia, e.g. green spaces in urban areas and hedgerows or small islands in agricultural areas, which could increase the diversity of decomposing beetles and microbes in agricultural and urban areas.

Besides the conversion of natural habitats and landscapes, agricultural land use impacts biodiversity in and around agricultural sites through the use of pesticides and fertilizers. The global demand for fertilizers is steadily increasing (FAO 2019) although they cause severe harm to the environment (Dudley and Alexander 2017). An accurate application of pesticides, for instance, is not guaranteed and pesticides might dispense in the surrounding. Damages through pesticides have been observed for invertebrates, amphibians, and birds already (Dudley and Alexander 2017) and might be one reason for the observed declined beetle abundance in agricultural landscapes (Chapter III).

### *Climate change*

From an evolutionary perspective, there are two theories on how communities might react to climate change. One is that communities, consisting of different species, co-evolve as one assemblage. The second theory, which is supported by paleoecological evidence, says that species within a community adapt individually to climate change due to individual life-history characteristics and thresholds (Graham and Grimm 1990). For instance, single species migrate to different geographic regions and build new communities there. The results of Chapters III-V make apparent that necromass-inhabiting bacteria, fungi and beetles respond differently to temperature and precipitation. This supports the second theory and suggests that responses to climate change are highly variable among species, indicating that some species might be able to adapt faster than others (Bellard et al. 2012). Climate change modifies ecological niches and forces individuals to adapt to these changes. Bellard et al. (2012) described three axes (directions) along which species can adapt to climate change: The first axis – the spatial axis – describes latitudinal or altitudinal shifts in species distributions, as, for instance, reviewed in Parmesan (2006). The second axis is the temporal axis. By changes in phenology, organisms can adjust the timing of certain events to climate, such as reproduction or seasonal migrations (Root et al. 2003). Phenological shifts can support the synchronization between life cycle events and climate. However, it can also cause asynchrony in biotic interactions like predator-prey interactions (Visser and Both 2005). The last axis is the self-axis. This implies physiological or behavioural changes, as observed in ectotherms, for instance, that help to acclimatize to climate change without the need for spatial or temporal shifts (Bellard et al. 2012).

Applying a space-for-time approach in this thesis, I will discuss the results based on the spatial axis, to account for potential future effects caused by climate change. I give evidence that warm and moist regions will preferably be inhabited by (resource-specialized) bacteria. Nevertheless, finding a new region with appropriate climatic conditions does not imply that other factors such as biotic interactions also match the ecological niche of the organism and other adaptations, e.g. micro-evolution might be necessary to survive (Bellard et al. 2012). For host-specialized deadwood microbes, as reported in Chapter V, this would imply that appropriate wood resources, for instance, are required for the successful colonization of new regions. In summary, I suggest that different decomposer groups apply different mechanisms to adapt to climate change in terms of climate niches and community specialization. However, in case that species are no longer able to acclimatize to new climatic conditions (fast enough), this might result in local or global extinctions (Bellard et al. 2012).

In general, it is important to note that climate change does not only imply an increase in temperatures. Climate change is an umbrella term for an increased frequency and intensity of extreme weather events, drought, increasing temperatures and shifts in precipitation rates (Ipcc 2021) that might all have varying effects on biodiversity. This, of course, complicates the interpretation of results addressing ‘climate-change effects’ on biodiversity. Moreover, climate change modifies habitat structures (Mantyka-Pringle et al. 2015), hence, organisms need to adapt to the modifications in two ways: they need to adapt to new climatic conditions as well as to new habitat structures.

### *Consequences for ecosystems and their services*

A greater diversity of functional groups reduces the risk of species extinction, which supports the ecosystem insurance hypothesis. This hypothesis states that a more diverse community, with abundant and dominant species as well as rare species, promotes the stability and resilience of ecosystems (Mooney et al. 2009). Particularly, a decline in abundant species, as observed in Chapter III, might disturb trophic interactions and important ecosystem functions and services (Wagner 2020). Modifications in biodiversity through species shifts or loss, changes in species distribution, phenology, or physiology may lead to alterations in ecosystems and consequently in services provided by them, such as the provisioning of food, the regulation and maintenance of ecosystems, and the cultural and religious value of natural places (Mooney et al. 2009).

## Conclusion

In a nutshell, with this thesis, I show that both global change drivers, land-use intensification and climate change, can affect biodiversity. Anthropogenic land use, particularly settlements and urban landscapes, had negative impacts on decomposer communities of all three necromass types. Climate effects on decomposer communities and decomposition processes, however, were ambiguous. Therefore, I support the statement of prior studies that intensive land use is a stronger threat to biodiversity than climate (Díaz et al. 2019) in temperate zones. However, both threats are to a certain extent coupled. The increase in agricultural areas is accompanied by an increase in greenhouse gases (through livestock and transport of food) (Dudley and Alexander 2017), which enhances the greenhouse effect and climate change. Hence, to promote decomposer communities and consequently decomposition processes, I suggest not only expanding the establishment of protected areas (that are not fragmented or polluted) but to support less intensive land use, reducing the use of pesticides and fertilizers, and tackling land-use threats on the respective spatial scales.

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# Affidavit

## Eidesstattliche Erklärung

### nach §7 Abs. 2 Satz 3, 4, 5 der Promotionsordnung der Fakultät für Biologie

Hiermit erkläre ich an Eides statt, die Dissertation: „**Folgen von Klimawandel und intensiver Landnutzung für Zersetzergemeinschaften und Abbauprozesse**“, eigenständig, d. h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben. Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

Weiterhin erkläre ich, dass bei allen Abbildungen und Texten bei denen die Verwertungsrechte (Copyright) nicht bei mir liegen, diese von den Rechtsinhabern eingeholt wurden und die Textstellen bzw. Abbildungen entsprechend den rechtlichen Vorgaben gekennzeichnet sind sowie bei Abbildungen, die dem Internet entnommen wurden, der entsprechende Hypertextlink angegeben wurde.

## Affidavit

I hereby declare that my thesis entitled: „**Consequences of climate change and land-use intensification for decomposer communities and decomposition processes**” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis. Furthermore, I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form.

Besides I declare that if I do not hold the copyright for figures and paragraphs, I obtained it from the rights holder and that paragraphs and figures have been marked according to law or for figures taken from the internet the hyperlink has been added accordingly.

Würzburg, den ______________________ ______________________

Jana Englmeier

# Author contributions

# Chapter II

## Diverse effects of climate, land use, and insects on dung and carrion decomposition

Jana Englmeier, Oliver Mitesser, M. Eric Benbow, Torsten Hothorn, Christian von Hoermann, Caryl Benjamin, Ute Fricke, Cristina Ganuza, Maria Haensel, Sarah Redlich, Rebekka Riebl, Sondra Rojas-Botero, Thomas Rummler, Ingolf Steffan-Dewenter, Elisa Stengel, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jie Zhang, Jörg Müller

published in *Ecosystems*

*Contribution*

SR, ISD, JZ, and JM developed the underlying study design. JE designed the experimental set-up with support from CvH, MEB, and JM. JE, CB, UF, CG, MH, RR, SRB, CT, JU, and LU conducted field work. JE and ES processed samples. TR provided climate data. JE analyzed the data in close collaboration with OM, TH, CvH, MEB, and JM. JE led the writing of the manuscript. All authors commented critically on the drafts and approved the final version.

*Contribution of the candidate*

| **Publication details** | **Description of the own contribution** |
|---|---|
| **Writing of the article**<br>Which parts of the article have been written to which extent by the candidate? | The writing of the manuscript was led by me, Jana Englmeier, including writing of the first draft and the implementation of comments from co-authors and reviewers |
| **Performed research**<br>Which experimental procedures have been conducted by the candidate? | Planning and preparation of decomposition experiments on multiple study sites was performed by me, Jana Englmeier. |
| **Conceptual design of the research**<br>To which extent did the candidate contribute to the conceptional design of the research project? | Experimental design and set-up were developed by me, Jana Englmeier. Additionally, a protocol for the sampling procedure was provided by me. |
| **Data analysis**<br>To which extent did the candidate contribute to the data analysis? | Data analysis was primarily conducted by me, Jana Englmeier, with contributions from Oliver Mitesser, Torsten Hothorn, and Jörg Müller. |
| **Overall contribution of the candidate** | 80-90 % |

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# Chapter III

## Dung-visiting beetle diversity is mainly affected by land use, while community specialization is driven by climate

Jana Englmeier, Christian von Hoermann, Daniel Rieker, M. Eric Benbow, Caryl Benjamin, Ute Fricke, Cristina Ganuza, Maria Haensel, Tomáš Lackner, Oliver Mitesser, Sarah Redlich, Rebekka Riebl, Sandra Rojas-Botero, Thomas Rummler, Jörg-Alfred Salamon, David Sommer, Ingolf Steffan-Dewenter, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jie Zhang, Jörg Müller

published in *Ecology and Evolution*

*Contribution*

SR, ISD, JZ, and JM developed the underlying study design. JE designed the experimental set-up with support from CvH, MEB, and JM. JE, CB, UF, CG, MH, RR, SRB, CT, JU, and LU conducted field work. TL, JAS, and DS identified beetles. TR provided climate data. JE analyzed the data in close collaboration with OM, DR, and JM. JE led the writing of the manuscript. All authors commented critically on the drafts and approved the final version.

*Contribution of the candidate*

| **Publication details** | **Description of the own contribution** |
|---|---|
| **Writing of the article**<br>Which parts of the article have been written to which extent by the candidate? | The writing of the manuscript was led by me, Jana Englmeier, including writing of the first draft and the implementation of comments from co-authors and reviewers |
| **Performed research**<br>Which experimental procedures have been conducted by the candidate? | Planning and preparation of pitfall-trap experiments on multiple study sites was performed by me, Jana Englmeier. |
| **Conceptual design of the research**<br>To which extent did the candidate contribute to the conceptional design of the research project? | Experimental design and set-up were developed by me, Jana Englmeier. Additionally, a protocol for pitfall-trap establishment and sample collection was provided by me. |
| **Data analysis**<br>To which extent did the candidate contribute to the data analysis? | Data analysis was primarily conducted by me, Jana Englmeier, with contributions from Oliver Mitesser, Jörg Müller, and Daniel Rieker |
| **Overall contribution of the candidate** | 80-90 % |

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# Chapter IV

## Bacteria community composition and climate drive carrion decomposition – not beetles or land use

Jana Englmeier

*Contribution of the candidate*

| Publication details | Description of the own contribution |
|---|---|
| **Writing of the article**<br>Which parts of the article have been written to which extent by the candidate? | The writing of the manuscript was led by me, Jana Englmeier, including writing of the first draft and the implementation of comments from co-authors |
| **Performed research**<br>Which experimental procedures have been conducted by the candidate? | Planning and preparation of pitfall-trap and microbial swab experiments on multiple study sites was performed by me, Jana Englmeier. |
| **Conceptual design of the research**<br>To which extent did the candidate contribute to the conceptional design of the research project? | Experimental design and set-up were developed by me, Jana Englmeier. Additionally, a protocol for sample collection (pitfall traps and microbial swabs) was provided by me. |
| **Data analysis**<br>To which extent did the candidate contribute to the data analysis? | Data analysis was primarily conducted by me, Jana Englmeier, with support from Jörg Müller |
| **Overall contribution of the candidate** | 95-100 % |

# Chapter V

## Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria

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Oliver Mitesser, Daniel Rieker, Caryl Benjamin, Ute Fricke, Cristina Ganuza, Maria Haensel, Janina Lorz, Sarah Redlich, Rebekka Riebl, Sandra Rojas-Botero, Thomas Rummler, Ingolf Steffan-Dewenter, Elisa Stengel, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jie Zhang, Jörg Müller, Claus Bässler

Submitted to *Diversity and Distribution*

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*Contribution*

SR, ISD, JZ, and JM developed the underlying study design. JE designed the experimental set-up with support from CBa and JM. JE, CBe, UF, CG, MH, RR, SRB, CT, JU, and LU conducted field work. JE, JL, and ES processed samples. TR provided climate data. JE analyzed the data in close collaboration with OM, DR, and CB. JE led the writing of the manuscript. All authors commented critically on the drafts and approved the final version.

*Contribution of the candidate*

| **Publication details** | **Description of the own contribution** |
|---|---|
| **Writing of the article**<br>Which parts of the article have been written to which extent by the candidate? | The writing of the manuscript was led by me, Jana Englmeier, including writing of the first draft and the implementation of comments from co-authors and reviewers |
| **Performed research**<br>Which experimental procedures have been conducted by the candidate? | Planning and preparation deadwood experiments on multiple study sites was performed by me, Jana Englmeier. |
| **Conceptual design of the research**<br>To which extent did the candidate contribute to the conceptional design of the research project? | Experimental design and set-up were developed by me, Jana Englmeier. Additionally, a protocol for deadwood exposure and sample collection was provided by me. |
| **Data analysis**<br>To which extent did the candidate contribute to the data analysis? | Data analysis was primarily conducted by me, Jana Englmeier, with contributions from Oliver Mitesser and Claus Bässler |
| **Overall contribution of the candidate** | 80-90 % |

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# Publication list

*First authorship articles originating from this thesis:*

**Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria**

2022

**Jana Englmeier**, Oliver Mitesser, Daniel Rieker, Caryl Benjamin, Ute Fricke, Cristina Ganuza, Maria Haensel, Janina Lorz, Sarah Redlich, Rebekka Riebl, Sandra Rojas-Botero, Thomas Rummler, Ingolf Steffan-Dewenter, Elisa Stengel, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jie Zhang, Jörg Müller, Claus Bässler. Submitted in **Diversity and Distributions** (13.12.2022)

**Dung-visiting beetle diversity is mainly affected by land use, while community specialization is driven by climate**

2022

**Jana Englmeier**, Christian von Hoermann, Daniel Rieker, M. Eric Benbow, Caryl Benjamin, Ute Fricke, Cristina Ganuza, Maria Haensel, Tomáš Lackner, Oliver Mitesser, Sarah Redlich, Rebekka Riebl, Sandra Rojas-Botero, Thomas Rummler, Jörg-Alfred Salamon, David Sommer, Ingolf Steffan-Dewenter, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jie Zhang, Jörg Müller. Published in **Ecology and Evolution**

**Diverse effects of climate, land use, and insects on dung and carrion decomposition**

2022

**Jana Englmeier**, Oliver Mitesser, M. Eric Benbow, Torsten Hothorn, Christian von Hoermann, Caryl Benjamin, Ute Fricke, Cristina Ganuza, Maria Haensel, Sarah Redlich, Rebekka Riebl, Sandra Rojas Botero, Thomas Rummler, Ingolf Steffan-Dewenter, Elisa Stengel, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jie Zhang, Jörg Müller. Published in **Ecosystems**

*Co-authored articles that did not originate from this thesis:*

**Interactive effects of climate and land use on pollinator diversity differ among taxa and scales**

2022

Cristina Ganuza, Sarah Redlich, Johannes Uhler, Cynthia Tobisch, Sandra Rojas-Botero, Marcell K. Peters, Jie Zhang, Caryl Benjamin, **Jana Englmeier,** Jörg Ewald, Ute Fricke, Maria Haensel, Johannes Kollmann, Rebekka Riebl, Lars Uphus, Jörg Müller, Ingolf Steffan-Dewenter. Published in **Science Advances**

**Modelling the Relative Abundance of Roe Deer (*Capreolus capreolus* L.) along a Climate and Land-Use Gradient**

2022

Caryl Benjamin, Lars Uphus, Marvin Lüpke, Sandra Rojas-Botero, Maninder Singh Dhillon, Jana Englmeier, Ute Fricke, Cristina Ganuza, Maria Haensel, Sarah Redlich, Rebekka Riebl, Cynthia Tobisch, Johannes Uhler, Jie Zhang, Annette Menzel, Wibke Peters. Published in **Animals**

**Plant richness, land use and temperature differently shape invertebrate leaf-chewing herbivory on plant functional groups**

2022

Ute Fricke, Sarah Redlich, Jie Zhang, Cynthia Tobisch, Sandra Rojas-Botero, Caryl Benjamin, **Jana Englmeier**, Cristina Ganuza, Rebekka Riebl, Johannes Uhler, Lars Uphus, Jörg Ewald, Johannes Kollmann, Ingolf Steffan-Dewenter. Published in **Oecologia**

**Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types**

2022

Ute Fricke, Ingolf Steffan-Dewenter, Jie Zhang, Cynthia Tobisch, Sandra Rojas-Botero, Caryl Benjamin, Jana Englmeier, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Johannes Uhler, Jörg Ewald, Johannes Kollmann, Sarah Redlich. Published in **PlosOne**

**Relationships of insect biomass and richness with land use along a climate gradient**

2021

Johannes Uhler, Sarah Redlich, Jie Zhang, Torsten Hothorn, Cynthia Tobisch, Jörg Ewald, Simon Thorn, Sebastian Seibold, Oliver Mitesser, Jerome Moriniere, Vedran Bozicevic, Caryl Benjamin, **Jana Englmeier**, Ute Fricke, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Sandra Botero, Thomas Rummler, Lars Uphus, Stefan Schmidt, Ingolf Steffan-Dewenter, Jörg Müller. Published in **Nature Communications**

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2021

Sarah Redlich, Jie Zhang, Caryl Benjamin, Maninder Dhillon, **Jana Englmeier**, Jörg Ewald, Ute Fricke, Cristina Ganuza, Maria Haensel, Thomas Hovestadt, Johannes Kollmann, Thomas Koellner, Carina Kuebert-Flock, Harald Kunstmann, Annette Menzel, Christoph Moning, Wibke Peters, Rebekka Riebl, Thomas Rummler, Sandra Rojas Botero, Cynthia Tobisch, Johannes Uhler, Lars Uphus, Jörg Müller, Ingolf Steffan-Dewenter. Published in **Methods in Ecology and Evolution**

**Temperature drives variation in flying insect biomass across a German malaise trap network**

2021

Ellen A.R. Welti, Petr Zajicek, Manfred Ayasse, Tim Bornholdt, Jörn Buse, Frank Dziock, Rolf A. Engelmann , **Jana Englmeier**, Martin Fellendorf, Marc I. Förschler, Mark Frenzel, Ute Fricke, Cristina Ganuza, Mathias Hippke, Günter Hoenselaar, Andrea Kaus-Thiel, Klaus Mandery, Andreas Marten, Michael T. Monaghan , Carsten Morkel, Jörg Müller, Stephanie Puffpaff, Sarah Redlich, Ronny Richter, Sandra Rojas Botero, Tobias Scharnweber, Gregor Scheiffarth, Paul Schmidt Yáñez, Rhena Schumann, Sebastian Seibold , Ingolf Steffan-Dewenter, Stefan Stoll, Cynthia Tobisch, Sönke Twietmeyer, Johannes Uhler, Juliane Vogt, Dirk Weis, Wolfgang W. Weisser, Martin Wilmking, Peter Haase. Published in **Insect Conservation and Diversity**

### Climate effects on vertical forest phenology of Fagus sylvatica, sensed by Sentinel-2, time lapse camera and ground observations

2021

Lars Uphus, Marvin Lüpke, Ye Yuan, Caryl Benjamin, **Jana Englmeier**, Ute Fricke, Cristina Ganuza, Michael Schwindl, Johannes Uhler, Annette Menzel. Published in **Remote Sensing**

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