

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 1200km 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; Fadrigue 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 1200km 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 1200km 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

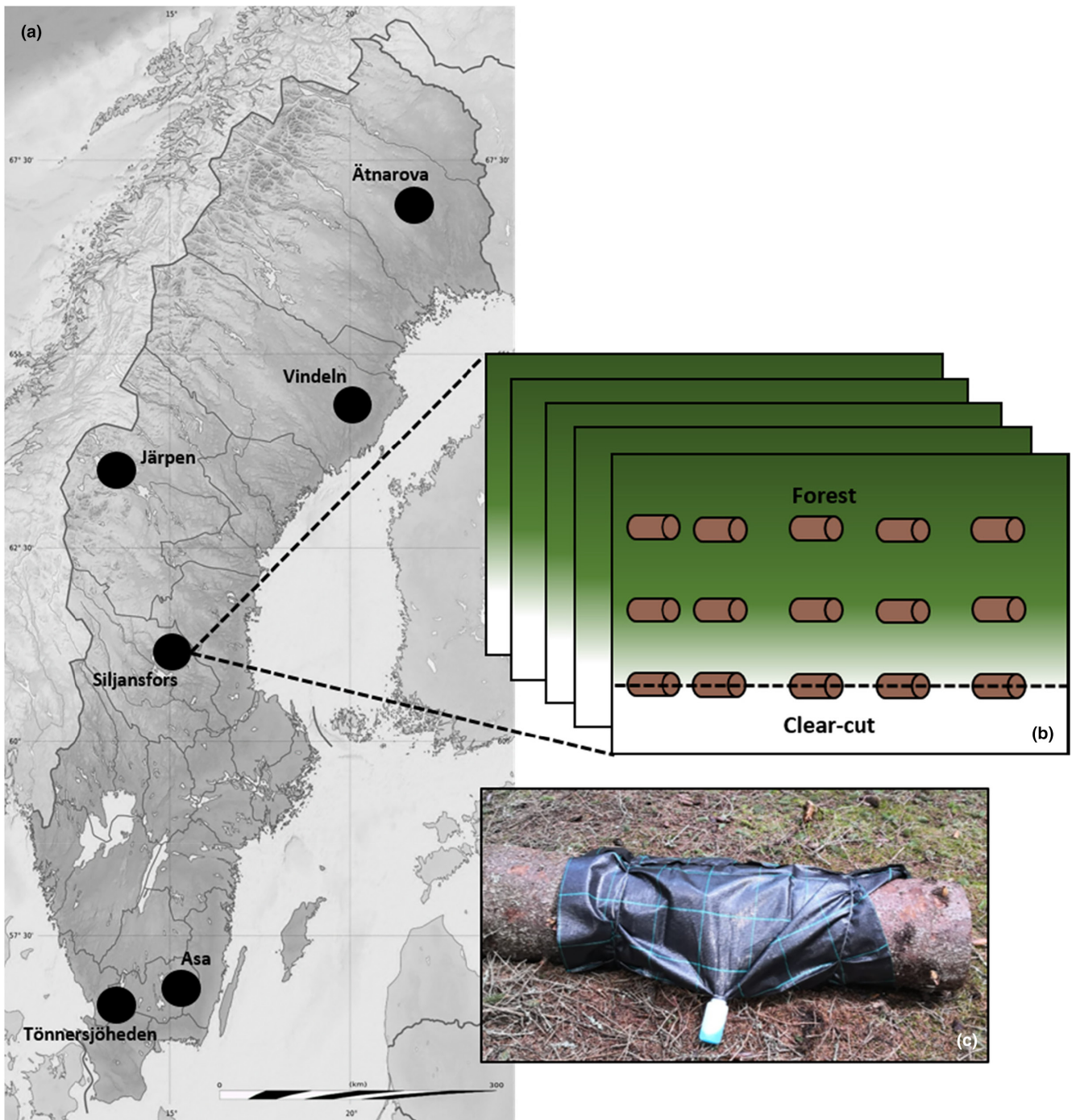


FIGURE 1 Six study regions, which consist of five study plots each (except Siljansfors, where there were four), were distributed over Sweden (a). A plot consists of 15 stem sections on three different shade levels: (i) sun-exposed, (ii) intermediately shaded and (iii) fully shaded (b). The dashed line 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]
Ätnarova	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); Hågglund 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	Study region/Plot/Shade	Gaussian		.13
		Shade level				
		Aspect				
Species richness	Linear mixed effects model	Regional temperature	Study region/Plot	Gaussian	498.5	.62
		Shade level				
		Aspect				
		Diameter				
		Bark				
Abundance	Generalized linear mixed effects model	Shade level*Regional temperature	Study region/Plot	Negative binomial	1422.36	.73
		Regional temperature				
		Shade level				
		Aspect				
		Diameter				
Species richness	Linear mixed effects model	Bark	Study region/Plot	Gaussian	509.3	.49
		Aspect				
		Diameter				
		Bark				
		Shade level*Regional temperature				
Abundance	Generalized linear mixed effects model	Regional temperature	Study region/Plot	Negative binomial	1447.47	.51
		Bark				
		Aspect				
		Diameter				
		Shade level*Regional temperature				
Species richness	Linear mixed effects model	Shade level	Study region/Plot	Gaussian	501.8	.64
		Bark				
		Aspect				
		Diameter				
		Bark				
Abundance	Generalized linear mixed effects model	Shade level	Study region/Plot	Negative binomial	1424.55	.71
		Bark				
		Aspect				
		Diameter				
		Bark				

TABLE 2 (Continued)

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

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: $\geq 5.17^\circ\text{C}$), whereas a species with minimum -10% of the STI over whole Sweden was considered as 'northern' (northern species: $\leq 4.25^\circ\text{C}$). Species with a STI between 4.25 and 5.17 were considered as intermediate. We analysed also $\pm 20\%$ and $\pm 25\%$ cutoff, but apart from fewer data points, it showed no essential difference to $\pm 10\%$ 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 ($\Delta\text{temp} = 3.1^\circ\text{C}$) than the difference in the microclimatic temperature between the sun-exposed and fully shaded logs (mean $\Delta\text{temp} = 1.5^\circ\text{C}$). 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 220km 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 $STI \geq 5.17^\circ\text{C}$. 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 $STI \leq 4.25^\circ\text{C}$. 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

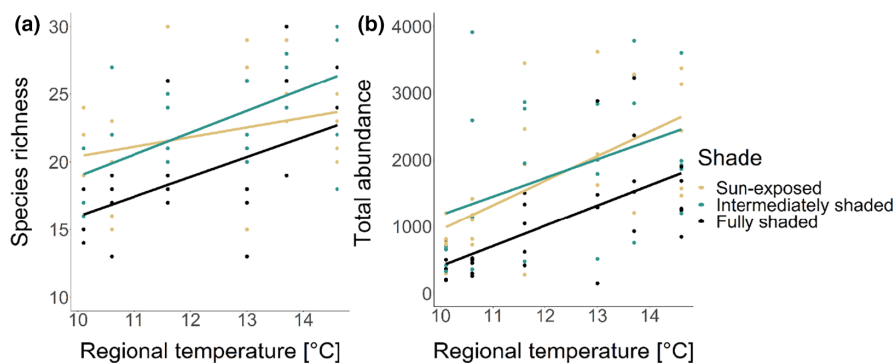


FIGURE 2 Species richness (a) and abundance (b) of saproxylic beetles of the three shade levels (sun-exposed, intermediately shaded and fully shaded) along the regional temperature gradient. The dots represent species richness and total abundance per plot and shade level. There was a significant effect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

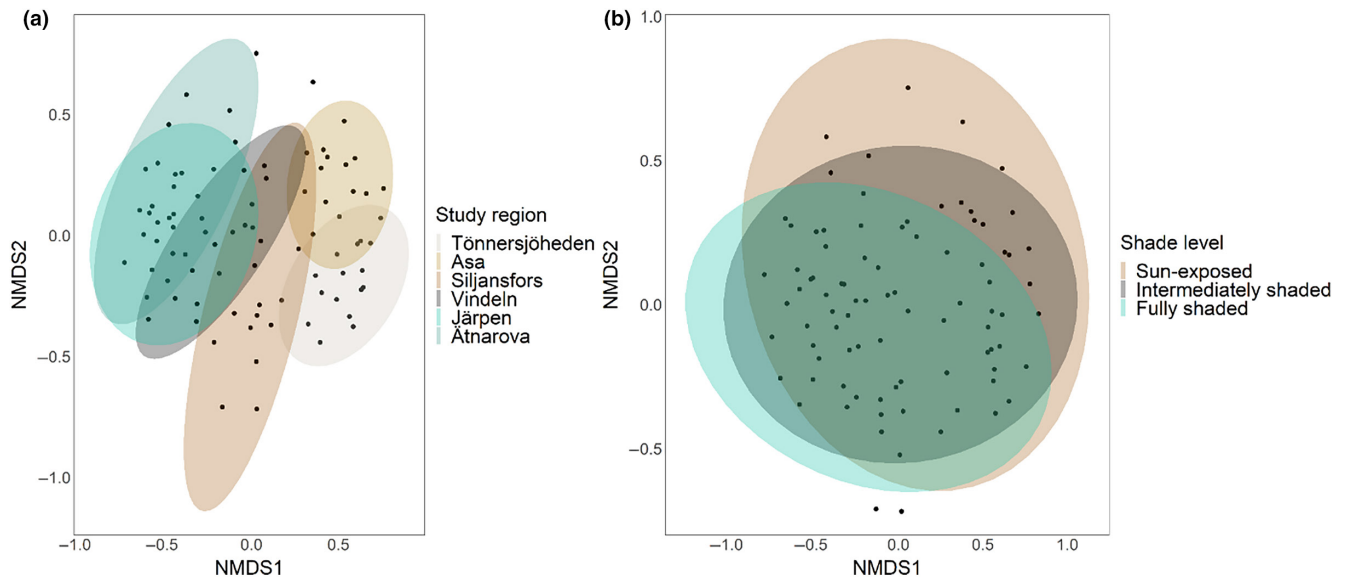
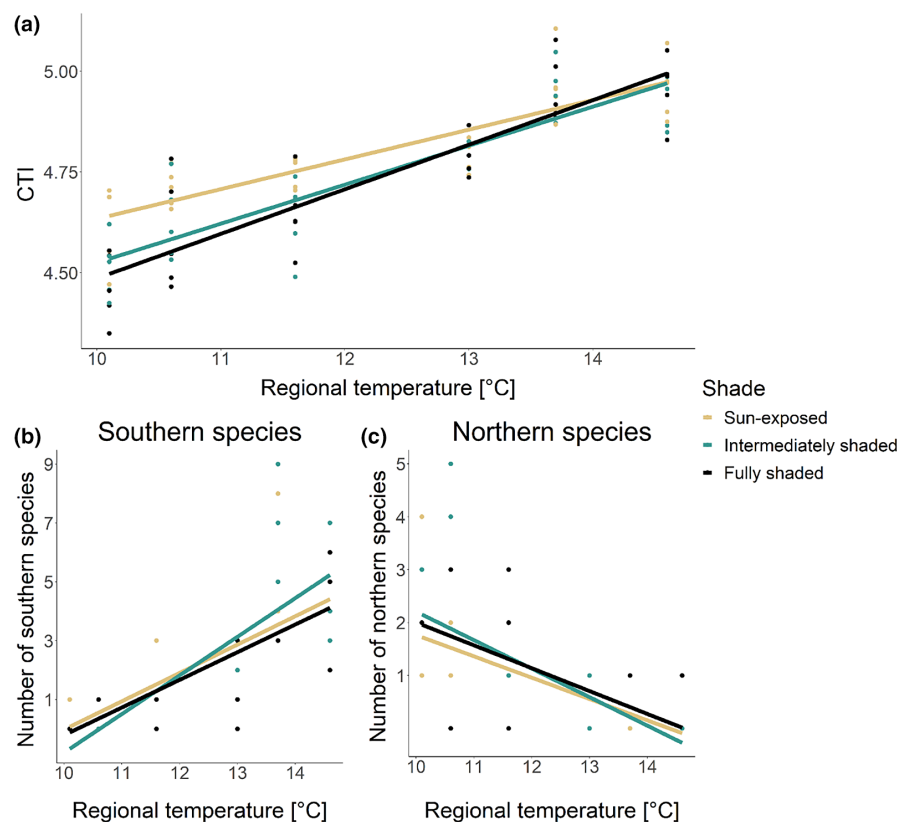


FIGURE 3 Nonmetric multidimensional scaling of saproxylic beetle communities based on abundance data differentiated along a regional gradient from south (Tönnersjöheden) to north (Ätnarova) (a) and along a shade gradient (b). The dots represent species composition per plot and shade level. There were 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 220km 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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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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