


ORIGINAL ARTICLE

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.

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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

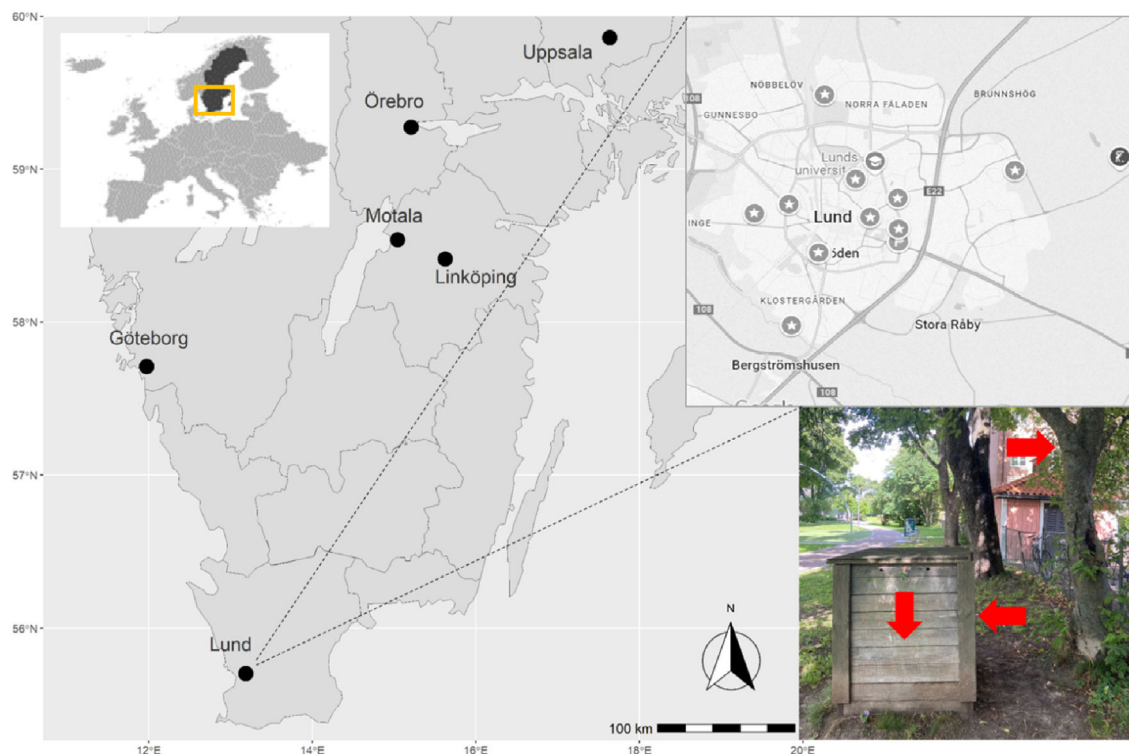


FIGURE 1 Six study cities distributed over southern Sweden containing 10 wood mould boxes resembling tree hollows. The microclimatic mean temperature was measured (i) in the wood mould of each box, (ii) inside the box attached to the north-facing wall, (iii) outside the box at the closest tree (red arrows 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 m³ 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 $+40^{\circ}\text{C}$, 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 $+50^{\circ}\text{C}$ 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 Markttäckedata, 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 *betadis* 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.

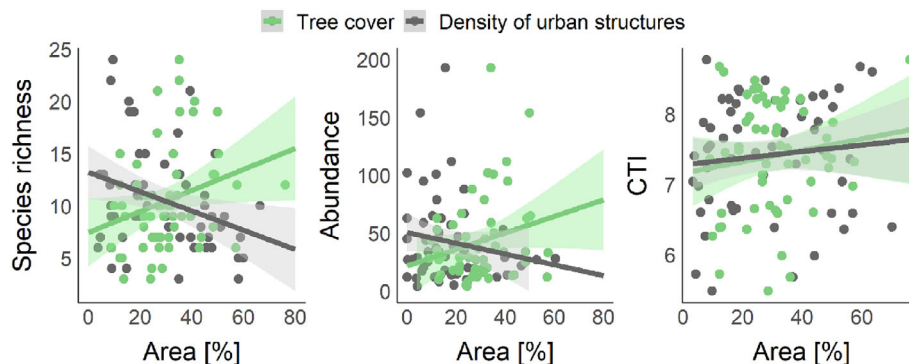


FIGURE 2 Effect of tree cover and density of urban structures on species richness, abundance, and CTI. Dots represent species richness and abundance per box. The buffer sizes used for the density of urban structures and tree cover refer to those that generated the lowest AIC in the respective models.

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).

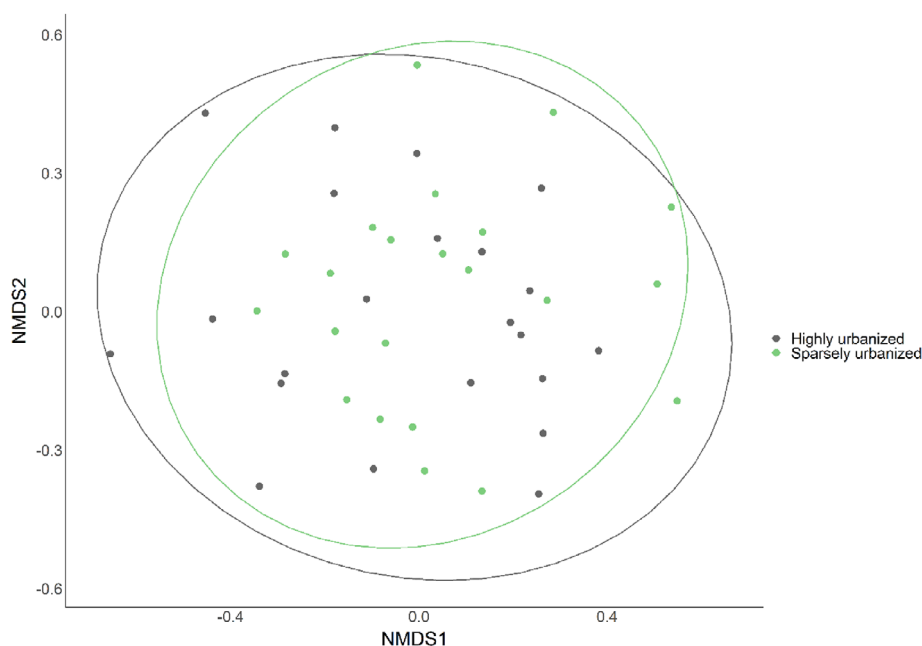


FIGURE 3 NMDS of saproxylic beetle compositions across highly urbanised sites, that is with a high density of urban structures around wood mould boxes, and sparsely urbanised sites, that is with a low density of urban structures around wood mould boxes, across all studied cities.

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 (Klysik 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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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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