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Life in the dead: Biodiversity in dead wood along macro- and microclimatic gradients

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Cover: Photos and painting by Anika Gossmann, edited by Lina Gossmann. Middle: *Mycena crocata*, Upper left: dead wood with *Fomitopsis pinicola*, Lower left: *Saperda scalaris*, Upper right: *Fomitopsis pinicola*, Lower right: *Lucanus cervus.*

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Life in the dead: Biodiversity in dead wood along macro- and microclimatic gradients

Abstract

Climate is a major driver of biodiversity at both large and small spatial scales. My research focuses on the diversity of saproxylic (= dead wood dependent) species across macro- and microclimatic gradients in both forested and urban areas. I sampled beetles, fungi, and bacteria from spruce logs placed out in production forests along a 1200 km latitudinal gradient in Sweden, and along shade gradients from sun-exposed to fully shaded logs. I also measured the decomposition rates of these logs. Additionally, I surveyed saproxylic beetles in wood mould boxes, which resemble hollow trees, along urban-rural gradients in six cities in southern Sweden. For beetles and bacteria, I found a latitudinal diversity gradient with a higher diversity in the south. Moreover, the diversity of saproxylic beetles and brown-rot fungi (a key functional group in decomposition) followed the "hydroclimatic compensation model". This model suggests that the species' habitat requirements can alter along a regional climatic gradient to maintain consistent microclimatic conditions. For brown-rot fungi, I found a positive relationship between fungal diversity and saproxylic beetle abundance, which indicates that beetles serve as dispersal vectors. Furthermore, I observed increasing decomposition rates with increasing regional temperature. Interestingly, in the south, high fungal diversity reduced decomposition rates – likely due to antagonistic interactions – especially when the diversity of nitrogen-fixing bacteria was high. In contrast, this effect was reversed in the north under the same conditions. In urban landscapes, saproxylic beetle diversity was positively associated with habitat amount, but negatively associated with dispersal barriers, such as roads and buildings. Generally, I found microclimate to be a strong driver for the saproxylic biodiversity. Therefore, I conclude that dead wood creation with varying microclimatic conditions is needed to promote saproxylic species with different thermal requirements, both in forests and urban areas.

Keywords: Microclimate, thermophilous, saproxylic, wood-inhabiting fungi, wood-inhabiting bacteria, veteran tree, wood decay, dead wood, dispersal

Livet i det döda: Biologisk mångfald i död ved längs makro- och mikroklimatiska gradienter

Abstract

Klimatet är en viktig faktor för biologisk mångfald i både stora och små rumsliga skalor. Min forskning fokuserar på mångfalden av vedlevande arter längs klimatgradienter i både skog och stadsmiljöer. Jag provtog vedlevande skalbaggar, svampar och bakterier från granstockar utlagda i produktionsskogar längs en 1200 km gradient från södra till norra Sverige, samt längs en skuggradient från solbelysta till helt beskuggade stockar. Jag mätte även nedbrytningshastigheten av veden i dessa stockar. I ett annat experiment undersökte jag vedskalbaggar i mulmlådor – konstgjorda livsmiljöer som efterliknar ihåliga träd – längs gradienter från innerstaden och utåt i sex städer i södra Sverige, där jag även mätte temperaturen inuti lådorna. Jag fann en latitudinell gradient i artantalet av vedlevande skalbaggar och bakterier, med högre artrikedom i söder än i norr. Framför allt för vedskalbaggar och brunrötesvampar (en funktionell grupp som är viktig för nedbrytning) följde artrikedomsmönstret ”modellen för hydroklimatisk kompensation”. Det innebär att arter ändrar sina habitatpreferenser längs en regional klimatgradient för att få liknande mikroklimatiska förhållanden där de förekommer. Jag fann också att mångfalden av svampar var högre när det var fler vedskalbaggar, som jag tolkar som att de fungerar som spridningsvektorer. Intressant nog visade resultaten att i södra Sverige kan hög mångfald av svampar leda till lägre nedbrytningshastighet, troligen på grund av antagonistiska interaktioner – särskilt när mångfalden av kvävefixerande bakterier var hög, medan i norr var effekten den motsatta under samma förhållanden. I urbana landskap ökade artrikedomen av vedskalbaggar med omgivande areal av habitat med träd, men minskade med mängden spridningsbarriärer. Generellt fann jag att mikroklimatet är en stark drivkraft för mångfalden av vedlevande arter. Därför drar jag slutsatsen att skapandet av död ved med varierande mikroklimat behövs för att gynna vedlevande arter med olika habitat krav, både i skogar och urbana miljöer.

Keywords: Mikroklimat, vedlevande svampar, vedlevande bakterier, ihåliga träd, nedbrytning, död ved, spridning

Das Leben im Toten: Biodiversität in Totholz entlang makro- und mikroklimatischer Gradienten

Abstract

Das regionale sowie das Mikroklima sind ein zentraler Faktor für die Biodiversität. In meiner Forschung habe ich mich auf die Vielfalt saproxyler (= totholzabhängiger) Arten konzentriert entlang klimatischer Gradienten in Wäldern und Städten. Ich habe Daten zu saproxylen Käfern, Pilzen und Bakterien aus toten Fichtenstämmen entlang eines 1200 km langen Breitengrad-Gradienten in Schweden und entlang von Beschattungsgradienten erhoben, wobei auch Totholzzersetzungsraten gemessen wurden. Zusätzlich untersuchte ich saproxyle Käfer in Baumhöhlenkästen entlang von Stadt-Land-Gradienten. Für Käfer und Bakterien fand ich höhere Artenzahlen im Süden als im Norden von Schweden. Außerdem folgten Käfer und Braunfäulepilze (eine wichtige funktionelle Gruppe zur Totholzzersetzung) dem „hydroklimatischen Kompensationsmodell“. Dieses besagt, dass Arten ihre Habitatpräferenzen entlang eines klimatischen Gradienten anpassen können, um ähnliche mikroklimatische Bedingungen beizubehalten. Für Braunfäulepilze fand ich eine positive Korrelation zwischen Artenzahl und Käferabundanz, was auf Käfer als mögliche Verbreitungsvektoren hinweist. Zudem beobachtete ich zunehmende Totholzzersetzungsraten mit steigender regionaler Temperatur. Interessanterweise führte aber eine zu hohe Pilzartenzahl zu geringeren Zersetzungsraten im Süden – vermutlich aufgrund antagonistischer Interaktionen – insbesondere bei gleichzeitig hoher Vielfalt stickstofffixierender Bakterien, während dieser Effekt im Norden unter denselben biotischen Bedingungen umgekehrt war. In urbanen Landschaften war die Diversität von saproxylen Käfern positiv mit Habitatverfügbarkeit assoziiert, jedoch negativ mit urbanen Strukturen wie Straßen und Gebäuden. Grundsätzlich lässt sich zusammenfassen, dass die Schaffung von Totholz unter variierenden mikroklimatischen Bedingungen notwendig ist, um saproxyle Arten mit unterschiedlichen klimatischen Ansprüchen in Wäldern wie auch urbanen Landschaften zu fördern.

Keywords: Mikroklima, holzbewohnende Pilze, holzbewohnende Bakterien, Baumhöhle, Zersetzung, Totholz

Dedication

To my beloved family and partner – and to all the microbes that make life possible.

"A dead tree is not the end. It
is the beginning of a thousand
lives."

Fieldwork in May in northern Sweden (2021).

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Anika Goßmann, Öckinger, E., Schroeder, M., Lindman, L., Ranius, T. 2024. Interaction between regional temperature and shade level shapes saproxylic beetle communities. Diversity and Distributions, 30: e13836.

II. Anika Goßmann, Runnel, K., Bahram, M., Ranius, T. Contrasting diversity patterns of brown- and white-rot wood saprotrophs in response to climate and dispersal vectors. (submitted)

III. Anika Goßmann, Ranius, T., Bahram, M., Runnel, K. Wood-inhabiting fungi and bacteria contribute to dead wood decomposition along a regional climatic gradient. (submitted)

IV. Anika Goßmann, Jansson, N., Öckinger, Ryding, C., Ranius, T. 2025. Tree cover increases species richness and shapes species composition of saproxylic beetles along with the microclimate. Ecological Entomology.

All published papers are published open access.

The contribution of Anika Gossmann to the papers included in this thesis was as follows:

I. Participated in the development of ideas, performed field work, and led the data analyses and the writing and revisions of the manuscript.

II. Participated in the development of ideas and design of the study, led field work, and led the data analyses and the writing and revisions of the manuscript.

III. Participated in the development of the ideas and design of the study, led field work, and led the data analyses and the writing of the manuscript.

IV. Participated in the development of the ideas and design of the study, contributed to the field work, led the data analyses and the writing of the manuscript.

1. Introduction

As ecologists, we seek to uncover patterns in nature and explore the relationships between organisms and their environments. We analyse complex ecological processes, identify species, and develop hypotheses and theories. Our goal is to find simplicity in the vast complexity of life. With this challenge in mind, I wrote my doctoral thesis – a small, but hopefully meaningful puzzle piece in the large picture of *Ecology*.

1.1 Climate as a major driver of biodiversity

1.1.1 Biodiversity along macro- and microclimatic gradients

A central question in ecology is understanding the factors that drive species communities. Climate is one of the most important abiotic factors shaping species communities at different spatial scales (Lee-Yaw et al., 2016; Thomas, 2010). Thus, by reflecting differences in average temperatures, regional species pools can vary along large-scale latitudinal and altitudinal gradients (Pianka, 1966). In particular, it has been shown that biodiversity increases towards warmer regions, generating a latitudinal diversity gradient (Rosenzweig, 1995). Greater resource availability and increased metabolism (Brown et al., 2004) in warmer climates can result in higher numbers of individuals, which in turn can promote greater species richness (i.e. energy-richness hypothesis; Wright et al., 1993). Such a latitudinal diversity gradient has been observed for different taxonomic groups, such as mammals (Buckley et al., 2010), birds (Hawkins et al., 2003), and insects (Müller et al., 2015), whereas for fungi and bacteria, this pattern is not as consistent across studies (Bahram et al., 2018; Li et al., 2023; Mikryukov et al., 2023; Tedersoo et al., 2014; Větrovský et al., 2019).

Climate on a small spatial scale, i.e., microclimate, plays a crucial role in habitat selection, survival and reproduction and can thus affect biodiversity (Chen et al., 1999). Forest ecosystems that vary in canopy openness can provide different microclimatic conditions due to the interception of solar radiation, air mixing, and evapotranspiration (De Frenne et al., 2021; Zellweger et al., 2020). Furthermore, microclimatic temperature extremes can be strongly buffered due to reduced sunlight and wind speed (De Frenne et al., 2019; Meeussen et al., 2021), providing microrefugia especially for cold-adapted organisms (Ashcroft et al., 2012; Greiser et al., 2020). In contrast, clear-cut forests provide warmer microclimatic conditions and can thus be dominated by thermophilous, i.e., warm-adapted, species (e.g., plant species, Christiansen et al., 2021). However, many studies investigating the effect of microclimate on forest biodiversity, such as insects, fungi and plants, are based on the degree of canopy openness (Chen et al., 1999; Seibold et al., 2016a; Seibold et al., 2016b), whereas direct measurements of the microclimatic temperature are scarce.

1.1.2 Hydroclimatic compensation model

Species with large geographical distributions may adapt their habitat requirements along a macroclimatic gradient to maintain similar microclimatic conditions across their entire distribution range. This has been termed the “hydroclimatic compensation model” (Ackerly et al., 2020) or “concept of relative constancy of habitats” (Walter and Breckle, 1985). Thus, to compensate for the regional climate, species might occur in warmer habitats at their cold-range margins, and in cooler habitats at their warm-range margins. Although the hydroclimatic compensation model has not been explicitly mentioned, several recent studies provide evidence for such a pattern. For instance, some cold-adapted northern plant species can grow in warm regions, if habitats with cooler microclimatic conditions, such as forests, are accessible (Hylander et al., 2015). In contrast, thermophilous plant species can survive in cold regions at sites with warmer microclimatic temperatures, such as on forest clear-cuts (Christiansen et al., 2021). For butterflies (Davies et al., 2006, Fourcade et al., 2017), ants, grasshoppers, and sand lizards (Thomas et al., 1999) it has also been shown that they can be limited at their northern range margins to microrefugia with warmer microclimatic conditions. Understanding the different habitat requirements of species along macroclimatic gradients is important to improve biodiversity conservation efforts.

1.1.3 Community temperature index

A simple, yet powerful tool to investigate the extent to which a local species composition reflects climatic conditions is to calculate the Community Temperature Index (CTI; Devictor et al., 2008; Fourcade et al., 2021). The CTI is calculated as the mean STI (Species Temperature index) of all species in a community, whereas the STI represents the average temperature a species experiences over its spatial distribution range (Devictor et al., 2008; Fadrique et al., 2018). Thus, a high CTI reflects a local species community that is dominated by thermophilous species, whereas a low CTI reflects a large proportion of cold-adapted species. This index has been used to understand shifts in species communities with climate warming. For instance, Fourcade et al. (2019) observed that climate warming led to an increase in CTI of bumblebee communities between 1960 and 2012, as communities became increasingly dominated by thermophilous species. Habitat changes can also lead to a shift in CTI due to changes in microclimatic conditions. Thus, an increased forest cover resulted in more cold-adapted bird species due to cooler microclimatic temperatures (Barnagaud et al., 2012). Thus, the CTI is an effective tool to study biodiversity patterns in relation to species' thermal preferences along macroclimatic gradients. Moreover, it can be used to test the hydroclimatic compensation model by comparing the CTI of species communities along microclimatic gradients dependent on the regional climate. However, to my knowledge, this model has not yet been tested using this index.

1.2 Biodiversity in dead wood

Boreal forests constitute an enormous biome, comprising approximately 30 % of the world's forests. They encompass around half of the world's remaining (near-) natural forests and provide important ecological, economic, social, and cultural services (Gauthier et al., 2015). Compared to other forested regions, the tree species diversity in European boreal forests is low, with Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) being the most dominant tree species (Girona et al., 2023). In this thesis, I focus mainly on biodiversity in the dead wood of Norway spruce, while one project focuses on beetles in hollow deciduous trees.

1.2.1 Dead wood dependent beetles

Dead wood is a key element for biodiversity. In European boreal forests, around 25 % of all forest-living species are classified as saproxylic, meaning they depend on wood decay or its by-products, whether in living or dead trees (Alexander, 2008). They can be separated into facultative saproxylic, i.e., they may use dead wood or other saproxylic organisms, and obligate saproxylic, i.e., dependent on dead wood or on other saproxylic organisms.

Saproxylic organisms play a crucial role in dead wood decomposition and nutrient cycling (Seibold et al., 2021) and can be specialized on certain tree species (Müller et al., 2020), decay stages (Stokland et al., 2012), and microclimatic conditions (Seibold et al., 2016a). Due to habitat loss and degradation caused by intensified forestry and agriculture, many saproxylic organisms are threatened (Nieto and Alexander, 2010).

Among saproxylic organisms, beetles are one of the best studied taxonomic groups. Their diversity has been shown to follow a latitudinal diversity gradient (Franzén et al., 2025; Kriegel et al., 2023; Müller et al., 2015) and to increase in sun-exposed conditions. Thus, higher microclimatic temperatures lead to higher species richness and abundance of saproxylic beetles (Müller et al., 2015; Seibold et al., 2016b). However, when studying their occurrence patterns, the effects of macro- and microclimate have mostly been investigated separately. Only for the European spruce bark beetle *Ips typographus* (LINNAEUS, 1758) both gradients have been considered simultaneously, indicating that in colder regions the species is more frequently in sun-exposed compared to shaded logs, whereas this difference is much smaller in warmer regions (Lindman et al., 2023). This result supports the hydroclimatic compensation model, but it remains unknown to what extent this model also applies to broader diversity of saproxylic beetles.

Figure 1. A saproxylic beetle (Björkvedbock / Leiterbock, *Saperda scalaris*, LINNAEUS (1758)) on dead wood in Uppsala, Sweden (Photo by A. Gossmann).

Besides their important role in nutrient cycling and dead wood decomposition, saproxylic beetles can also serve as dispersal vectors for other saproxylic organisms. In particular, beetles can transport fungal spores and thus disperse wood-inhabiting fungi (Birkemoe et al., 2018). For instance, the European spruce bark beetle *I. typographus* has been observed to vector over 30 fungal species (Solheim, 1993). However, it can be assumed that the extent to which saproxylic beetles serve as dispersal vectors might differ along a macroclimatic gradient due to shorter activity periods and reduced beetle abundances in colder compared to warmer regions (Lindman et al., 2023). Thus, it has yet to be studied whether saproxylic beetles are a limiting factor for the establishment of wood-inhabiting fungi in cold regions.

In European boreal forests, one of the most prominent saproxylic beetle species is the European spruce bark beetle *I. typographus*. It is considered one of the most destructive pests of mature Norway spruce forests killing millions of spruce trees in Central and Northern Europe during periodic large-scale outbreaks (Schelhaas et al., 2003). Mainly triggered by drought, this species has doubled the impact of tree mortality in the last decades (Patacca et al., 2023). In Sweden, a severe drought event in 2018 resulted in 34 million m^3 of bark-beetle infested trees, reflecting approximately 70 % of the spruce forests lost to outbreaks over the last 50 years (Schroeder and Kärvemo, 2022). Due to climate warming, it becomes even more important to apply forest management strategies that mitigate spruce bark beetle outbreaks, but, at the same time, promote biodiversity conservation by improving the habitat for saproxylic organisms.

1.2.2 Wood-inhabiting fungi and bacteria

Fungi are one of the most species-rich taxa in dead wood (Niskanen et al., 2023). Compared to dead wood dependent beetles, microbes (including fungi and bacteria) are usually referred to in the literature as wood-inhabiting rather than saproxylic, since it remains unknown for many species to what extent they are restricted to wood (Stokland et al., 2012). Saprotrophic fungi, i.e., decomposer fungi, are the most functionally important, exhibiting diverse decay strategies such as brown- and white-rot. White-rot fungi are able to decompose all wood components (lignin, cellulose, and hemicellulose), whereas brown-rot fungi decompose only cellulose and hemicellulose (Highley and Kirk, 1979). Biodiversity patterns of wood-inhabiting fungi are governed by climate, with increasing fungal richness towards warmer regions (Tedersoo et al., 2014), although this pattern is not consistently observed (Li et al., 2023; Větrovský et al 2019). On smaller spatial scales, microclimate affects the diversity and function of wood-inhabiting fungi (Bradford et al., 2014; Gilbertson, Lindhe et al., 2004; 1980; Rayner and Boddy, 1988). Many species are favoured by closed canopies (Bässler et al., 2010; Thorn et al., 2018) with cooler, more humid microclimatic conditions. In contrast, brown-rot fungi are favoured by open canopies with higher temperatures and dry conditions (Brabcová et al., 2022; Fukasawa, 2021), which might be due to adaptation to stressful conditions in order to lower competitive pressure (Fukasawa, 2021). However, as for saproxylic beetles, the effect of macro- and microclimate on the diversity of wood-inhabiting fungi have so far only been studied separately, while the hydroclimatic compensation model has not yet been considered for wood-inhabiting fungi.

Figure 2. Brown-rot fungus (Red-belted conk / Klibbticka / Rotrandiger Baumschwamm, *Fomitopsis pinicola*, P. KARST) on a dead stump in Småland, Sweden (Photo by A. Gossmann).

In contrast to saproxylic beetles and wood-inhabiting fungi, wood-inhabiting bacteria have not received much attention in previous research. So far, a latitudinal diversity gradient has only been observed for soil bacteria across boreal-arctic to temperate zones (Bahram et al., 2018), and it remains unknown whether this trend applies to bacteria in wood. In Bavaria, Germany, bacterial richness in wood increased with warmer regional temperature, although this study did not span a large latitudinal gradient (Englmeier et al., 2023). On a small spatial scale, bacterial richness in wood decreased with increasing microclimatic temperature (Englmeier et al., 2023). Thus, to fully understand diversity patterns of wood-inhabiting bacteria, the interaction between macro- and microclimate needs to be taken into account.

1.3 Dead wood decomposition

1.3.1 Dead wood decomposition along macro- and microclimatic gradients

Forests are an important carbon sink, with dead wood storing around 8 % of the global forest carbon stock (Pan et al., 2011). Dead wood decomposition is a key process that returns carbon and nutrients back into the environment (Russel et al., 2015). It is governed by climate and mediated by microbial communities, with elevated temperatures typically enhancing decomposition rates (Berg et al., 1993; Bradford et al., 2014; Davidson and Janssens, 2006). Changes in climate may alter microbial composition and decomposition rates (Currie et al., 2010; Perreault et al., 2023), directly affecting carbon storage and nutrient cycling. However, the combined effects of climate and microbes on dead wood decomposition remain poorly understood.

1.3.2 Fungi and bacteria as main wood decomposers

Fungi are the principal decomposers of wood due to their ability to produce extracellular enzymes and actively transfer carbon, nutrients, water, and oxygen (Boddy, 1993). A central assumption in functional ecology is that more diverse communities perform better (Cadotte et al., 2011; Cardinale et al., 2012), but this may not apply to wood decomposition (Runnel et al., 2025). Notably, high fungal diversity can reduce decomposition efficiency due to antagonistic interactions among species, including competition for space and resources (Fukami et al., 2010; Fukasawa et al., 2021; Hiscox et al., 2015).

When studying dead wood decomposition, wood-inhabiting bacteria are often overlooked. Yet, they can degrade simpler carbon compounds (Johnston et al., 2016) and alter the wood, making it more accessible for fungi (Greaves, 1971). Nitrogen-fixing bacteria can enable fungi to meet their nitrogen requirements for vegetative and generative growth (Hoppe et al., 2014). Conversely, competitive interactions between bacteria and fungi for resources and habitat may alter microbial community structures and reduce diversity (Bahram et al., 2018; Rinta-Kanto et al., 2016). These contrasting roles of bacteria – as mutualists and as competitors – highlight the complexity of microbial interactions in regulating decomposition. This complexity is further complicated by climatic conditions, since they may modulate not only microbial communities but also their interactions, potentially shifting fungal–bacterial relationships between facilitative and competitive (Glassman et al., 2018). This underscores the importance to consider context in diversity–function relationships.

1.4 Urbanization shapes biodiversity

Urbanization poses a major threat to biodiversity by reducing and fragmenting natural habitats. Natural habitats remaining in cities often have a reduced value for biodiversity due to habitat degradation, negative edge effects (i.e., species being more abundant in the habitat interior than at the edge), and habitat isolation (Beninde et al., 2015; McKinney, 2008). However, cities can also support valuable microhabitats for biodiversity, such as veteran trees and dead wood, which serve as critical resources for many organisms. Veteran trees with cavities serve as key habitats for saproxylic insects (Horák, 2018). Warm and stable microclimatic conditions within tree hollows are favourable to many saproxylic species (Lindman et al., 2023). However, intensive forestry and agriculture have resulted in a severe reduction in veteran trees in production landscapes (Lindenmayer et al., 2012; Siitonen, 2001). Since economic production is rarely a priority in urban areas, veteran trees can be found in urban landscapes providing potential refugia for saproxylic insects (Fröhlich and Ciach, 2020). Indeed, several rare saproxylic beetle species have been observed in hollow trees located in urban settings (Andersson, 1999; Carpaneto et al., 2010; Peuhu et al., 2019). Despite their ecological importance, large old trees in cities are frequently removed for aesthetic or safety reasons (Carpaneto et al., 2010). Consequently, assessing saproxylic biodiversity in urban areas and developing targeted conservation strategies is of critical importance.

1.4.1 Habitat amount and dispersal barriers

Environmental filters, such as habitat quality and quantity, can shape species communities (Vellend, 2016). In particular, increasing habitat amount can promote species diversity (Fahrig, 2013). However, in urban areas, the effect of habitat amount has shown contrasting results on insects: the abundance of dung beetles has been found to increase with urban forest cover (Bernardino et al., 2024), whereas saproxylic insects appear to be largely unaffected (Meyer et al., 2021). When assessing the effects of habitat amount in urban areas, potential negative impacts by dispersal barriers must be taken into account. Urban structures such as roads and buildings can hinder species movement, thereby negatively affecting their distribution and persistence. These negative relationships are well documented for vertebrates, while studies for invertebrates remain limited (Teixeira et al., 2020). Nevertheless, some studies indicated that streets and buildings can act as dispersal barriers for insects, including Tachinid flies (Corcos et al., 2019), butterflies, bees, and wasps (Dániel-Ferreira et al., 2022; Johansson et al., 2018). However, for saproxylic insects, the role of urban structures as dispersal barriers remains largely unexplored.

1.4.2 Urban heat island effect

Due to heat-absorbing artificial surfaces, cities can have temperatures 2-4 °C warmer than surrounding rural areas. This is termed the “urban heat island effect” (Kłysik and Fortuniak, 1999), and can have vast effects on biodiversity (Oke, 1995). Thus, due to warmer microclimatic temperatures in urban areas, insect communities may be dominated by more thermophilous species (Franzén et al., 2020; Menke et al., 2011; Piano et al., 2017). In contrast, urban forests with high tree densities can lower the surrounding temperature and thereby buffer the urban heat island effect (Grilo et al., 2020). Hence, microclimate can also act as an environmental filter that generates differences in species communities between urban and rural areas. However, the extent to which the urban heat island effect and the cooling effect of urban forests shape species communities remains to be studied.

2. Aims and objectives

The main aim of my thesis is to study the biodiversity patterns of beetles, fungi, and bacteria in dead wood along macro- and microclimatic gradients in both forests and urban areas. Furthermore, I examine how these biodiversity patterns relate to dead wood decomposition along the same climatic gradients. I established two field experiments: one was along a 1200 km latitudinal gradient in Sweden, and another was along urban-rural gradients in Swedish cities. In particular, I tested:

- effects of macro- and microclimate on saproxylic beetle diversity. Specifically, I tested the hydroclimatic compensation model with respect to saproxylic beetle diversity (**Paper I**).
- effects of macro- and microclimate on brown- and white-rot fungi, and the role of saproxylic beetles as dispersal vectors for wood-inhabiting fungi (**Paper II**).
- interaction between wood-inhabiting fungi and bacteria influencing dead wood decomposition along macro- and microclimatic gradients (**Paper III**).
- effects of environmental filters and microclimatic temperature on saproxylic beetle diversity along urban-rural gradients (**Paper IV**).

3. Material and Methods

3.1 Study regions and study design

The data for **Paper I-III** were collected in mature spruce forests along a 1200 km latitudinal gradient in Sweden (Fig. 3A), whereas the data for **Paper IV** were collected in six Swedish cities: Lund, Göteborg, Linköping, Motala, Örebro, and Uppsala

Paper I-III

The main aim of **Paper I-III** was to study biodiversity in dead wood along macro-and microclimatic gradients. This was possible with a unique study setup by establishing crossed gradients in macroclimate, i.e., 1200 km latitudinal gradient in Sweden, and microclimate, i.e., shade gradient. In 2020, one year before my PhD studies started, six study regions were selected along the macroclimatic gradient (Fig. 3A), consisting of managed Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) forests. The mean annual temperature ranges from 7.8 °C in the southernmost to 0.3 °C in the northernmost region (SMHI, 1991-2020). At each study region, five study plots were established (Fig. 3C and D). However, due to destruction by forestry management, only four plots were remaining in Siljansfors in 2021 (**Paper I**), whereas in 2023, only three plots were remaining in Siljansfors and four in Vindeln (**Paper II** and **III**). Each study plot consisted of a 1-2 year old clear-cut and an adjacent mature forest stand to obtain a gradient in microclimate (Fig. 3C).

In 2020, 15 freshly cut spruce logs of 1.5 m length were placed at each study plot along five transects and at three different shade levels: (i) sun-exposed: five logs were placed at the forest edge between the clear-cut and the mature spruce forest; (ii) intermediately shaded: five logs were placed 10 m into the forest; and (iii) fully shaded: five logs were placed 50 m from the forest edge into the forest (Fig. 3C). In total, this resulted in 435 spruce logs. Logs within each transect originated from the same tree and ranged between 15 and 35 cm in diameter.

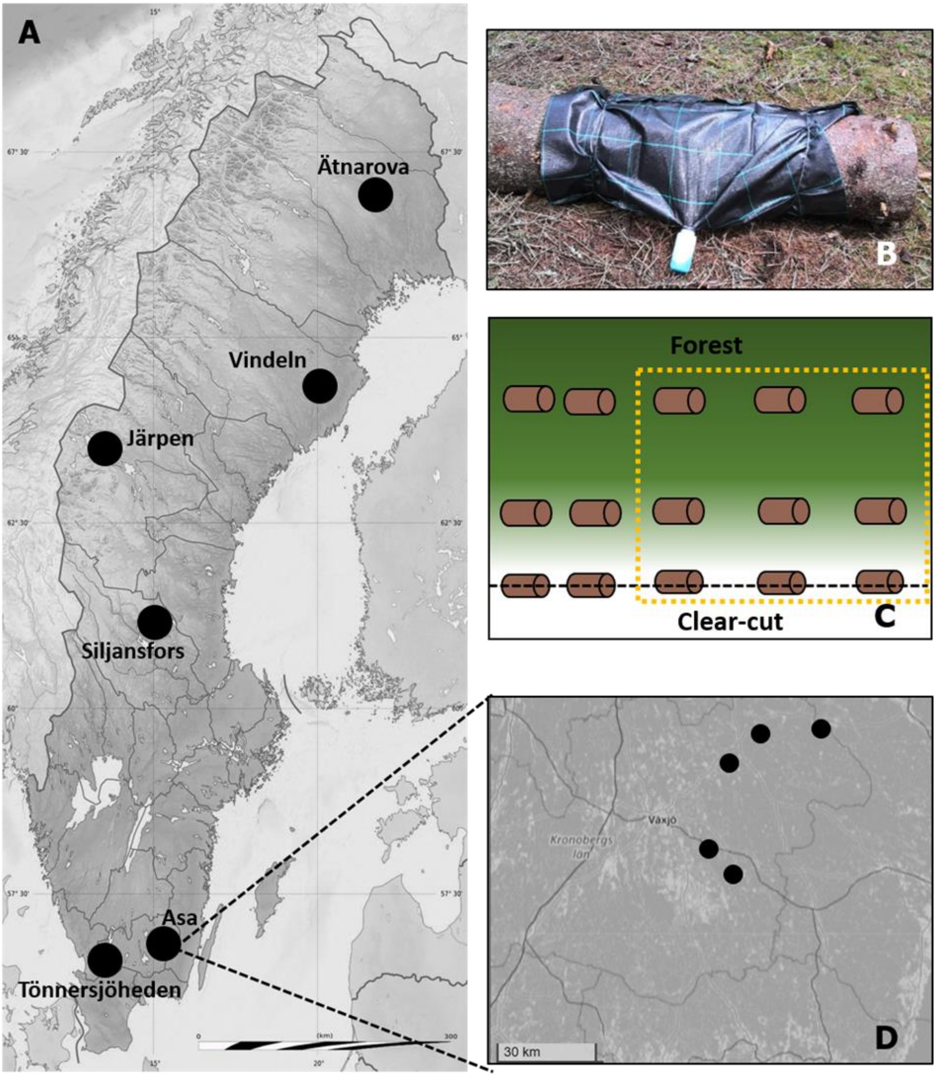

Figure 3. Six study regions, each with five study plots distributed over Sweden (A). 15 spruce logs distributed on three different shade levels: (i) sun-exposed, (ii) intermediately shaded, and (iii) fully shaded (C). The forest edge is represented by a black dashed line (C). For **Paper II** and **III**, only the logs surrounded by a yellow dashed line were sampled (C). Distribution of study plots (black dots) at the study region Asa (map was extracted from Open Street Map (July, 2025)) (D). In spring 2021, every log was equipped with an emergence trap to collect saproxylic beetles (B).

Paper IV

Six cities in southern Sweden were selected: Lund, Göteborg, Motala, Linköping, Örebro, and Uppsala (Fig. 4A), with annual mean temperatures ranging from 8.7 °C in the southernmost city (Lund) to 6.6 °C in the northernmost city (Uppsala). In 2014, ten wooden boxes (but only eight in Motala and Linköping) were placed along an urban-rural gradient in each city (Fig. 4B) with distances to the city centres ranging from 0.5 to 15 km. The boxes were designed to emulate tree hollows in old deciduous trees (Fig. 4C, cf. Jansson et al., 2009). Thus, all boxes were placed at sites with trees in the surrounding area, with oak (*Quercus sp*.) being the dominant tree species.

The boxes, each with a volume of 1 m^3, were made of spruce wood with 25 mm thick walls, including a roof, and placed on the ground (Fig. 5). To emulate wood mould, each box was filled with 400 l of leaves from the surrounding area and 400 L of wood chips from deciduous trees. Below the roof on each side of the boxes, two holes (20 mm in diameter) allowed small animals to enter the box.

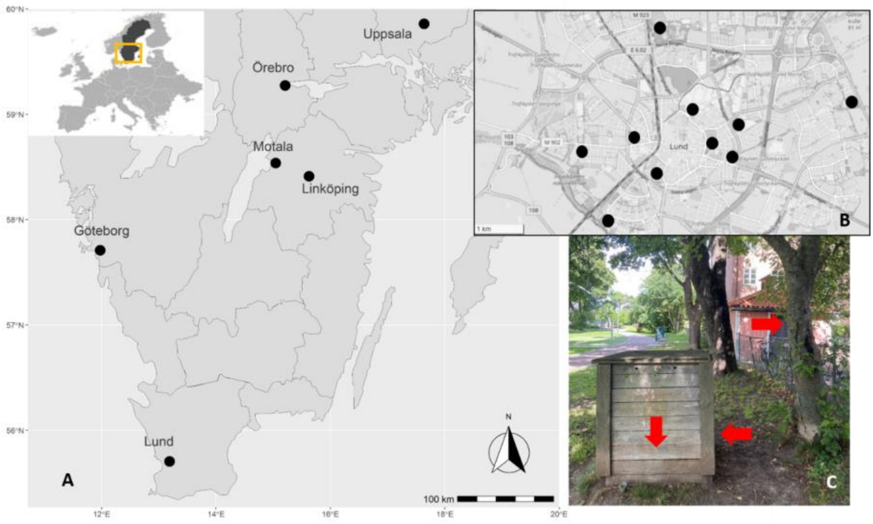

Figure 4. Ten wood mould boxes resembling hollow trees distributed over six cities in southern Sweden (A). Inside and around each would mould box, microclimatic mean temperature was measured at different positions: (i) inside the wood mould of each box, (ii) inside the box attached to the north-facing wall, (iii) outside the box at the closest tree (red arrows represent

logger locations, C), and when available, (iv) inside hollow trees. As an example for the distribution of the wood mould boxes along an urban-rural gradient, a map of Lund was extracted from Open Street Map (July, 2025), with black dots representing box locations (B).

Figure 5. Wood mould box from the outside and pitfall trap inside the wood mould of the box to sample saproxylic insects (Photo by C. Ryding, 2019).

3.2 Data collection

3.2.1 Beetle sampling

Paper I

In 2021, each log was equipped with emergence traps to sample saproxylic beetles that developed in the logs (Fig. 3B). The traps enclosed a 1 m wide strip around the log, and were positioned in the centre of each stem section. A bottle filled with 50 % water/propylene glycol mix was attached to collect the emerging beetles. As insect hatching starts earlier in the south, emergence traps were set up in the beginning of April in southern Sweden, and in the beginning of May in northern Sweden. Thus, mainly beetles that originated from oviposition from 2020 were collected. The sampling was finished in the beginning of September 2021, and subsequently, the sampled beetles were identified to species level. Only species classified as saproxylic (obligate or facultative) were extracted for the analyses (listed at least in one of the following publications: Ekström, 2020; Hägglund and Hjältén, 2018; Schmidl and Bußler, 2004).

Paper IV

In 2019, each wood mould box was equipped with two pitfall traps to collect saproxylic beetles, consisting of a plastic jar (Ø 65 mm) and filled with a 50 % water/propylene glycol mix and detergents (Fig. 5). From the beginning of May, the traps were emptied and exchanged every four weeks until the end of August. The sampled beetles were identified to species level, and only saproxylic (both obligate and facultative according to Ekström, 2020; Hägglund and Hjältén, 2018; Schmidl and Bußler, 2004) species were extracted for the analyses.

3.2.2 Microbial sampling

In 2023, for fungal and bacterial analyses, sawdust from nine of the 15 spruce logs of each study plot were sampled (Fig. 3C). For **Paper II** and **III**, two different sampling types were applied:

(i) Sawdust was collected from three holes drilled perpendicularly to the log surface, with two on the underside, and one on the top centre (Fig. 6, grey arrows). In the field, sawdust was pooled per plot and shade level, resulting in 81 samples (3 shade levels across 27 plots).

(ii) Sawdust was collected from three holes drilled perpendicularly into the lower section of the wider end of each log (Fig. 6, white arrows). Sawdust was pooled at log level, resulting in 243 samples (9 logs per plot and 27 plots in total).

For **Paper II**, both sample types were used and the data were combined by calculating the weighted mean of Operational Taxonomic Unit (OUT) read counts, whereas for **Paper III**, only the second sample type was used.

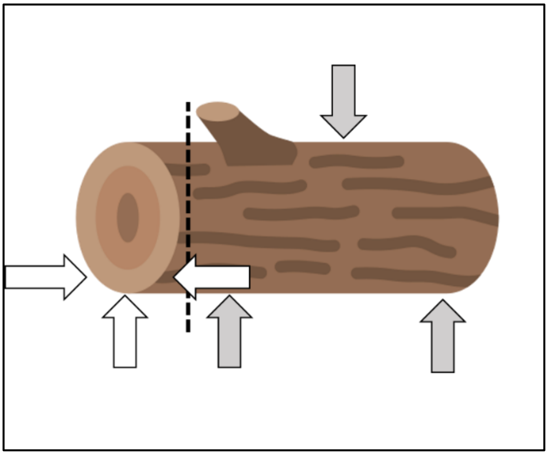

Figure 6. Two types of sawdust samples (grey arrows (i), white arrows (ii)). Dashed line represents where wood discs have been cut in 2020 and 2023, respectively, from each log.

Figure 7: Drilling into spruce log in September 2023 (Photo by A. Gossmann).

The sampling technique was the same for both sample types: first, the bark was removed with an ethanol-flamed knife, and subsequently, sawdust was collected by drilling into the logs (Ø 1 cm, length 10 cm, Fig. 7). The sawdust samples were freeze-dried at -50 °C for 24 hours and homogenized using a swing mill and plastic beads. Using the NucleoMag DNA Microbiome kit (Macherey-Nagel, Germany), fungal and bacterial DNA was extracted from 100 mg of each homogenized wood sample, and subsequently, DNA concentration and quality were measured for each sample. The fungal ITS (internal transcribed spacer) region was amplified by using the primers fITS7 (forward) (Ihrmark et al., 2012) and ITS4 (reverse) (White et al., 1980), whereas the bacterial 16S region was amplified by using the primers 341F (forward) and 805R (reverse) (Herlemann et al., 2011). For fungal DNA, PacBio sequencing was performed externally by SciLifeLab, Uppsala (Sweden), whereas for bacterial DNA, Illumina sequencing was performed by SciLifeLab, Stockholm (Sweden).

3.2.3 Microclimatic temperature data

Paper I-III

In 2020, the microclimatic temperature was measured at each study plot to confirm that the shade gradient clearly corresponded to microclimate. Therefore, six logs on each study plot (two of each shade level) were equipped with temperature loggers (SL52T, Signatrol) directly under the bark. They measured the microclimatic temperature hourly from beginning of May until mid-September, and thus covered the time of the year when saproxylic beetles were collected with emergence traps the following year. Error-measurements were excluded (22 of 1.136.500 measurements). Subsequently, mean microclimatic temperature per day and plot-shade level was calculated.

Paper IV

In 2022, temperature loggers (SL52T, Signatrol) were installed inside and around each wood mould box and in hollow trees nearby to assess the microclimatic temperature (Fig. 4). Due to missing boxes, only for 49 of the initial 56 wood mould boxes, microclimatic temperature was measured. Temperature loggers were located at four different positions in and around each box:

(i) one logger was placed 20 cm below the surface of the wood mould at the centre of each box;

(ii) one logger was attached to the north-facing wall inside each box;

(iii) one logger was attached to the closest tree of each box (max. 2 m distance), 2 m from the ground, and at the north-facing side;

(iv) one logger was placed into the wood mould of a hollow tree in the close surrounding (max. 20 m distance), if available.

The temperature was measured hourly from the beginning of April until the end of September. Due to lost loggers and destroyed boxes in September, the total number of temperature loggers was 29 in the wood mould of the boxes, 39 on the walls inside the boxes, and 42 outside the boxes. Only six loggers were placed in hollow trees in the close surrounding. Error-measurements were excluded (0.04 % of all measurements). Subsequently, the mean microclimatic temperature and daily mean temperature fluctuation (standard deviation) per logger type across the whole sampling season were calculated.

3.2.4 Environmental data

Paper I-III

In spring 2021, the diameter of each spruce log was measured at the centre of each log, and the percentage of remaining bark on each log estimated.

For **Paper II**, I used the abundance of emerging beetles from 2021 as a proxy for dispersal vectors. The abundances of only those logs were extracted, which were also sampled for fungal DNA.

As a proxy for the regional climate, 30-year (1991-2020) mean temperature measurements from nearby weather stations were extracted (SMHI, 2022).

Paper IV

Canopy openness above each box was measured by taking photographs with a fisheye lens 1 m above the ground. The photos were analysed with Gap Light Analyzer (Frazer, 1999), calculating the percentages of the area not covered by canopy. Furthermore, the number of hollow trees (entrance hole diameter > 10 cm) was counted in a radius of 20 m around each box. Canopy openness and number of hollow trees were measured and counted around 49 of the initial 56 wood mould boxes.

ArcGIS Pro 3.0.3 was used to assess the density of urban structures (i.e. dispersal barriers) and tree cover (i.e. habitat amount) around each box. Map data from the NMD database (Nationella Marktäckedata, 2023) with a resolution of 10 × 10 m was extracted, which is provided in raster format and included 25 land cover categories. Subsequently, these were reclassified into two groups: “tree cover” and “density of urban structures”, with fourteen categories representing areas with >10 % tree canopy cover (e.g., forests, parks) grouped as “tree cover” and three categories representing artificial built areas without vegetation grouped as “density of urban structures”. Subsequently, the percentage areas of density of urban structures and tree cover were calculated in a 3000 m, 1000 m, 500 m, and 100 m buffer around each box.

As a proxy for regional climate, mean annual temperature data from 1995-2020 (SMHI, 2023) was used. To compare the regional climate with my measured microclimatic temperature, temperature data from April to September 2022 was extracted from nearby weather stations (SMHI, 2023).

3.3 Community temperature index

The Community Temperature Index (CTI) was calculated to assess how saproxylic beetle communities respond to regional climate and microclimate (Devictor et al., 2008).

Paper I

In **Paper I**, the CTI was based on species distributions only in Sweden. This is adequate, since the distributions of saproxylic beetles in Sweden are well documented, and I am interested in the relative difference in CTI as an estimate of the dominance of species with different climatic niches within local communities. Therefore, a mean annual temperature (1991-2020; SMHI, 2022) was calculated for each Swedish province. The Species Temperature Index (STI) for a given species was calculated by averaging the annual mean temperatures of those provinces where the species occurs, according to Lundberg and Gustafsson (1995). Subsequently, the CTI was calculated by averaging STI values based on species presence only. The CTI was not weighted by species abundance as some species with an intermediate STI were highly abundant (for instance the three most abundant species constituted 89.6 % of all collected individuals) and thus, might suppress the effect of species with high or low STI.

Paper IV

In **Paper IV**, the CTI was based on global species occurrences. The STI of each species was calculated by averaging the mean temperature (1970–2000; WorldClim 2.1 dataset (Fick and Hijmans, 2017)) of those pixels (4.5 x 4.5 km resolution in R (package geodata; Hijmans et al., 2023)), where the species occurs (GBIF, Global Biodiversity Information Facility, Chamberlain et al., 2023). Subsequently, the CTI for each box was calculated by averaging the STI values of the species present in that box weighted by species abundance.

3.4 Dead wood decomposition

In 2020, a 3 cm wide wood disc was cut from the larger cut-end of each log, and stored under dry conditions. In 2023, another 3 cm wide wood disc was cut from the same end of each log (Fig. 6). Thus, the decomposition rate was based on the loss of wood density in 2023 compared to 2020. One quarter from the bottom, and one quarter from the top of each wood disc were cut for density measurement, as wood density within a single wood item can vary. Bark, soil, and fungi were removed from those wood pieces, and dried at 60 °C for a minimum of 48 hours until a constant mass was reached. The volume of the dried disc pieces was measured with the water displacement method by pressing the pieces under water with an almost volumeless needle. The displaced water represents the volume of the disc piece. Wood density was further calculated with the following equation:

$$Density\left(\frac{g}{L}\right) = \frac{Dry\ mass\ (g)}{Dry\ volume\ (L)}$$

The density was then converted to density loss in percentage (%).

3.5 Bioinformatics

The LotuS pipeline (ver. 2.32) was used to quality-filter, demultiplex, and process the filtered reads into OTUs (Özkurt et al., 2022), which was configured with the following settings: dereplication threshold of -derepMin 2, and clustering algorithm described by Fu et al. (2012). Both de novo and reference chimera filtering (via Uchime (Edgar, 2016)) were applied. Taxonomy was assigned using the SILVA (ver. 138.1) and UNITE (ver. 8.1) databases for bacterial and fungal sequences, respectively. For bacterial functional annotation, FAPROTAX was used (Louca et al., 2016), and FungalTraits tool (Põlme et al., 2020) for fungal functional annotation. Global and local singletons (OTUs represented by single sequences) were removed for the Illumina sequenced data (bacterial OTUs). All bacterial and fungal DNA sampled from the spruce logs are referred to as wood-inhabiting. Finally, although OTUs are not equivalent to species, the term 'species' is used throughout the thesis for readability.

3.6 Statistical analyses

All statistical analyses were conducted in R 4.2.0 (R Core Team, 2022).

Paper I

Linear mixed-effects models (lme from package nlme, Pinheiro et al., 2013) were applied to test the effects of study region and shade level on microclimatic temperature, and to assess the effects of regional temperature, shade level and their interaction on species richness and CTI of saproxylic beetles. The daily mean microclimatic temperature was calculated by averaging the temperature on plot shade level. I included *study_region/study_plot* as a nested random effect variable. Bark cover, log diameter, and aspect were included as fixed effects.

Paper II

Generalized linear mixed-effects models were applied to test the effects of regional climate, shade level, their interaction, and the abundance of dispersal vectors on the richness (number of OTUs) of all sampled fungi, and on the richness and relative abundance of brown- and white-rot fungi. Relative abundance refers to the proportion of sequencing reads belonging to a specific functional group relative to all sequencing reads. I included *study_region/study_plot* as a nested random effect variable.

Paper III

Generalized linear mixed-effects models were applied to test the effects of regional climate and shade level on wood density loss and on microbial metrics, including fungal and bacterial richness, and nitrogen-fixing bacterial richness and relative abundance. Furthermore, I tested the effects of fungal and bacterial metrics on wood density loss, and extracted the model with the lowest AIC (second-order Akaike's information criterion, AICc from package MuMIn, Barton, 2009). In all models, *study_region/study_plot* was included as a nested random effect.

Paper IV

Generalized linear mixed-effects models were applied to test the effects of environmental filters (i.e., density of urban structures, tree cover and microclimate) on species richness, abundance, and CTI of saproxylic beetles. The AIC was calculated to compare the model fit of the four different buffer models, and the results of the models with the lowest AIC are presented. Linear mixed effects-models were applied to test the effects of density of urban structures and tree cover on the microclimatic temperature. Additionally, the same linear mixed-effects models were applied with temperature fluctuation as response variable. City identity was included as random effect variable in all models.

4. Results and Discussion

In these PhD projects, I gained novel insights into how biodiversity in dead wood changes along macro- and microclimatic gradients. In the following sections, I synthesize my findings from the four papers and discuss the separate and combined effects of macro- and microclimate on biodiversity in dead wood and dead wood decomposition in forest ecosystems and the effects of environmental filters on saproxylic beetle diversity along urban-rural gradients.

4.1 Microclimatic temperature reflects shade gradient

As expected, microclimatic temperature decreased from sun-exposed to fully shaded logs across all study regions (**Paper I**, Fig. 8), with an average temperature difference of 1.5 °C between sun-exposed and fully-shaded logs. In contrast, between the southernmost and northernmost region, the temperature difference was 3.1 °C. Thus, the difference in microclimatic temperature between sun-exposed and fully shaded logs corresponded to 577 km along the latitudinal gradient, indicating a strong impact of tree canopy on the microclimatic temperature.

I used shade level rather than microclimatic temperature as the basis for comparison, since the temperature measurements reflected variation not only along a shade gradient, but also along the regional climatic gradient.

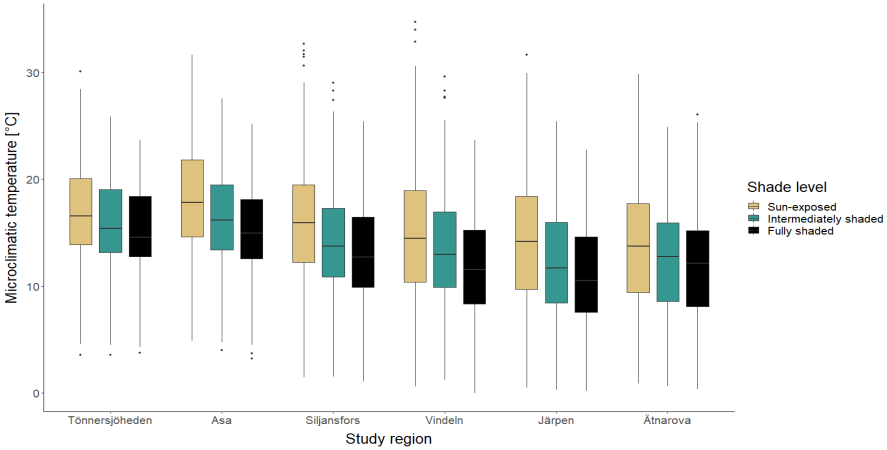

Figure 8: Mean microclimatic temperature from southern (Tönnersjöheden) to northern Sweden (Ätnarova), and along a shade gradient from sun-exposed (yellow) to fully shaded logs (black). Microclimatic temperature was measured inside spruce logs from April to September 2020.

4.2 Biodiversity in dead wood along macro- and microclimatic gradients

4.2.1 Diversity in dead wood follows a latitudinal diversity gradient

In total, I collected 209 saproxylic beetle species (~158.000 individuals) (**Paper I**), 2.415 wood-inhabiting fungal species, including 40 brown-rot and 109 white-rot fungal species (**Paper II**), and 5.040 wood-inhabiting bacterial species including 56 nitrogen-fixing bacterial species (**Paper III**) along the regional climatic gradient. Species richness of saproxylic beetles and wood-inhabiting bacteria increased significantly with regional temperature (Fig. 9), whereas for wood-inhabiting fungi, regional temperature had only a marginally positive effect. Thus, the diversity of saproxylic beetles and wood-inhabiting bacteria follows a latitudinal diversity gradient (Rosenzweig, 1995). Englmeier et al. (2023) found an increasing richness of wood-inhabiting bacteria with regional temperature, but this study did not cover a large climatic gradient. Detecting a latitudinal diversity gradient for organisms in dead wood is critical for two reasons: first, these species play a crucial role in ecosystem functions such as nutrient cycling and decomposition (Seibold et al., 2021), which may vary along macroclimatic gradients. Second, as the climate warms, thermophilous species are expected to expand their ranges into colder regions (De Frenne et al., 2013), potentially altering patterns of species richness and, in turn, reshaping forest biodiversity and ecosystem functioning along macroclimatic gradients.

4.2.2 Microclimate shapes biodiversity in dead wood

In contrast to the species richness patterns along a macroclimatic gradient, I found less consistent patterns along microclimatic gradients. Across all study regions, species richness of saproxylic beetles was higher in sun-exposed compared to shaded logs (**Paper I**, Fig. 9). This finding aligns with the literature (Lettenmaier et al., 2022; Seibold et al., 2016b; Vogel et al., 2020), suggesting that saproxylic beetles are favoured by warmer microclimatic temperatures. As ectothermic organisms, the life cycle of insects – including saproxylic beetles – is strongly influenced by temperature.

Fungal and bacterial richness did not exhibit a clear response towards the different shade levels (**Paper II** and **III**, Fig. 9). In fact, although not significant, I observed higher fungal and bacterial richness in sun-exposed compared to shaded logs. This is in contrast to previous studies reporting that fungal and bacterial richness is higher under closed canopies (Bässler et al., 2010; Brabcová et al., 2022; Englmeier et al., 2023; Hagge et al., 2024; Thorn et al., 2018), exhibiting cooler and more humid microclimatic conditions. However, those studies have all been conducted in the Bavarian Forest National Park in south-eastern Germany, where macroclimatic temperatures are generally higher than in Sweden. Thus, sun-exposed conditions there may be detrimental for fungal spores (Krah et al., 2021; Norros et al., 2015). In contrast, as the macroclimatic conditions are generally cooler in my study regions, the whole shade gradient seemed to serve as suitable habitat for wood-inhabiting fungi. This suggests that the regional climate may modulate species' habitat requirements – a possibility examined in more detail in the next section.

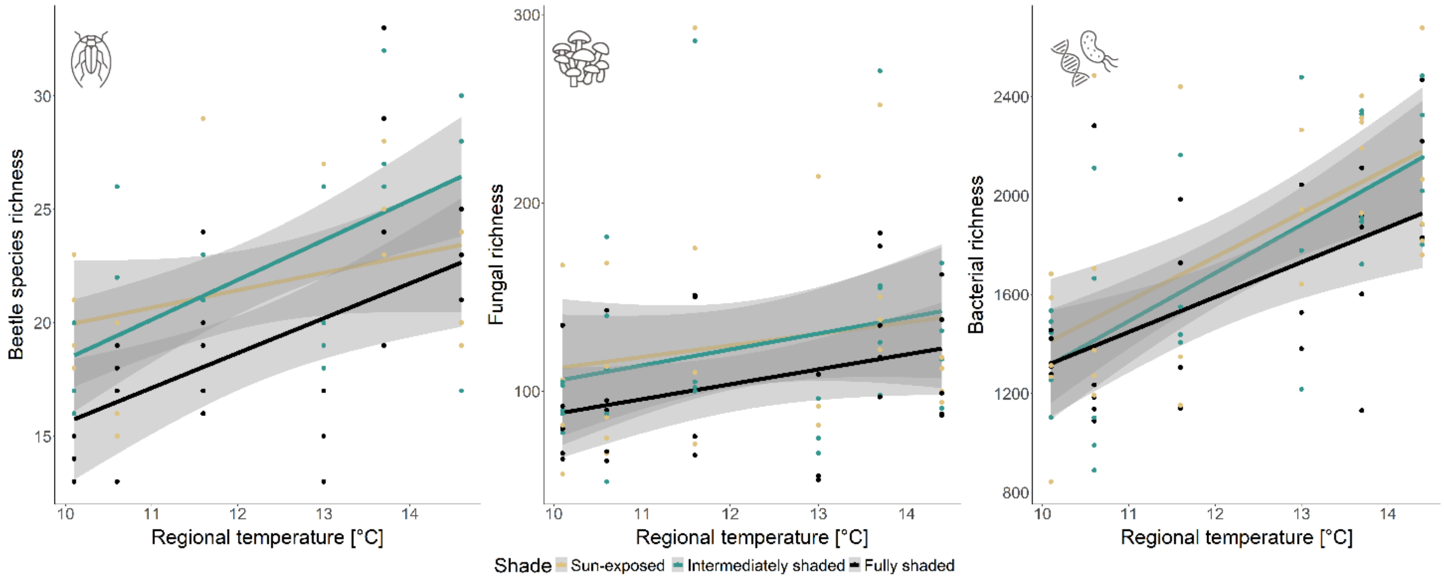

Figure 9. Species richness of saproxylic beetles, and wood-inhabiting fungi and bacteria sampled in dead wood of spruce logs along a regional climatic gradient from northern to southern Sweden and along a shade gradient from sun-exposed (yellow) to fully shaded (black) logs. Each dot represents sample per plot shade level.

4.2.3 Hydroclimatic compensation model partly explains biodiversity in dead wood

In **Paper I**, I refer to the concept of relative constancy of habitats, whereas in **Paper II**, I chose to use the term "hydroclimatic compensation model". In the following, I will present and discuss the results of both.

In **Paper I**, I found an interaction effect between regional temperature and shade level on the saproxylic beetle CTI, which supports the hydroclimatic compensation model. Thus, in northern Sweden, the CTI varied clearly along the shade gradient, whereas in southern Sweden, the CTI was more consistent across the shade gradients (Fig. 10). In other words, in colder regions, thermophilous species dominated in sun-exposed but not shaded logs, whereas in warmer regions, there was no such distinction. This indicates that in colder regions, saproxylic beetles may be more limited by microclimatic temperatures, whereas in warmer regions, the whole shade gradient might serve as suitable habitat. Such an interaction pattern has also been observed for a woodland-dependent butterfly species, which was less dependent on woodlands in regions with warmer winters and wetter summers (Pateman et al., 2016), and for the European spruce bark beetle *I. typographus*, with higher abundances in sun-exposed than shaded logs in colder regions, but no such distinction in warmer regions (Lindman et al., 2023).

In **Paper I**, the CTI was based on species distribution data only across Sweden. This means that I may not have captured distribution patterns of cold-adapted species at their true southern range margin, which could explain why I did not find a strong effect of shade level at study sites with a warmer regional climate. Conclusively, I provide evidence for the hydroclimatic compensation model for saproxylic beetles at least at their true northern range margin.

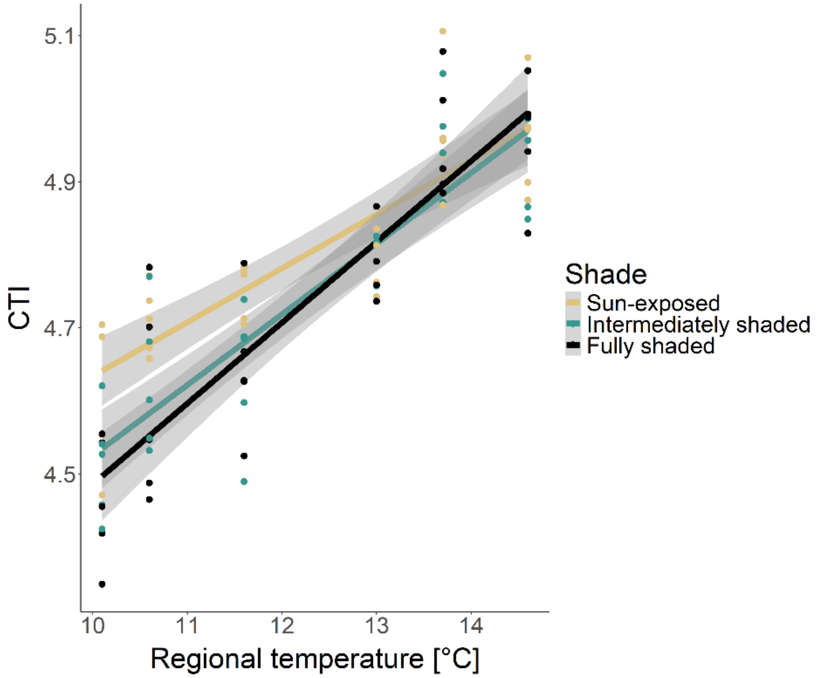

Figure 10. Community Temperature Index (CTI) of saproxylic beetle communities along a regional climatic gradient from northern to southern Sweden and along shade gradients from sun-exposed (yellow) to fully shaded (black) spruce logs. Each dot represents sample per plot shade level.

Besides saproxylic beetles, I found that particularly the diversity of brown-rot fungi follows the hydroclimatic compensation model (**Paper II**, Fig. 11). However, here I did not base the analysis on the CTI, but on fungal richness patterns. Thus, fungal richness was similar across the shade gradients in warmer regions, but significantly higher in sun-exposed logs in colder regions. This indicates that in the south, the whole shade gradient provides suitable microclimatic conditions for brown-rot fungi, whereas in the north, they are limited by microclimatic conditions. Since this analysis is solely based on fungal richness, it remains unclear whether fungi in sun-exposed logs in northern regions are truly thermophilous species at their northern range margin or cold-adapted species that perform better under warmer microclimatic conditions. However, as distribution data for fungi are not as well documented as for saproxylic beetles, and since most of the fungal sequences were not identified to species level, it is not possible to calculate a Species Temperature Index, and thus a Community Temperature Index. Nevertheless, this result supports the hydroclimatic compensation model, as the habitat requirements of the brown-rot diversity vary along a regional climatic gradient. Thus, especially clear-cutting regimes in colder regions may favour brown-rot fungi, which in turn can result in overall shifts of fungal communities, and consequently alter decomposition.

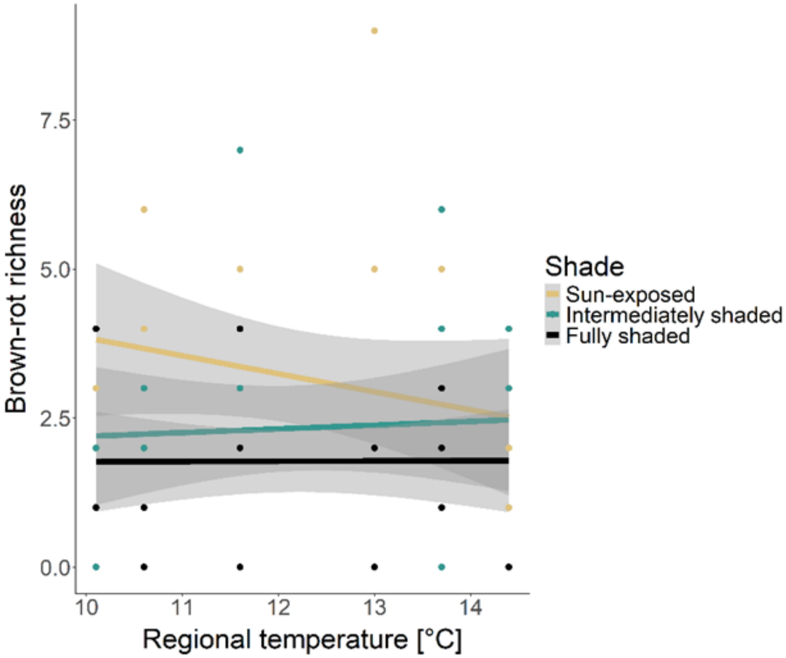

Figure 11. Species richness of brown-rot fungi along a regional climatic gradient from northern to southern Sweden and along shade gradients from sun-exposed (yellow) to fully shaded (black) spruce logs. Each dot represents sample per plot shade level.

For all wood-inhabiting fungi, white-rot fungi, and wood-inhabiting bacteria, I did not find any response to shade level and varying habitat requirements along the studied regional climatic gradient. This indicates that regardless of the regional climate, the whole shade gradient may serve as suitable habitat. One explanation for this can be within-species variation, so that southern and northern populations might be adapted to the climatic conditions of the respective region (Barley et al., 2021; Bennett et al., 2019). Therefore, populations at their southern or northern range margin do not have strong associations with certain microclimatic conditions.

4.2.4 Dispersal vectors shape brown-rot diversity in dead wood

Besides the direct effects of macro- and microclimate on the fungal diversity, fungal communities can also be indirectly affected through their associations with other organisms. The title of Seibold et al. (2019): "Fungi associated with beetles dispersing from dead wood – Let's take the beetle bus!" metaphorically conveys this idea, since saproxylic beetles can serve as dispersal vectors for wood-inhabiting fungi. In this context, the body surface, digestive system, and mycangia, which is a special structure on the beetle body (Six and Paine, 1996), may serve as dispersal media for fungal spores (Birkemoe et al., 2018; Jacobsen et al., 2017). In **Paper II**, I found additional evidence for this assumption. Whereas all wood-inhabiting fungi and white-rot fungi were not affected by dispersal vectors, richness and relative abundance of brown-rotters increased with beetle abundance across all study regions. This result may explain why brown-rot fungi mostly occurred in sun-exposed logs: not only are they physiologically suited to dry, sun-exposed wood, but they also benefit from increased colonization opportunities via beetles, which prefer similar microclimatic conditions. Thus, beetle-facilitated dispersal and favourable microclimate may jointly reinforce brown-rot success in sun-exposed dead wood. In contrast, all wood-inhabiting fungi and white-rot fungi were not associated with sun-exposed conditions, and thus might not benefit from the dispersal by saproxylic beetles.

In further research, it would be interesting to investigate how dispersal vectors affect wood-inhabiting bacterial diversity. It can be assumed that beetles also carry bacteria into wood, but I am not aware of any study investigating this. Ideally, bacterial DNA should be directly sampled from the body surface of the saproxylic beetles before they enter the wood. Although bacteria contribute substantially to the decomposition process (Johnston et al., 2016), little is known about how decomposing bacteria access dead wood.

4.3 Dead wood decomposition along a macroclimatic gradient

Why is the world green? The world is green not just because of the colour of plants, but because of the many ecological functions that sustain life around us: pollination, nutrient-cycling, or decomposition – just to name a few. As part of my doctoral studies, I looked into dead wood decomposition along climatic gradients and related it to the diversity of wood-inhabiting microbes. I present these results in the following.

In **Paper III**, I found dead wood decomposition rates to increase towards warmer regions (Fig. 12), whereas shade level had no effect. The average wood density loss at the southernmost study region (Tönnersjöheden) was 11.2 % over three years, whereas at the northernmost study region (Ätnarova), it was 0.3 %. This result supports the general pattern of higher decomposition rates in the south compared to the north (Davidson and Janssens, 2006), likely due to higher metabolic rates and enzymatic activity of decomposers (Gillooly et al., 2001).

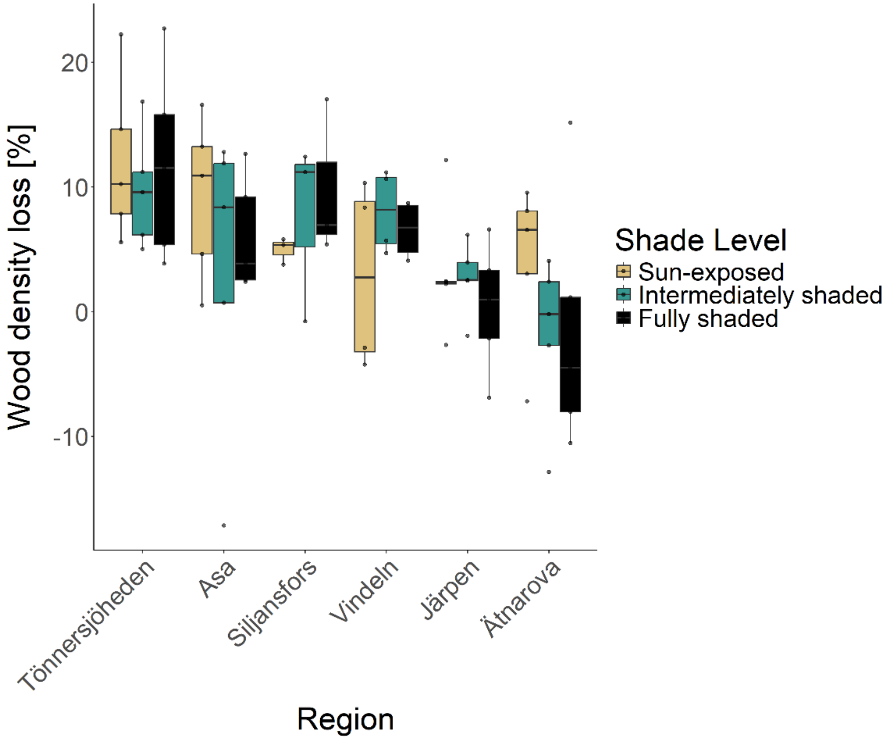

Figure 12. Wood density loss [%] from 2020 to 2023 from southern (Tönnersjöheden) to northern (Ätnarova) Sweden and from sun-exposed to fully shaded logs.

4.3.1 Wood-inhabiting fungi as principal decomposers

Although regional climate was a strong predictor of dead wood decomposition, adding fungal richness significantly improved the model beyond what could be explained by climatic variables alone. This indicates a significant contribution of fungi to the decomposition process. I found a non-linear, hump-shaped relationship between fungal richness and decomposition rates (Fig. 13), indicating that decomposition rates increase with fungal richness to a certain level, but then decrease. In previous studies, increasing decomposition rates have only been observed when the number of fungal species was low (up to ten species) (Setälä and McLean, 2004; Tiunov and Scheu, 2005). This may be due to antagonistic interactions among fungi, such as competition (Fukami et al., 2010; Fukasawa et al., 2021; Hiscox et al., 2015). Thus, a high number of fungal species may result in fungi allocating more resources to antagonistic interactions than to decomposition (Boer et al., 2005), consequently reducing decomposition rates.

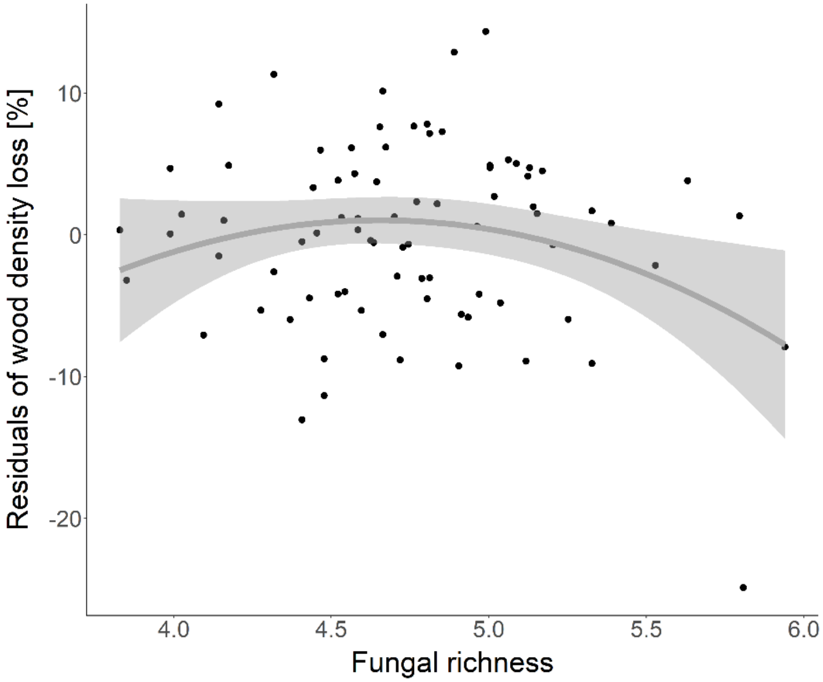

Figure 13. Residuals extracted from decomposition model, i.e., wood density loss as response variable and regional climate and shade level as explanatory variables, against a gradient of log-transformed fungal richness.

4.3.2 Interaction between wood-inhabiting fungi and nitrogen-fixing bacteria affects dead wood decomposition

I detected a marginally significant interaction effect between regional climate and fungal richness on wood density loss, indicating that decomposition rates decrease with fungal richness in the south, but increase with fungal richness in the north. This interaction became highly significant when nitrogen-fixing bacterial richness was included into the interaction term (Fig. 14). Thus, in warmer regions, decomposition rates and fungal richness were negatively correlated when nitrogen-fixing bacterial richness was high, but positively correlated under the same conditions in the north (Fig. 14). This result suggests antagonistic interactions among microbes in warmer regions, and facilitative interactions in colder regions. Specifically, there are two possible mechanisms driving this antagonistic effect in warmer regions: first, fungi and bacteria may directly compete for the same substrate investing more into antagonistic interactions than into decomposition (Boer et al., 2005). Second, high richness of nitrogen-fixing bacteria increases nitrogen content in dead wood, which may favor highly competitive, fast growing fungi (Lustenhouwer et al., 2020), thereby intensifying interspecific competition among fungi. In the north, I observed the opposite: decomposition rates increased with fungal richness when nitrogen-fixing bacterial richness was high. This aligns with the “stress-gradient hypothesis”, which posits that antagonistic interactions decrease with increasing abiotic stress (Bertness and Callaway, 1994). Previously, this stress-gradient has been detected for plants and bacteria, whereas fungi shifted towards more negative interactions under stressful conditions (reviewed by Adams et al., 2022). In my study, colder regions likely represent higher abiotic stress, potentially reducing fungal antagonism and promoting facilitative interactions among fungi.

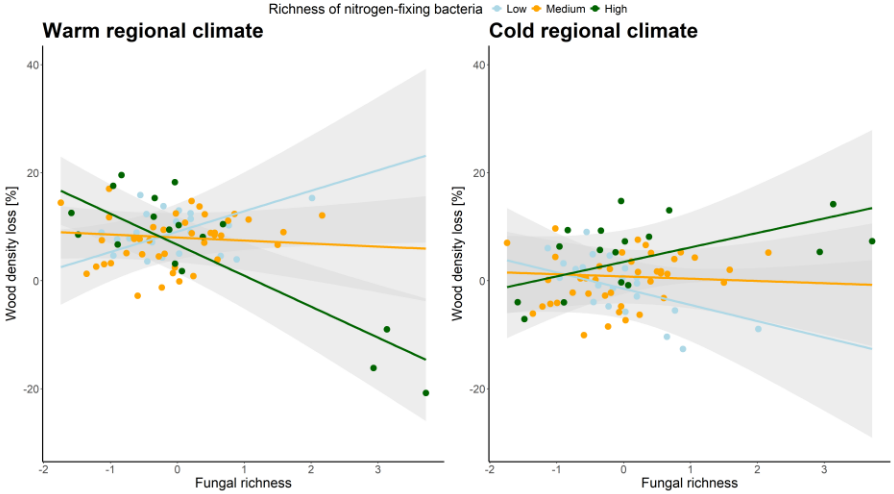

Figure 14. Wood density loss against the residuals of fungal richness (residuals extracted from linear model with bacterial richness as predictor variable) in warmer and colder regions. Regional temperature was divided into quantiles (10.6 °C, 11.6 °C, and 13.7 °C), with 10.6 °C and 13.7 °C selected to represent colder and warmer regions, respectively. Residuals of nitrogen-fixing bacterial richness (residuals extracted from linear model with regional climate and shade level as predictor variables) were grouped into

quantiles (−1.14, 0.01, 1.39), corresponding to low, medium, and high richness levels.

4.4 Saproxylic beetle biodiversity along urban-rural gradients

4.4.1 Microclimate along urban-rural gradients

In **Paper IV**, I found evidence for an urban heat island effect in the studied cities, since microclimatic temperatures increased significantly with density of urban structures, i.e., built areas without vegetation, in a 3000 m buffer (Fig. 15). In contrast, microclimatic temperatures decreased marginally with tree cover, i.e., areas with tree canopy cover > 10 %, in a 3000 m buffer (Fig. 15), which can be due to the cooling effect of tree canopies (Grilo et al., 2020). Canopy openness above the wood mould boxes also had strong positive effects on the microclimatic mean temperature, and explained the microclimatic temperature better than density of urban structures and tree cover. This indicates that the close environmental surrounding has a stronger effect on microclimate than the large-scale surrounding (tree cover and density of urban structures). Thus, the urban heat island effect may be buffered by increasing canopy cover.

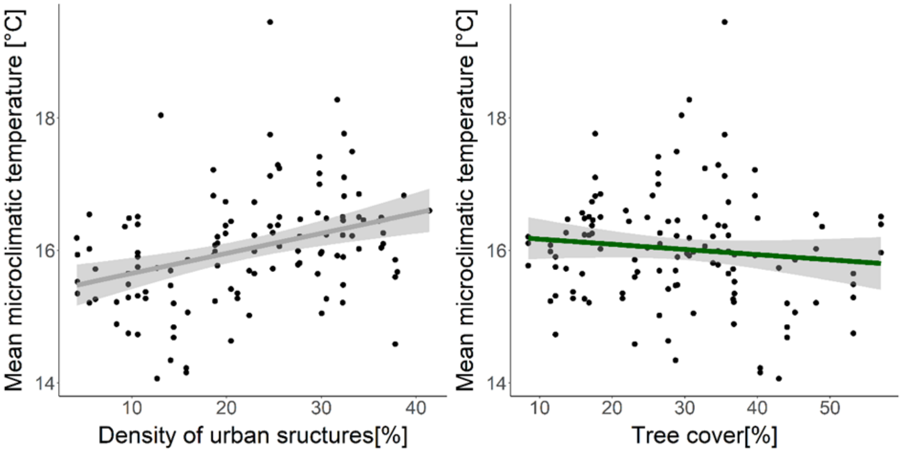

Figure 15. Microclimatic mean temperature [°C] along density of urban structures [%] and tree cover [%] in a 3000 m buffer across the six study

cities. Microclimatic mean temperature was calculated by averaging the temperature per logger type across the whole sampling season.

I found the microclimatic mean temperature inside the wood mould of the boxes (15.9 °C) to be similar to the temperature measured inside hollow trees (15.7 °C), and the microclimatic mean temperature fluctuation to be lower inside the wood mould of the boxes (0.54 °C) and inside hollow trees (1.45 °C) compared to the ambient mean temperature fluctuation (2.68 °C). This indicates stable microclimatic conditions both inside wood mould boxes and inside hollow trees, and suggests that wood mould boxes resemble microclimatic conditions inside hollow trees. Since a stable microclimate seems to be a key factor for saproxylic insects specialized on tree hollows (Ranius et al. 2024), wood mould boxes may have the potential to serve as artificial habitat for invertebrates living in tree hollows.

4.4.2 Effect of environmental filters on saproxylic beetle diversity along urban-rural gradients

In **Paper IV**, I tested the effects of three environmental filters on saproxylic beetle diversity in urban areas: density of urban structures (i.e. dispersal barriers), tree cover (i.e. habitat amount), and microclimate. As described above, I found an urban heat island effect, but this had no effect on the CTI. In other words, thermophilous species did not dominate in areas with a high density of urban structures (Fig. 16). Instead, CTI increased significantly with tree cover, and decreased significantly with canopy openness, meaning that thermophilous species dominated in wood mould boxes with cooler microclimatic temperatures. However, I did not find any effect of the microclimatic temperature on CTI, indicating that the cooler microclimatic temperatures resulting from decreasing canopy openness and increasing tree cover were not the driver of the observed CTI pattern.

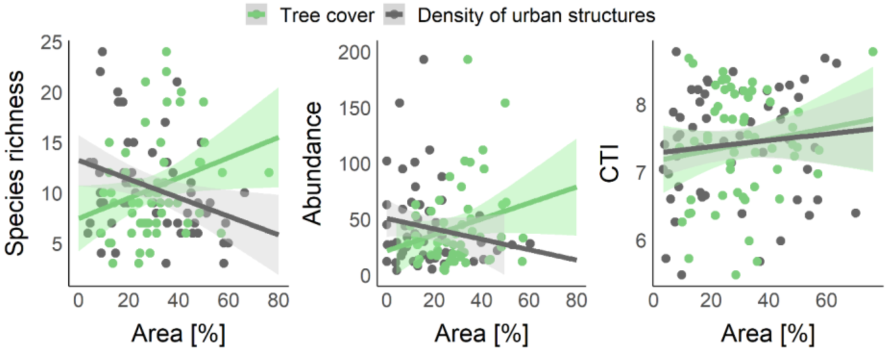

Figure 16. Effects of tree cover and density of urban structures on species richness, abundance, and CTI. Dots represent species richness, abundance and CTI per box. Effects of tree cover on species richness, abundance and CTI are based on a 500 m buffer. The effect of density of urban structures on species richness is based on a 1000 m buffer, on abundance on a 100 m buffer, and on CTI on a 500 m buffer.

Besides microclimate, I found the density of urban structures and tree cover to act as environmental filters. Species richness and abundance of saproxylic beetles increased significantly with tree cover in the 500 m buffer (Fig. 16), while species richness decreased significantly with the density of urban structures both in the 1000 m and 100 m buffer (Fig. 16). However, as tree cover and density of urban structures are tightly correlated, it is not possible to disentangle their effects on beetle diversity. Nevertheless, the positive effect of tree cover indicates to some extent that increasing habitat amount promotes saproxylic beetle diversity. These findings are consistent with Fattorini and Galassi (2016), who reported increasing diversity of saproxylic beetles with urban forest area, and Marker (2019), who observed higher species richness of saproxylic beetles in proximity to urban forests. The negative effect of density of urban structures is likely driven by both the strong negative correlation between density of urban structures and tree cover, and by greater habitat isolation, as urban structures can act as dispersal barriers (Corcos et al., 2019; Leidner and Haddad, 2011). However, to better understand these dynamics, future studies should aim to disentangle the effects of habitat amount and dispersal barriers on different insect groups, including saproxylic species. This would require study designs where these variables are not correlated, as well as the use of more precise proxies for measuring dispersal barriers.

I found that 33 % of the saproxylic beetle species in the sampled wood mould boxes were associated with hollow trees. A previous study, where pitfall traps were placed in cavities of oaks in the same part of Sweden, found a similar proportion (37 %) of saproxylic beetles associated with hollow trees (Ranius and Jansson 2002). This indicates that the studied boxes are indeed harboring a fauna similar to that found in tree hollows. Due to safety and aesthetic reasons, large old trees are often removed in urban environments (Carpaneto et al., 2010), and trees need a long time to develop until hollows are formed (Ranius et al., 2009). Therefore, boxes with wood mould may serve as artificial microhabitats for saproxylic insects at least during a few years after the establishment.

5. Conclusion and management recommendation

This thesis provides valuable insights into less commonly referenced ecological concepts, including the hydroclimatic compensation model and the stress gradient hypothesis. At the same time, I was able to support several well-established theories, such as the latitudinal diversity gradient and the urban heat island effect. Ultimately, my findings not only enhance our understanding of biodiversity patterns per se, but also provide a foundation for developing more targeted and effective management recommendations for wood-inhabiting organisms. Given the focus on species inhabiting dead wood, the following recommendations center on forest and urban forest management that promotes their conservation, while also helping to mitigate pest outbreaks, such as those caused by the European spruce bark beetle.

Dead wood volume has declined significantly due to forestry practices. The current amount of dead wood in managed forests represents only 10–20 % of that found in natural forests (Seibold and Thorn, 2018). Therefore, it is widely recognized that dead wood creation is an important tool for the natural restoration of managed boreal forests. Although dead wood creation promotes the diversity of saproxylic species in boreal managed forests, large amounts of recently dead trees raise concerns about the increased risk of bark beetle outbreaks in surrounding managed forests. Based on my research, it is essential to address this apparent trade-off by incorporating a microclimatic perspective.

In my study, I found a higher species richness of beetles and brown-rot fungi in sun-exposed dead wood, particularly in colder regions (**Papers I** and **II**). These sun-exposed microhabitats – functioning as warmer microrefugia – appear to provide favorable thermal conditions that compensate for the otherwise harsh climate in the north. As such, they may play a critical role in supporting the persistence of saproxylic species at higher latitudes, where suitable habitats are often limited by climatic constraints.

From a conservation perspective, this underscores the importance of maintaining and promoting small-scale, sun-exposed microhabitats within forest landscapes. Carefully targeted management practices, such as preserving or creating small canopy openings, retaining sun-exposed dead wood, and ensuring a continuous, natural input of deadwood, can significantly enhance habitat quality for communities living in dead wood without compromising overall forest integrity. Furthermore, it is especially important to provide a diverse array of dead wood types, including standing dead trees (snags), stumps, coarse, and fine woody debris, as well as a range of decay stages. This structural and compositional variety supports a broad spectrum of saproxylic species, each with different ecological requirements and degrees of specialization (Stokland et al., 2012; Uhl et al., 2022).

Simultaneously, these management practices may contribute to broader forest health. For example, ensuring that dead wood is well-distributed may help limit the risk of pest outbreaks, such as those caused by the European spruce bark beetle (*I. typographus*), which colonizes freshly dead logs (Eriksson et al., 2007). Thus, biodiversity conservation and disturbance regulation can be mutually reinforced through deadwood management strategies tailored to local climatic conditions.

In **Paper I**, I found a significant discrepancy in the CTI of saproxylic beetle communities between different shading conditions, particularly in colder regions. This suggests that species with specific thermal preferences are more likely to occur in dead wood that matches their preferred microclimatic conditions. Specifically, a lower CTI in shaded dead wood indicates a dominance of cold-adapted saproxylic beetle species. Therefore, to support cold-adapted beetle species, it is essential to maintain forests with a dense canopy, which generates cooler microclimatic conditions. As mentioned before, providing a diversity of dead wood types and decay stages is important to meet different habitat requirements. A study by Lindman et al. (2023) showed that *I. typographus* prefers sun-exposed dead wood especially in colder regions. Thus, in northern forests, dead wood creation in dense forests is unlikely to increase the risk of bark beetle outbreaks.

Based on my results from **Paper IV**, it is possible to favor saproxylic beetles in cities by maintaining and increasing landscape-level tree cover. Specifically, as large old trees have become increasingly scarce, there is a need for restoring microhabitats to favor saproxylic insects, which depend on hollow trees. With my study, I also showed that the microclimatic conditions inside artificial wood mould boxes are similar to those inside hollow trees and that these boxes can harbor many saproxylic beetle species that are usually found inside hollow trees. Thus, wood mould boxes serve, at least partly, as an artificial substitute for tree hollows.

Finally, these results can be interpreted in the context of climate change. As climate is warming, species may shift their distribution northwards (Zellweger et al., 2020), potentially suppressing cold-adapted species. Since I found cold-adapted saproxylic beetle species to be less abundant in sun-exposed dead wood in the north, climate change makes it increasingly important to maintain forests with a dense canopy especially in colder regions to support cold-adapted species. Furthermore, I found that the whole shade gradient in warmer regions may serve as suitable habitat for saproxylic beetles and wood-inhabiting microbes. However, with a warming climate, thermophilous species from southern and central Europe might colonize southern Sweden, potentially suppressing the native species diversity in dead wood. This highlights the importance of maintaining forests with a dense canopy also in warmer regions. In line with the literature, I found higher decomposition rates in warmer climates. Furthermore, nitrogen-fixing bacterial richness and relative abundance increased with regional temperature. As a result, warming climate may lead to increased nitrogen availability in northern forests, which could promote wood decaying fungal species, probably modulating dead wood decomposition. Together with changes in forest growth and tree mortality, this may have far-reaching consequences for carbon storage in northern forest ecosystems. Finally, the combined effects of urban heat island and climate warming may lead to too warm and dry conditions for biodiversity in urban areas. Thus, it is of high importance to create and maintain urban forests, which can buffer elevated temperatures.

In conclusion, my thesis provides detailed insights into biodiversity in dead wood and its patterns along macro- and microclimatic gradients. Nonetheless, there is still much to explore about *life in the dead*.

6. Future perspective

In **Paper I**, I studied saproxylic beetle communities in spruce dead wood along macro- and microclimatic gradients. However, this study did not cover the entire distribution range of the species – specifically, the true southern range margin was missing for almost all species. Thus, to fully understand the extent to which the diversity of cold-adapted species is structured along microclimatic gradients at their actual southern range margin, it is necessary to study a broader regional climatic gradient. In other words, the distribution of cold-adapted saproxylic beetle species could be studied along shade gradients in southern or central Europe to determine whether these species depend more on fully shaded conditions at their southern range margin. Additionally, it may be valuable to explore how these patterns change over time – for instance, how interannual climatic variation affects these patterns, or how species' responses shift during forest regeneration after logging.

Paper II examined the diversity of wood-inhabiting fungi, particularly brown- and white-rot fungi, along macro- and microclimatic gradients, and the influence of dispersal vectors such as saproxylic beetles. However, it remains unclear to what extent bacteria are dispersed by saproxylic beetles. This is particularly important, as wood-inhabiting bacteria play a significant role in the decomposition process. Studying their dispersal could therefore enhance our understanding of ecosystem functioning. Furthermore, this paper examined the hydroclimatic compensation model on wood-inhabiting fungi based on their richness. As in **Paper I**, calculating the Species Temperature Index also for fungal species could help to assess the extent to which thermophilous species dominate in sun-exposed dead wood in colder regions, and cold-adapted species in shaded dead wood in warmer regions. Since many fungal species, particularly those that cannot be visually detected, are still poorly studied, this approach is less feasible for the entire wood-inhabiting fungal community. Thus, an alternative might be to focus on the most common and visually detectable fungal species, whose distribution ranges are better understood.

A major component of **Paper III** focused on the diversity of wood-inhabiting bacteria. Compared to wood-inhabiting fungi or soil bacteria, bacterial communities in dead wood remain poorly studied. For example, it is still unclear which bacterial functional groups, beyond nitrogen-fixing bacteria, contribute to decomposition and how they respond to environmental variables. One way to address this knowledge gap would be to cultivate specific bacterial functional groups and experimentally assess their contribution to wood decomposition.

Finally, I studied in **Paper IV** the effects of environmental filters on the diversity of saproxylic beetles in urban landscapes. As habitat amount and dispersal barriers were highly correlated, I could not determine which variable plays a more important role for the saproxylic beetle diversity. In future research, it is therefore essential to disentangle their effects, which can be achieved by designing the study so that these two variables are uncorrelated and by using more precise proxies for dispersal barriers. Furthermore, to more precisely evaluate the extent to which wood mould boxes can serve as artificial substitutes for hollow trees in urban areas, the diversity of saproxylic beetles in both hollow trees and wood mould boxes within urban landscapes should be assessed and compared.

By addressing these questions, conservation efforts for saproxylic organisms can be optimized in both urban and forest landscapes, while also improving our understanding of the underlying mechanisms driving key ecosystem functions, such as the decomposition process.

References

Ackerly, D., Kling, M., Clark, M., Papper, P., Oldfather, M., Flint, A., Flint, L. 2020. Topoclimates, refugia, and biotic responses to climate change. *Frontiers in Ecology and the Environment*, 18(5), 288-297. https://doi.org/10.1002/fee.2204

Adams, A., Besozzi, E., Shahrokhi, G., Patten, M. 2022. A case for associational resistance: Apparent support for the stress gradient hypothesis varies with study system. *Ecology Letters*, 25(1), 202-217. https://doi.org/10.1111/ele.13917

Andersson, H. 1999. Rödlistade eller sällsynta evertebrater knutna till ihåliga, murkna eller savande träd samt trädsvampar i Lunds stad. [Red-listed or rare invertebrates associated with hollow, rotting, or sapping trees or polypores in the town of Lund. In Swedish with an English abstract]. *Entomologisk Tidskrift*, 120(4), 169-183.

Alexander, K. 2008. Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. *Revue d'écologie*, 9-13.

Ashcroft, M., Gollan, J., Warton, D., Ramp, D. 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18(6), 1866-1879. https://doi.org/10.1111/j.1365-2486.2012.02661.x

Bässler, C., Müller, J., Dziock, F., Brandl, R. 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. *Journal of Ecology*, 98(4), 822–832. https://doi.org/10.1111/j.1365-2745.2010.01669.x

Bahram, M., Hildebrand, F., Forslund, S. K., Anderson, J. L., Soudzilovskaia, N. A., Bodegom, P. M., ... & Bork, P. 2018. Structure and function of the global topsoil microbiome. *Nature*, 560(7717), 233-237. https://doi.org/10.1038/s41586-018-0386-6

Barley, J. M., Cheng, B. S., Sasaki, M., Gignoux-Wolfsohn, S., Hays, C. G., Putnam, A. B., ..., Kelly, M. 2021. Limited plasticity in thermally tolerant ectotherm populations: evidence for a trade-off. *Proceedings of the Royal Society B*, 288(1958), 20210765. https://doi.org/10.1098/rspb.2021.0765

Barnagaud, J. Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Viol, I., Archaux, F. 2012. Relating habitat and climatic niches in birds. *PLoS One*, 7(3), e32819. https://doi.org/10.1371/journal.pone.0032819

Barton, K. 2009. MuMIn : multi-model inference. Httpr-Forg.-Proj.

Beninde, J., Veith, M., Hochkirch, A. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters,* 18(6), 581-592. https://doi.org/10.1111/ele.12427

Bennett, S., Duarte, C. M., Marbà, N., Wernberg, T. 2019. Integrating within-species variation in thermal physiology into climate change ecology. *Philosophical Transactions of the Royal Society B,* 374(1778), 20180550. https://doi.org/10.1098/rstb.2018.0550

Berg, B., Berg, M. P., Bottner, P., Box, E., Breymeyer, A., De Anta, R. C., ..., de Santo, A. V. 1993. Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry,* 20(3), 127-159. https://doi.org/10.1007/BF00000785

Bernardino, G. V. D. S., Mesquita, V. P., Bobrowiec, P. E. D., Iannuzzi, L., Salomão, R. P., Cornelius, C. 2024. Habitat loss reduces abundance and body size of forest-dwelling dung beetles in an Amazonian urban landscape. *Urban Ecosystems,* 27(4), 1175-1190. https://doi.org/10.1007/s11252-024-01520-6

Bertness, M. and Callaway, R. 1994. Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191-193.

Birkemoe, T., Jacobsen, R. M., Sverdrup-Thygeson, A., Biedermann, P. H. 2018. Insect-fungus interactions in dead wood systems. In Saproxylic insects: diversity, ecology and conservation (pp. 377-427). *Cham: Springer International Publishing*. https://doi.org/10.1007/978-3-319-75937-1_12

Boddy, L. 1993. Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. *Mycological research*, 97(6), 641-655.

Boer, W. D., Folman, L. B., Summerbell, R. C., Boddy, L. 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews*, 29(4), 795-811. https://doi.org/10.1016/j.femsre.2004.11.005

Brabcová, V., Tláskal, V., Lepinay, C., Zrůstová, P., Eichlerová, I., Štursová, M., ..., Baldrian, P. 2022. Fungal community development in decomposing fine deadwood is largely affected by microclimate. *Frontiers in Microbiology,* 13, 835274. https://doi.org/10.3389/fmicb.2022.835274

Bradford, M. A., Warren Ii, R. J., Baldrian, P., Crowther, T. W., Maynard, D. S., Oldfield, E. E., ..., King, J. R. 2014. Climate fails to predict wood decomposition at regional scales. *Nature Climate Change*, 4(7), 625-630. https://doi.org/10.1038/nclimate2251

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ..., Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., West, G. B. 2004. Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771-1789. https://doi.org/10.1890/03-9000

Buckley, L. B., Davies, T. J., Ackerly, D. D., Kraft, N. J., Harrison, S. P., Anacker, B. L., ..., Wiens, J. J. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 277(1691), 2131-2138. https://doi.org/10.1098/rspb.2010.0179

Cadotte, M. W., Carscadden, K., Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079-1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ..., Naeem, S. 2012. Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59-67. https://doi.org/10.1038/nature11148

Carpaneto, G. M., Mazziotta, A., Coletti, G., Luiselli, L., Audisio, P. 2010. Conflict between insect conservation and public safety: the case study of a saproxylic beetle (Osmoderma eremita) in urban parks. *Journal of Insect Conservation*, 14(5), 555-565. https://doi.org/10.1007/s10841-010-9283-5

Chamberlain, S., Barve, V., Mcglinn, D. 2023. Package rgbif: interface to the global biodiversity information facility API. *R package version 3.7. 2.*

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., ..., Franklin, J. F. 1999. Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, 49(4), 288-297. https://doi.org/10.2307/1313612

Christiansen, D. M., Iversen, L. L., Ehrlén, J., Hylander, K. 2022. Changes in forest structure drive temperature preferences of boreal understorey plant communities. *Journal of Ecology*, 110(3), 631-643. https://doi.org/10.1111/1365-2745.13825

Corcos, D., Cerretti, P., Caruso, V., Mei, M., Falco, M., Marini, L. 2019. Impact of urbanization on predator and parasitoid insects at multiple spatial scales. *PloS One*, 14(4), e0214068. https://doi.org/10.1371/journal.pone.0214068

Currie, W. S., Harmon, M. E., Burke, I. C., Hart, S. C., Parton, W. J., Silver, W. 2010. Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. *Global Change Biology*, 16(6), 1744-1761. https://doi.org/10.1111/j.1365-2486.2009.02086.x

Dániel-Ferreira, J., Berggren, Å., Wissman, J., Öckinger, E. 2022. Road verges are corridors and roads barriers for the movement of flower-visiting insects. *Ecography,* 2022(2). https://doi.org/10.1111/ecog.05847

Davidson, E. A., and Janssens, I. A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165-173. https://doi.org/10.1038/nature04514

Davies, Z. G., Wilson, R. J., Coles, S., Thomas, C. D. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, 75(1), 247-256. https://doi.org/10.1111/j.1365-2656.2006.01044.x

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., ..., Verheyen, K. 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, 110(46), 18561-18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ..., Lenoir, J. 2019. Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744-749. https://doi.org/10.1038/s41559-019-0842-1

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., ..., Hylander, K. 2021. Forest microclimates and climate change:

Importance, drivers and future research agenda. *Global Change Biology*, 27(11), 2279-2297. https://doi.org/10.1111/gcb.15569

Devictor, V., Julliard, R., Couvet, D., Jiguet, F. 2008. Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, 275(1652), 2743-2748. https://doi.org/10.1098/rspb.2008.0878

Edgar, R. 2016. UCHIME2: improved chimera prediction for amplicon sequencing. *BioRxiv*, 074252. https://doi.org/10.1101/074252

Ekström, A. 2020. The importance of ecoparks for saproxylic beetles. *Swedish University of Agricultural Sciences, Umeå.*

Englmeier, J., Rieker, D., Mitesser, O., Benjamin, C., Fricke, U., Ganuza, C., ..., Bässler, C. 2023. Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria. *Ecography*, 2023(11), e06807. https://doi.org/10.1111/ecog.06807

Eriksson, M., Neuvonen, S., Roininen, H. 2007. Retention of wind-felled trees and the risk of consequential tree mortality by the European spruce bark beetle Ips typographus in Finland. *Scandinavian Journal of Forest Research*, 22(6), 516-523. https://doi.org/10.1080/02827580701800466

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., ..., Feeley, K. J. 2018. Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, 564(7735), 207-212. https://doi.org/10.1038/s41586-018-0715-9

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40(9), 1649-1663. https://doi.org/10.1111/jbi.12130

Fattorini, S., and Galassi, D. M. 2016. Role of urban green spaces for saproxylic beetle conservation: a case study of tenebrionids in Rome, Italy. *Journal of Insect Conservation,* 20(4), 737-745. https://doi.org/10.1007/s10841-016-9900-z

Fick, S. E., and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302-4315. https://doi.org/10.1002/joc.5086

Fourcade, Y., Ranius, T., Öckinger, E. 2017. Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. *Journal of Animal Ecology*, 86(6), 1339-1351. https://doi.org/10.1111/1365-2656.12740

Fourcade, Y., Åström, S., Öckinger, E. 2019. Climate and land-cover change alter bumblebee species richness and community composition in subalpine areas. *Biodiversity and Conservation*, 28(3), 639-653. https://doi.org/10.1007/s10531-018-1680-1

Fourcade, Y., WallisDeVries, M. F., Kuussaari, M., van Swaay, C. A., Heliölä, J., Öckinger, E. 2021. Habitat amount and distribution modify community dynamics under climate change. *Ecology Letters*, 24(5), 950-957. https://doi.org/10.1111/ele.13691

Franzén, M., Betzholtz, P. E., Pettersson, L. B., Forsman, A. 2020. Urban moth communities suggest that life in the city favours thermophilic multi-dimensional generalists. *Proceedings of the Royal Society B*, 287(1928), 20193014. https://doi.org/10.1098/rspb.2019.3014

Franzén, M., Jansson, N., Avci, M., Brin, A., Brustel, H., Budka, J., ..., Milberg, P. 2025. Taxonomic and Trophic Groups Mediate Latitudinal Variation in Saproxylic Beetle Species Richness and Body Size Across Western Palaearctic Oak Forests. *Ecology and Evolution*, 15(6), e71574. https://doi.org/10.1002/ece3.71574

Frazer, G. 1999. Gap light analyzer (GLA). Users Man. Program Doc. Version 20 36.

Fröhlich, A., and Ciach, M. 2020. Dead wood resources vary across different types of urban green spaces and depend on property prices. *Landscape and Urban Planning*, 197, 103747. https://doi.org/10.1016/j.landurbplan.2020.103747

Fu, L., Niu, B., Zhu, Z., Wu, S., Li, W. 2012. CD-HIT: accelerated for clustering the next-generation sequencing data. *Bioinformatics*, 28(23), 3150-3152. https://doi.org/10.1093/bioinformatics/bts565

Fukami, T., Dickie, I. A., Paula Wilkie, J., Paulus, B. C., Park, D., Roberts, A., ..., Allen, R. B. 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecology Letters*, 13(6), 675-684. https://doi.org/10.1111/j.1461-0248.2010.01465.x

Fukasawa, Y. 2021. Ecological impacts of fungal wood decay types: A review of current knowledge and future research directions. *Ecological Research*, 36(6), 910-931. https://doi.org/10.1111/1440-1703.12260

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349(6250), 819-822. 10.1126/science.aaa9092

Gilbertson, R. L. 1980. Wood-rotting fungi of North America. *Mycologia*, 72(1), 1-49. https://doi.org/10.1080/00275514.1980.12021153

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., Charnov, E. L. 2001. Effects of size and temperature on metabolic rate. *Science*, 293(5538), 2248-2251. 10.1126/science.1061967

Girona, M. M., Morin, H., Gauthier, S., Bergeron, Y. 2023. Boreal forests in the face of climate change: sustainable management (p. 837). *Springer Nature*. 10.1007/978-3-031-15988-6

Glassman, S. I., Weihe, C., Li, J., Albright, M. B., Looby, C. I., Martiny, A. C., ..., Martiny, J. B. 2018. Decomposition responses to climate depend on microbial community composition. *Proceedings of the National Academy of Sciences*, 115(47), 11994-11999. https://doi.org/10.1073/pnas.1811269115

Greaves, H. 1971. The bacterial factor in wood decay. *Wood Science and Technology*, 5(1), 6-16. https://doi.org/10.1007/BF00363116

Greiser, C., Ehrlén, J., Meineri, E., Hylander, K. 2020. Hiding from the climate: Characterizing microrefugia for boreal forest understory species. *Global Change Biology*, 26(2), 471-483. https://doi.org/10.1111/gcb.14874

Grilo, F., Pinho, P., Aleixo, C., Catita, C., Silva, P., Lopes, N., ..., Branquinho, C. 2020. Using green to cool the grey: Modelling the cooling effect of green spaces with a high spatial resolution. *Science of the Total Environment*, 724, 138182. https://doi.org/10.1016/j.scitotenv.2020.138182

Hägglund, R., and Hjältén, J. 2018. Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides. *Forest Ecology and Management*, 425, 45-58.

Hagge, J., Müller, J., Bässler, C., Brandl, R., Schuldt, A., Thorn, S., Seibold, S. 2024. Change in saproxylic beetle, fungi and bacteria assemblages along horizontal and vertical gradients of sun-exposure in forest. *Biological Conservation*, 291, 110493. https://doi.org/10.1016/j.biocon.2024.110493

Hawkins, B. A., Porter, E. E., Felizola Diniz-Filho, J. A. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, 84(6), 1608-1623. https://doi.org/10.1890/00129658(2003)084[1608:PAHAPO]2.0.CO;2

Herlemann, D. P., Labrenz, M., Jürgens, K., Bertilsson, S., Waniek, J. J., Andersson, A. F. 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME Journal*, 5(10), 1571-1579. https://doi.org/10.1038/ismej.2011.41

Highley, T. L., and Kirk, T. K. 1979. Mechanisms of wood decay and the unique features of heartrots. 10.1094/Phyto-69-1151

Hijmans, R. J., Barbosa, M., Ghosh, A., Mandel, A., Hijmans, M. R. J. 2024. Package ‘geodata’. CRAN https://doi. org/10.32614/cran.

Hiscox, J., Savoury, M., Vaughan, I. P., Müller, C. T., Boddy, L. 2015. Antagonistic fungal interactions influence carbon dioxide evolution from decomposing wood. *Fungal Ecology*, 14, 24-32. https://doi.org/10.1016/j.funeco.2014.11.001

Hoppe, B., Kahl, T., Karasch, P., Wubet, T., Bauhus, J., Buscot, F., Krüger, D. 2014. Network analysis reveals ecological links between N-fixing bacteria and wood-decaying fungi. *PLoS One*, 9(2), e88141. https://doi.org/10.1371/journal.pone.0088141

Horák, J. 2018. The role of urban environments for saproxylic insects. In Saproxylic insects: Diversity, ecology and conservation (pp. 835-846). *Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-75937-1_24*

Hylander, K., Ehrlén, J., Luoto, M., Meineri, E. (2015). Microrefugia: Not for everyone. *Ambio*, 44(1), 60-68. https://doi.org/10.1007/s13280-014-0599-3

Ihrmark, K., Bödeker, I. T., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., ..., Lindahl, B. D. 2012. New primers to amplify the fungal ITS2 region–evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology*, 82(3), 666-677. https://doi.org/10.1111/j.1574-6941.2012.01437.x

Jacobsen, R. M., Kauserud, H., Sverdrup-Thygeson, A., Bjorbækmo, M. M., Birkemoe, T. 2017. Wood-inhabiting insects can function as targeted vectors for decomposer fungi. *Fungal Ecology*, 29, 76-84. https://doi.org/10.1016/j.funeco.2017.06.006

Jansson, N., Ranius, T., Larsson, A., Milberg, P. 2009. Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodiversity and*

Conservation, 18(14), 3891-3908. https://doi.org/10.1007/s10531-009-9687-2

Johansson, V., Koffman, A., Hedblom, M., Deboni, G., Andersson, P. 2018. Estimates of accessible food resources for pollinators in urban landscapes should take landscape friction into account. *Ecosphere*, 9(10), e02486. https://doi.org/10.1002/ecs2.2486

Johansson, V., Kindvall, O., Askling, J., Franzén, M. 2020. Extreme weather affects colonization–extinction dynamics and the persistence of a threatened butterfly. *Journal of Applied Ecology*, 57(6), 1068-1077. https://doi.org/10.1111/1365-2664.13611

Johnston, S. R., Boddy, L., Weightman, A. J. 2016. Bacteria in decomposing wood and their interactions with wood-decay fungi. *FEMS Microbiology Ecology*, 92(11), fiw179. https://doi.org/10.1093/femsec/fiw179

Kłysik, K., and Fortuniak, K. 1999. Temporal and spatial characteristics of the urban heat island of Łódź, Poland. *Atmospheric Environment*, 33(24-25), 3885-3895. https://doi.org/10.1016/S1352-2310(99)00131-4

Krah, F. S., Hess, J., Hennicke, F., Kar, R., Bässler, C. 2021. Transcriptional response of mushrooms to artificial sun exposure. *Ecology and Evolution*, 11(15), 10538-10546. https://doi.org/10.1002/ece3.7862

Kriegel, P., Vogel, S., Angeleri, R., Baldrian, P., Borken, W., Bouget, C., ..., Thorn, S. 2023. Ambient and substrate energy influence decomposer diversity differentially across trophic levels. *Ecology Letters*, 26(7), 1157-1173.

Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M., ..., Angert, A. L. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, 19(6), 710-722. https://doi.org/10.1111/ele.12604

Leidner, A. K., and Haddad, N. M. 2011. Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conservation Biology*, 25(5), 1022-1031. https://doi.org/10.1111/j.1523-1739.2011.01720.x

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J., Hagge, J. 2022. Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. *Oecologia*, 198(3), 825-834. https://doi.org/10.1007/s00442-022-05141-8

Li, P., Tedersoo, L., Crowther, T. W., Wang, B., Shi, Y., Kuang, L., ..., Jiang, J. 2023. Global diversity and biogeography of potential phytopathogenic fungi in a changing world. *Nature Communications*, 14(1), 6482. https://doi.org/10.1038/s41467-023-42142-4

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F. 2012. Global decline in large old trees. *Science,* 338(6112), 1305-1306. 10.1126/science.1231070

Lindhe, A., Åsenblad, N., Toresson, H. G. 2004. Cut logs and high stumps of spruce, birch, aspen and oak–nine years of saproxylic fungi succession. *Biological Conservation*, 119(4), 443-454. https://doi.org/10.1016/j.biocon.2004.01.005

Lindman, L., Öckinger, E., Ranius, T. 2022. Microclimatic conditions mediate the effect of deadwood and forest characteristics on a threatened beetle species, Tragosoma depsarium. *Oecologia*, 199(3), 737-752. https://doi.org/10.1007/s00442-022-05212-w

Lindman, L., Ranius, T., Schroeder, M. 2023. Regional climate affects habitat preferences and thermal sums required for development of the Eurasian spruce bark beetle, Ips typographus. *Forest Ecology and Management*, 544, 121216. https://doi.org/10.1016/j.foreco.2023.121216

Louca, S., Parfrey, L. W., Doebeli, M. 2016. Decoupling function and taxonomy in the global ocean microbiome. *Science*, 353(6305), 1272-1277. 10.1126/science.aaf4507

Lundberg, S., and B. Gustafsson. 1995. Catalogus Coleopterorum Sueciae. *Naturhistoriska riksmuseet.*

Lustenhouwer, N., Maynard, D. S., Bradford, M. A., Lindner, D. L., Oberle, B., Zanne, A. E., Crowther, T. W. 2020. A trait-based understanding of wood decomposition by fungi. *Proceedings of the National Academy of Sciences,* 117(21), 11551-11558. https://doi.org/10.1073/pnas.1909166117

Marker, J. 2019. Effect of distance to urban areas on saproxylic beetles in urban forests (Master Thesis). *Karlstad University.*

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, 11(2), 161-176. https://doi.org/10.1007/s11252-007-0045-4

Meeussen, C., Govaert, S., Vanneste, T., Calders, K., Bollmann, K., Brunet, J., ..., De Frenne, P. 2020. Structural variation of forest edges across Europe. *Forest Ecology and Management*, 462, 117929. https://doi.org/10.1016/j.foreco.2020.117929

Menke, S. B., Guénard, B., Sexton, J. O., Weiser, M. D., Dunn, R. R., Silverman, J. 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystems*, 14(2), 135-163. https://doi.org/10.1007/s11252-010-0150-7

Meyer, S., Rusterholz, H. P., Baur, B. 2021. Saproxylic insects and fungi in deciduous forests along a rural–urban gradient. *Ecology and Evolution*, 11(4), 1634-1652. https://doi.org/10.1002/ece3.7152

Mikryukov, V., Dulya, O., Zizka, A., Bahram, M., Hagh-Doust, N., Anslan, S., ..., Tedersoo, L. 2023. Connecting the multiple dimensions of global soil fungal diversity. *Science Advances*, 9(48), eadj8016. 10.1126/sciadv.adj8016

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., ..., Gossner, M. M. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography*, 38(5), 499-509. https://doi.org/10.1111/ecog.00908

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., ..., Thorn, S. 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos*, 129(10), 1579-1588. https://doi.org/10.1111/oik.07335

Nationella Marktäckedata (NMD) [WWW Document], 2023. URL https://www.naturvardsverket.se/verktyg-och-tjanster/kartor-och-karttjanster/nationella-marktackedata/ (accessed 6.30.23).

Nieto, A., and Alexander, K. 2010. European red list of saproxylic beetles. *Cuardernos de Biodiversidad* 33, 3-10. http://dx.doi.org/10.14198/cdbio.2010.33.01

Niskanen, T., Lücking, R., Dahlberg, A., Gaya, E., Suz, L. M., Mikryukov, V., ..., Antonelli, A. 2023. Pushing the frontiers of biodiversity research: Unveiling the global diversity, distribution, and conservation of fungi. *Annual Review of Environment and Resources*, 48(1), 149-176. https://doi.org/10.1146/annurev-environ-112621-090937

Norros, V., Karhu, E., Nordén, J., Vähätalo, A. V., Ovaskainen, O. 2015. Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecology and Evolution*, 5(16), 3312-3326. https://doi.org/10.1002/ece3.1589

Özkurt, E., Fritscher, J., Soranzo, N., Ng, D. Y., Davey, R. P., Bahram, M., Hildebrand, F. 2022. LotuS2: an ultrafast and highly accurate tool for amplicon sequencing analysis. *Microbiome*, 10(1), 176. https://doi.org/10.1186/s40168-022-01365-1

Oke, T. R. 1995. The heat island of the urban boundary layer: characteristics, causes and effects. In Wind climate in cities (pp. 81-107). *Dordrecht: Springer Netherlands*. https://doi.org/10.1007/978-94-017-3686-2_5

Oksanen, J. 2015. Vegan: community ecology package. *R package version, 2, 3*.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., ..., Hayes, D. 2011. A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988-993. 10.1126/science.1201609

Patacca, M., Lindner, M., Lucas-Borja, M. E., Cordonnier, T., Fidej, G., Gardiner, B.,…, Schelhaas, M. J. 2023. Significant increase in natural disturbance impacts on European forests since 1950. *Global Change Biology*, 29(5), 1359-1376. https://doi.org/10.1111/gcb.16531

Pateman, R. M., Thomas, C. D., Hayward, S. A., Hill, J. K. 2016. Macro-and microclimatic interactions can drive variation in species' habitat associations. *Global Change Biology*, 22(2), 556-566. https://doi.org/10.1111/gcb.13056

Perreault, L., Forrester, J. A., Lindner, D. L., Jusino, M. A., Fraver, S., Banik, M. T., Mladenoff, D. J. 2023. Linking wood-decay fungal communities to decay rates: Using a long-term experimental manipulation of deadwood and canopy gaps. *Fungal Ecology*, 62, 101220. https://doi.org/10.1016/j.funeco.2022.101220

Peuhu, E., Thomssen, P. M., Siitonen, J. 2019. Comparison of three trap types in sampling saproxylic beetles living in hollow urban trees. *Journal of Insect Conservation*, 23(1), 75-87. https://doi.org/10.1007/s10841-018-0115-3

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, 100(910), 33-46. https://doi.org/10.1086/282398

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., ... & Hendrickx, F. 2017. Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales.

Global Change Biology, 23(7), 2554-2564. https://doi.org/10.1111/gcb.13606

Pinheiro, J. 2011. nlme: Linear and nonlinear mixed effects models. *R package version, 3, 1.*

Põlme, S., Abarenkov, K., Henrik Nilsson, R., Lindahl, B. D., Clemmensen, K. E., Kauserud, H., ..., Tedersoo, L. 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, 105(1), 1-16. https://doi.org/10.1007/s13225-020-00466-2

R Core Team. 2020. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. http://www.R-project.org/.

Ranius, T., and Jansson, N. 2002. A comparison of three methods to survey saproxylic beetles in hollow oaks. *Biodiversity and Conservation*, 11(10), 1759-1771. https://doi.org/10.1023/A:1020343030085

Ranius, T., Svensson, G. P., Berg, N., Niklasson, M., Larsson, M. C. 2009. The successional change of hollow oaks affects their suitability for an inhabiting beetle, Osmoderma eremita. *Annales Zoologici Fennici*, 46(3), 205-216. https://doi.org/10.5735/086.046.0305

Ranius, T., Gibbons, P., Lindenmayer, D. 2024. Habitat requirements of deadwood-dependent invertebrates that occupy tree hollows. *Biological Reviews*, 99(6), 2022-2034. https://doi.org/10.1111/brv.13110

Rayner, A. D. M., and Boddy, L. 1988. Fungal communities in the decay of wood. In: Advances in microbial ecology, 115-166. *Boston, MA: Springer US.* https://doi.org/10.1007/978-1-4684-5409-3_4

Rinta-Kanto, J. M., Sinkko, H., Rajala, T., Al-Soud, W. A., Sørensen, S. J., Tamminen, M. V., Timonen, S. 2016. Natural decay process affects the abundance and community structure of Bacteria and Archaea in Picea abies logs. *FEMS Microbiology Ecology*, 92(7), fiw087. https://doi.org/10.1093/femsec/fiw087

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. *Cambridge Univ. Press.* 10.1017/cbo9780511623387

Runnel, K., Tedersoo, L., Krah, F. S., Piepenbring, M., Scheepens, J. F., Hollert, H., ..., Bässler, C. 2025. Toward harnessing biodiversity–ecosystem function relationships in fungi. *Trends in Ecology and Evolution*, 40(2), 180-190. 10.1016/j.tree.2024.10.004

Russell, M. B., Fraver, S., Aakala, T., Gove, J. H., Woodall, C. W., D'Amato, A. W., Ducey, M. J. 2015. Quantifying carbon stores and decomposition in dead wood: A review. *Forest Ecology and Management*, 350, 107-128. https://doi.org/10.1016/j.foreco.2015.04.033

Schelhaas, M. J., Nabuurs, G. J., Schuck, A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, 9(11), 1620-1633. https://doi.org/10.1046/j.1365-2486.2003.00684.x

Schmidl, J. V., and Bußler, H. 2004. Ökologische gilden xylobionter käfer Deutschlands. *Naturschutz und Landschaftsplanung*, 36(7), 202-218.

Schroeder, M., and Kärvemo, S. 2022. Rekordstort utbrott av granbarkborre–orsaker och vad man kan göra. *Kungliga Skogs-och Lantbruksakademiens Tidskrift*, 7, 16-19.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M. D., ..., Müller, J. 2016a. Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological Conservation*, 204, 181-188. https://doi.org/10.1016/j.biocon.2016.09.031

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., ..., Müller, J. 2016b. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53(3), 934-943. https://doi.org/10.1111/1365-2664.12607

Seibold, S., and Thorn, S. 2018. The importance of dead-wood amount for saproxylic insects and how it interacts with dead-wood diversity and other habitat factors. In Saproxylic insects: Diversity, ecology and conservation (pp. 607-637). *Cham: Springer International Publishing.* https://doi.org/10.1007/978-3-319-75937-1_18

Seibold, S., Müller, J., Baldrian, P., Cadotte, M. W., Štursová, M., Biedermann, P. H., ..., Bässler, C. 2019. Fungi associated with beetles dispersing from dead wood–Let's take the beetle bus!. *Fungal Ecology*, 39, 100-108. https://doi.org/10.1016/j.funeco.2018.11.016

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., ..., Müller, J. 2021. The contribution of insects to global forest deadwood decomposition. *Nature*, 597(7874), 77-81. https://doi.org/10.1038/s41586-021-03740-8

Setälä, H., and McLean, M. A. 2004. Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia*, 139(1), 98-107. https://doi.org/10.1007/s00442-003-1478-y

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 11-41. http://www.jstor.org/stable/20113262.

Six, D. L., and Paine, T. D. 1996. A technique for the introduction of fungi to bark beetle mycangia. *Journal of Entomological Science*, 31(4), 466-468.

SMHI. 2022. Historical data. https://www.smhi.se/data/meteorologi/temperatur. Accessed in March 2022.

SMHI. 2023. Historical data. https://www.smhi.se/data/meteorologi/temperatur. Accessed in March 2023.

Solheim, H. 1993. Fungi associated with the spruce bark beetle Ips typographus in an endemic area in Norway. *Scandinavian Journal of Forest Research*, 8(1-4), 118-122. https://doi.org/10.1080/02827589309382760

Stokland, J. N., Siitonen, J., Jonsson, B. G. 2012. Biodiversity in dead wood. *Cambridge University Press.*

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., ..., Abarenkov, K. 2014. Global diversity and geography of soil fungi. *Science*, 346(6213), 1256688. 10.1126/science.1256688

Teixeira, F. Z., Rytwinski, T., Fahrig, L. 2020. Inference in road ecology research: what we know versus what we think we know. *Biology Letters*, 16(7), 20200140. https://doi.org/10.1098/rsbl.2020.0140

Thomas, C. D., and Jones, T. M. 1993. Partial recovery of a skipper butterfly (Hesperia comma) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology*, 472-481. https://doi.org/10.2307/5196

Thomas, J. A., Rose, R. J., Clarke, R. T., Thomas, C. D., Webb, N. R. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range.

Functional Ecology, 13, 55-64. https://doi.org/10.1046/j.1365-2435.1999.00008.x

Thomas, C. D. 2010. Climate, climate change and range boundaries. *Diversity and Distributions*, 16(3), 488-495. https://doi.org/10.1111/j.1472-4642.2010.00642.x

Thorn, S., Förster, B., Heibl, C., Müller, J., Bässler, C. 2018. Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. *Biodiversity and Conservation*, 27(12), 3119-3135. https://doi.org/10.1007/s10531-018-1592-0

Tiunov, A. V., and Scheu, S. 2005. Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. *Ecology Letters*, 8(6), 618-625. https://doi.org/10.1111/j.1461-0248.2005.00757.x

Uhl, B., Krah, F. S., Baldrian, P., Brandl, R., Hagge, J., Müller, J., ..., Bässler, C. 2022. Snags, logs, stumps, and microclimate as tools optimizing deadwood enrichment for forest biodiversity. *Biological Conservation*, 270, 109569. https://doi.org/10.1016/j.biocon.2022.109569

Vellend, M. 2016. The theory of ecological communities. In The theory of ecological communities. *Princeton University Press*. https://doi.org/10.1515/9781400883790

Větrovský, T., Kohout, P., Kopecký, M., Machac, A., Man, M., Bahnmann, B. D., ..., Baldrian, P. 2019. A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nature communications*, 10(1), 5142. https://doi.org/10.1038/s41467-019-13164-8

Vogel, S., Gossner, M. M., Mergner, U., Müller, J., Thorn, S. 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. Journal of *Applied Ecology*, 57(10), 2075-2085. https://doi.org/10.1111/1365-2664.13648

Walter, H., and Breckle, S. 1985. The law of relative constancy of habitat—ecotypes and ecoclines. *Ecological Systems of the Geobiosphere*, 1, 194-202.

White, T. J., Bruns, T., Lee, S. J. W. T., Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR protocols: a guide to methods and applications, 18(1), 315-322.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. *Oikos*, 496-506. https://doi.org/10.2307/3544109

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., ..., Coomes, D. 2020. Forest microclimate dynamics drive plant responses to warming. *Science*, 368(6492), 772-775. 10.1126/science.aba6880

Popular science summary

Climate plays a key role for the life on Earth. Climate warming and land use change, such as urbanization and changes in agriculture and forestry, can alter the climate on a small spatial scale, known as microclimate. In turn, this can influence the organisms living there. In my research, I have studied the microclimate in urban green spaces and in forests (ranging from clear-cuts to dense forests), and the climate on a big scale (regional climate) along a latitudinal gradient in Sweden. I related these climatic conditions to organisms living in dead wood. These organisms are highly important for keeping forest ecosystems healthy by decomposing dead wood and recycling nutrients back into the ecosystem. However, as the amount of dead wood strongly declined in both managed forests and urban areas over the past decades, it is of high importance to conduct conservation measures that support species living in dead wood.

In my studies, I found more species in dead wood, including beetles and bacteria, in southern compared to northern Sweden. Increased metabolism allows organisms to grow and reproduce faster. This increased biological activity can support more individuals, contributing to a higher species richness in warmer regions. In simple terms: more energy means more diversity of life.

Researchers have discovered that populations of the same species can occur in different habitat types, like sunny or shaded spots, dependent on the regional climate. With this, species keep their preferred climatic conditions. For example, species can inhabit sunny spots in colder regions, but stick to shady spots in warmer regions. In my research, I found that dead wood dependent beetles mostly occurring in warmer regions inhabited sun-exposed dead wood in colder regions. At the same time, beetles mostly occurring in colder regions inhabited shaded dead wood. I also noticed a similar trend in a group of fungi known as brown-rot fungi (functionally important group of fungi that break down dead wood), which occurred more in sun-exposed dead wood in colder regions. Based on these results, I suggest that especially in colder regions, it is important to keep and create a mix of forest habitats – from natural open forest gaps to forests with a dense canopy cover. With this, many species with different climatic preferences are supported.

The fungal richness of brown-rotters was higher in sun-exposed dead wood, and in dead wood with more dead wood dependent beetles. These beetles likely transport fungal spores into dead wood. This might explain why I found brown-rot fungi mostly in sun-exposed dead wood: these fungi are not just well adapted to dry and warm conditions, they also benefit from dispersal by beetles, which also prefer warm conditions.

Dead wood may look lifeless, but it is full of microbial activity. Wood-inhabiting fungi are the main players in decomposition of dead wood, but also bacteria contribute to the decomposition process. Since organisms are generally more active in warmer regions, it is not surprising that I found dead wood decomposing faster in southern compared to northern Sweden. But here is the twist: when too many fungal species were present, I found that the decomposition rates decreased – especially in warmer regions, when the number of nitrogen-fixing bacteria was high. These bacteria provide fungi with nitrogen, which they need to grow. In turn, this might encourage competition among fungi, making them focus more on outcompeting each other than breaking down wood.

Dead wood inhabiting organisms do not only occur in forest landscapes, they can also inhabit urban areas, if green spaces with dead wood and large old trees are accessible. Boxes filled with artificial wood mould can mimic hollow trees and support beetles that are usually found inside tree hollows. In my study, I found more dead wood dependent beetle species in wood mould boxes surrounded by areas with a high proportion of tree habitats, but less in wood mould boxes surrounded by areas with a high proportion of urban structures, such as roads and buildings. In these boxes, I also found many beetle species that are usually found inside hollow trees. Also the temperature I measured inside these wood mould boxes was similar to that I measured inside hollow trees. Therefore, I suggest that wood mould boxes can support dead wood dependent organisms in areas where large old trees are scarce.

Taking the findings from my four studies together, I conclude that organisms living in dead wood are strongly influenced by both the regional climate and microclimate. Especially in colder regions, I found that microclimate plays an important role. Therefore, conservation efforts in the north should take microclimate into account. For example, dead wood creation under different shading conditions – from sun-exposed to dense forest canopies – can support species with different climatic needs. In urban areas, I conclude that rich tree areas are needed to support dead wood living organisms, and wood mould boxes can be used in areas where large old trees are scarce to support species that depend on tree hollows. Still, there is a lot we do not know about *life in the dead*, and future research is needed to fill these gaps.

Populärvetenskaplig sammanfattning

Klimatet spelar en nyckelroll för livet på jorden. Ett varmare klimat och förändrad markanvändning, såsom urbanisering och förändringar i jordbruk och skogsbruk kan förändra klimatet på en liten skala – det vi kallar mikroklimat. Detta kan i sin tur påverka de organismer som lever där. I min forskning har jag studerat mikroklimatet i urbana områden och i skogar (från kalhyggen till täta skogar), samt klimatet i större skala (regionalt klimat) längs en nord-sydlig gradient i Sverige. Jag kopplade dessa klimatvariabler till organismer som lever i död ved. Dessa organismer är mycket viktiga för att hålla skogsekosystemen friska genom att bryta ner död ved och återföra näringsämnen till ekosystemet. Dock, eftersom mängden död ved har minskat kraftigt både i brukade skogar och i urbana områden, är det av stor vikt att genomföra bevarandeåtgärder som stödjer arter som lever i död ved.

I mina studier fann jag fler arter som lever i död ved, inklusive skalbaggar och bakterier, i södra Sverige jämfört med norra. Ökad ämnesomsättning i varmare ekosystem gör att organismer kan växa och föröka sig snabbare. Denna ökade biologiska aktivitet gör att det blir fler individer, vilket bidrar till högre artrikedom i varmare regioner. Enkelt uttryckt: mer energi innebär mer liv.

Arter kan föredra olika livsmiljöer, som soliga eller skuggiga platser, beroende på det regionala klimatet. På så sätt kan de bibehålla sina föredragna klimatförhållanden. Till exempel kan arter leva i soliga platser i kallare områden, men föredra skuggiga platser i varmare områden. I min forskning fann jag att skalbaggar som är beroende av död ved och som huvudsakligen förekommer i varmare regioner, levde i solbelyst död ved i kallare regioner. Samtidigt levde skalbaggar som föredrar kallare klimat i skuggig död ved i kallare regioner. Jag såg också en liknande trend hos en grupp svampar som kallas brunrötesvampar brunrötesvampar (en funktionellt viktig grupp av svampar som bryter ner död ved), som oftare förekom i solbelyst död ved i kallare regioner. Baserat på dessa resultat föreslår jag att det är viktigt att bevara och skapa en variation av skogsmiljöer – från naturliga öppna skogsgläntor till skogar med tät trädkrona – i kallare regioner. På så vis gynnas många arter med olika klimatpreferenser.

Mångfalden av brunrötesvampar var högre i solbelyst död ved och i död ved med fler vedlevande skalbaggar. Dessa skalbaggar transporterar troligen svampsporer in i veden. Detta kan förklara varför jag främst fann brunrötande svampar i solbelyst död ved: dessa svampar är inte bara väl anpassade till torra och varma förhållanden, de gynnas också av spridning via skalbaggar, som i sin tur också föredrar varma miljöer.

Död ved kan verka livlös, men den är full av mikrobiell aktivitet. Vedlevande svampar är de främsta aktörerna i nedbrytningen, men även bakterier bidrar till nedbrytningsprocessen. Eftersom organismer i allmänhet är mer aktiva i varmare regioner, var det inte förvånande att jag fann att död ved bröts ned snabbare i södra Sverige jämfört med norra. Men här kommer det oväntade: när det fanns för många svampar minskade nedbrytningshastigheten – särskilt i varmare regioner, där mängden kvävefixerande bakterier var hög. Dessa bakterier förser svampar med kväve, vilket de behöver för att växa. Detta kan i sin tur leda till ökad konkurrens mellan svampar, så att de fokuserar mer på att konkurrera med varandra än att bryta ner veden.

Organismer som lever i död ved förekommer inte bara i skog. De kan även finnas i städer, om det finns grönområden med död ved och stora gamla träd. Lådor fyllda med artificiell mulm kan efterlikna ihåliga träd och utgöra livsmiljö för skalbaggar som normalt lever i trädens håligheter. I min studie fann jag fler död-veds-beroende skalbaggar i mulmlådor omgivna med en stor andel områden med träd, som parker och urbana skogar, men färre arter i lådor omgivna av en stor andel vägar och byggnader. Jag hittade många skalbaggsarter i dessa lådor som är knutna till ihåliga träd. Temperaturen i mulmlådorna var dessutom lik den jag mätte inne i ihåliga träd. Därför kan mulmlådor bidra till mängden livsmiljö för vedlevande organismer i områden där gamla, stora träd är sällsynta.

Mina fyra studier visar att organismer i död ved påverkas starkt av både det regionala klimatet och mikroklimatet. Särskilt i kallare regioner spelar mikroklimatet en viktig roll för dessa organismer. Därför bör bevarandeåtgärder i norr ta hänsyn till mikroklimat. Exempelvis kan skapandet av död ved under olika ljusförhållanden – från solbelysta platser till täta trädkronor – gynna arter med olika klimatpreferenser. I städer drar jag slutsatsen att trädrika områden är viktiga som livsmiljö för organismer som lever i död ved, och att mulmlådor kan användas i områden där stora gamla träd är sällsynta för att förbättra förutsättningarna arter som är beroende av trädens håligheter. Men det finns fortfarande mycket vi inte vet om *livet i det döda*, och mer forskning behövs för att fylla dessa kunskapsluckor.

Populärwissenschaftliche Zusammenfassung

Das Klima nimmt eine Schlüsselrolle für das Leben auf der Erde ein. Die Erderwärmung und Landnutzungsänderungen, wie etwa Urbanisierung, Landwirtschaft, Aufforstung oder Kahlschläge, können das Klima auf kleiner räumlicher Skala (Mikroklima) verändern. Dies wiederum kann die dort lebenden Organismen beeinflussen. In meiner Forschung untersuchte ich das Mikroklima in städtischen Grünflächen und in Wäldern (von Kahlschlägen bis zu dichten Waldbeständen) sowie das Klima auf großer räumlicher Skala (regionales Klima) entlang eines Breitengrad-Gradienten in Schweden. Diese klimatischen Bedingungen setzte ich anschließend in Beziehung zu Totholzorganismen. Diese Organismen sind wesentlich zur Aufrechterhaltung von Waldökosystemen, da sie Totholz abbauen und Nährstoffe in die Umwelt zurückführen. Jedoch nahm die Menge an Totholz in den letzten Jahrzehnten rapide ab sowohl in Wäldern als auch in Städten, weshalb der Schutz dieser Arten besonders wichtig ist.

In meinen Studien fand ich mehr totholzbewohnende Arten – darunter Käfer und Bakterien – im Süden als im Norden von Schweden. Ein erhöhter Stoffwechsel ermöglicht es Organismen schneller zu wachsen und sich zu vermehren. Diese erhöhte biologische Aktivität kann mehr Arten unterstützen und zu einer höheren Artenvielfalt in wärmeren Regionen führen. Einfach gesagt: mehr Energie bedeutet mehr Leben.

Studien haben gezeigt, dass Arten je nach regionalem Klima unterschiedliche Lebensräume, wie zum Beispiel sonnige oder schattige Habitate besiedeln können, um ihre bevorzugten klimatischen Bedingungen beizubehalten. Beispielsweise können wärmeliebende Arten sonnige Plätze in kälteren Regionen besiedeln, während sie in wärmeren Gegenden oft schattige Bereiche bevorzugen. In meiner Forschung stellte ich fest, dass wärmeliebende Totholzkäfer in kälteren Gebieten vor allem sonnenexponiertes Totholz besiedelten. Gleichzeitig fand ich kälteliebende Arten vor allem in beschattetem Totholz in kälteren Regionen. Ein ähnlicher Trend zeigte sich bei Braunfäulepilzen (eine wichtige funktionelle Gruppe von Pilzen, die Totholz zersetzen), die häufiger in sonnenexponiertem Totholz in kälteren Regionen auftraten. Auf Grund dieser Ergebnisse empfehle ich, besonders in kälteren Regionen eine Mischung aus verschiedenen Waldhabitaten – von natürlichen offenen Lichtungen bis hin zu dichten Baumkronen – zu erhalten und zu kreieren. So können Arten mit unterschiedlichen Klimaansprüchen unterstützt werden.

Braunfäulepilze traten in größerer Artenzahl in sonnenexponiertem Totholz sowie in solchem mit mehr Totholzkäfern auf. Diese Käfer können vermutlich Pilzsporen in das Holz transportieren. Das könnte erklären, warum ich Braunfäulepilze vor allem in sonnenexponiertem Totholz gefunden habe: Diese Pilze sind nicht nur gut an trockene und warme Bedingungen angepasst, sondern profitieren auch von der Ausbreitung durch Käfer, die ebenfalls warme Bedingungen bevorzugen.

Totholz mag leblos erscheinen, ist jedoch voller mikrobieller Aktivität. Pilze sind besonders wichtig für die Zersetzung von Totholz, wobei auch Bakterien zur Zersetzung beitragen. Da Organismen in wärmeren Regionen im Allgemeinen aktiver sind, ist es nicht überraschend, dass ich in Südschweden eine schnellere Totholzzersetzungsrate feststellen konnte als im Norden. Doch hier kommt der überraschende Aspekt: Wenn zu viele Pilzarten vorkamen – insbesondere in wärmeren Regionen und in Kombination mit einer hohen Anzahl stickstofffixierender Bakterien – nahm die Zersetzungsrate ab. Diese Bakterien liefern den Pilzen Stickstoff, den sie für ihr Wachstum benötigen. Das wiederum könnte die Konkurrenz unter den Pilzen verstärken und sich dadurch negativ auf die Zersetzungsrate ausüben.

Totholzorganismen kommen nicht nur in Wäldern vor, sondern auch in Städten – vorausgesetzt, es gibt dort grüne Flächen mit Totholz und alten Bäumen. Künstliche Baumhöhlenkästen (= Kästen mit Holzmulm gefüllt, die Baumhöhlen ähneln) können Käferarten unterstützen, die normalerweise in Baumhöhlen leben. In meiner Studie fand ich mehr Totholzkäfer in Baumhöhlenkästen, die von baumreichen Gebieten wie Parks oder Stadtwäldern umgeben waren als in Kästen in städtisch bebauter Umgebung. Außerdem waren viele dieser Käferarten mit Baumhöhlen assoziiert, und die Mikrotemperatur in den Kästen ähnelte jener in echten Baumhöhlen. Das deutet darauf hin, dass Baumhöhlenkästen insbesondere in Gebieten mit geringerem Altbaumbestand als Naturschutzmaßnahme dienen können.

Basierend auf den Ergebnissen meiner vier Studien sind Totholzorganismen sowohl vom regionalen Klima als auch vom Mikroklima stark beeinflusst. Besonders in kälteren Regionen spielt das Mikroklima eine entscheidende Rolle, sodass die dortigen Naturschutzmaßnahmen das

Mikroklima berücksichtigen sollten. Beispielsweise kann die Schaffung von Totholz in verschiedenen Waldhabitaten – von offenen bis hin zu dichten Waldbeständen – Arten mit verschiedenen klimatischen Anforderungen unterstützen. In Städten sollten baumreiche Flächen erhalten bleiben und gefördert werden. Außerdem könnten Baumhöhlenkästen dort eingesetzt werden, wo alte Bäume fehlen, um Arten zu unterstützen, die auf Baumhöhlen angewiesen sind. Trotzdem gibt es noch viel, was wir über das *Leben im Totholz* nicht wissen, sodass zukünftige Forschung nötig ist, um diese Wissenslücken zu schließen.

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RESEARCH ARTICLE

Diversity and Distributions WILEY

Interaction between regional temperature and shade level shapes saproxylic beetle communities

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Abstract

Aim: The 'concept of relative constancy of habitats' assumes that species differ in their habitat preferences depending on the regional temperature so that all populations experience similar microclimatic conditions. Our aim was to assess the relevance of this concept by disentangling the effects of shade level and regional temperature on southern and northern distributed saproxylic (=dead wood dependent) beetle species.

Location: Sweden.

Methods: We established a field experiment by placing 435 logs of Norway spruce (*Picea abies*) along shade gradients in six regions differing in regional temperature (along a 1200 km latitudinal gradient). For each log, we sampled the saproxylic beetle community and calculated the Community Temperature Index (CTI), indicating to what extent the community is dominated by southern or northern species.

Results: Species richness and total abundance were better explained by shade level, whereas species composition was better explained by study region. In colder regions, CTI varied along the shade gradient, whereas in warmer regions, CTI was more similar along the shade gradient. Moreover, in colder regions, the number of southern species was higher in sun-exposed logs, whereas in warmer regions, the number of southern species was higher in shaded logs. This supports the concept of relative constancy of habitats. In contrast, northern species preferred shaded conditions regardless of the regional temperature.

Main Conclusions: Regional temperature, shade level and resulting microclimate are important drivers of species richness, total abundance and composition. Occurrence patterns of saproxylic beetle species follow to some extent the concept of relative constancy of habitats since their habitat preferences vary with regional temperature. Northern species are of conservation concern due to disadvantages by climate warming and clear-cutting. They are favoured by preserving forests with rarely disturbed canopies.

KEYWORDS
community index, dead wood, forest edge, forestry, microclimate, relative constancy of habitats, temperature

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1 | INTRODUCTION

A fundamental goal in ecology is to identify mechanisms driving the composition of species communities via dispersal, environmental filtering, biotic interactions and ecological drift (i.e. stochastic changes in species abundances; Vandermeer, 1972; Vellend, 2010). Environmental filtering arises from fitness differences among species resulting from abiotic and biotic conditions (Vellend, 2010). One of the most influential abiotic factors is the climate, which can shape species communities at different spatial scales (Lee-Yaw et al., 2016; Thomas, 2010). Regional species pools differ along latitudinal and altitudinal gradients, reflecting differences in average temperature (Pianka, 1966). Also the climate on a small spatial scale, that is, the microclimate, affects environmental filtering, survival and reproduction and thus generates differences in local species composition (Chen et al., 1999). However, the relative importance of large-scale climatic conditions and microclimate driving the local species diversity and composition is still poorly understood.

Species with large geographical distributions might differ in their habitat preferences between regions to experience similar microclimatic conditions over their whole distribution range. This is termed the 'concept of relative constancy of habitats' (Walter & Breckle, 1985). Although the concept has not been explicitly stated, it has been supported by several recent studies; for instance, cold-adapted northern plant species can survive in warm regions, if cool habitats, such as dense forests, are accessible (Hylander et al., 2015). Also, plant species with preferences for higher temperatures can occur in cold regions at sites with warmer microclimatic temperatures, such as on clear-cuts (Christiansen et al., 2021). Moreover, for certain ectothermic animal species, it has been observed that they are limited at their northern range boundaries to microrefugia with warmer microclimatic conditions (Davies et al., 2006; Fourcade et al., 2017; Thomas et al., 1999).

One way to investigate to what extent species composition reflects thermal requirements is to calculate the community temperature index (CTI; Devictor et al., 2008; Fourcade et al., 2021). It is estimated as the mean STI (Species Temperature index), which in turn is the average temperature experienced by a species over its geographical range (Devictor et al., 2008; Fadrique et al., 2018). Thus, a high CTI of a local community reflects a large proportion of species that mainly occur in a warm climate, whereas a low CTI of a local community reflects a large proportion of species that mainly occur in a cold climate. The CTI measure can be used to study the concept of relative constancy of habitats of species communities along macroclimatic gradients with variation in small-scale gradients affecting the microclimate.

Differences in how CTI changes along microclimatic gradients between regions supports the concept of relative constancy of habitats, since it indicates that species choose different habitats with certain microclimatic conditions dependent on the macroclimate.

Dead wood is a key factor for forest biodiversity. In European boreal forests, around 25% of all forest-living species have been classified as saproxylic (Siitonen, 2001), that is, they are dependent, during some part of their life cycle, on dead wood (Speight, 1989). Such insects play a crucial role in decomposition and nutrient recycling in forest ecosystems (Seibold et al., 2021). The level of habitat specialization varies widely among species, with tree species (Müller et al., 2020), diameter, decay stage (Stokland et al., 2012) and sun-exposure (Seibold, Bässler, Baldrian, et al., 2016) being important factors for many species.

Forestry practices, such as clear-cutting, modify the canopy and thus the microclimatic conditions (Hylander, 2005; Reynolds, 1970), which in turn affect the diversity and composition of saproxylic beetles (Chen et al., 1999; Seibold, Bässler, Baldrian, et al., 2016; Seibold, Bässler, Brandl, et al., 2016). However, only few studies have measured the microclimate in dead wood and related it to the saproxylic beetle fauna (Lettenmaier et al., 2022; Lindman et al., 2022, 2023). Usually, sun-exposed dead wood harbours more species and a higher abundance of saproxylic beetles than dead wood in dense forests (Thorn et al., 2016). On a larger scale, species richness and abundance of saproxylic beetles are higher in warmer regions (Kriegel et al., 2023; Müller et al., 2015). By studying species' occurrence patterns in relation to both regional temperature and shade level, it has been shown for the European spruce bark beetle that in colder regions, the species occurs more frequently in sun-exposed compared to shaded logs, whereas this difference is much smaller in warmer regions (Lindman et al., 2023). This supports the concept of relative constancy of habitats. However, it remains unknown to what extent this concept applies to the broad diversity of saproxylic insects.

We conducted a large-scale field experiment using forestry-induced variation in microclimate along a 1200 km latitudinal gradient in Sweden by placing 435 logs of Norway spruce (*Picea abies*) under contrasting shading conditions, hence creating a series of gradients in microclimate along the larger regional temperature gradient (Figure 1a). Our aim was to assess how the diversity and composition of saproxylic beetle communities vary along the regional temperature and shade gradients, and determine the relative importance of these gradients for saproxylic beetle communities. Furthermore, this unique setup allowed us to assess to what extent saproxylic beetle species select habitats with favourable microclimatic conditions to compensate for regional temperature differences, and thus follow the concept of relative constancy of habitats. Specifically, we asked how the CTI was related to the regional temperature and shade gradient. Furthermore, we tested the hypothesis that in colder regions, the number of southern species is higher in sun-exposed compared to shaded logs, whereas in warmer regions, the number of northern species is higher in shaded compared to sun-exposed logs.

2 | MATERIALS AND METHODS

2.1 | Study regions and study design

We selected six study regions along a 1200 km latitudinal gradient in Sweden, ranging from 56.7° N to 66.9° N, in 2020 (Table 1, Figure 1a). All regions are dominated by managed forests of

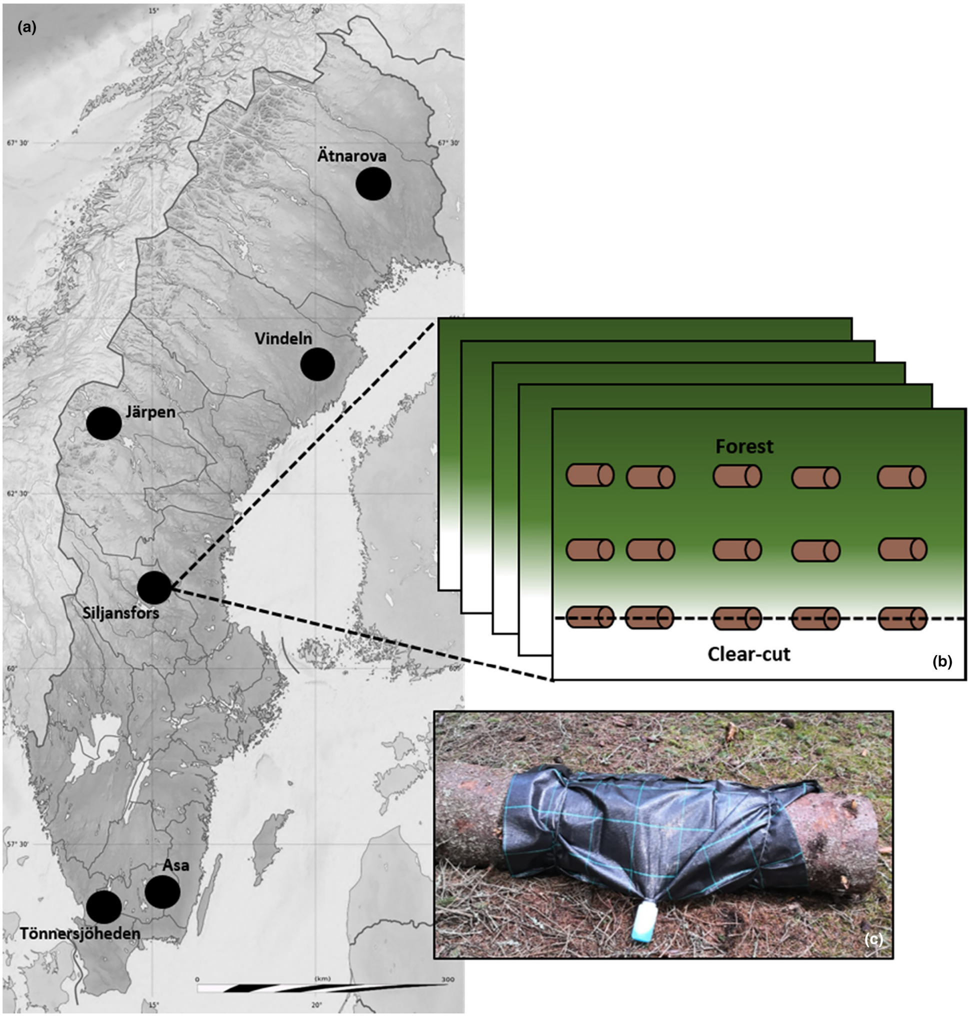


FIGURE 1 Six study regions, which consist of five study plots each (except Siljansfors, where there were four), were distributed over Sweden (a). A plot consists of 15 stem sections on three different shade levels: (i) sun-exposed, (ii) intermediately shaded and (iii) fully shaded (b). The dashed line represents the forest edge (b). In early spring, 1 year after the logs were placed out, every log was equipped with an emergence trap, which were emptied in autumn (c).

Norway spruce and Scots pine (*Pinus sylvestris*), but with a tendency to more Norway spruce and deciduous tree species in the south (Kyaschenko et al., 2022). The mean annual temperature of the study regions varies between 7.8°C in the southernmost region to 0.3°C in the northernmost region (SMHI, 2022; Appendix S1: Table S1). The temperatures in 2020 were very similar to the 30-year mean temperatures during the period April until September (SMHI, 2022), indicating that the weather conditions were close to normal during the year when the collected beetles were in their larval stage. In each study region, we established five study plots (except in Siljansfors, where there were only four plots due to destruction of one plot by forestry management). The median distance between the plots within a study region was 27 km. To obtain contrasting microclimates within plots, each study plot

TABLE 1 Study regions with coordinates, altitude, average temperature and precipitation from nearby weather stations from May to September 1991–2020 and 2020 (SMHI, 2022), microclimatic temperature (T_{micro}), temperature range (min; max) of T_{micro}. T_{micro} is the mean temperature measured in our study from May to September 2020.

Study region	Latitude/longitude	Altitude [m]	Prec. [mm/month] (1991–2020)	T [°C] (1991–2020)	T [°C] (2020)	T_{micro} [°C]	Range T_{micro} [°C]
Tönnersjöheden	56.664232/13.2177121	168	76.6	14.4	13.8	15.6	[3.2; 31.7]
Asa	56.952086/15.3095396	265	66.7	13.7	14.2	16.4	[3.5; 30.1]
Siljansfors	61.0672399/14.9730381	325	68.3	13.0	13.1	14.2	[1; 32.7]
Vindeln	64.2025559/19.5711812	154	64.7	11.6	9.5	13.1	[−0.04; 34.7]
Järpen	63.3382683/13.4049215	425	75.4	10.6	11.7	12.4	[0.2; 31.7]
Åtnarova	66.9144614/21.7243836	199	61.5	10.1	10.2	12.5	[0.3; 29.9]

consisted of a 1–2 year-old clear-cut and an adjacent mature forest stand (Figure 1b).

At each study plot, we placed 15 freshly cut spruce logs of 1.5 m length along five transects at three different shade level: (i) five logs were placed at the forest edge between the clear-cut and the mature spruce stand, that is, sun-exposed, (ii) five logs were placed 10 m into the forest stand, that is, intermediately shaded and (iii) five logs were placed 50 m from the forest edge into the forest, that is, fully shaded. This resulted in 435 spruce logs in total. The diameter of the logs was 15–35 cm. Logs within each transect originated from the same tree. The order of the logs, cut at different heights from the tree, was randomized along transects. The distance between four of the logs at the same shade level was 15 m, and 1 m between two of the logs (Figure 1b). This setup was established in March and April 2020.

2.2 | Temperature data collection and measurement of environmental variables

To confirm that the regional temperature and shade gradient were clearly related to microclimate, we measured the microclimatic temperature on each study plot. We equipped six spruce logs on each study plot (two for each shade level) with temperature loggers (SL52T (Signatrol)) directly under the bark and measured the microclimatic temperature hourly from May 1st until September 17th 2020. This time period was chosen since it covers the time range when adult saproxylic beetles are mainly collected with traps (indicating an active phase) in spruce logs in Sweden (Wikars et al., 2005). We calculated the daily mean for every temperature logger and excluded error-measurements for subsequent analyses (22 of 1,136,500 measurements). Furthermore, in spring 2021, we recorded the diameter of the spruce logs at the centre of each log, the percentage of remaining bark on each log and the aspect of the forest edges of every study plot. We defined aspect by dividing the circle (360°) into four sections, which were numbered according to the distance from the south (180°). This resulted in three categories: 1 (136°–225°) being the southernmost, 2 (46°–135° and 226°–315°) being east and west, 3 (316°–45°) being the northernmost.

2.3 | Beetle data collection

In 2021, we used emergence traps to sample beetles from each stem section (Figure 1c). The traps enclosed a 1 m wide strip around the log, positioned in the centre of each stem section to catch the emerging beetles that developed in the logs. To collect the emerging saproxylic beetles, we used a 50% water/propylene glycol mix as sampling fluid in the collection jar. Since insect hatching starts earlier in the south, we set up emergence traps in southern Sweden in the beginning of April 2021 and in northern Sweden in the beginning of May 2021. Thus, we mainly collected insects that originated from oviposition that took place in the spruce logs in 2020. The sampling ended in the beginning of

September 2021. Sampled beetle adults were identified to species level. For the analysis, we extracted species classified as saproxylic (obligate or facultative) at least in one of the following publications: Ekström (2020); Hägglund and Hjältén (2018); Schmidl and Bußler (2004). We used several lists, since not all collected species were covered by one single list. Since species of the genus *Crypturgus* (*C. pusillus*, *C. subcribrosus*, *C. cinereus*, *C. hispidulus*) have a similar STI and were very numerous in the collected samples, we merged them to *Crypturgus* spp.

2.4 | Calculation of Community Temperature Index

To examine how the community composition of saproxylic beetles responds to regional temperature and shade, we calculated the Community Temperature Index (CTI; Devictor et al., 2008). First, we calculated a mean annual temperature (1991–2020; SMHI, 2022) for each of Sweden's provinces. There are 25 provinces, but the largest—Lapland – was subdivided into five smaller regions (Lundberg & Gustafsson, 1995, Appendix S1: Figure S1). To obtain the Species Temperature Index (STI) for a given species, the mean temperature was calculated of those provinces where the species occurs, according to Lundberg and Gustafsson (1995). We excluded 18 taxa (95 individuals) from the CTI analysis since they were only identified to genus level, and thus, it was impossible to calculate a STI for them. We used the Swedish province scale, since reliable knowledge about species distribution is accessible at this resolution, whereas that is not the case at a European or global scale. Since beetles inhabiting fresh dead wood show a high level of specialization to certain tree species (Wende et al., 2017), it was important that we used logs of Norway spruce. The native distribution of Norway spruce in Europe is separated into the boreal region and the mountain regions in the south-central temperate zone (Schwörer et al., 2015). Both the southern and northern limit of the boreal distribution area are situated within Sweden, whereas the south-central distribution area has a similar climate as the southern part of Sweden (European Environment Agency, 2022). Therefore, it is adequate to estimate STI for Swedish provinces alone. This is especially true since we are only using the relative differences in CTI as an estimate of the dominance of species with different climatic niches in local communities. We calculated CTI for each shade level on every study plot by averaging STI values based on species presence patterns only. We did not weigh for species' abundance, because some species with an intermediate STI were highly abundant (for instance, the three most abundant species constituted 89.6% of all collected individuals) and thus suppress the effect of species with high or low STI when weighing for abundance.

2.5 | Statistical analyses

Statistical analyses were conducted in R 4.2.0 (R Core Team, 2020). To assess to what extent microclimatic temperature reflects both shade level and regional temperature, we applied a linear mixed-effects model (*lme* from package *nlme*, Pinheiro et al., 2013) with a Gaussian distribution (Table 2). The daily mean of the microclimatic temperature was calculated for each shade level on every study plot, which were based on 24 temperature measurements per day. The six study regions and the three different shade levels were included as explanatory variables, whereas microclimatic mean temperature was used as response variable. Aspect was used as additional predictor variable. A combined variable of study region, study plot and shade level (*region_plot_shade*) was used as random variable. Since the daily temperature is correlated with the time variable *day* (Julian calendar day), we included the variables *plot_shade* and *day* as autocorrelation factors.

To assess how the diversity of saproxylic beetle communities varies along the regional temperature and shade gradients, we analysed total number of individuals (hereafter *abundance*) and total number of species (hereafter *species richness*) in relation to regional temperature, shade level and their interaction. Species richness and abundance were calculated for each shade level on every study plot. We applied a linear mixed-effects model (*lme* from package *nlme*, Pinheiro et al., 2013) with Gaussian distribution (Table 2), and used species richness as response variable. For the model with abundance as response variable, we applied a generalized linear mixed-effects model with negative binomial distribution (*glmmTMB* from package *glmmTMB*, Brooks et al., 2017; Table 2). Thirty-year mean temperature (Table 1), that is, regional temperature, shade level and their interaction were included as fixed variables, whereas study region and study plot were used as nested random variables. Log diameter, bark coverage (both are proxies for habitat amount, since many saproxylic insects live under bark) and aspect were used as additional predictor variables.

To determine the relative importance of the regional temperature and shade gradient for saproxylic beetle communities, we fitted one model only with regional temperature as explanatory variable, and one model only with shade level as explanatory variable (Table 2). The additional predictor variables were included in both models. Subsequently, we compared the calculated Akaike's information criterion (AIC) for these models (Table 2).

To analyse how the composition of saproxylic beetle communities varies along the regional temperature and shade gradients, we assessed the dissimilarity in saproxylic beetle composition between shade levels and study regions. We applied analysis of similarities (Anosim from package vegan, Oksanen et al., 2022) using abundance data and compared the mean rank similarities within and between categories (shade level and study region). Anosim addresses dissimilarities in abundance data and provides a robust statistical approach to study the impact of the predefined categories on species compositions.

To test the concept of relative constancy of habitats, we analysed how the CTI was related to the regional temperature and shade gradient. Therefore, we fitted a linear mixed effects model (*lme* from package *nlme*, Pinheiro et al., 2013) with Gaussian distribution (Table 2) and used CTI as response variable and regional

TABLE 2 All linear and generalized linear mixed effects models fitted in this study with response variable, fixed effects, random effects and family distribution. Conditional R^2 and second-order Akaike criterion (AICc) calculated for each model.

Response variable	Model type	Fixed effects	Random effects	Family distribution	AICc	R^2
Mean microclimatic temperature	Linear mixed effects model	Study region Shade level Aspect	Study region/Plot/Shade	Gaussian		.13
Species richness	Linear mixed effects model	Regional temperature Shade level Aspect Diameter Bark Shade level*Regional temperature	Study region/Plot	Gaussian	498.5	.62
Abundance	Generalized linear mixed effects model	Regional temperature Shade level Aspect Diameter Bark Shade level*Regional temperature	Study region/Plot	Negative binomial	1422.36	.73
Species richness	Linear mixed effects model	Regional temperature Bark Aspect Diameter	Study region/Plot	Gaussian	509.3	.49
Abundance	Generalized linear mixed effects model	Regional temperature Bark Aspect Diameter	Study region/Plot	Negative binomial	1447.47	.51
Species richness	Linear mixed effects model	Shade level Bark Aspect Diameter	Study region/Plot	Gaussian	501.8	.64
Abundance	Generalized linear mixed effects model	Shade level Bark Aspect Diameter	Study region/Plot	Negative binomial	1424.55	.71

TABLE 2 (Continued)

Response variable	Model type	Fixed effects	Random effects	Family distribution	AICc	R^2
CTI	Linear mixed effects model	Regional temperature	Study region/Plot	Gaussian		.87
		Shade level				
		Aspect				
		Shade level*Regional temperature				
Number of southern/northern species	Generalized linear mixed effects model	Regional temperature	Study region/Plot	Negative binomial		.79/0.62
		Shade level				
		Bark				
		Diameter				
		Aspect				
		Shade level*Regional temperature				

temperature, shade level and their interaction as explanatory variables (Table 2). Study region and study plot were used as nested random variables. Aspect was used as an additional predictor variable.

To more precisely assess the concept of relative constancy of habitats, we analysed species specifically with clear thermal preferences, that is, with a high or low STI. We categorized species into those with a high STI, hereafter referred to as 'southern' species, and species with a low STI, hereafter referred to as 'northern' species, and species with an intermediate STI (Appendix S1: Table S4). When a species occurred over whole Sweden, the STI was 4.82°C. We considered a species as 'southern', when its STI was minimum +10% of the STI over whole Sweden (southern species: ≥5.17°C), whereas a species with minimum −10% of the STI over whole Sweden was considered as 'northern' (northern species: ≤4.25°C). Species with a STI between 4.25 and 5.17 were considered as intermediate. We analysed also ±20% and ±25% cutoff, but apart from fewer data points, it showed no essential difference to ±10% cutoff, and therefore we do not present the results with these cutoff levels. It is adequate to refer to the species groups as 'northern' and 'southern' since the mean temperature of the Swedish provinces showed a clear gradient from south to north, and with the highest altitudes being in the north, strengthening the south–north gradient in temperature. We fitted a generalized linear mixed effects model (*glmmTMB*) with species richness of southern and northern saproxylic beetle species, respectively, as response variable and regional temperature, shade level and their interaction as fixed variables. We included aspect as additional predictor variable (Table 2).

3 | RESULTS

3.1 | Effect of regional temperature and shade on microclimate and saproxylic beetles

As expected, the mean microclimatic temperature decreased from the southern to the northern study regions (Appendix S1: Tables S3 and S4) and along the shade gradient from sun-exposed to fully shaded logs (Appendix S1: Tables S3 and S4), indicating that both the latitudinal and shade gradient reflect gradients in microclimatic temperature. The difference in the microclimatic temperature between the southernmost and northernmost region was higher (Δtemp = 3.1°C) than the difference in the microclimatic temperature between the sun-exposed and fully shaded logs (mean Δtemp = 1.5°C). The difference in microclimatic temperature between sun-exposed to fully shaded logs corresponded to 577 km along the latitudinal gradient.

In total, we collected 158,203 individuals of 209 saproxylic beetle species (Appendix S1: Table S2). Species richness increased with regional temperature and was lower in fully shaded compared to sun-exposed and intermediate conditions. There was no effect of the interaction between regional temperature and shade level on species richness (Figure 2a, Appendix S1: Tables S3 and S4). The model with shade level as explanatory variable had a stronger explanatory power than the model with regional temperature (Table 2).

Beetle abundance increased with regional temperature and was lower in fully shaded compared to sun-exposed and intermediate conditions. There was no effect of the interaction between regional temperature and shade level on beetle abundance (Figure 2b, Appendix S1: Tables S3 and S4). The model with shade level as explanatory variable had a stronger explanatory power than the model with regional temperature (Table 2).

Species composition of saproxylic beetles differed between study regions ($p<.01$, $R=.37$), especially between the two southernmost (Asa and Tönnersjöheden) and the three northernmost (Vindeln, Järpen and Ätnarova) regions (Figure 3a). In contrast, there was only a small compositional difference between beetle communities along the shade gradient (Figure 3b, $p=.03$, $R=.04$).

3.2 | Effect of shade level and regional temperature on CTI and species richness of southern and northern species

CTI increased with regional temperature, and decreased along the shade gradient from sun-exposed to fully shaded logs. The difference in CTI between sun-exposed and fully shaded logs corresponded to a difference in CTI of approximately 220 km along the regional temperature gradient. There was an interaction effect between shade level and regional temperature on CTI, indicating that in cold regions, the CTI varied more along the shade gradient than in warm regions (Figure 4a, Appendix S1: Tables S2–S5).

In total, there were 50 species classified as 'southern', that is, with a STI ≥ 5.17°C. As expected, the number of southern species increased with regional temperature, but shade level had no effect. There was a marginally significant interaction effect between shade level and regional temperature on the number of southern species, indicating that in cold regions (Vindeln, Järpen and Ätnarova), there were more southern species in sun-exposed logs, whereas in warm regions (Tönnersjöheden, Asa and Siljansfors), there were more southern species in intermediately shaded logs (Figure 4b, Appendix S1: Tables S3 and S4).

There were in total 17 species classified as 'northern', that is, with STI ≤ 4.25°C. The number of northern beetle species decreased with regional temperature, whereas there was neither an effect of shade level, nor an interaction effect between regional temperature and shade level on the number of northern species (Figure 4c, Appendix S1: Tables S3 and S4).

4 | DISCUSSION

We found that regional temperature and shade level are important drivers of species richness, abundance and composition of saproxylic beetles. Species composition was better explained by study region than by shade level, whereas species richness and abundance were better explained by shade level than by regional temperature. The concept of relative constancy of habitats was supported by an observed interaction effect between regional temperature and shade level on CTI, since in colder regions, the CTI varied clearly along the shade gradient, whereas in warmer regions, the CTI was rather similar along the shade gradient. Furthermore, the concept was supported by a weak interaction between regional temperature and shade level on the number of southern species, whereas northern species preferred shaded conditions regardless of the regional temperature.

4.1 | Species richness, total abundance and species composition of saproxylic beetle communities

Consistent with previous studies, we showed that species richness and abundance of saproxylic beetles are lowest in fully shaded dead wood (Figure 2; Lettenmaier et al., 2022; Seibold, Bässler, Brandl, et al., 2016; Vogel et al., 2020), and increase with regional temperature (Figure 2; Kriegel et al., 2023; Müller et al., 2015), generating a latitudinal diversity gradient. In the south, species richness tended to be higher in intermediately shaded logs compared to sun-exposed logs, indicating that in warmer regions, sun-exposed conditions might be too warm and dry for some beetle species. Besides temperature, also humidity might change along the shade gradient, which could also affect species richness and abundance of saproxylic beetles (Hanks et al., 1999; Meeussen et al., 2020). However, other studies have shown weak relationships between canopy openness and humidity in dead wood (Lindman et al., 2022, 2023). Due to standardized conditions in our study, no other characteristics of the sampled dead wood items than microclimate varied along the shade

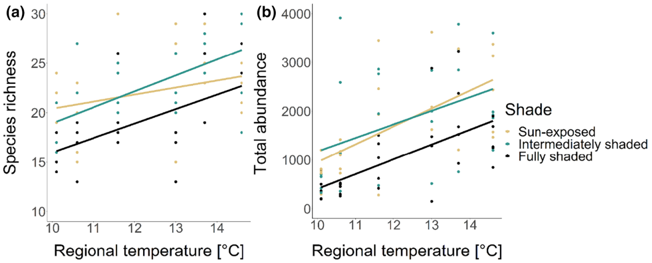


FIGURE 2 Species richness (a) and abundance (b) of saproxylic beetles of the three shade levels (sun-exposed, intermediately shaded and fully shaded) along the regional temperature gradient. The dots represent species richness and total abundance per plot and shade level. There was a significant effect of shade level ($p<.01$) and regional temperature ($p<.01$) on species richness and total abundance.

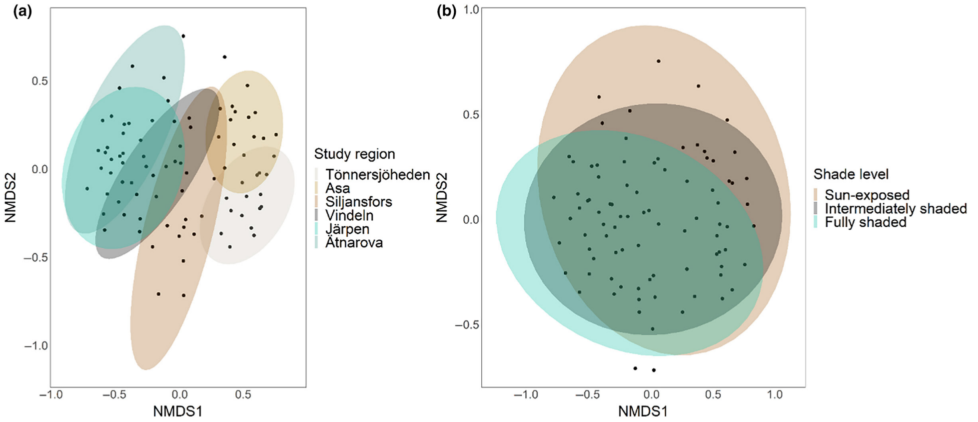
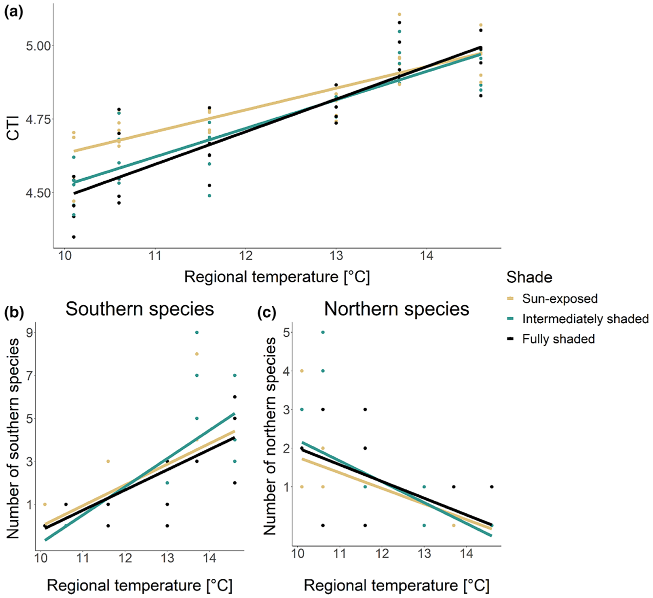


FIGURE 3 Nonmetric multidimensional scaling of saproxylic beetle communities based on abundance data differentiated along a regional gradient from south (Tönnersjöheden) to north (Ätnarova) (a) and along a shade gradient (b). The dots represent species composition per plot and shade level. There were significant differences in species composition between study regions ($p < .01$) and between shade levels ($p = .03$).

FIGURE 4 CTI along the regional temperature gradient and on three shade levels (sun-exposed, intermediately shaded and fully shaded) (a). Number of southern (b) and northern beetle species (c) along the regional temperature gradient on three shade levels (sun-exposed, intermediately shaded and fully shaded). The dots represent the CTI and number of southern and northern species, respectively, per plot and shade level. There was a significant effect of shade level ($p < .01$), regional temperature ($p < .01$) and their interaction ($p < .01$) on CTI. There was a significant effect of regional temperature on number of southern and northern species and a marginally significant effect of interaction between regional temperature and shade level on number of southern species ($p = .08$).



gradient. Thus, we can conclude that saproxylic beetle communities are shaped by the regional temperature and small-scale habitat conditions, both affecting microclimatic temperature.

The shade level explained the observed pattern of species richness and abundance better than the regional temperature. This is in contrast to Thorn et al. (2018), who found that the diversity of saproxylic beetles was equally determined by proxies for macroclimate and microclimate. We showed that the difference in microclimatic temperature between sun-exposed and fully shaded logs corresponded to 577 km along the latitudinal gradient. This steep gradient in microclimatic temperature along the shade gradients implies a high heterogeneity in microclimatic conditions. Studies have shown that a high microclimatic heterogeneity can increase saproxylic beetle diversity (Lettenmaier et al., 2022; Seibold, Bässler, Baldrian, et al., 2016; Seibold, Bässler, Brandl, et al., 2016). Due to large differences in microclimatic temperature along both gradients and much shorter geographical distances, saproxylic beetles can select habitats with optimal microclimatic conditions without long dispersal distances, which could explain the strong effect of shade level compared to the regional temperature.

In contrast to the patterns for species richness and abundance, we found a stronger effect of study region on saproxylic beetle composition compared to shade level, indicating that the species pools in southern and northern Sweden are different (Figure 3a). One explanation for the distinct species composition between study regions but not between shade levels might be the wider variation in temperature from southern to northern Sweden, whereas another might be large geographical distances between study regions impeding dispersal. Species richness and abundance were better explained by shade level than by regional temperature indicating that the wide variation in regional temperature does not have large effects on the conditions for the saproxylic beetle species in general, and thus gives some support for the view that the large geographical distances along the regional temperature gradient are important. Also Fattorini and Baselga (2012) suggested that the variation in species richness of Tenebrionid beetles was rather explained by climate, whereas species composition was more affected by dispersal limitation or stochastic colonization.

In comparison to the distinct species composition between southern and northern regions, species composition was more similar between shaded and sun-exposed logs (Figure 3b). Saproxylic beetles can easily disperse between different shade levels at a site, and therefore species are at least occasionally inhabiting also logs with non-optimal microclimatic conditions. Thus, the wide difference in distances along the two climatic gradients (the regional temperature and the shade gradient) have large consequences for the species composition. This limits to some extent the relevance of the concept of relative constancy of habitats for saproxylic beetle species: species with a limited distribution area are often not able to use logs with optimal microclimatic conditions in other regions due to long distances.

4.2 | The effect of regional temperature and shade level on CTI and species richness of southern and northern species

CTI increased with regional temperature (Figure 4a). Such changes in CTI along large-scale climatic gradients are expected, given how CTI values are estimated, and thus have been shown for many taxa (Devictor et al., 2008; Kwon, 2017; Mingarro et al., 2021). Consistent with the steep gradient in microclimatic temperature along the shade gradient, we found significant differences in CTI along the shade gradient (Figure 4a), with a difference in CTI between sun-exposed and fully shaded logs corresponding to 220 km along the latitudinal gradient. To our knowledge, our study is the first on saproxylic insects using CTI. Similar studies on other insects have investigated altitudinal gradients and found a decrease in CTI with increasing elevation (Fourcade et al., 2019; Nieto-Sánchez et al., 2015). They all conclude that thermal preferences affect species communities both at larger and smaller spatial scales.

The observed interaction effect between regional temperature and shade level on CTI supports the concept of relative constancy of habitats (Figure 4a). In colder regions, the CTI varied clearly along the shade gradient, whereas in warm regions, the CTI was more similar along the shade gradient. This indicates that in colder regions, saproxylic beetles are more selective regarding their microclimatic preferences. Such an interaction pattern has also been detected for a woodland-dependent butterfly, which was less restricted to woodlands in regions with warmer winters and wetter summers (Pateman et al., 2016). One possible explanation for this interaction pattern in our study could be that in northern regions, climate is a limiting factor, whereas in southern regions, biotic interactions limit to a higher extent species' distributions (Paquette & Hargreaves, 2021). Already Darwin (1859) hypothesized that the importance of biotic interactions decreases with latitude. Thus, towards high latitudes, climate is the dominating factor shaping species communities, whereas towards low latitudes, fitness is increasingly constrained by biotic interactions (Darwin, 1859; MacArthur, 1984).

We found a weak effect of the interaction between regional temperature and shade level on the number of southern species (Figure 4b). In colder regions, there were more southern species in sun-exposed logs, whereas in warmer regions, there were more southern species in intermediately shaded logs. This could be due to too warm and dry conditions in sun-exposed logs in southern regions to serve as suitable habitat for many saproxylic beetle species. Thus, the observed pattern supports the concept of relative constancy of habitats. It indicates that the distribution of southern saproxylic beetle is directly limited by microclimatic temperature and that they experience similar microclimatic conditions over their whole distribution range. In contrast, northern species were mostly present in shaded logs across all regions (Figure 4c). This might be attributed to the fact that many of them suffer from competition from southern species in more sun-exposed logs (Paquette & Hargreaves, 2021), or drought sensitivity. Northern species could be of conservation concern due to their sensitivity towards climate warming and clear-cutting.

Previously, the concept of relative constancy of habitats has only been studied for individual species (Lindman et al., 2023; Pateman et al., 2016; Walter & Breckle, 1985). We were able to study the concept on community level by calculating the CTI for species communities and classifying species into those with a southern and northern distribution. Thus, we reveal a broader picture of species communities and test the more general relevance of this concept, in comparison to studies only providing examples by focusing on single species per se.

Our study covers almost the whole width of the Swedish belt of boreal and hemiboreal forests (Ahti et al., 1968). A few species in our study have a broader distribution occurring in the temperate zone. Therefore, the patterns resulting from the concept of relative constancy of habitats might be even clearer at this larger scale. However, for saproxylic beetles in early decay stages it is difficult to study this concept over several climate biomes, since they are often associated with certain tree species. We studied the natural distribution range of Norway spruce, which in Europe covers the boreal region and the mountain regions (south-central temperate zone of Europe). Thus, it is adequate to restrict our experimental set-up to Sweden only.

5 | CONCLUSION

With this study, we can draw three main conclusions. First, climate acts as an important driver of the saproxylic beetle fauna. The main patterns for species richness, abundance and CTI were similar along the regional temperature and shade gradient. This suggests that the species patterns along both gradients are mainly resulting from differences in microclimate. Species composition was better explained by study region than by shade level, whereas species richness and abundance were better explained by shade level than by regional temperature. One explanation for this could be geographical distances, which create distinct species pools along the regional temperature gradient, but not along the shade gradient. The fact that the temperature range was wider along the regional temperature gradient than along the shade gradient can also be important for the observed patterns.

Occurrence patterns of saproxylic beetle species follow to some extent the concept of relative constancy of habitats, since their habitat preferences vary with the regional temperature. One limiting factor of the relevance of the concept of relative constancy of habitats are the large geographical distances, so that species are often not able to use habitats with optimal microclimatic conditions in other regions.

Finally, northern species preferred shaded conditions. Ongoing climate warming and clear-cutting might favour southern species and they can repress northern species. Thus, northern species are of conservation concern, and are favoured by preserving forests with rarely disturbed canopies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13836.

DATA AVAILABILITY STATEMENT

Data openly available in a public repository. Data is stored in SND, https://snd.gu.se/en/catalogue/study/preview/caa02825-959d-471d-9db9-0a82a6770f5d

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REFERENCES

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, *5*, 169–211.

Brooks, M., K. Kristensen, K., van Benthem, A., Magnusson, C., Berg, A., Nielsen, H., Skaug, M., Machler, B., & Bolker., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., Brookshire, B. L., & Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*, *49*, 288–297.

Christiansen, D. M., Iversen, L. L., Ehrlén, J., & Hylander, K. (2021). Changes in forest structure drive temperature preferences of boreal understorey plant communities. *Journal of Ecology*, *110*, 631–643.

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. Murray.

Davies, Z. G., Wilson, R. J., Coles, S., & Thomas, C. D. (2006). Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, *75*, 247–256.

Devictor, V., Julliard, R., Couvet, D., & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 2743–2748.

Ekström, A. L. (2020). *The importance of ecoparks for saproxylic beetles*. Swedish University of Agricultural Sciences.

European Environment Agency. (2022). *Main climates of Europe*. https://www.eea.europa.eu/data-and-maps/figures/climate

Fadrique, B., Báez, S., Duque, A., Malizia, A., Blundo, C., Carilla, J., & Osinaga-Acosta, O. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, *564*, 207–212.

Fattorini, S., & Baselga, A. (2012). Species richness and turnover patterns in European Tenebrionid beetles. *Insect Conservation and Diversity*, *5*, 331–345.

Fourcade, Y., Åström, S., & Öckinger, E. (2019). Climate and land-cover change alter bumblebee species richness and community composition in subalpine areas. *Biodiversity and Conservation*, *28*, 639–653.

Fourcade, Y., Ranius, T., & Öckinger, E. (2017). Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. *Journal of Animal Ecology*, *86*, 1339–1351.

Fourcade, Y., Wallis De Vries, M. F., Kuussaari, M., Swaay, C. A. M., Heliölä, J., & Öckinger, E. (2021). Habitat amount and distribution modify community dynamics under climate change. *Ecology Letters*, *24*, 950–957.

Hägglund, R., & Hjältén, J. (2018). Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides. *Forest Ecology and Management*, *425*, 45–58.

Hanks, L. M., Paine, T. D., Millar, J. G., Campbell, C. D., & Schuch, U. K. (1999). Water relations of host tree and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). *Oecologia*, *119*, 400–407.

Hylander, K. (2005). Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology*, *42*, 518–525.

Hylander, K., Ehrlén, J., Luoto, M., & Meineri, E. (2015). Microrefugia: Not for everyone. *Ambio*, *44*, 60–68.

Kriegel, P., Vogel, S., Angeleri, R., Baldrian, P., Borken, W., Bouget, C., & Thorn, S. (2023). Ambient and substrate energy influence decomposer diversity differentially across trophic levels. *Ecology Letters*, *26*, 1157–1173.

Kwon, T. S. (2017). Temperature and ant assemblages: Biased values of community temperature index. *Journal of Asia-Pacific Entomology*, *20*, 1077–1086.

Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H., & Ranius, T. (2022). Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests. *Journal of Environmental Management*, *313*, 114993.

Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M., & Angert, A. L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, *19*, 710–722.

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J., & Hagge, J. (2022). Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. *Oecologia*, *198*, 825–834.

Lindman, L., Öckinger, E., & Ranius, T. (2022). Microclimatic conditions mediate the effect of deadwood and forest characteristics on a threatened beetle species, *Tragosoma desparium*. *Oecologia*, *199*, 1–16.

Lindman, L., Ranius, T., & Schroeder, M. (2023). Regional climate affects habitat preferences and thermal sums required for development of the Eurasian spruce bark beetle, *Ips typographus*. *Forest Ecology and Management*, *544*, 121216.

Lundberg, S., & Gustafsson, B. (1995). *Catalogus Coleopterorum Sueciae*. Naturhistoriska riksmuseet.

MacArthur, R. H. (1984). *Geographical ecology: Patterns in the distribution of species*. Princeton University Press.

Meeussen, C., Govaert, S., Vanneste, T., Calders, K., Bollmann, K., Brunet, J., & De Frenne, P. (2020). Structural variation of forest edges across Europe. *Forest Ecology and Management*, *462*, 117929.

Mingarro, M., Cancela, J. P., BurÓn-Ugarte, A., García-Barros, E., Munguira, M. L., Romo, H., & Wilson, R. J. (2021). Butterfly communities track climatic variation over space but not time in the Iberian Peninsula. *Insect Conservation and Diversity*, *14*, 647–660.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., & Heidinger, I. M. M. (2015). Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography*, *38*, 499–509.

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., & Vogel, S. (2020). Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos*, *129*, 1579–1588.

Nieto-Sánchez, S., Gutiérrez, D., & Wilson, R. J. (2015). Long-term change and spatial variation in butterfly communities over an elevational gradient: Driven by climate, buffered by habitat. *Diversity and Distributions*, *21*, 950–961.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *Vegan: Community ecology package*. R package version 2.6.4.

Paquette, A., & Hargreaves, A. L. (2021). Biotic interactions are more often important at species' warm versus cool range edges. *Ecology Letters*, *24*, 2427–2438.

Pateman, R. M., Thomas, C. D., Hayward, S. A. L., & Hill, J. K. (2016). Macro- and microclimatic interactions can drive variation in species' habitat associations. *Global Change Biology*, *22*, 556–566.

Pianka, E. R. (1966). Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist*, *100*, 33–46.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & the R Development Core Team. (2013). *Nlme: Linear and nonlinear mixed effects models*. R Package Version 3.1.108.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Reynolds, P. (1970). Effects of forestry practices on forest microclimate. *WIT Transactions on Ecology and the Environment*, *46*, 623–634.

Schmidl, J., & Bußler, H. (2004). Ökologische Gilden xylobionter Käfer Deutschlands. *Naturschutz Und Landschaftsplanung*, *36*, 202–218.

Schwörer, C., Colombaroli, D., Kaltenrieder, P., Rey, F., & Tinner, W. (2015). Early human impact (5000–3000 BC) affects mountain forest dynamics in the Alps. *Journal of Ecology*, *103*, 281–295.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M. D., Weiß, I., & Müller, J. (2016). Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological Conservation*, *204*, 181–188.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D., & Müller, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, *53*, 934–943.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., & Cadotte, M. W. (2021). The contribution of insects to global forest deadwood decomposition. *Nature*, *597*, 77–81.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, *49*, 11–42.

SMHI. (2022). Historical data. https://www.smhi.se/data/meteorologi/temperatur

Speight, M. C. (1989). *Saproxylic invertebrates and their conservation*. Council of Europe.

Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). *Biodiversity in dead wood*. Cambridge University Press.

Thomas, C. D. (2010). Climate, climate change and range boundaries. *Diversity and Distributions*, *16*, 488–495.

Thomas, J. A., Rose, R. J., Clarke, R. T., Thomas, C. D., & Webb, N. R. (1999). Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, *13*, 55–64.

Thorn, S., Bußler, H., Fritze, M., Goeder, P., Müller, J., Weiß, I., & Seibold, S. (2016). Canopy closure determines arthropod assemblages in microhabitats created by windstorms and salvage logging. *Forest Ecology and Management*, *381*, 188–195.

Thorn, S., Förster, B., Heibl, C., Müller, J., & Bässler, C. (2018). Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. *Biodiversity and Conservation*, *27*, 3119–3135.

Vandermeer, J. H. (1972). Niche theory. *Annual Review of Ecology and Systematics*, *3*, 107–132.

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, *85*, 183–206.

Vogel, S., Gossner, M. M., Mergner, U., Müller, J., & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. *Journal of Applied Ecology*, *57*, 2075–2085.

Walter, H., & Breckle, S. (1985). The law of relative constancy of habitat—ecotypes and ecoclines. Springer, Berlin. In *Ecological Systems of the Geobiosphere: 1 Ecological Principles in Global Perspective* (pp. 194–202).

Wende, B., Gossner, M. M., Grass, I., Arnstadt, T., Hofrichter, M., Floren, A., & Steffan-Dewenter, I. (2017). Trophic level, successional age and trait matching determine specialization of deadwood-based interaction networks of saproxylic beetles. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170198.

Wikars, L. O., Sahlin, E., & Ranius, T. (2005). A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *The Canadian Entomologist*, *137*, 304–324.

BIOSKETCHES

Our research aims at contributing to knowledge needed to make decisions related to forest biodiversity. A large part of our field studies are in spatial and climate-related ecology. These include studies of land use and climate change on populations and communities, and strategies to preserve, restore and monitor biodiversity. The main interest of the corresponding author lays in forestry-induced alterations of microclimate and its effect on deadwood-dependent organisms.

Author contributions: M.S., T.R. and E.Ö. designed the study. L.L. set up the logs in the field and measured the temperature. A.G. and L.L. collected the beetle data and A.G. analysed the data. A.G. wrote the first draft and all co-authors contributed to the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Appendix S1

Research article in *Diversity and Distributions*

Interaction between regional temperature and shade level shapes saproxylic beetle communities

Table 1. Weather stations of every study region. More than one weather station indicates that the average values of both were taken. This was the case, when there was no weather station directly nearby the study region. Mean annual temperature from 1991-2020 SMHI.

Study site	SMHI Weather station	Mean annual temperature [°C]
Tönnersjöheden	Halmstad/Ljungby	7.8
Asa	Kosta	6.7
Siljansfors	Mora	5.0
Vindeln	Vindeln/Sunnansjönäs	3.0
Järpen	Åre/Björnängen	3.0
Ätnarova	Gällivare/Nattavaara/Sattavaara	0.3

Table 2. Study sites with species richness, total abundance and CTI for saproxylic beetles, which were sampled in a total of 435 logs from May until September 2021.

Study Site	Species richness	Total abundance	CTI
Tönnersjöheden	92	29519	4.75
Asa	111	46253	4.74
Siljansfors	77	26313	4.73
Vindeln	81	31086	4.61
Järpen	76	16371	4.61
Ätnarova	68	8661	4.4

Table 3. Wald-χ^2 test of linear and generalized linear mixed effects models with mean microclimatic temperature, species richness, abundance, CTI and number of southern and

northern species as response variables. Numbers in bold indicate significant effects (<0.05), numbers in italic indicate marginally significant effects (<0.1).

Model with predictor variables	χ^2	**DF**	***p*-value**
Microclimatic temperature			
Aspect	29.69	3	**0.02**
Shade level	29.69	2	**<0.01**
Study region	80.02	5	**<0.01**
Species richness			
Diameter	2.62	1	0.11
Aspect	1.1	3	0.78
Bark coverage	2.0e^{-4}	1	0.99
Shade level	16.26	2	**<0.01**
Regional temperature	9.65	1	**<0.01**
Regional temperature: Shade level	3.96	2	0.14
Species richness			
Diameter	4.33	1	**0.04**
Aspect	1.29	3	0.73
Bark coverage	5.0e^{-4}	1	0.98
Regional temperature	11.5	1	**<0.01**
Species richness			
Diameter	0.58	1	0.45
Aspect	0.64	3	0.89
Bark coverage	0.02	1	0.89
Shade level	16.15	1	**<0.01**
Abundance			
Diameter	0.1	1	0.75
Aspect	12.37	3	**<0.01**
Bark coverage	0.02	1	0.88
Shade level	46.19	2	**<0.01**
Regional temperature	11.64	1	**<0.01**
Regional temperature: Shade level	3.86	2	0.14
Abundance			
Diameter	0.29	1	0.59
Aspect	11.79	3	**<0.01**
Bark coverage	0.24	1	0.62
Regional temperature	13.47	1	**<0.01**
Abundance			
Diameter	1.95	1	0.16
Aspect	10.22	3	**0.02**
Bark coverage	0.02	1	0.88
Shade level	45.91	1	**<0.01**
CTI			
Aspect	2.72	3	0.44
Shade level	17.29	2	**<0.01**
Regional temperature	84.29	1	**<0.01**
Regional temperature: Shade level	12.89	2	**<0.01**
Number of southern species			

Diameter	0.91	1	0.39
Aspect	0.33	3	0.95
Bark coverage	3.17	1	*0.07*
Shade level	0.29	2	0.86
Regional temperature	24.54	1	**<0.01**
Regional temperature : Shade level	4.86	2	*0.08*
Number of northern species			
Diameter	0.25	1	0.62
Aspect	2.64	3	0.45
Bark coverage	0.15	1	0.69
Shade level	0.54	2	0.76
Regional temperature	19.45	1	**<0.01**
Regional temperature: Shade level	1.15	5	0.56

Table 4. Fitted linear and generalized linear mixed effects models with mean microclimatic temperature, species richness, abundance, CTI and number of southern and northern species as response variables. Numbers in bold indicate significant effects (<0.05), numbers in italic indicate marginally significant effects (<0.1). Estimate and Std. error were extracted from the summary tables. Lower and upper confidence intervals were calculated with the function *confint*.

Model with predictor variables	**Estimate**	**Std. Error**	**Lower CI**	**Upper CI**	***p*-value**
Mean microclimatic temperature					
Aspect					
South	-0.54	0.75	-2.04	0.95	0.47
North	-2.04	0.82	-3.66	-0.41	**0.01**
West	-1.47	0.73	-2.92	-0.02	0.47
Shade level					
Shade II	-1.55	0.47	-2.49	-0.62	**<0.01**
Shade III	-2.55	0.47	-3.49	-1.61	**<0.01**
Study region					
Asa	0.01	0.73	-1.44	1.45	0.99
Siljansfors	-2.25	0.69	-3.63	-0.86	**<0.01**
Vindeln	-3.25	0.68	-4.61	-1.89	**<0.01**
Järpen	-4.22	0.69	-5.6	-2.83	**<0.01**
Ätnarova	-4.08	0.69	-5.46	-2.69	**<0.01**
Species richness					
Regional temperature	1.29	0.71	-0.67	3.27	0.14
Regional temperature: Shade					
Regional temperature: Shade II	0.97	0.53	-0.09	2.02	*0.07*
Regional temperature: Shade III	0.84	0.53	-0.22	1.91	0.12
Shade level					
Shade II	-11.00	6.52	-24.08	2.08	*0.09*
Shade III	-12.87	6.56	-26.04	0.29	*0.06*
Diameter	0.51	0.32	-0.12	1.15	0.11
Aspect					

North	-1.35	2.61	-6.79	4.09	0.61
South	0.32	2.45	-4.79	5.43	0.89
West	-0.68	2.35	-5.59	4.23	0.78
Bark coverage	0.001	0.04	-0.09	0.09	0.99
Abundance					
Regional temperature	0.29	0.09	0.12	0.47	**<0.01**
Regional temperature: Shade					
Regional temperature: Shade II	-0.12	0.07	-0.26	0.03	0.12
Regional temperature: Shade III	0.02	0.07	-0.12	0.17	0.77
Shade level					
Shade II	1.31	0.93	-0.51	3.12	0.16
Shade III	-1.03	0.91	-2.82	0.76	0.26
Diameter	-0.01	0.04	-0.1	0.07	0.75
Aspect					
North	-0.73	0.37	-1.46	0.003	**0.05**
South	0.12	0.35	-0.56	0.79	0.73
West	0.03	0.33	-0.63	0.68	0.93
Bark coverage	0.001	0.01	-0.01	0.01	0.88
Species richness					
Regional temperature	2.03	0.59	0.37	3.69	**0.03**
Diameter	0.69	0.33	0.03	1.35	**0.04**
Aspect					
North	-1.18	2.57	-6.55	4.19	0.65
South	0.56	2.41	-4.46	5.59	0.82
West	-0.58	2.32	-5.42	4.25	0.8
Bark coverage	0.001	0.05	-0.09	0.09	0.98
Species richness					
Shade level					
Shade II	0.81	0.88	-0.95	2.58	0.36
Shade III	-2.56	0.88	-4.32	-0.8	**<0.01**
Diameter	0.25	0.33	-0.4	0.9	0.45
Aspect					
North	-1.02	2.69	-6.63	4.59	0.71
South	0.42	2.59	-4.99	5.83	0.87
West	-0.31	2.44	-5.39	4.77	0.89
Bark coverage	0.01	0.04	-0.08	0.09	0.89
Abundance					
Regional temperature	0.28	0.08	0.13	0.43	**<0.01**
Diameter	0.03	0.05	-0.07	0.12	0.59
Aspect					
North	-0.89	0.39	-1.66	-0.12	**0.02**
South	-0.05	0.36	-0.75	0.65	0.88
West	-0.11	0.35	-0.79	0.57	0.75
Bark coverage	0.004	0.01	-0.01	0.02	0.62
Abundance					
Shade level					
Shade II	-0.11	0.12	-0.35	0.13	0.36
Shade III	-0.76	0.12	-1.0	-0.53	**<0.01**
Diameter	-0.07	0.05	-0.16	0.03	0.16
Aspect					
North	-0.71	0.39	-1.45	0.07	*0.07*
South	0.09	0.38	-0.65	0.84	0.8
West	0.08	0.36	-0.62	0.78	0.83
Bark coverage	0.001	0.01	-0.01	0.01	0.88

CTI					
Regional temperature	0.07	0.01	0.04	0.11	**<0.01**
Regional temperature: Shade					
Regional temperature: Shade II	0.02	0.01	0.002	0.04	**0.03**
Regional temperature: Shade III	0.04	0.01	0.02	0.06	**<0.01**
Shade level					
Shade II	-0.34	0.13	-0.59	-0.08	**0.01**
Shade III	-0.52	0.13	-0.77	-0.26	**<0.01**
Aspect					
North	-0.04	0.06	-0.16	0.07	0.44
South	0.02	0.05	-0.09	0.12	0.76
West	-0.01	0.05	-0.12	0.09	0.8
Number of southern species					
Regional temperature	0.55	0.15	0.25	0.85	**<0.01**
Regional temperature: Shade					
Regional temperature: Shade II	0.41	0.19	0.05	0.78	**0.03**
Regional temperature: Shade III	0.11	0.16	-0.19	0.43	0.47
Shade level					
Shade II	-5.59	2.58	-10.06	-0.55	**0.03**
Shade III	-1.57	2.16	-5.79	2.65	0.47
Diameter	0.06	0.06	-0.06	0.17	0.34
Aspect					
North	-0.09	0.68	-1.42	1.25	0.9
South	0.08	0.66	-1.22	1.38	0.9
West	0.001	0.65	-1.26	1.27	0.99
Bark coverage	0.02	0.01	-0.002	0.04	*0.07*
Number of northern species					
Regional temperature	-0.68	0.22	-1.09	-0.25	**<0.01**
Regional temperature: Shade					
Regional temperature: Shade II	-0.18	0.27	-0.72	0.35	0.49
Regional temperature: Shade III	0.09	0.24	-0.38	0.56	0.7
Shade level					
Shade II	2.13	2.98	-3.70	7.97	0.47
Shade III	-0.82	2.64	-5.99	4.35	0.76
Diameter	-0.04	0.09	-0.22	0.13	0.62
Aspect					
North	0.47	0.64	-0.79	1.73	0.47
South	0.23	0.58	-0.91	1.36	0.69
West	0.69	0.55	-0.39	1.77	0.21
Bark coverage	-0.004	0.01	-0.03	0.02	0.69

Table 5. Collected saproxylic beetle species, their STI and abundance. Based on their STI, beetles were categorized into intermediate, southern and northern species. Species without a STI were excluded from CTI analysis.

Species	STI	Abundance	Type
Acidota crenata	4.81	19	Intermediate
Acrulia inflate	4.60	15	Intermediate
Agathidium atrum	4.90	1	Intermediate
Agathidium mandibulare	4.91	1	Intermediate
Agathidium pisanum	4.62	1	Intermediate

Agathidium seminulum	4.71	8	Intermediate
Ampedus balteatus	5.00	34	Intermediate
Ampedus nigrinus	4.60	11	Intermediate
Ampedus pomorum	5.60	2	Southern
Ampedus sanguineus	6.71	7	Southern
Ampedus tristis	4.38	18	Intermediate
Amphicyllis globus	4.92	2	Intermediate
Anaspis flava	6.28	4	Southern
Anaspis marginicollis	4.93	52	Intermediate
Anaspis rufilabris	4.81	6	Intermediate
Anaspis sp		2	
Anastrangalia sanguinolenta	5.23	7	Southern
Anidorus nigrinus	6.63	1	Southern
Anisotoma castanea	4.81	2	Intermediate
Anisotoma glabra	4.71	2	Intermediate
Arpedium quadrum	4.62	12	Intermediate
Aspidiphorus orbiculatus	5.23	5	Southern
Atheta fungi	4.82	18	Intermediate
Atheta hypnorum	4.80	1	Intermediate
Atheta lativentris	4.59	3	Intermediate
Atheta paracrassicornis	4.69	3	Intermediate
Atheta picipes	4.59	1	Intermediate
Atheta pilicornis	4.73	35	Intermediate
Atheta sodalis	4.82	18	Intermediate
Atheta sp		7	
Atheta subtilis	4.82	14	Intermediate
Atomaria bella	4.99	216	Intermediate
Atomaria ornata	5.77	3	Southern
Atomaria sp		1	
Atomaria subangulata	4.19	1	Northern
Atomaria umbrina	4.62	1	Intermediate
Atomaria vespertina	4.59	33	Intermediate
Atrecus longiceps	4.39	10	Intermediate
Atrecus pilicornis	2.21	1	Northern
Bibloporus bicolor	5.03	8	Intermediate
Bitoma crenata	5.19	2	Southern
Bolitochara mulsanti	5.61	2	Southern
Bolitochara pulchra	4.82	23	Intermediate
Bryoporus cernuus	4.68	2	Intermediate
Cardiophorus ruficollis	5.34	1	Southern
Cartodere nodifer	6.16	2	Southern
Cerylon fagi	6.24	1	Southern
Cerylon histeroides	4.70	29	Intermediate
Chrysobothris chrysostigma	4.25	4	Intermediate
Cis bidentatus	4.70	1	Intermediate
Cis castaneus	7.39	1	Southern
Cis dentatus	5.01	1	Intermediate
Cis punctulatus	4.83	3	Intermediate

Corticaria foveola	5.41	1	Southern
Corticaria longicollis	4.82	5	Intermediate
Corticaria orbicollis	1.94	2	Northern
Corticaria rubripes	4.61	30	Intermediate
Corticaria sp		8	
Corticarina minuta	7.66	1	Southern
Corticarina parvula	4.65	1	Intermediate
Corticeus linearis	5.00	104	Intermediate
Cortinicara gibbosa	5.21	1	Southern
Cryphalus abietis	6.99	1	Southern
Cryphalus asperatus	6.23	65	Southern
Cryphalus saltuarius	3.89	1	Northern
Cryptophagus scanicus	4.82	2	Intermediate
Cryptophagus setulosus	4.71	1	Intermediate
Crypturgus sp.	4.82	10639	Intermediate
Curtimorda maculosa	5.07	8	Intermediate
Cyphon padi	4.82	22	Intermediate
Dacne bipustulata	4.91	2	Intermediate
Dadobia immersa	4.98	7	Intermediate
Danosoma conspersum	3.75	1	Northern
Dasytes caeruleus	7.26	2	Southern
Dasytes niger	4.90	1	Intermediate
Dasytes obscurus	4.76	3	Intermediate
Dendroctonus micans	4.72	20	Intermediate
Dinaraea aequata	4.71	3	Intermediate
Dinaraea arcana	3.86	2	Northern
Dolichocis laricinum	3.11	1	Northern
Drusilla canaliculata	4.82	1	Intermediate
Dryocoetes autographus	4.71	3597	Intermediate
Dryocoetes hectographus	4.1	34	Northern
Enicmus rugosus	4.71	12	Intermediate
Enicmus testaceus	6.77	5	Southern
Epuraea angustula	4.23	1	Northern
Epuraea laeviuscula	4.57	10	Intermediate
Epuraea marseuli	4.82	29	Intermediate
Epuraea neglecta	7.45	1	Southern
Epuraea pygmaea	4.75	172	Intermediate
Epuraea sp		1	
Ernobius mollis	5.99	1	Southern
Euglenes pygmaeus	5.98	6	Southern
Euplectus decipiens	5.23	2	Southern
Euplectus karstenii	4.91	5	Intermediate
Euplectus nanus	5.49	11	Southern
Euplectus punctatus	5.12	2	Intermediate
Euplectus sp		5	
Gabrius splendidulus	5.09	28	Intermediate
Glischrochilus quadripunctatus	4.71	4	Intermediate

Hadrobregmus pertinax	5.00	2	Intermediate
Hylastes cunicularius	4.65	519	Intermediate
Hylastes opacus	6.01	5	Southern
Hylobius abietis	4.82	35	Intermediate
Hylobius pinastri	4.90	26	Intermediate
Hylurgops glabratus	3.03	1214	Northern
Hylurgops palliatus	4.82	1081	Intermediate
Ipidia binotata	6.72	17	Southern
Ips typographus	4.71	21944	Intermediate
Ischnoglossa prolixa	6.16	1	Southern
Judolia sexmaculata	4.71	1	Intermediate
Latridius hirtus	4.76	1	Intermediate
Latridius sp		1	
Leptusa fumida	5.86	4	Southern
Leptusa norvegica	5.52	3	Southern
Leptusa pulchella	4.81	5	Intermediate
Leptusa ruficollis	6.90	1	Southern
Leptusa sp		1	
Liotrichus affinis	3.55	1	Northern
Lordithon speciosus	3.44	2	Northern
Malthodes brevicollis	4.90	2	Intermediate
Malthodes fuscus	4.71	1	Intermediate
Malthodes marginatus	4.98	2	Intermediate
Malthodes sp		3	
Melanotus castanipes	4.59	64	Intermediate
Melanotus sp		36	
Microambe abietis	5.29	2	Southern
Micrambe longitarsis	5.07	2	Intermediate
Monochamus sutor	4.7	7	Intermediate
Mycetina cruciata	6.63	1	Southern
Mycetoporus punctus	4.77	1	Intermediate
Mycetoporus sp		1	
Nepachys cardiacae	4.08	1	Northern
Nudobius lentus	4.69	49	Intermediate
Omalium rivulare	4.82	1	Intermediate
Omalium rugatum	5.32	14	Southern
Omalium sp		3	
Orthocis alni	4.92	1	Intermediate
Orthoperus atomus	4.92	1	Intermediate
Orthotomicus laricis	5.21	2	Southern
Orthotomicus proximus	5.00	6	Intermediate
Orthotomicus suturalis	4.71	7	Intermediate
Oxymirus cursor	4.79	3	Intermediate
Pediacus fuscus	3.66	7	Northern
Pella cognata	4.87	1	Intermediate
Pella lugens	6.71	1	Southern
Peltis ferruginea	4.75	3	Intermediate
Phaenops cyanea	5.1	1	Intermediate

Phloeonomus punctipennis	4.79	1	Intermediate
Phloeonomus pusillus	4.82	214	Intermediate
Phloeonomus sjobergi	5.11	209	Intermediate
Phloeopora corticalis	5.45	3	Southern
Phloeopora testacea	4.91	1	Intermediate
Phloeostiba lapponica	4.63	4	Intermediate
Pissodes gyllenhalii	4.95	38	Intermediate
Pityogenes bidentatus	4.82	9	Intermediate
Pityogenes chalcographus	4.71	109508	Intermediate
Pityophagus ferrugineus	4.71	8	Intermediate
Pityophthorus micrographus	4.71	2	Intermediate
Placusa atrata	4.55	2	Intermediate
Placusa complanata	4.71	44	Intermediate
Placusa depressa	4.73	4	Intermediate
Placusa sp.		14	
Placusa tachyporoides	5.00	1	Intermediate
Platysoma lineare	5.07	1	Intermediate
Plegaderus vulneratus	4.71	205	Intermediate
Podistra schoenherri	4.47	3	Intermediate
Podistra sp		1	
Pogonocherus fasciculatus	4.71	2	Intermediate
Polygraphus poligraphus	4.91	79	Intermediate
Polygraphus punctifrons	3.33	469	Northern
Pteryx suturalis	4.82	2	Intermediate
Ptiliidae sp		1	
Ptinus subpillosus	5.65	3	Southern
Pytho depressus	4.82	1	Intermediate
Quedius mesomelinus	4.82	15	Intermediate
Quedius scitus	6.71	1	Southern
Quedius sp		4	
Rabocerus foveolatus	3.72	1	Northern
Rhagium inquisitor	4.82	10	Intermediate
Rhizophagus bipustulatus	4.90	1	Intermediate
Rhizophagus dispar	4.82	105	Intermediate
Rhizophagus fenestralis	4.47	1	Intermediate
Rhizophagus ferrugineus	4.71	22	Intermediate
Rhyncolus ater	4.82	143	Intermediate
Scaphisoma agaricinum	4.82	37	Intermediate
Scaphisoma boleti	6.51	1	Southern
Sepedophilus constans	4.61	1	Intermediate
Sepedophilus immaculatus	6.05	1	Southern
Sepedophilus littoreus	4.56	51	Intermediate
Sepedophilus marshami	5.56	87	Southern
Sepedophilus sp		4	
Sepedophilus testaceus	5.29	16	Southern
Serropalpus barbatus	5.69	1	Southern
Silvanoprus fagi	6.71	5	Southern
Stenichnus bicolor	4.71	1	Southern

Stenichnus godarti	6.82	1	Southern
Stictoleptura rubra	6.47	40	Southern
Tetropium castaneum	4.99	338	Intermediate
Tetropium fuscum	4.81	14	Intermediate
Thanasimus formicarius	4.71	8	Intermediate
Tomicus piniperda	4.81	30	Intermediate
Trypodendron lineatum	4.73	5380	Intermediate
Tyrus mucronatus	5.43	10	Southern
Xantholinus sp		2	
Xantholinus tricolor	5.08	3	Intermediate
Xylechinus pilosus	3.23	4	Northern
Xylostiba monilicornis	5.73	2	Southern
Zilora ferruginea	4.39	1	Intermediate

Figure 1. Sweden and its provinces with the biggest province – Lapland – separated into five smaller ones (Sk=Skåne, Bl=Blekinge, Öl=Öland, Go=Gotland, GS=Gotska sandön, Ha=Halland, Sm=Småland, Vg=Västergötland, Ög=Östergötland, Bo=Bohuslän, Ds=Dalsland, Nä=Närke, Sö=Södermanland, Vs=Västmanland, Vr=Värmland, Up=Uppland, Gä=Gästrikland, Dr=Dalarna, Hs=Hälsingland, Hr=Härjedalen, Me=Medelpad, Jä=Jämtland, Ån=Ångermanland, Ås=Åsele lappmark, Vb=Västerbotten, Ly=Lycksele lappmark, Pi=Pite lappmark, Nb=Norrbotten, Lu=Lule lappmark, To=Torne lappmark; Figure is according to Lundberg and Gustafsson (1995)).

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ORIGINAL ARTICLE

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In urban areas, tree cover increases species richness and shapes species composition of saproxylic beetles along with the microclimate

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Abstract

1. Urbanisation constitutes a major threat to biodiversity due to the reduction and fragmentation of natural habitats. However, with appropriate conservation measures, cities can harbour valuable microhabitats for biodiversity such as hollow trees and dead wood.
2. We tested the effects of environmental filters, such as tree cover (reflecting habitat amount), density of urban structures (reflecting dispersal barriers), and microclimate on species richness, abundance and species composition of saproxylic beetles along urbanisation gradients. According to the urban homogenisation hypothesis, we expected more homogeneous communities across highly urbanised sites than across sparsely urbanised sites. Furthermore, we assessed whether communities at highly urbanised sites are more dominated by thermophilous species due to the urban heat island effect.
3. In six cities in southern Sweden, we placed ten wood mould boxes emulating hollow trees along urbanisation gradients and sampled saproxylic beetles inside those boxes. To determine to what extent communities were dominated by thermophilous species, we calculated the Community Temperature Index (CTI).
4. Species richness of saproxylic beetles decreased with the density of urban structures, whereas the abundance increased with tree cover. Microclimate and tree cover affected saproxylic beetle species composition significantly, but we did not find support for the urban homogenisation hypothesis. Despite an observed urban heat island effect and a cooling effect of tree canopies, CTI did not increase with the density of urban structures or decrease with tree cover.
5. We conclude that it is possible to promote saproxylic insects in cities by maintaining and creating tree cover with varying canopy densities, leading to a variety of microclimatic conditions. Artificial microhabitats, such as wooden boxes, have similar microclimatic conditions as hollow trees and can be used to increase the supply of habitats for saproxylic species in cities.

KEYWORDS
Community Temperature Index, dead wood, hollow trees, microclimate, urbanisation, wood mould boxes

INTRODUCTION

Urbanisation leads to a reduction and fragmentation of natural habitats (Parris, 2016). The remaining small patches of natural habitats often have a reduced value for biodiversity due to habitat degradation, negative edge effects (i.e. species are more abundant in the habitat interior than at the edge), and habitat isolation (Beninde et al., 2015; McKinney, 2008).

Urbanisation can also affect biodiversity by a warmer climate due to heat-absorbing artificial surfaces (Oke, 1995). Cities can have temperatures 2–4°C higher than surrounding rural areas, which is referred to as the 'urban heat island effect' (Kłysik & Fortuniak, 1999). This can explain why urban insect communities are often dominated by more thermophilous species (Franzén et al., 2020; Menke et al., 2011; Piano et al., 2017). The urban heat island effect can be buffered by urban forests with high tree densities that reduce the surrounding temperature (Grilo et al., 2020). However, it remains unknown whether this cooling effect clearly promotes species dependent on cooler microclimatic conditions.

Cities within a region often share similar biotic and abiotic conditions regarding, for instance, anthropogenic disturbances, vegetation, and the level of habitat fragmentation. These conditions can lead to the loss of habitat specialists and poorly dispersing species, while favouring mobile, thermophilous, and generalist species (Sidemo-Holm et al., 2022). This process, known as urban homogenisation, can lead to an increasing similarity of communities across multiple cities (Lokatis & Jeschke, 2022; McKinney, 2006). Thus, an increasing homogenisation can threaten biodiversity on larger scales, especially in highly urbanised regions. Most studies investigating urban homogenisation have focused on birds (Blair & Johnson, 2008; Catterall et al., 2010; Clergeau et al., 2006) or plants (Knapp & Wittig, 2012; McKinney, 2006; Schwartz et al., 2006), but insects have rarely been studied in this regard (but see Baldock et al., 2015; Blair, 2001; Knop, 2016).

Species communities are shaped by environmental filters, such as habitat quality and quantity (Vellend, 2016). An increasing habitat amount in a landscape can lead to a higher local species richness (Fahrig, 2013) and affect species composition (Pilskog et al., 2020; Dianzinga et al., 2020) due to a possible correlation between habitat amount and habitat heterogeneity (Seibold et al., 2016). In urban areas, studies investigating the effect of habitat amount on insects have shown contrasting results, with positive effects of a high urban forest cover on dung beetle abundance (Bernardino et al., 2024) but no effect of urban forest cover on saproxylic (=dead wood-dependent) insects (Meyer et al., 2021), highlighting the need for more research in this field. In contrast, species can be negatively affected by dispersal barriers due to urban structures, such as roads and buildings. The negative effect of roads on vertebrates is well documented, while studies on invertebrates are rather rare (Teixeira et al., 2020). However, studies on Tachinid flies (Corcos et al., 2019), butterflies, bees and wasps (Dániel-Ferreira et al., 2022; Johansson et al., 2018) indicate that streets and buildings can act as dispersal barriers.

Saproxylic organisms depend on dead wood and play a crucial role in dead wood decomposition and consequently also in nutrient recycling (Seibold et al., 2021). Due to habitat loss and deterioration, many saproxylic species, including beetles, are today threatened (Calix et al., 2018). Certain structures only found in old trees, such as tree hollows, serve as important microhabitats for saproxylic invertebrates since they provide long-lasting habitats and stable microclimatic conditions (Lindman et al., 2023; Ranius et al., 2024). However, intensive forestry and agriculture have led to a severe reduction of large old trees and dead wood in production landscapes (Lindenmayer et al., 2012; Siitonen, 2001). Since the production of agricultural and forest products is rarely important in urban areas, urban trees have the potential to serve as refugia for saproxylic organisms (Fröhlich & Ciach, 2020). Indeed, several rare saproxylic beetles have been found to occur in dead wood and hollow trees in urban areas (Andersson, 1999; Carpaneto et al., 2010; Fattorini & Galassi, 2016; Peuhu et al., 2019). However, to our knowledge, only one study has examined how the saproxylic insect fauna is affected by environmental filters reflecting an urbanisation gradient (in that case, forest size and degree of urbanisation; Meyer et al., 2021).

Warm and stable microclimatic conditions can be important for the occurrence of saproxylic beetle species in tree hollows (Lindman et al., 2023). It has also been shown that saproxylic beetles with certain thermal preferences (revealed from their geographical distributions) are mostly found in dead wood with microclimatic conditions consistent with those preferences (Goßmann et al., 2024). In an urban environment, microclimate can act as an environmental filter that generates a difference between urban and rural areas, but studies on the effect of microclimate on saproxylic insects in urban areas are scarce. Consequently, the possible impact of the urban heat island effect on saproxylic insects is poorly understood.

In this study, we investigated the effects of environmental filters of particular importance in urban areas, such as the density of urban structures (reflecting dispersal barriers), tree cover (reflecting habitat amount), and microclimate on the saproxylic beetle fauna. We placed wooden boxes filled with artificial wood mould (= loose material in tree hollows, mainly consisting of decaying wood) to emulate tree hollows along urbanisation gradients in six Swedish cities. We predicted the following:

I. Species richness, abundance, and composition of saproxylic beetles are affected by environmental filters that differ between urban and rural areas (density of urban structures, tree cover, and microclimate). In particular, we predict that species richness and abundance increase with tree cover but decrease with the density of urban structures.

II. According to the urban homogenisation hypothesis, communities are more homogeneous across highly urbanised sites, that is sites

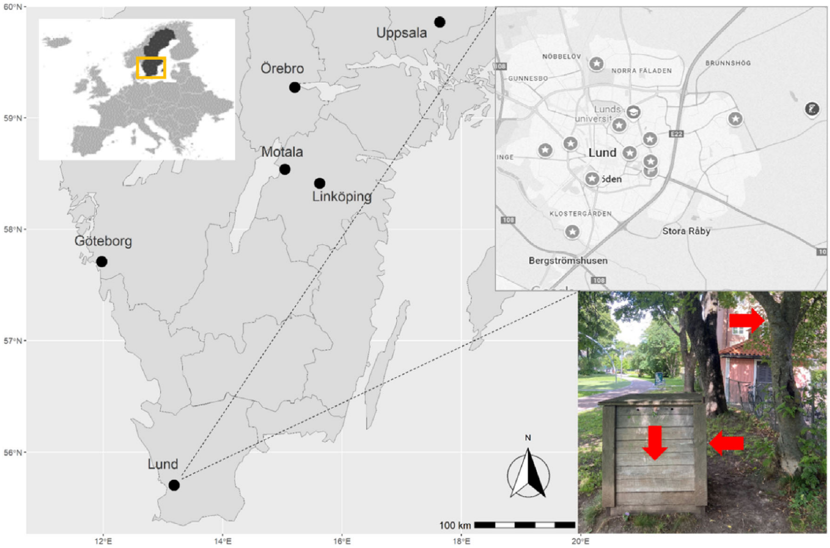

FIGURE 1 Six study cities distributed over southern Sweden containing 10 wood mould boxes resembling tree hollows. The microclimatic mean temperature was measured (i) in the wood mould of each box, (ii) inside the box attached to the north-facing wall, (iii) outside the box at the closest tree (red arrows represent logger locations), and when available, (iv) inside hollow trees. The picture of the wood mould box was taken by Anika Gossmann. The map of Lund in the upper right was extracted from Google Maps (March, 2025), and serves as an example of the distribution of the wood mould boxes along an urbanisation gradient. The grey stars represent the box locations.

with a high density of urban structures, than across sparsely urbanised sites, that is sites with a low density of urban structures.

III. Reflecting the urban heat island effect, highly urbanised sites are more dominated by thermophilous species, whereas we predict the opposite for sites with a high tree cover.

MATERIALS AND METHODS

Study design

The study was conducted in six cities in southern Sweden (Lund, Göteborg, Motala, Linköping, Örebro, and Uppsala) ranging from 55.7°N to 59.9°N (Figure 1). The human population sizes in these cities vary between 30,000 (Motala) and 600,000 (Göteborg) inhabitants. The annual mean temperatures range from 8.7°C in the southernmost city (Lund) to 6.6°C in the northernmost city (Uppsala) (Appendix S1: Tables S1 and S2). In 2014, ten wooden boxes (but only eight in Motala and Linköping), serving as artificial microhabitats for saproxylic beetles (cf. Jansson et al., 2009) were placed in each city with different distances to the city centres ranging from 0.5 to 15 km (Figure 1). All boxes were placed at sites with trees in the surrounding area. Apart from one site in Uppsala, the majority of the trees in the surrounding area of the boxes were deciduous, with oak (*Quercus* sp.) being the dominant tree species.

In accordance with Jansson et al. (2009), the boxes were designed to emulate tree hollows in old deciduous trees. Since Jansson et al. (2009) recommended bigger boxes to generate more stable microclimatic conditions, we constructed boxes of 1 m^3 in size (1 × 1 × 1 m) and placed them on the ground (Figure 1). Also among natural tree hollows, a significant proportion have entrances close to the ground (Ranius et al., 2009). In 2014, each box was filled with 400 L of leaves from the surrounding area and 400 L of wood chips from deciduous trees to emulate wood mould, which typically accumulates in tree hollows. The boxes were constructed of 25 mm-thick walls of spruce wood and a lid. Two holes (20 mm in diameter) just below the roof on each side of the boxes allowed small animals to interact with the interior, while four holes in the lid allowed rainwater to enter. To enhance decomposition, 25 L of water was added while the floor of the boxes was covered with a tarpaulin to promote moisture retention. When necessary, leaf litter and wood chips were added in the following years to keep the original amount of wood mould. Thus, the boxes allowed us to study the saproxylic beetle fauna under highly standardised local conditions.

Beetle data collection

In 2019, two pitfall traps were placed inside each box to collect saproxylic beetles. The traps consisted of a plastic jar with a top diameter of 65 mm and were filled with a 50% water/propylene glycol mix and detergents to reduce surface tension. Emptying and exchange of traps were performed every four weeks from the beginning of May until the end of August. In total, species richness and abundance of 56 wood mould boxes were sampled. Since saproxylic beetles were strongly dominating among the collected invertebrates, only this insect group was chosen for the subsequent analysis. The sampled beetles were identified to species level by Stanislav Snäll and Gunnar Sjödin. For the analysis, those species were extracted which were classified as saproxylic (both obligate and facultative) at least in one of the following sources: Ekström (2020), and Schmidl and Bußler (2004). We also retrieved information on red-list status in the national Swedish Red List (Eide, 2020). All beetle species were categorised into one of the following microhabitat groups: (i) *Rot*: Rotten wood in any part of the trunks, even on the outside of the trunk, (ii) *Hollow*: Rotten wood in trunks, exclusively from the inside, in hollows (not associated with animal nests), (iii) *Nest*: Animal nests in tree hollows, (iv) *Fungi*: Fruiting bodies of saproxylic fungi, (v) *Mould*: Mycelia or mould, (vi) *Dry*: Dead, dry wood in trunks, (vii) *Fresh*: Under fresh bark and sap runs, according to a development of the categorisation by Ranius and Jansson (2002) (Appendix S1: Table S10).

Temperature data collection and measurement of environmental variables

In April 2022, we installed temperature loggers (SL52T, Signatrol) to assess the microclimatic temperature inside and around each box and in hollow trees nearby. Due to missing boxes in 2022, microclimatic temperature was measured in 49 of the initial 56 wood mould boxes. One logger was placed 20 cm below the surface of the wood mould at the centre of each box. A second logger was attached to the north-facing wall inside each box, while a third logger was attached at the closest tree to each box (max. 2 m distance), 2 m from the ground and at the north-facing side (Figure 1). If possible, a fourth logger was placed into the wood mould of a hollow tree in the close surroundings (max. 20 m distance). These trees were oak, beech, or birch, and the entrance holes with loggers were, on average, 1.20 m above the ground and 30 cm in diameter. We installed temperature loggers both inside and outside the boxes and in hollow trees since saproxylic beetles can be affected by both the microclimatic temperature inside the box, where larval development occurs, and outside air temperatures during the time between beetle emergence and oviposition. The loggers measured the temperature hourly from April 11th until September 26th, 2022. Due to lost loggers and destroyed boxes, the total number of functioning temperature loggers was 29 in the wood mould of the boxes, 39 on the walls inside the boxes, and 42 outside the boxes. Only six loggers were placed in tree cavities due to a lack of available hollow trees around the wood mould boxes. We compared the hourly measurements of all loggers with the hourly measurements of weather stations nearby. The lowest and highest temperatures measured by the weather stations across all cities were −5 and +40°C, respectively (hourly measurements from April until September 2022). Temperature loggers with poorly charged batteries had a tendency to record unrealistic measurements. Therefore, we excluded values below −10°C and above +50°C in our dataset, resulting in 0.04% of all data points being excluded. As a proxy for regional climate, we used mean annual temperature data from 1995 to 2020 (SMHI, 2023; Appendix S1: Table S2). To compare macroclimate with our measured microclimatic temperature, we used temperature data from April to September 2022 from nearby weather stations (SMHI, 2023; Appendix S1: Table S2). Furthermore, to compare our measured microclimatic temperature with temperature from 2019, when beetles were collected, we extracted temperature from April to September 2019 from nearby weather stations (SMHI, 2023; Appendix S1: Table S2). In that way, we found that the measured microclimatic temperatures from 2022 were similar to the temperatures in 2019 for the same months when the beetles were collected.

We estimated canopy openness above each box by taking photographs with a fisheye lens 1 m above the ground. The photos were analysed with Gap Light Analyser (Frazer, 1999), which calculates the percentage of the area not covered by a canopy. Further, as a measure of habitat amount, the number of cavity trees was counted in a radius of 20 m around each box. Hereby, we considered living trees with a cavity with at least one entrance hole (with a diameter >10 cm) as a cavity tree. Cavities with smaller entrance holes were excluded since the amount of wood mould is then often at a magnitude of decilitres, whereas with a larger entrance hole it is typically between one or a few hundred litres (Ranius et al., 2009), and thus harbours much more habitat for saproxylic invertebrates. Again, due to missing boxes in 2022, canopy openness and the number of hollow trees were measured and counted around 49 of the initial 56 wood mould boxes.

To assess the density of urban structures (i.e. potential dispersal barriers) and tree cover (i.e. habitat amount) around each box, we used ArcGIS Pro 3.0.3 and extracted map data from the NMD database (Nationella Marktäckedata, 2023) with a resolution of 10 × 10 m. The data are provided in raster format and include 25 land cover categories. These were reclassified into two groups: 'tree cover' and 'density of urban structures'. Fourteen categories representing areas with >10% tree canopy cover (e.g. forests, parks) were grouped as 'tree cover,' while three categories representing artificial built areas without vegetation were grouped as 'density of urban structures' (Appendix S1: Table S11). Subsequently, we calculated the percentage area of density of urban structures and tree cover in a 3000, 1000, 500, and 100 m buffer around each box. We tested this range of radii since it reflects the spatial scales of response for individual species of saproxylic invertebrates in hollow trees (Bergman et al., 2012; Ranius et al., 2024). We identified the spatial scale of response in our study by comparing which of them generated the best fit with our data. Furthermore, the boxes were categorised into those with the highest ('highly urbanised') and the lowest ('sparsely urbanised') density of urban structures within the 100 m buffer (Appendix S1: Table S1). We considered four with the highest density of urban structures as 'highly urbanised', and four boxes with the lowest density of urban structures as 'sparsely urbanised' (three when there were a total of eight boxes per city).

Calculation of Community Temperature Index

To examine how the community composition of saproxylic beetles responds to a warmer urban microclimate, we calculated the Community Temperature Index (CTI; Devictor et al., 2008). It is estimated as the mean STI (Species Temperature Index) for all species in a community (Devictor et al., 2008; Fadrique et al., 2018). STI, in turn, is the long-term average temperature experienced by a given species over its occurrence range (Devictor et al., 2008). We calculated STI as the mean temperature (1970–2000) for each species' occurrence range from the WorldClim 2.1 dataset (Fick & Hijmans, 2017) with a 2.5 min (*c.* 4.5 × 4.5 km) resolution in R (package *geodata*; Hijmans et al., 2023). The STI was calculated without weighting by the number of observations of each species in each pixel. To estimate the occurrence range of each species, we used occurrence maps available from GBIF (Global Biodiversity Information Facility, Chamberlain et al., 2023). We calculated the CTI for each box by averaging STI values of the species present in that box weighted by species abundance (Appendix S1: Tables S3 and S10).

Statistical analyses

Statistical analyses were conducted in R 4.2.0 (R Core Team, 2020). The number of saproxylic beetle species (hereafter *species richness*) and the number of individuals (hereafter *abundance*) were calculated at the box level. Due to missing values for canopy openness, the number of hollow trees, and microclimatic mean temperature, 49 of the initial 56 wood mould boxes were analysed, with 22 wood mould boxes classified as highly and sparsely urbanised, respectively.

To test the effect of environmental filters (density of urban structures, tree cover, and microclimate) on species richness and abundance (prediction I), we fitted generalised linear mixed effects models and included species richness and abundance, respectively, as response variables (*glmmTMB* from package *glmmTMB*, Brooks et al., 2017). For the model with species richness as the response variable, we used a negative binomial distribution, whereas for the abundance model, we log-transformed the abundance data and used a Gaussian distribution. Due to a strong correlation ($r = -0.54$, $p < 0.01$), tree cover and the density of urban structures were used as explanatory variables in separate models, but the same additional predictor variables were included: regional temperature, canopy openness, and number of hollow trees. As a measure of regional temperature, we used the mean annual temperature (1995–2020) of each city (SMHI, 2023; Appendix S1: Table S2). City identity was included as a random effect variable. We applied eight different models four with the density of urban structures (100, 500, 1000, 3000 m) and four with tree cover (100, 500, 1000, 3000 m), and calculated the second-order Akaike's information criterion (*AICc* from package *MuMIn*; Barton, 2023). We compared the AIC of the four different spatial scales and presented only results using scales that generated the lowest AIC, both for the models including the density of urban structure and tree cover. In separate models, we tested the effect of microclimatic mean temperature on species richness and abundance and included regional climate as covariates.

To test the effect of environmental filters on saproxylic beetle species composition, we applied a permutational multivariate analysis of variance (PERMANOVA, function *adonis* from R package *vegan*; Oksanen, 2010) with microclimatic mean temperature, density of urban structures, and tree cover as explanatory variables. To control for the climate in the study cities, we included regional temperature (mean annual temperature, 1995–2020, SMHI, 2023; Appendix S1: Table S2) as covariates. We present only those results that generated the highest R^2, both for the models including the density of urban structures and tree cover.

To test the urban homogenisation hypothesis (prediction II), we applied a betadispersion analysis (function *betadisper* from R package *vegan*; Oksanen, 2010) with the identity of highly and sparsely urbanised wood mould boxes as a grouping factor. Subsequently, we performed an ANOVA.

To test whether the microclimatic mean temperature increases with the density of urban structures and decreases with tree cover, we applied linear mixed-effects models with a Gaussian distribution for each buffer (*lme* from package *nlme*, Pinheiro, 2012). Microclimatic mean temperature was used as the response variable, and tree cover and the density of urban structures were used as explanatory variables in separate models, but the same additional predictor variables were included: regional temperature, logger position, and canopy openness. As a measure of regional temperature, we used the mean temperature from April until September 2022 for each city (SMHI, 2023; Appendix S1: Table S2), while city identity was used as the random effect variable. Subsequently, we calculated the effect size for each explanatory variable (only for the models that received the lowest AIC) with *cohens_f_squared* from the function *effectsize* (Ben-Shachar et al., 2020). Additionally, we ran the same linear mixed-effects model with daily microclimatic temperature fluctuation as the response variable. The daily mean microclimatic temperature fluctuation was calculated as the mean standard deviation across all measurements per logger and per day. Again, only results using scales that generated the lowest AIC were presented, both for the models including the density of urban structure and tree cover.

To test the urban heat island effect on saproxylic beetle species (prediction III), we used generalised linear mixed-effects models *glmmTMB* with CTI as the response variable and used a Gaussian distribution. The density of urban structures and tree cover was used as explanatory variables in separate models, but the same additional predictor variables were included: regional temperature and canopy openness. As a measure of regional temperature, we used the mean annual temperature (1995–2020) of each city (SMHI, 2023; Appendix S1: Table S2). City identity was included as a random effect variable. Only results using scales that generated the lowest AIC were presented, both for the models including the density of urban structure and tree cover. In separate models, we tested the effect of microclimatic mean temperature on the CTI and included regional climate as covariates.

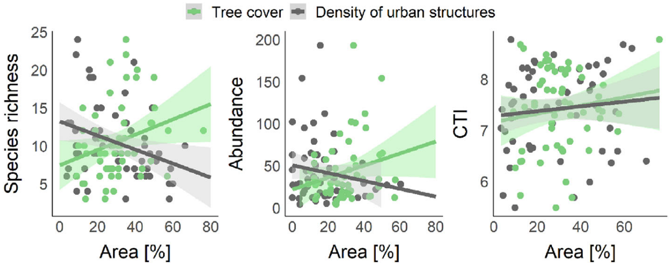

FIGURE 2 Effect of tree cover and density of urban structures on species richness, abundance, and CTI. Dots represent species richness and abundance per box. The buffer sizes used for the density of urban structures and tree cover refer to those that generated the lowest AIC in the respective models.

RESULTS

In total, we collected 3464 individuals of 105 saproxylic beetle species with an average number of 62 individuals and 11 species per box. Among all species, five were red-listed as near-threatened (NT): *Ptenidium gressneri*, *Trinodes hirtus*, *Mycetophagus quadriguttatus*, *Aderus populneus*, and *Uloma culinaris*. According to our urbanisation categories, two of the red-listed species occurred in highly urbanised boxes, and three in sparsely urbanised boxes. We classified 33% of all collected saproxylic species as associated with tree hollows (*Hollow* and *Nest*; Appendix S1: Table S10), 20% with rotten wood (*Rot*), 23% with fungi (*Fungi* and *Mould*), 18% with fresh dead wood (*Fresh*), and 3% with dry dead wood in trunks (*Dry*).

Effect of environmental filters on species richness and abundance of saproxylic beetles

In the models with the best fit, species richness of saproxylic beetles decreased significantly with the density of urban structures (within a 1000 m buffer), but increased significantly with tree cover (within a 500 m buffer) (Figure 2, Table 1; Appendix S1: Tables S3, S4 and S7). Microclimatic mean temperature had no effect on species richness (Appendix S1: Table S8).

Saproxylic beetle abundance was not affected by the density of urban structures, whereas tree cover had a strong positive effect (within a 500 m buffer) (Figure 2, Table 1; Appendix S1: Tables S3, S4 and S7). In contrast, saproxylic beetle abundance decreased significantly with both microclimatic mean temperature and canopy openness (Table 1, Appendix S1: Tables S4, S7 and S8).

Effect of environmental filters on species composition and test of urban homogenisation hypothesis

Saproxylic beetle species composition changed marginally with the density of urban structures (within a 100 m buffer) (PERMANOVA: $R^2 = 0.03$, $p = 0.09$), and significantly with the microclimatic mean temperature (PERMANOVA: $R^2 = 0.04$, $p = 0.02$) and tree cover (within a 3000 m buffer) (PERMANOVA: $R^2 = 0.03$, $p = 0.02$) (Appendix S1: Table S9).

There was no difference in the average community similarity between wood mould boxes in highly versus sparsely urbanised sites ($F = 1.1$, $p = 0.35$; Figure 3).

Effect of environmental filters on microclimate and CTI

The microclimatic mean temperature was not affected by the regional temperature and did not differ between logger positions (inside the wood mould in boxes: 15.9°C, inside boxes: 16.02°C, outside boxes: 16.09°C, inside tree cavities: 15.75°C). Microclimatic mean temperature increased with canopy openness and density of urban structures (within 3000 m buffer) but decreased marginally with tree cover (within 3000 m buffer) (Table 2; Appendix S1: Table S5 and S7).

Canopy openness had the highest effect size in both models—either including density of urban structures or tree cover—with Cohen's $d = 0.24$ and 0.18, respectively. For the density of urban structures, Cohen's *d* was 0.12, while tree cover had the lowest effect size with Cohen's $d = 0.02$.

The daily microclimatic temperature fluctuations (mean standard deviation across all measurements per logger and per day) differed strongly between logger positions, with much narrower temperature fluctuations inside the wood mould in the boxes than outside the boxes (inside the wood mould in the boxes: 0.55°C, inside boxes: 2.96°C, outside boxes: 2.68, inside tree cavities: 1.45°C). Regional temperature and density of urban structures had no effect, whereas daily microclimatic temperature fluctuation increased significantly with canopy openness and decreased significantly with tree cover (within 3000 m buffer) (Table 2, Appendix S1: Table S6 and S7).

CTI increased significantly with regional temperature and decreased, surprisingly, with canopy openness (Figure 2, Table 1;

TABLE 1 Wald-Chi square test with species richness, abundance and CTI as response variables and regional temperature (1995–2020, SMHI), canopy openness, number of cavity trees, density of urban structures, and tree cover, respectively, as explanatory variables.

	Species richness			Abundance			CTI		
	AICc: 284.1			AICc: 139.6			AICc: 120.9		
	1000 m			100 m			500 m		
	χ^2	df	*p*-value	χ^2	df	*p*-value	χ^2	df	*p*-value
Regional temperature	7.5	1	**0.03**	2.2	1	0.14	9.3	1	**<0.01**
Number of cavity trees	0.1	1	0.72	0.9	1	0.32	–	–	–
Canopy openness	3.8	1	**0.05**	4.6	1	**0.03**	4.6	1	**0.03**
Urban structures	7.0	1	**<0.01**	2.9	1	*0.09*	0.09	1	0.77
	Species richness			**Abundance**			**CTI**		
	AICc: 286.5			**AICc: 134.7**			**AICc: 116.5**		
	500 m			**500 m**			**500 m**		
	χ^2	df	*p*-value	χ^2	df	*p*-value	χ^2	df	*p*-value
Regional temperature	11.4	1	**<0.01**	2.7	1	0.1	7.6	1	**<0.01**
Number of cavity trees	0.02	1	0.88	0.2	1	0.66	–	–	–
Canopy openness	2.2	1	0.14	6.7	1	**<0.01**	7.4	1	**<0.01**
Tree cover	4.9	1	**0.03**	8.4	1	**<0.01**.	4.7	1	**0.03**

Note: Each model was calculated in a 3000, 1000, 500 and 100 m buffer, but only those buffer models are presented that received the lowest AIC value (all buffer models are presented in the Appendix S1). Numbers in bold indicate a significant effect (<0.05), numbers in italic indicate a marginal significant effect (<0.1).

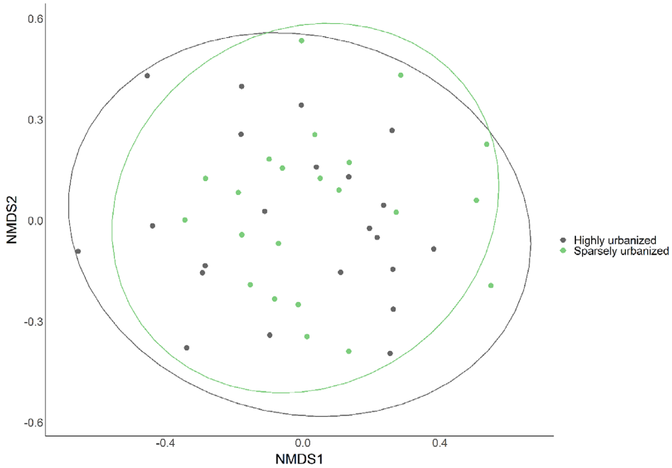

FIGURE 3 NMDS of saproxylic beetle compositions across highly urbanised sites, that is with a high density of urban structures around wood mould boxes, and sparsely urbanised sites, that is with a low density of urban structures around wood mould boxes, across all studied cities.

Appendix S1: Tables S3, S4 and S7). Density of urban structures and microclimatic mean temperature had no effect (Appendix S1: Tables S4, S7 and S8), but tree cover affected CTI positively (within 500 m buffer) (Figure 2, Table 1; Appendix S1: Tables S4 and S7).

DISCUSSION

Species richness of saproxylic beetles decreased with the density of urban structures, while abundance was positively affected by tree cover. Species composition was strongly shaped by microclimate and

TABLE 2 Wald-Chi square test with microclimatic mean temperature and microclimatic temperature fluctuation as response variables and regional temperature (SMHI, 2023), logger location, density of urban structures, and tree cover, respectively, as explanatory variables.

	Microclimatic temperature			**Microclimatic temperature fluctuation**		
	AICc: 299.2			**AICc: 235.8**		
	3000 m			**100 m**		
	χ^2	**df**	***p*-value**	χ^2	**df**	***p*-value**
Regional temperature	0.01	1	0.91	1.4	1	0.24
Logger position	3.0	3	0.39	416.7	3	**<0.01**
Canopy openness	8.6	1	**<0.01**	64.9	1	**<0.01**
Urban structures	4.2	1	**<0.01**	1.9	1	0.17

	Microclimatic temperature			**Microclimatic temperature fluctuation**		
	AICc: 304.9			**AICc: 232.9**		
	3000 m			**3000 m**		
	χ^2	**df**	***p*-value**	χ^2	**df**	***p*-value**
Regional temperature	0.001	1	0.97	1.6	1	0.21
Logger position	3.6	3	0.31	423.2	3	**<0.01**
Canopy openness	10.9	1	**<0.01**	47.6	1	**<0.01**
Tree cover	3.6	1	*0.06*	5.1	1	**0.02**

Note: Each model was calculated in a 3000, 1000, 500, and 100 m buffer, but only those buffer models are presented that received the lowest AIC value (all buffer models are presented in the Appendix S1). Numbers in bold indicate a significant effect (<0.05), numbers in italic indicate a marginal significant effect (<0.1).

tree cover. This supports the hypothesis that those factors can act as environmental filters for saproxylic beetle communities. We did not find support for the urban homogenisation hypothesis, and despite an observed urban heat island effect and cooling effect of high canopy cover, CTI did not increase with the density of urban structures or decrease with tree cover.

Effects of environmental filters on diversity patterns of saproxylic beetles

The density of urban structures and tree cover was highly correlated, making it impossible to determine which factor is the more important driver of saproxylic beetle fauna. Nevertheless, species richness decreased with the density of urban structures (reflecting dispersal barriers), whereas saproxylic beetle abundance increased with tree cover (reflecting habitat amount), supporting prediction (I). The increasing abundance of saproxylic beetles with tree cover indicates that at least to some extent habitat amount has positive effects on the saproxylic beetle fauna. This is in line with Fattorini and Galassi (2016), who observed an increasing diversity of saproxylic beetles particularly in urban forest areas, and Marker (2019), who reported a higher species richness of saproxylic beetles closer to urban forests. It has been shown that especially passive dispersers, such as rotifers and cladocerans, are not affected by urbanisation, whereas the diversity of active dispersers, such as butterflies and ground beetles, decreases with urbanisation (Piano et al., 2020). As the dispersal ability can highly vary between saproxylic beetle species (Feldhaar and Schauer, 2018), the saproxylic beetle species in our study might be differently affected by urbanisation. In a non-urban context, studies on saproxylic beetles and other forest organisms have also found a positive relationship between habitat amount in the surrounding landscape and local species richness (Sverdrup-Thygeson et al., 2014) or abundance (Undin et al., 2024). Furthermore, species richness decreased with the density of urban structures, which can be explained by the strong negative correlation with tree cover but also by an increasing habitat isolation, since urban structures can act as dispersal barriers (Corcos et al., 2019; Leidner and Haddad, 2011). In further research, it would be useful to disentangle the separate effects of habitat amount and dispersal barriers on various insect groups, including saproxylic insects. That can be possible by designing the study so these two variables are not correlated and using more precise proxies of dispersal barriers.

We found that 33% of the saproxylic beetle species in the sampled wood mould boxes were associated with hollow trees. A previous study, where pitfall traps were placed in cavities of oaks in the same part of Sweden, found a similar proportion (37%) of saproxylic beetles associated with hollow trees (Ranius and Jansson 2002). This indicates that our boxes are indeed harbouring a fauna similar to that found in tree hollows. Due to safety and aesthetic reasons, dead wood and large old trees have often been removed in urban environments (Carpaneto et al., 2010), and trees need a long time to develop until hollows are formed (Ranius et al., 2009). Therefore, boxes with wood mould can be useful since they constitute microhabitats for the saproxylic insect fauna within only a few years after the establishment.

Besides the density of urban structures, we found the saproxylic beetle abundance to decrease with microclimatic temperature and canopy openness. This is in contrast to previous studies, reporting higher abundances in sun-exposed dead wood (Lettenmaier et al., 2022; Goßmann et al., 2024; Seibold et al., 2016). The negative effect of a warmer microclimate can be due to its strong correlation with the density of urban structures, which might suppress the effect of microclimate per se on saproxylic beetles. However, the fact that saproxylic beetle abundance decreases also with canopy openness could be related to too-warm and dry conditions in sun-exposed wood mould boxes. In line with that, Goßmann et al. (2024) found saproxylic beetle species richness to be highest in intermediately shaded dead wood in southern Sweden. Note that the summer in 2018 was extraordinarily warm (and we sampled adult beetles in 2019). Thus, the survival rate of the larvae might have been reduced in wood mould boxes with the highest microclimatic temperatures. For other insect species, it has been found that the summer of 2018 had a strong detrimental effect (Johansson et al., 2020). Thus, in urban areas, saproxylic beetle diversity might be promoted by increasing canopy cover, especially when considering the effect of a warming climate.

Species composition is strongly shaped by microclimate and tree cover, but no support for the urban homogenisation hypothesis

Saproxylic beetle species composition changed significantly with microclimatic mean temperature, indicating that saproxylic beetle species composition differs among microhabitats with different microclimatic temperatures. Also, Schauer et al. (2018) observed species turnover of saproxylic beetles with varying temperature. The differences in species composition with varying microclimatic temperatures could be due to different thermal preferences of saproxylic beetle species. Goßmann et al. (2024) have indeed shown that the extent to which shade level affects saproxylic beetles depends on the species' thermal preferences. Conclusively, also in urban areas, different degrees of canopy openness resulting in various microclimatic conditions lead to differences in saproxylic beetle species composition.

We found the saproxylic beetle species composition to change with tree cover within a 3000 m buffer. This is in line with Meyer et al. (2021), who found a change in saproxylic insect composition with different forest sizes within a 500 m buffer. It has previously been shown that differences in habitat amount can lead to differences in species composition due to a correlation between habitat amount and habitat heterogeneity (Seibold et al., 2016). In our study, different tree species and the amount and type of dead wood in the surrounding habitat of the wood mould boxes could have led to different species compositions of saproxylic beetles.

Species composition differed similarly across highly and sparsely urbanised wood mould boxes, indicating that communities across highly urbanised sites were not more homogeneous than species compositions across sparsely urbanised sites. This is in contrast to prediction (II) and several previous studies on different species groups, which have provided clear support for the urban homogenisation hypothesis (McKinney, 2006; Merckx and Van Dyck, 2019; Sidemo-Holm et al., 2022). One reason why we did not find support for this hypothesis might be that the trees and forest habitats around highly urbanised boxes were equally homogenous as those around sparsely urbanised boxes. For instance, along the whole urbanisation gradient, the majority of the trees in the surrounding area of all boxes were deciduous, with oaks being the dominating tree species.

Effect of environmental filters on microclimate and CTI

Microclimatic mean temperature increased with the density of urban structures, which is consistent with the urban heat island effect (Kłysik and Fortuniak, 1999) and decreased with tree cover, indicating a cooling effect of tree habitats. Furthermore, canopy openness (measured at each box) had strong positive effects on the microclimatic mean temperature and explained the microclimatic temperature best. This means that the close environmental surroundings (canopy above each wood mould box) affect the microclimate more than the large-scale surroundings (tree cover and density of urban structures in a 3000 m buffer), indicating that the urban heat island effect can be buffered by increasing canopy cover. The microclimatic temperature inside the wood mould in the boxes and inside hollow trees was similar and slightly lower than ambient temperatures. The daily microclimatic temperature fluctuation inside the wood mould in the boxes was even narrower than inside hollow trees, and both were narrower than the daily ambient temperature fluctuation, indicating stable microclimatic conditions especially inside wood mould boxes, but also inside hollow trees. This suggests that wood mould boxes can resemble the microclimatic conditions of hollow trees, which is important since a stable microclimate seems to be a key factor for saproxylic insects specialised on tree hollows (Ranius et al. 2024).

Despite the significant effect of the density of urban structures on the microclimatic temperature, there was no effect on the CTI, which contrasts with prediction (III). In fact, we found a higher CTI at sites with a low canopy openness in the close surroundings of the boxes and high tree cover in the surrounding landscape. This contrasts with our prediction that tree cover might decrease the occurrence of thermophilous species and thus promote species that depend on cooler microclimatic conditions. An explanation for why we found contradictory effects might be that CTI does not truly reflect the thermal preferences of saproxylic beetle species. STI and CTI are based on large-scale ambient temperatures, whereas saproxylic beetles are highly dependent on microclimatic conditions in dead wood. Microclimatic temperature can differ greatly from ambient temperatures (De Frenne et al., 2019), and thus, species might select microhabitats that do not correspond directly to the ambient temperatures captured by the temperature indices.

CONCLUSIONS

We conclude that it is possible to favour saproxylic insects in cities by maintaining and increasing the landscape-level tree cover. Specifically, since we found the species composition to differ depending on microclimatic conditions in urban areas, the diversity of saproxylic beetles can be promoted by maintaining and establishing variation in canopy openness. Since large old trees are often absent in urban environments, there is also a need for restoring microhabitats to favour saproxylic insects. Wood mould boxes can be used to establish microhabitats for the saproxylic insect fauna. We showed that the microclimatic conditions inside the wood mould of the boxes are similar to those inside hollow trees and that those boxes harbour many saproxylic beetle species that are usually found inside hollow trees. This supports the idea that wood mould boxes could at least partly serve as artificial substitutes for tree hollows.

AUTHOR CONTRIBUTIONS

Anika Gossmann: Conceptualization; methodology; data curation; formal analysis; investigation; visualization; writing – original draft. **Nicklas Jansson:** Conceptualization; methodology; writing – review and editing. **Erik Öckinger:** Supervision; writing – review and editing. **Caroline Ryding:** Methodology. **Thomas Ranius:** Conceptualization; methodology; supervision; resources; project administration; validation; investigation; funding acquisition; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data is archived in SND (Swedish Nationell Datatjänst) and can be found here: https://doi.org/10.5878/kvn2-4q83.

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REFERENCES

Andersson, H. (1999) Rödlistade eller sällsynta evertebrater knutna till ihåliga, murkna eller savande träd samt trädsvampar i Lunds stad [Red-listed or rare invertebrates associated with hollow, rotting, or sapping trees or polypores in the town of Lund. In Swedish with an English abstract]. *Entomologisk Tidskrift*, 120, 169–183.

Baldock, K., Goddard, M., Hicks, D., Kunin, W., Mitschunas, N., Osgathorpe, L. et al. (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142849.

Barton, K. 2023. MuMIn: Multi-Model Inference. R package version 1.47.5. – https://CRAN.R-project.org/package=MuMIn.

Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18, 581–592.

Ben-Shachar, M., Lüdecke, D. & Makowski, D. (2020) Effectsize: estimation of effect size indices and standardized parameters. *Journal of Open Source Software*, 5, 2815.

Bergman, K., Jansson, N., Claesson, K., Palmer, M. & Milberg, P. (2012) How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management*, 265, 133–141.

Bernardino, G., Mesquita, V., Bobrowiec, P., Iannuzzi, L., Salomão, R. & Cornelius, C. (2024) Habitat loss reduces abundance and body size of forest-dwelling dung beetles in an Amazonian urban landscape. *Urban Ecosystems*, 27, 1175–1190.

Blair, R. (2001) Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna? In: Lockwood, J.L. & McKinney, M.L. (Eds.) *Biotic homogenization*. Boston, MA: Springer US, pp. 33–56.

Blair, R. & Johnson, E. (2008) Suburban habitats and their role for birds in the urban–rural habitat network: points of local invasion and extinction? *Landscape Ecology*, 23, 1157–1169.

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Calix, M., Alexander, K., Nieto, A., Dodelin, B., Soldati, F., Telnov, D. et al. (2018) *European red list of saproxylic beetles*. Brussels, Belgium: IUCN.

Carpaneto, G., Mazziotta, A., Coletti, G., Luiselli, L. & Audisio, P. (2010) Conflict between insect conservation and public safety: the case study of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *Journal of Insect Conservation*, 14, 555–565.

Catterall, C., Cousin, J., Piper, S. & Johnson, G. (2010) Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? *Diversity and Distributions*, 16, 559–570.

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L. et al. (2023) *rgbif: Interface to the global biodiversity information facility API*. R package version 3.7.2.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M. & Dinetti, M. (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation*, 127, 336–344.

Corcos, D., Cerretti, P., Caruso, V., Mei, M., Falco, M. & Marini, L. (2019) Impact of urbanization on predator and parasitoid insects at multiple spatial scales. *PLoS One*, 14, e0214068.

Dániel-Ferreira, J., Berggren, Å., Wissman, J. & Öckinger, E. (2022) Road verges are corridors and roads barriers for the movement of flower-visiting insects. *Ecography*, 2022, 5847.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B., Hylander, K., Luoto, M. et al. (2019) Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3, 744–749.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2743–2748.

Dianzinga, N., Moutoussamy, M., Sadeyen, J., Ravaomanarivo, L. & Frago, E. (2020) The interacting effect of habitat amount, habitat diversity and fragmentation on insect diversity along elevational gradients. *Journal of Biogeography*, 47, 2377–2391.

Eide, W. (2020) *Rödlistade arter i Sverige 2020*. Uppsala: SLU Artdatabanken.

Ekström, L. (2020) *The importance of ecoparks for saproxylic beetles* [WWW document]. Available from: https://stud.epsilon.slu.se/15764/ [Accessed 21st June 2023].

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J. et al. (2018) Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, 564, 207–212 h.

Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663.

Fattorini, S. & Galassi, D. (2016) Role of urban green spaces for saproxylic beetle conservation: a case study of tenebrionids in Rome, Italy. *Journal of Insect Conservation*, 20, 737–745.

Feldhaar, H. & Schauer, B. (2018) Dispersal of saproxylic insects. In: *Saproxylic insects: diversity, ecology and conservation*, Cham: Springer International Publishing, pp. 515–546.

Fick, S. & Hijmans, R. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Franzén, M., Betzholtz, P., Pettersson, L. & Forsman, A. (2020) Urban moth communities suggest that life in the city favours thermophilic multi-dimensional generalists. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20193014.

Frazer, G. (1999) *Gap light analyzer (GLA)*. Users Manual Program Document Version 20 36.

Fröhlich, A. & Ciach, M. (2020) Dead wood resources vary across different types of urban green spaces and depend on property prices. *Landscape and Urban Planning*, 197, 103747.

Goßmann, A., Öckinger, E., Schroeder, M., Lindman, L. & Ranius, T. (2024) Interaction between regional temperature and shade level shapes saproxylic beetle communities. *Diversity and Distributions*, 30, e13836.

Grilo, F., Pinho, P., Aleixo, C., Catita, C., Silva, P., Lopes, N. et al. (2020) Using green to cool the grey: modelling the cooling effect of green spaces with a high spatial resolution. *Science of the Total Environment*, 724, 138182.

Hijmans, R., Ghosh, A. & Mandel, A. (2023) *Geodata: download geographic data*. R package.

Jansson, N., Ranius, T., Larsson, A. & Milberg, P. (2009) Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodiversity and Conservation*, 18, 3891–3908.

Johansson, V., Kindvall, O., Askling, J. & Franzén, M. (2020) Extreme weather affects colonization extinction dynamics and the persistence of a threatened butterfly. *Journal of Applied Ecology*, 57, 1068–1077.

Johansson, V., Koffman, A., Hedblom, M., Deboni, G. & Andersson, P. (2018) Estimates of accessible food resources for pollinators in urban landscapes should take landscape friction into account. *Ecosphere*, 9, e02486.

Kłysik, K. & Fortuniak, K. (1999) Temporal and spatial characteristics of the urban heat Island of Łódź, Poland. *Atmospheric Environment*, 33, 3885–3895.

Knapp, S. & Wittig, R. (2012) An analysis of temporal homogenisation and differentiation in Central European village floras. *Basic and Applied Ecology*, 13, 319–327.

Knop, E. (2016) Biotic homogenization of three insect groups due to urbanization. *Global Change Biology*, 22, 228–236.

Leidner, A. & Haddad, N. (2011) Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conservation Biology*, 25, 1022–1031.

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J. et al. (2022) Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. *Oecologia*, 198, 825–834.

Lindenmayer, D., Laurance, W. & Franklin, J. (2012) Global decline in large old trees. *Science*, 338, 1305–1306.

Lindman, L., Öckinger, E. & Ranius, T. (2023) Microclimate in hollow trees and how it affects an inhabiting beetle species, Osmoderma eremita. *Ecological Entomology*, 48, 112–126.

Lokatis, S. & Jeschke, J. (2022) Urban biotic homogenization: approaches and knowledge gaps. *Ecological Applications*, 32, e2703.

Marker, J. (2019) *Effect of distance to urban areas on saproxylic beetles in urban forests* (Master Thesis). Karlstad University.

McKinney, M. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247–260.

McKinney, M. (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, 11, 161–176.

Menke, S., Guénard, B., Sexton, J., Weiser, M., Dunn, R. & Silverman, J. (2011) Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystems*, 14, 135–163.

Merckx, T. & Van Dyck, H. (2019) Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecology and Biogeography*, 28, 1440–1455.

Meyer, S., Rusterholz, H. & Baur, B. (2021) Saproxylic insects and fungi in deciduous forests along a rural–urban gradient. *Ecology and Evolution*, 11, 1634–1652.

Nationella Marktäckedata (NMD) [WWW document], 2023. Available from: https://www.naturvardsverket.se/verktyg-och-tjanster/kartor-och-karttjanster/nationella-marktackedata/ [Accessed 30th June 2023].

Oke, T. (1995) *The heat Island of the urban boundary layer: characteristics, causes and effects*. Wind climate in cities, pp. 81–107.

Oksanen, J. (2010) *Vegan: community ecology package*. Available from: https://cran.r-project.org

Parris, K. (2016) *Ecology of urban environments*. Hoboken, NJ: John Wiley & Sons.

Peuhu, E., Thomssen, P. & Siitonen, J. (2019) Comparison of three trap types in sampling saproxylic beetles living in hollow urban trees. *Journal of Insect Conservation*, 23, 75–87.

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D., Isaia, M. et al. (2017) Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23, 2554–2564.

Piano, E., Souffreau, C., Merckx, T., Baardsen, L., Backeljau, T., Bonte, D. et al. (2020) Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, 26, 1196–1211.

Pilskog, H., Birkemoe, T., Evju, M. & Sverdrup-Thygeson, A. (2020) Species composition of beetles grouped by host association in hollow oaks reveals management-relevant patterns. *Journal of Insect Conservation*, 24, 65–86.

Pinheiro, J. (2012) *nlme: linear and nonlinear mixed-effects models*. R package version 3.1-103.

R Core Team. (2020) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: http://www.R-project.org/

Ranius, T., Gibbons, P. & Lindenmayer, D. (2024) Habitat requirements of deadwood-dependent invertebrates that occupy tree hollows. *Biological Reviews*, 99, 2022–2034.

Ranius, T. & Jansson, N. (2002) A comparison of three methods to survey saproxylic beetles in hollow oaks. *Biodiversity and Conservation*, 11, 1759–1771.

Ranius, T., Svensson, G., Berg, N., Niklasson, M. & Larsson, M. (2009) The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Annales Zoologici Fennici*, 46, 205–216.

Schauer, B., Steinbauer, M., Vailshery, L., Müller, J., Feldhaar, H. & Obermaier, E. (2018) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. *Biodiversity and Conservation*, 27, 853–869.

Schmidl, V. & Bußler, H. (2004) Ökologische gilden xylobionter käfer Deutschlands. *Naturschutz und Landschaftsplanung*, 36, 202–218.

Schwartz, M., Thorne, J. & Viers, J. (2006) Biotic homogenization of the California flora in urban and urbanizing regions. *Biological Conservation*, 127, 282–291.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S. et al. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53, 934–943.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M., Lorz, J. et al. (2021) The contribution of insects to global forest deadwood decomposition. *Nature*, 597, 77–81.

Sidemo-Holm, W., Ekroos, J., Reina García, S., Söderström, B. & Hedblom, M. (2022) Urbanization causes biotic homogenization of woodland bird communities at multiple spatial scales. *Global Change Biology*, 28, 6152–6164.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11–41.

SMHI. (2023) *Historical data*. Available from: https://www.smhi.se/data/meteorologi/temperaturee

Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J. (2014) Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodiversity and Conservation*, 23, 513–535.

Teixeira, F., Rytwinski, T. & Fahrig, L. (2020) Inference in road ecology research: what we know versus what we think we know. *Biology Letters*, 16, 20200140.

Undin, M., Atrena, A., Carlsson, F., Edman, M., Jonsson, B. & Sandström, J. (2024) To what extent does surrounding landscape explain stand-level occurrence of conservation-relevant species in fragmented boreal and hemi-boreal forest? A systematic review. *Environmental Evidence*, 13, 19.

Vellend, M. (2016) *The theory of ecological communities (MPB-57)*. Princeton, NJ: Princeton University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1.

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Appendix S1

Research article in *Ecological Entomology*

In urban areas, tree cover increases species richness and shapes species composition of saproxylic beetles along with the microclimate

Table S1: Studied cities with population, area (SCB, 2023), and microclimatic mean temperature (= average temperature across all logger locations per city). The boxes of each city were categorized into those with the highest (“highly urbanized”) and the lowest (“sparsely urbanized”) density of urban structures within a 100 m buffer. Four with the highest density of urban structures were considered as “highly urbanized”, and four boxes with the lowest density of urban structures as “sparsely urbanized” (three each in cities with totally eight boxes). The average percentage of the highest and lowest density of urban structures was calculated for each city.

Study city	Population	Area [km^2]	Microclimatic mean temperature [°*C*]	Min / max microclimatic temperature [°*C*]	Highly urbanized [%]	Sparsely urbanized [%]
Linköping	115 682	42.16	16.6	-8.5 / 48.1	27.15	10.03
Motala	29 823	19.18	15.5	-2.5 / 43.1	15.52	1.04
Lund	94 393	26.3	16.2	1.5 / 39.6	21.55	4.25
Göteborg	607 882	447.8	15.7	-3.9 / 40.1	13.38	4.78
Örebro	126 604	50.64	16.3	-8.0 / 39.6	41.16	8.99
Uppsala	166 698	43.74	15.9	-3.9 / 38.1	39.81	8.92

Table S2: Average temperature across April – September in 2022 and in 2019, and mean annual temperature from 1995-2020. Measurements were extracted from nearby weather stations (SMHI).

City	2022 SMHI [°*C*]	2022 SMHI min / max [°*C*]	Mean annual temperature [°*C*]	2019 SMHI [°*C*]
Linköping	13.2	-3.3 / 36.2	6.8	13.3
Motala	12.6	-1.4 / 33.1	6.8	12.8
Lund	14.6	-2 / 27.4	8.7	14.8

Göteborg	14.7	-0.9 / 32.9	8.9	15.3
Örebro	13.9	-3.1 / 35.5	7.1	13.9
Uppsala	12.9	-5.1 / 32.9	6.6	12.8

Table S3: Species richness, abundance, and CTI of saproxylic beetles, canopy openness, and microclimatic mean temperature of each box across the six study cities. Temperature refers to the average temperature of the four logger types per box. NA refers to missing microclimatic temperature and canopy openness data due to missing boxes in 2022.

City	**Box identity**	**Species richness**	**Abundance**	**CTI [°*C*]**	**Canopy openness [%]**	**Temperature [°*C*]**
Linköping	1	21	547	8.3	14.1	15.9
Linköping	2	13	63	7.2	33.1	16.7
Linköping	3	20	95	7.3	20.2	16.1
Linköping	4	10	27	6.6	26.6	17.7
Linköping	5	7	19	7.3	11.4	15.9
Linköping	6	19	50	7.3	21.4	16.6
Linköping	7	13	193	8.2	17.9	17.1
Linköping	8	8	11	5.6	28.0	16.9
Motala	1	13	34	7.4	28.1	15.6
Motala	2	10	44	6.3	20.8	15.4
Motala	3	12	63	5.7	23.7	15.3
Motala	4	8	25	7.7	16.2	15.4

Motala	5	14	18	7.4	24.7	15.5
Motala	6	9	37	6.7	52.8	18.0
Motala	7	11	59	8.3	18.4	15.2
Motala	8	4	12	5.5	17.2	15.5
Lund	1	9	30	7.5	13.9	15.8
Lund	2	10	27	8.2	NA	NA
Lund	3	11	67	7.9	15.2	16.1
Lund	4	9	47	8.5	13.5	15.9
Lund	5	6	17	8.5	16.6	16.5
Lund	6	11	39	7.9	24.1	16.0
Lund	7	7	16	8.4	18.8	15.9
Lund	8	6	15	8.2	37.1	17.2
Lund	9	7	29	7.8	16.2	16.5
Lund	10	6	20	8.4	9.9	15.9
Göteborg	1	7	8	8.2	NA	NA
Göteborg	2	12	437	8.8	19.2	14.9

Göteborg	3	6	13	7.0	86.1	16.4
Göteborg	4	15	102	8.1	11.7	15.7
Göteborg	5	10	45	6.6	15.3	15.3
Göteborg	6	4	4	7.8	11.0	15.5
Göteborg	7	9	20	7.6	13.6	16.5
Göteborg	8	6	12	6.9	73.7	16.3
Göteborg	9	7	14	6.6	54.8	15.9
Göteborg	10	12	57	7.5	NA	NA
Örebro	1	9	29	8.3	20.3	16.5
Örebro	2	5	10	6.6	NA	NA
Örebro	3	6	28	7.4	NA	NA
Örebro	4	3	14	8.6	NA	NA
Örebro	5	3	5	6.7	NA	NA
Örebro	6	9	34	8.2	18.6	16.2
Örebro	7	15	65	7.9	17.1	15.9
Örebro	8	12	33	7.3	26.1	16.8

Örebro	9	17	88	7.1	10.2	16.0
Örebro	10	5	53	8.7	5.7	16.4
Uppsala	1	19	112	8.0	34.2	17.2
Uppsala	2	11	79	7.8	13.7	14.2
Uppsala	3	22	101	7.5	12.5	15.3
Uppsala	4	15	35	6.4	24.1	16.5
Uppsala	5	10	27	6.4	15.1	16.6
Uppsala	6	8	22	6.4	9.9	16.3
Uppsala	7	9	39	5.7	18.1	16.2
Uppsala	8	7	12	7.0	10.8	16.8
Uppsala	9	24	208	6.8	13.5	15.3
Uppsala	10	19	154	7.4	17.7	14.9

Table S4: Wald-Chi square test with species richness, abundance and CTI of saproxylic beetles as response variables and regional temperature (1995-2020, SMHI), canopy openness, number of cavity trees, density of urban structures, and tree cover as explanatory variables.

Species richness	**Buffer 3000** (AICc: 290.6)			**Buffer 500** (AICc: 286.5)			**Buffer 100** (AICc: 285.1)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	10.0	1	**<0.01**	7.1	1	**0.03**	10.8	1	**<0.01**
Number of cavity trees	0.01	1	0.91	0.1	1	0.76	1.4	1	0.23
Canopy openness	1.2	1	0.28	3.3	1	**0.07**	2.8	1	*0.09*
Urban structures	0.57	1	0.45	6.2	1	**0.01**	6.3	1	**0.01**

Species richness	**Buffer 3000** (AICc: 290.5)			**Buffer 1000** (AICc: 287.9)			**Buffer 100** (AICc: 288.5)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	8.9	1	**<0.01**	9.6	1	**<0.01**	10.4	1	**<0.01**
Number of cavity trees	0.01	1	0.92	0.01	1	0.92	0.4	1	0.51
Canopy openness	1.7	1	0.19	2.2	1	0.14	0.8	1	0.37
Tree cover	1.7	1	0.19	3.3	1	*0.07*	2.6	1	0.1

Abundance	**Buffer 3000** (AICc: 142.2)			**Buffer 1000** (AICc: 140.6)			**Buffer 500** (AICc: 140.0)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	2.2	1	0.14	1.6	1	0.21	1.5	1	0.22
Number of cavity trees	0.1	1	0.77	0.2	1	0.64	0.2	1	0.63
Canopy openness	2.8	1	*0.09*	4.3	1	**0.04**	4.7	1	**0.03**
Urban structures	0.3	1	0.59	1.9	1	0.17	2.5	1	0.12

Abundance	**Buffer 3000** (AICc: 141.2)			**Buffer 1000** (AICc: 139.6)			**Buffer 100** (AICc: 137.1)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value

Regional temperature	1.7	1	0.19	1.6	1	0.17	2.0	1	0.15
Number of cavity trees	0.1	1	0.74	0.2	1	0.76	1.3	1	0.25
Canopy openness	3.8	1	**0.05**	6.6	1	**0.03**	3.0	1	*0.08*
Tree cover	1.2	1	0.27	3.9	1	*0.09*	5.7	1	**0.02**

CTI	**Buffer 3000** (AICc: 120.9)			**Buffer 1000** (AICc: 120.9)			**Buffer 100** (AICc: 120.9)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	10.3	1	**<0.01**	9.6	1	**<0.01**	9.8	1	**<0.01**
Canopy openness	4.2	1	**0.04**	4.1	1	**0.04**	4.6	1	**0.03**
Urban structures	0.1	1	0.79	0.01	1	0.94	0.1	1	0.82

CTI	**Buffer 3000** (AICc: 120.9)			**Buffer 1000** (AICc: 119.2)			**Buffer 100** (AICc: 120.9)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	9.3	1	**<0.01**	10.2	1	**<0.01**	9.7	1	**<0.01**
Canopy openness	4.4	1	**0.03**	6.4	1	**0.01**	4.8	1	**0.03**
Tree cover	0.02	1	0.89	1.8	1	0.18	0.01	1	0.92

Table S5: Wald-Chi square test with microclimatic mean temperature as response variable and regional temperature (SMHI, 2022), logger location, density of urban structures, and tree cover as explanatory variables.

Microclimatic temperature	**Buffer 1000** (AICc: 304.2)			**Buffer 500** (AICc: 302.3)			**Buffer 100** (AICc: 304.5)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	0.03	1	0.85	0.04	1	0.84	0.01	1	0.91
Logger position	3.4	3	0.34	3.3	3	0.35	3.0	3	0.39
Canopy openness	12.3	1	**<0.01**	13.9	1	**<0.01**	8.6	1	**<0.01**
Urban structures	5.6	1	**0.02**	7.9	1	**<0.01**	4.2	1	**0.04**

Microclimatic temperature	**Buffer 1000** (AICc: 307.5)			**Buffer 500** (AICc: 305.6)			**Buffer 100** (AICc: 307.8)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	0.01	1	0.91	0.04	1	0.84	0.03	1	0.86
Logger position	3.7	3	0.29	4.3	3	0.23	4.1	3	0.25
Canopy openness	8.9	1	**<0.01**	10.0	1	**<0.01**	5.6	1	**0.02**
Tree cover	1.3	1	0.25	3.6	1	*0.06*	2.1	1	0.14

Table S6: Wald-Chi square test with microclimatic temperature fluctuation as response variable and regional temperature (SMHI, 2022), logger location, density of urban structures, and tree cover as explanatory variables.

Microclimatic temperature fluctuation	**Buffer 3000** (AICc: 236.6)			**Buffer 1000** (AICc: 236.6)			**Buffer 500** (AICc: 238.0)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	0.8	1	0.36	0.8	1	0.37	1.1	1	0.3
Logger position	413.9	3	**<0.01**	416.5	3	**<0.01**	410.7	3	**<0.01**
Canopy openness	52.2	1	**<0.01**	48.6	1	**<0.01**	52.4	1	**<0.01**
Urban structures	0.9	1	0.33	1.8	1	0.18	0.52	1	0.47

Microclimatic temperature fluctuation	**Buffer 1000** (AICc: 235.4)			**Buffer 500** (AICc: 238.2)			**Buffer 100** (AICc: 234.6)		
	Chi2	DF	*p* value	Chi2	DF	*p* value	Chi2	DF	*p* value
Regional temperature	2.1	1	0.15	1.3	1	0.25	1.1	1	0.29
Logger position	416.4	3	**<0.01**	408.1	3	**<0.01**	428.4	3	**<0.01**
Canopy openness	46.9	1	**<0.01**	59.9	1	**<0.01**	59.6	1	**<0.01**
Tree cover	3.0	1	*0.08*	0.02	1	0.89	4.6	1	**0.03**

Table S7: Generalized linear mixed-effects models with species richness, abundance, CTI, microclimatic mean temperature, and microclimatic temperature fluctuation as response variable and regional temperature (SMHI, 2019), canopy openness, number of cavity trees, and density of urban structures, and tree cover, respectively as explanatory variables.

	Buffer 3000				**Buffer 1000**				**Buffer 500**				**Buffer 100**			
	Estimate	SE	Lower CI	Upper CI	Estimate	SE	Lower CI	Upper CI	Estimate	SE	Lower CI	Upper CI	Estimate	SE	Lower CI	Upper CI
Species richness																
Regional temp	-0.19	0.06	-0.32	-0.08	-0.17	0.06	-0.29	-0.05	-0.17	0.06	-0.29	-0.05	-0.19	0.06	-0.31	-0.08
Canopy openness	-0.005	0.005	-0.01	0.004	-0.01	0.004	-0.02	0.0001	-0.01	0.004	-0.02	0.001	-0.01	0.004	-0.02	0.001
Urban structure	-0.004	0.006	-0.02	0.01	-0.01	0.004	-0.02	-0.002	-0.01	0.003	-0.01	-0.002	-0.01	0.01	-0.02	-0.003
Number of cavity trees	-0.001	0.006	-0.02	0.01	-0.003	0.01	-0.02	0.01	-0.002	0.01	-0.02	0.01	-0.01	0.01	-0.03	0.01
Species richness																
Regional temp	-0.19	0.06	-0.31	-0.06	-0.19	0.07	-0.31	-0.07	-0.2	0.06	-0.32	-0.09	-0.19	0.06	-0.32	-0.08
Canopy openness	-0.01	0.004	-0.01	0.01	-0.01	0.004	-0.02	0.002	-0.01	0.004	-0.01	0.002	-0.004	0.004	-0.01	0.005
Tree cover	0.01	0.01	-0.003	0.02	0.01	0.005	-0.001	0.02	0.01	0.004	0.001	0.02	0.004	0.003	-0.001	0.01
Number of cavity trees	-0.01	0.01	-0.02	0.01	-0.001	0.01	-0.02	0.02	-0.001	0.01	-0.02	0.01	-0.01	0.01	-0.02	0.01
Abundance																
Regional temp	-0.2	0.14	-0.47	0.07	-0.17	0.14	-0.44	0.09	-0.17	0.14	-0.44	0.09	-0.19	0.13	-0.46	0.06
Canopy openness	-0.02	0.01	-0.03	0.003	-0.02	0.01	-0.04	-0.001	-0.02	0.01	-0.04	-0.002	-0.02	0.01	-0.04	-0.002
Urban structure	-0.01	0.01	-0.03	0.02	-0.01	0.01	-0.03	0.005	-0.01	0.01	-0.03	0.003	-0.02	0.01	-0.04	0.003
Number of cavity trees	-0.01	0.02	-0.04	0.03	-0.01	0.02	-0.04	0.03	-0.01	0.02	-0.04	0.02	-0.02	0.02	-0.06	0.02
Abundance																
Regional temp	-0.18	0.14	-0.45	0.09	-0.19	0.15	-0.45	0.08	-0.21	0.13	-0.46	0.04	-0.19	0.13	-0.44	0.07
Canopy openness	-0.02	0.01	-0.04	$2.1e^{-4}$	-0.02	0.01	-0.04	$-2.1e^{-3}$	-0.02	0.01	-0.04	-0.01	-0.01	0.01	-0.03	$1.8e^{-3}$
Tree cover	0.01	0.01	-0.01	0.04	0.02	0.01	$-2.8e^{-3}$	0.04	0.03	0.01	0.01	0.05	0.01	0.01	$2.6e^{-3}$	0.03
Number of cavity trees	-0.01	0.02	-0.04	0.03	-0.01	0.02	-0.04	0.03	-0.01	0.02	-0.04	0.02	-0.02	0.02	-0.05	0.01
CTI																
Regional temp	0.46	0.12	0.23	0.46	0.46	0.12	0.23	0.46	0.47	0.12	0.24	0.47	0.46	0.12	0.23	0.46
Canopy openness	-0.01	0.01	-0.03	-0.01	-0.02	0.01	-0.03	-0.02	-0.02	0.01	-0.03	-0.02	-0.02	0.01	-0.03	-0.02
Urban structure	0.002	0.01	-0.02	0.002	0.001	0.001	-0.01	0.001	-0.002	0.01	-0.01	-0.002	0.01	0.01	-0.02	0.001

CTI

Regional temp	0.46	0.12	0.23	0.46	0.46	0.12	0.24	0.46	0.45	0.11	0.22	0.44	0.46	0.12	0.23	0.46
Canopy openness	-0.02	0.01	-0.03	-0.02	-0.02	0.01	-0.03	-0.02	-0.02	0.01	-0.03	-0.02	-0.02	0.01	-0.03	-0.02
Tree cover	-0.001	0.01	-0.02	-0.001	0.01	0.01	-0.01	0.01	0.01	0.01	-0.001	0.01	-0.0003	0.005	-0.01	-0.002
Microtemp																
Regional temp	-0.06	0.17	-0.54	0.43	-0.04	0.22	-0.66	0.57	-0.05	0.22	-0.67	0.58	0.03	0.23	-0.61	0.66
Logger position																
Inside Box	0.1	0.16	-0.21	0.42	0.11	0.16	-0.21	0.43	0.12	0.16	-0.19	0.43	0.13	0.16	-0.19	0.441
Outside Box	0.19	0.16	-0.13	0.51	0.17	0.16	-0.15	0.49	0.17	0.16	-0.15	0.49	0.17	0.16	-0.15	0.49
Hollow tree	-0.28	0.31	-0.89	0.34	-0.32	0.31	-0.93	0.29	-0.31	0.31	-0.92	0.3	-0.29	0.31	-0.91	0.33
Canopy openness	0.02	0.01	0.01	0.03	0.02	0.01	0.01	0.03	0.02	0.01	0.01	0.03	0.02	0.01	0.01	0.03
Urban structure	0.03	0.01	0.01	0.05	0.01	0.01	0.002	0.03	0.02	0.01	0.004	0.03	0.02	0.01	0.0003	0.04
Microtemp																
Regional temp	0.01	0.24	-0.66	0.68	0.03	0.26	-0.68	0.74	0.05	0.25	-0.63	0.73	0.04	0.23	-0.59	0.67
Logger position																
Inside Box	0.11	0.16	-0.2	0.43	0.1	0.16	-0.2	0.43	0.12	0.16	-0.2	0.43	0.12	0.16	-0.19	0.43
Outside Box	0.19	0.16	-0.14	0.51	0.17	0.16	-0.15	0.49	0.17	0.16	-0.15	0.49	0.16	0.16	-0.16	0.48
Hollow tree	-0.32	0.31	-0.94	0.29	-0.35	0.31	-0.98	0.26	-0.4	0.31	-1.01	0.22	-0.39	0.31	-1.01	0.22
Canopy openness	0.02	0.01	0.01	0.03	0.02	0.01	0.01	0.03	0.02	0.01	0.01	0.03	0.01	0.01	0.002	0.03
Tree cover	-0.02	0.01	-0.04	0.001	-0.01	0.01	-0.03	0.01	-0.01	0.01	-0.03	0.001	-0.06	0.005	-0.02	0.003
Fluctuation																
Regional temp	-0.12	0.14	-0.51	0.26	-0.12	0.13	-0.47	0.24	-0.13	0.13	-0.48	0.22	-0.15	0.12	-0.49	0.19
Logger position																
Inside Box	2.46	0.13	2.2	2.72	2.46	0.13	2.2	2.72	2.46	0.13	2.19	2.72	2.47	0.13	2.21	2.73
Outside Box	2.14	0.13	1.88	2.4	2.15	0.13	1.89	2.41	2.15	0.13	1.89	2.41	2.15	0.13	1.89	2.41
Hollow tree	0.85	0.24	0.36	1.33	0.85	0.24	0.37	1.33	0.86	0.24	0.38	1.33	0.93	0.24	0.44	1.42
Canopy openness	0.03	0.004	0.02	0.04	0.03	0.004	0.02	0.04	0.03	0.004	0.02	0.04	0.03	0.004	0.02	0.04
Urban structure	-0.01	0.01	-0.02	0.01	-0.01	0.004	-0.01	0.003	-0.003	0.004	-0.01	0.005	0.01	0.01	-0.003	0.02
Fluctuation																
Regional temp	-0.13	0.1	-0.41	0.16	-0.14	0.1	-0.42	0.13	-0.14	0.12	-0.48	0.2	-0.13	0.13	-0.49	0.22
Logger position																
Inside Box	2.46	0.12	2.2	2.72	2.46	0.13	2.2	2.72	2.46	0.13	2.2	2.73	2.47	0.13	2.22	2.73
Outside Box	2.14	0.13	1.88	2.39	2.16	0.13	1.89	2.42	2.15	0.13	1.89	2.41	2.14	0.13	1.88	2.39
Hollow tree	0.83	0.24	0.35	1.31	0.87	0.24	0.38	1.35	0.87	0.24	0.38	1.36	0.84	0.24	0.36	1.31
Canopy openness	0.03	0.004	0.02	0.03	0.03	0.004	0.02	0.03	0.03	0.004	0.02	0.04	0.03	0.004	0.02	0.04
Tree cover	0.01	0.01	0.001	0.02	0.01	0.005	-0.001	0.02	-0.001	0.004	-0.01	0.01	-0.01	0.003	-0.01	-0.0004

Table S8: Wald-Chi square test and summary table of generalized linear mixed-effects models with species richness, abundance, and CTI as response variables and regional temperature (1995-2020, SMHI), and microclimate as explanatory variables. Estimate and Std. error were extracted from the summary table, whereas degrees of freedom were calculated with the function *df.residual* and the lower and upper confidence intervals were calculated with the function *confint*.

	Species richness			**Abundance**			**CTI**		
	Chi2	df	*p* value	Chi2	df	*p* value	Chi2	df	*p* value
Regional temperature	13.8	1	**<0.01**	4.2	1	**0.03**	2.9	1	*0.09*
Microclimate	2.5	1	0.12	4.5	1	**0.05**	1.0	1	0.31

	Species richness					**Abundance**					**CTI**				
	Estimate	Std. Error	df	Lower CI	Upper CI	Estimate	Std. Error	df	Lower CI	Upper CI	Estimate	Std. Error	df	Lower CI	Upper CI
Regional temperature	-0.22	0.06	44	-0.33	-0.1	-0.34	0.17	44	-0.54	-0.02	0.23	0.16	44	-0.04	0.59
Microclimate	-0.12	0.07	44	-0.26	0.03	-0.28	0.13	44	-0.69	-0.01	-0.17	0.16	44	-0.47	0.15

Table S9: PERMANOVA results with species composition as response variable and density of urban structure, tree cover, and regional climate as explanatory variables.

	3000 m				**1000 m**				**500 m**			
	Sumof Sqs	R^2	F value	*p* value	Sum of Sqs	R^2	F value	*p* value	Sumof Sqs	R^2	F value	*p* value
Urban structure	0.22	0.01	0.65	0.86	0.3	0.02	0.9	0.56	0.28	0.01	0.82	0.67
Regional climate	1.12	0.06	3.3	< **0.01**	1.12	0.06	3.33	< **0.01**	1.12	0.06	3.32	< **0.01**

	1000 m				**500 m**				**100 m**			
	Sumof Sqs	R^2	F value	*p* value	Sum of Sqs	R^2	F value	*p* value	Sumof Sqs	R^2	F value	*p* value
Tree cover	0.42	0.02	1.26	0.21	0.37	0.02	1.09	0.34	0.47	0.02	1.42	0.11
Regional climate	1.12	0.06	3.35	< **0.01**	1.12	0.06	3.33	< **0.01**	1.13	0.06	3.39	< **0.01**

Table S10: All sampled saproxylic beetle species separated into their microhabitat groups according to a development of the categorization by Ranius and Jansson (2002). *Rot*: Rotten wood in any part of the trunks, even on the outside of the trunk. *Hollow*: Rotten wood in trunks, exclusively from the inside, in hollows. Not associated with animal nests. *Nest*: Animal nests in tree hollows. *Fungi*: Fruiting bodies of saproxylic fungi. *Mould*: Mycelia or mould. *Dry*: Dead, dry wood in trunks. *Fresh*: Under fresh bark and sap runs. For each species, we calculated a STI (species temperature index). Species with NA as STI had too few occurrences on GBIF, so that we did not calculate a STI and excluded them from the CTI analysis.

Species	Microhabitat	STI
Abraeus perpusillus	Hollow	9.88
Aderus populneus	Nest	8.44
Alosterna tabacicolor	Rot	7.63
Anaspis marginicollis	Rot	5.19
Anaspis rufilabris	Rot	6.3
Anaspis thoracica	Rot	6.88
Anidorus nigrinus	Rot	7.09
Anisotoma glabra	Mould	4.12
Aridius nodifer	Mould	7.52
Atheta nigricornis	Nest	7.95
Atomaria bella	Fungi	2.94
Atomaria fuscata	Hollow	7.75
Atomaria morio	Nest	5.76
Atomaria umbrina	Mould	4.6
Atomaria wollastoni	Fungi	4.99
Cartodere constricta	Mould	5.58
Cerylon histeroides	Rot	6.85

Cetonia aurata	Hollow	8.85
Chrysanthia geniculata	Rot	6.73
Corticaria longicollis	Mould	4.88
Corticaria rubripes	Mould	3.2
Corticaria serrata	Mould	8.11
Cortinicara gibbosa	Mould	6.62
Cryptophagus badius	Rot	4.86
Cryptophagus dentatus	Fungi	7.48
Cryptophagus labilis	Hollow	7.57
Cryptophagus micaceus	Nest	6.53
Cryptophagus pilosus	Nest	8.49
Cryptophagus saginatus	Fungi	7.02
Cryptophagus scanicus	Rot	6.76
Cryptophagus scutellatus	Hollow	7.08
Dasytes aeratus	Rot	9.38
Dasytes cyaneus	Rot	7.24
Dendrophilus corticalis	Hollow	6.55
Diaperis boleti	Fungi	7.99
Dienerella elongata	Fungi	8.89
Dorcus parallelipipedus	Rot	10.02
Enicmus rugosus	Mould	6.32
Enicmus testaceus	Mould	8.06
Epauloecus unicolor	Nest	5.0
Epuraea marseuli	Fresh	5.09
Epuraea melanocephala	Fresh	8.04
Epuraea pallescens	Fresh	6.4
Epuraea unicolor	Fresh	7.17
Euplectus bescidicus	Hollow	6.19
Euplectus karstenii	Hollow	5.76
Euplectus mutator	Rot	4.34

Euplectus nanus	Hollow	6.57
Euplectus punctatus	Rot	4.61
Gabrius splendidulus	Fresh	6.08
Glischrochilus hortensis	Fresh	6.92
Glischrochilus quadripunctatus	Fresh	5.01
Hadrobregmus pertinax	Dry	5.13
Hylobius abietis	Rot	6.53
Hylurgops palliatus	Fresh	5.6
Latridius minutus	Mould	6.73
Leptusa fumida	Fresh	6.8
Litargus connexus	Fresh	9.6
Megatoma undata	Nest	7.55
Melanotus castanipes	Rot	6.26
Melanotus villosus	Rot	9.73
Micrambe abietis	Mould	9.73
Mycetaea subterranea	Nest	8.46
Mycetina cruciata	Fungi	7.35
Mycetophagus quadriguttatus	Hollow	10.07
Orthoperus corticalis	Fungi	7.14
Orthoperus punctatus	Fungi	7.14
Palorus depressus	Nest	9.74
Paromalus flavicornis	Rot	9.87
Phloeocharis subtilissima	Fresh	9.87
Phloeonomus punctipennis	Fresh	8.36
Phloeonomus pusillus	Fresh	4.92
Phloeonomus sjobergi	Fresh	2.13
Phloeostibia plana	Nest	NA
Phyllodrepa gracilicornis	Fresh	7.46
Placusa tachyporoides	Fungi	6.72

Prionocyphon serricornis	Hollow	8.57
Prionychus ater	Hollow	8.41
Protaetia marmorata	Hollow	7.58
Ptenidium gressneri	Hollow	8.14
Pteryx suturalis	Rot	4.55
Ptilinus pectinicornis	Dry	9.06
Ptinus fur	Hollow	7.42
Ptinus raptor	Hollow	4.67
Ptinus subpillosus	Hollow	6.28
Ptinus villiger	Hollow	5.16
Quedius invreae	Nest	8.02
Quedius maurus	Nest	6.22
Quedius mesomelinus	Nest	6.48
Quedius scitus	Nest	7.87
Quedius xanthopus	Nest	5.59
Rhizophagus bipustulatus	Fresh	9.09
Rhizophagus dispar	Fresh	6.11
Scraptia fuscula	Nest	8.24
Scydmaenus hellwigii	Hollow	6.18
Sepedophilus marshami	Fungi	7.78
Sepedophilus testaceus	Fungi	7.14
Stenichnus godarti	Hollow	7.12
Stictoleptura rubra	Rot	8.06
Trinodes hirtus	Nest	10.13
Uloma culinaris	Rot	9.06
Xestobium rufovillosum	Dry	8.37
Xyleborinus saxesenii	Fresh	6.76
Xyleborus dispar	Fresh	9.57
Zyras lugens	Nest	7.01

Table S11: Habitat categories from Nationella Marktäckedata (NMD) that we included in tree cover (category 1-14) and density of urban structures (category 15-17) (NMD, 2023)

Category	Definition
1: Pine forest not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10% where >70% of the canopy cover consists of pine. Trees are higher than 5 meters.
2: Spruce forest not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10% where >70% of the canopy cover consists of spruce. Trees are higher than 5 meters
3: Mixed coniferous not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10% where >70% of consists of pine or spruce, but none of these species are >70%. Trees are higher than 5 meters.
4: Mixed forest not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10% where neither coniferous nor deciduous canopy cover reaches >70%. Trees are higher than 5 meters.
5: Deciduous forest not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10% where >70% of the canopy cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.
6: Deciduous hardwood forest not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10 where >70% of the canopy cover consists of deciduous trees, of which >50% is deciduous hardwood forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
7: Deciduous forest with deciduous hardwood forest not on wetland	Tree-covered areas outside of wetlands with a total canopy cover of >10 where >70% of the canopy cover consists of deciduous trees, of which 20 - 50% is deciduous hardwood forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
8: Pine forest on wetland	Tree-covered areas on wetlands with a total canopy cover of >10% where >70% of the canopy cover consists of pine. Trees are higher than 5 meters.
9: Spruce forest on wetland	Tree-covered areas on wetlands with a total canopy cover of >10% where >70% of the canopy cover consists of spruce. Trees are higher than 5 meters.

10: Mixed coniferous on wetland	Tree-covered areas on wetlands with a total canopy cover of >10% where >70% of consists of pine or spruce, but none of these species are >70%. Trees are higher than 5 meters.
11: Mixed forest on wetland	Tree-covered areas on wetlands with a total canopy cover of >10% where neither coniferous nor deciduous canopy cover reaches >70%. Trees are higher than 5 meters.
12: Deciduous forest on wetland	Tree-covered areas on wetlands with a total canopy cover of >10% where >70% of the canopy cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.
13: Deciduous hardwood forest on wetland	Tree-covered areas on wetlands with a total canopy cover of >10 where >70% of the canopy cover consists of deciduous trees, of which >50% is deciduous hardwood forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
14: Deciduous forest with deciduous hardwood forest on wetland	Tree-covered areas on wetlands with a total canopy cover of >10 where >70% of the canopy cover consists of deciduous trees, of which 20 - 50% is deciduous hardwood forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
15: Artificial surfaces, building	A durable construction consisting of roofs or roofs and walls and which is permanently placed on the ground or partly or wholly below ground or is permanently placed in a certain place in water and is intended to be designed so that people can stay in it.
16: Artificial surfaces, not building or road/railway	Artificial open and vegetation-free surfaces that are not building or road/railway.
17: Artificial surfaces, road/railway	Road or railway.

References

Nationella Marktäckedata (NMD) [WWW Document], URL https://www.naturvardsverket.se/verktyg-och-tjanster/kartor-och-karttjanster/nationella-marktackedata/ (accessed 6.30.23).

Ranius, T. and N. Jansson. 2002. A comparison of three methods to survey saproxylic beetles in hollow oaks. *Biodiversity and Conservation* **11**: 1759–1771.

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Climate is a major driver of biodiversity at both large and small spatial scales. My research shows that the interaction between micro- and macroclimate shapes the diversity of dead wood living organisms, such as beetles, fungi and bacteria, in forested landscapes. Additionally, I surveyed dead wood dependent beetles in urban areas. I conclude that dead wood creation with varying microclimatic conditions is needed to promote dead wood living species with different thermal requirements in both forests and urban areas.

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