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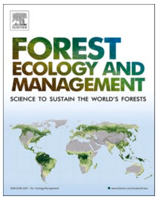

Regional climate affects habitat preferences and thermal sums required for development of the Eurasian spruce bark beetle, *Ips typographus*

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ABSTRACT

In recent years, the outbreaks of the Eurasian spruce bark beetle (*Ips typographus*) have become more frequent and severe, while temperatures have been rising. Our understanding of the consequences of climate warming can be improved by comparing the performance of *I. typographus* between geographical regions with different climates. We applied that approach by placing out Norway spruce logs at sites selected along a 1300 km north–south gradient in Sweden to study the effect of regional climate and microclimate on *I. typographus*. To obtain a microclimatic gradient at each site, we placed the logs at sun-exposed edges and in the shaded inner forest (10 m or 50 m from stand edges). We assessed the probability of colonisation of *I. typographus* and the thermal sums required for complete development.

The species' habitat preferences differed along the climate gradient including six geographical regions: in cooler regions, a higher proportion of sun-exposed logs was colonised in comparison to the shaded ones, while that difference was much smaller in warmer regions. The thermal sum needed for development tended to increase with warmer regional climate. Seasonal thermal sum exceeded the requirements for development of two generations *per* year in all three shade levels in the warmest region while in the coldest region two generations were only possible in some of the sun-exposed logs.

Outbreaks of *I. typographus* are more frequent and severe in regions with a warmer climate, and our study reveals two explanations for this: first, *I. typographus* has more suitable breeding sites in warmer regions, as shaded logs inside the forest offer additional suitable habitat; second, the potential population growth increases with the probability of completing two fully established generations *per* year. We recommend that after storm-fellings, wind-felled trees are removed before they are colonised by *I. typographus* to decrease the outbreak risk. The observed difference in habitat preferences between geographical regions implies that, in cooler sites in the north, it is enough to remove recently wind-felled spruces that are sun-exposed, such as along edges, while in the south, also trees in more shaded conditions inside forests are a suitable substrate for *I. typographus*. In a warming climate, the increased risk and severity of *I. typographus* outbreaks is a factor making it less attractive to use Norway spruce in forestry.

1. Introduction

The consequences of climate warming on species are often evaluated using space-for-time substitution, i.e. by replacing the temporal change in climate with spatial differences. Such evaluations have revealed that species abundances are affected by both climate and land use (Howard et al., 2015), and their interaction (Oliver et al., 2017). In most studies of climate effects on species, climatic conditions have been measured and predicted at a coarse resolution (Bennie et al., 2014), while the effect of habitat characteristics and management on microclimate has only recently been considered (e.g. Greiser et al., 2020). However, habitat characteristics can be important; modifications of habitat openness can cause a temperature change of a similar magnitude to that projected from anthropogenic climate change (Suggitt et al., 2011). Therefore, to evaluate the full effect of climatic conditions, both regional climate and factors affecting microclimate, including management, should be considered.

Insects are strongly affected by climatic conditions, since the temperature determines their physiological processes, activity patterns (Khaliq et al., 2014), and thus also population dynamics (Checa et al.,

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2014). For instance, with increasing temperature, the number of generations *per* year (i.e. voltinism) may increase (Corbet et al., 2006). Therefore, for many insect species, there are large-scale variations in voltinism, with more generations *per* year in regions with a warmer climate (Zeuss et al., 2017).

In forests, a large proportion of insect species (mainly beetles, hymenopterans, and dipterans) are dependent on deadwood (Siitonen 2001). In temperate regions, a warmer climate probably favours many deadwood-dependent insects (Müller et al., 2015; Lindman et al., 2022). Since the microclimate is affected both by local habitat characteristics and regional climate, it has been suggested that habitat preferences differ along north–south gradients (Chiari et al., 2012). However, to our knowledge, this has not been tested for any forest insects in replicated field studies.

The Eurasian spruce bark beetle *Ips typographus* (L.) is the most important insect pest on Norway spruce *Picea abies* (L.) Karst, which is an important tree species in production forestry in Northern Europe (Schlyter et al., 2006). Under endemic conditions, *I. typographus* mainly reproduces in wind-felled and otherwise weakened trees while during outbreaks it is also able to overcome defenses of more vigorous trees. Due to climate change, damage levels are projected to increase in the future (Seidl et al., 2014; 2017). The foremost factors initiating outbreaks of *I. typographus* are large-scale storm-fellings and exceptionally warm and dry summers, which are expected to become more frequent in a warming climate. In addition, warm summers may increase voltinism (Jönsson et al., 2011; Bentz et al., 2019). In northern Europe, univoltine populations of *I. typographus* are predominant (Fritscher & Schroeder, 2022), while in central Europe, *I. typographus* is usually bi- or trivoltine (Netherer and Hammerbacher, 2022).

For insects, a certain thermal sum (i.e. cumulative degree-days above a certain threshold temperature) is needed for development, and thus, the development time decreases with temperature. Thermal sums required for development may differ between regions as an adaptation to regional climate conditions, and this can affect the conclusions in space-for-time studies of climate warming effects. Such intraspecific variation between regions has been observed for some insect species (a bush-cricket: Černecká et al., 2020; a bark beetle: McManis et al., 2019). Also for *I. typographus*, it has been suggested that faster developmental rates are favoured in the north due to a higher risk of not being able to develop to adults before winter (Fritscher & Schroeder, 2022). However, no such comparisons have considered microclimatic thermal sums (i.e. thermal sums in the phloem of trees where *I. typographus* develops), but that is necessary to exclude that the effect is due to differences in habitat preferences between regions.

When projecting *I. typographus*' response to a warming climate, most studies have focused on voltinism (e.g. Jönsson et al., 2011; Bentz et al., 2019). However, we are not aware of any climate-related studies on *I. typographus* in the cooler parts of the boreal zone, where summer temperatures may currently be too low for the species to have even one generation, especially in shaded conditions, and that may change with a warming climate. Thus, it is possible to better understand the consequences of climate change by studying the extent to which *I. typographus* utilises sun-exposed and shaded breeding substrates in different regional climates.

In this study, we assessed the extent to which *I. typographus* colonises sun-exposed and shaded logs, and the thermal sums required for development, along a 1300 km long climatic gradient from northern to southern Sweden. We conducted a field experiment using existing variation in microclimate in logs and examined their effect on the development of *I. typographus*. This allowed us to analyse the combined effects of local habitat conditions, regional climate, and their interaction. We tested the following hypotheses:

(1) Habitat preferences differ with regional climate since both habitat characteristics and regional climate affect the microclimate. More specifically, the colonisation rate of logs by *I. typographus* is affected by regional climate and the level of shade, and an interaction between these two variables, so the species is able to use more shaded logs in the south. To examine whether the level of sun-exposure and regional climate do, indeed, reflect microclimatic conditions, we analysed these factors in relation to temperatures measured in the phloem of logs, where *I. typographus* developed.

(2) The potential for having two generations *per* year is higher in regions with a warmer climate. Populations in cooler regions require lower thermal sums for development of one generation, as an adaptation to regional climatic conditions.

2. Material and methods

2.1. Study area and design

The study was conducted in 2020 in six geographical regions in Sweden along a climatic gradient, with five study sites in each region. Each site consisted of a mature spruce stand facing a 1–2 year-old clear-cut. The stand edges of the five sites in each region were facing different compass directions to reflect the variation in sun-exposure of the edges of forests. At each study site, we established four transects with newly cut logs (1.5 m long) of Norway spruce at three different levels of shade: (*i*) on the edges between clear-cuts and mature spruce stands (sun-exposed), (*ii*) 10 m from the edge (intermediately shaded), and (*iii*) 50 m from the edge (totally shaded) (Fig. 1). Logs within transects always originated from the same tree and the order of them (cut at different heights from the tree) along transects was randomized. Three of the four transects were used for assessing the natural frequency of colonisation of *I. typographus* at different shade levels (colonisation experiment) and one transect for assessing the development time and thermal sum required for development of *I. typographus* (development experiment).

Since *I. typographus* are only breeding in the fresh phloem, they are only using wood from dying or recently dead trees. This means that the experimental logs are only used by the species during the year we studied them, and it is possible to fully assess the colonization rate and the time for development into adults only by searching for them under the bark.

At each site, the ambient and internal (i.e. under the bark of logs) temperatures were measured every hour from April to September 2020. To measure ambient temperature, we used one EL-USB-1 (Lascar Electronics) logger *per* shade level and site, placed at breast height (1.3 m) on the northern side of living trees in one of the transects. To measure temperature under the bark, we installed six SL52T (Signatrol) data-loggers in two transects at each site (Fig. 1). The loggers were placed to the log at the side facing the clear-cut with 45° angle from the ground. To install loggers, we carefully removed the bark with a putty knife, used a 24 mm drill (based on the size of the loggers) to make holes just deep enough for the loggers to be in contact with the reattached bark, which was fastened with staples and the bark edges covered by apple tree wax. In total, 90 EL-USB-1 and 180 SL52T loggers were used. From all analyses, we excluded three ambient data-loggers that measured very high temperatures and thus were suspected to have been sun-exposed, and 12 internal loggers that had no bark cover at the end of the season.

2.1.1. Colonisation experiment (to test hypothesis 1)

To analyse the frequency of colonisation of *I. typographus* in relation to habitat characteristics and ambient microclimatic variables, one log was placed at each of the three shade levels in each of the three transects *per* site (Fig. 1) in early spring (between April 2 and 20, 2020, earlier in the south), which is before the flight period of *I. typographus*. In the end of September, we assessed whether *I. typographus* had colonised the logs by looking for the species-specific galleries and *I. typographus* adults by removing small pieces of bark around bark beetle entrance and emergence holes. Furthermore, in the following year, as a part of another study, we collected adults of *I. typographus* together with other insects in eclector traps (from April to September) attached to all logs. Observing *I. typographus* in only one of these two assessments was enough for an

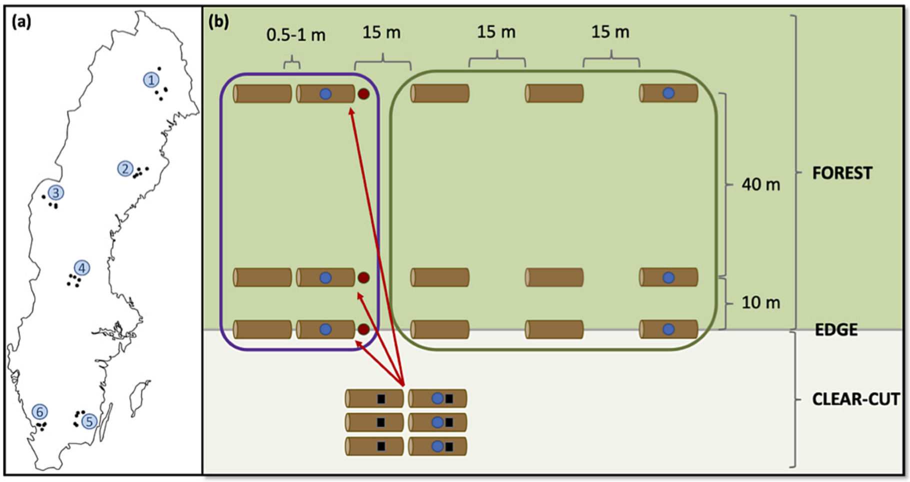

Fig. 1. (a) Study sites (black dots) of *Ips typographus* located in six climatically different geographical regions in Sweden: 1 – Ätnarova, 2 – Vindeln, 3 – Järpen, 4 – Siljansfors, 5 – Asa, 6 – Tönnersjöheden. (b) Design of each study site: logs for the development experiment (surrounded by a purple box), logs for the colonisation experiment (surrounded by a green box); location of ambient (red dots) and internal (inside the phloem; blue dots) temperature loggers. Prior to the start of flight of *Ips typographus* in the spring the logs for the development experiment were placed on the clear-cut and baited with pheromones (black squares) to ensure colonisation, after which the logs were moved (red arrows) into the transects for the development experiment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occurrence to be recorded. Of all recorded occurrences, 69 % were supported by both methods, 10 % only by checking for galleries, and 21 % only by eclector traps. The eclector traps only collected adults hibernating in the bark. In southern Sweden on average 40 % of the new-generation adults hibernates in the bark while the figure is lower in northern Sweden (Weslien et al., 2023).

2.1.2. *Development experiment (to test hypothesis 2)*

To assess the development time and thermal sum required for development of *I. typographus* at the three shade levels, six newly cut spruce logs were first placed on the clear-cut at each site before the start of the beetle flight period. To ensure colonisation, each log was baited with one *I. typographus* pheromone dispenser (Ipslure® Kjemikonsult, Norway). After colonisation, two logs were placed close to each other at each of the three different levels of shade along one transect at each site (Fig. 1). The logs were moved to the transects when the number of attacks (based on piles of boring dust) were deemed to be sufficient for the subsequent inspections of development stages. In all regions, except Asa, this happened within a week after the first attacks were recorded on the logs (logs moved 2–18 June). In Asa, a few attacks were recorded on a few of the logs four weeks before a a sufficient number of attacks occurred (logs moved 25–27 May). The sites in Tönnersjöheden were excluded from this part of the experiment as the baited logs were not colonised by *I. typographus*.

In summer 2020, we visited all sites once a week over a 10-week period (from June 15th to August 21st) to record the dates when the first *I. typographus* offspring had developed into adults and when they started to emerge from the logs. For this, we removed the bark from at least three maternal galleries *per* shade level and inspection date, and recorded occurrence of new generation adults and emergence holes. In Sweden, most *I. typographus* adults emerge from their brood tree to hibernate nearby in the ground after having finalized maturation feeding (Weslien et al., 2023). Thus, presence of emergence holes indicates that the new-generation adults have completed development.

2.2. *Habitat characteristics*

We measured or calculated habitat characteristics that had been previously reported to affect microclimate in deadwood (Romo et al., 2019; Lindman et al. 2022) or found to be important for deadwood-dependent insects (e.g. Chiari et al., 2012; Lindman et al., 2022; Appendix A). For each forest stand, we recorded *altitude* and the compass *direction* that the edge was facing. *Direction* was transformed to a linear scale by taking the absolute value of (180° – direction), where south is 0°, east and west 90° and north 180°.

For each log we recorded the middle *diameter*, log position along the transects, *canopy openness* and stand *basal area*. To estimate *canopy openness* (the percentage of the area above the log not covered by canopy), photographs were taken with a fisheye lens by placing the camera on the log. The photos were analysed with Gap Light Analyzer (Frazer et al., 1999). *Basal area* (the area in m^2 of the cross-sections of the tree trunks at breast height (1.3 m) *per* hectare), commonly used as an indicator of stand density, was measured with a relascope while standing above each log.

As a measure of regional climate, we used the average annual temperature over the last 25 years (i.e. 1998–2022) at the closest meteorological station (Swedish Meteorological and Hydrological Institute) in each study region. In all regions, the mean temperature from April to September in 2020 was close to the average for the last 25 years (Appendix B).

2.3. *Microclimatic variables*

We calculated mean temperature and weighed temperature fluctuations ((daily maximum – daily minimum)/mean) for loggers placed under the bark (internal temperature, two transects *per* site) and loggers attached to trees (ambient temperature, one transect *per* site) for the period from April 23 to September 11, 2020.

We calculated thermal sums (degree-days) based on the daily mean temperature from data collected by the loggers (ambient and internal), using the two most commonly applied lower developmental thresholds (LDT) of 5 °C and 8.3 °C for *I. typographus* (Fritscher & Schroeder, 2022). These thresholds have been determined by rearing beetles at different constant temperatures in the laboratory (Annila, 1969; Wermelinger & Seifert, 1998). In the colonisation experiment, the thermal sum was one of several climatic variables tested. It was calculated from the first day of at least 16.5 °C maximum air temperature in the region until 11th of September, using logged ambient temperature data. The threshold of 16.5 °C is the lowest temperature at which *I. typographus* is able to fly (Lobinger, 1994). In the developmental experiment, the thermal sum was calculated from internal temperatures (i.e. temperature experienced by egg-laying females and all developmental stages) in baited logs between the dates the logs were moved into the transects and when new generation adults and emergence holes were observed for the first time. To calculate thermal sums reached at different shade levels *per* region, we used temperature data from all internal loggers from April 23 to September 11 (the period for which we had temperature data for all the sites) and from the closest meteorological stations. We conducted linear regression analyses for each region and shade level to obtain 15 equations (Appendix C). The equations were applied to temperature data from the meteorological stations to predict the internal temperatures and also the degree-days accumulated from September 12 to December

31. We added the predicted values to collected data and calculated thermal sums from the first day with 16.5 °C until December 31 for each region and shade level. The predicted internal thermal sum from 12 September – 31 December constituted 22–23% of total thermal sum for Asa, 17–18 % for Siljansfors, 11–12 % for Järpen, 9–12 % for Vindeln and 10–11 % for Ätnarova (Appendix C).

2.4. Analyses

To analyse the effect of habitat characteristics on internal and ambient mean temperature and temperature fluctuations (variables described in Appendix A), we analysed each of the microclimatic variables as response variables, using linear mixed models with site ID as a random factor.

For the colonisation experiment, we used the three transects *per* site (with three logs *per* transect) that were established before the start of *I. typographus* flight. For the development experiment, we used one transect *per* site with two logs *per* shade level that were moved into the transect after being colonised by *I. typographus*. The two logs placed close to each other at each shade level were treated as a single sample. From all analyses of internal thermal sums we excluded logs (29 of 420) that had emergence holes only on the shady side, thus away from the placed data-loggers, since collected microclimatic data do not reflect the conditions experienced by the species in these cases.

To analyse the effect of habitat characteristics and ambient microclimatic variables (variables described in Appendix A) on the frequency of colonisation of *I. typographus*, we used generalised linear mixed models (binomial distribution) with site ID as a random factor.

To analyse the effect of habitat characteristics on the proportion of logs with *I. typographus* completing development (here defined as presence of emergence holes, indicating that new-generation adults have finalized maturation feeding), we used generalised linear models with a binomial distribution.

Thermal sums *per* regions were analysed with general linear models. To compare the potential of *I. typographus* to have two generations *per* year at different shade levels and in different regions, we used the thermal sum needed for one generation in each region (i.e. until formation of the first emergence holes) to calculate the requisite thermal sum for two generations and compared it with thermal sums accumulated at different shade levels from the first day with 16.5 °C until December 31, 2020.

In all analyses, we performed a first selection of variables, analysing one variable at a time, using second-order Akaike's information criterion corrected for small sample size (AICc; R package *AICcmodavg* (Mazerolle 2019)), as recommended when N *(sample size)* $\times$ k *(number of predictors)*$^{-1} < 40$ (Burnham & Anderson, 2002). We selected all variables that decreased the AICc value in comparison to the null model. We then built multivariable models by testing all possible combinations of selected variables using the R package *MuMIn* (Bartoń, 2019). Models were ranked using the difference between their AICc score and the score of the best-fitting model ($\Delta AICc_i = AICc_i – AICc_{min}$); we considered models with $\Delta AICc < 2$ to be plausible (Burnham & Anderson, 2002).

For the analysis of microclimatic variables, we present these plausible models (1–4 *per* variable) and their predictive performance. As a measure of the predictive performance of the models of mean ambient and internal temperature and temperature fluctuations, we report marginal R^2 (R^2_m, describing the proportion of variance explained by the fixed factors alone) and *conditional* R^2 (R^2_c, describing the proportion of variance explained by both the fixed and random factors, i.e. the variance explained by the whole model).

In species-related analyses, there was always more than one plausible model. Therefore, we performed model averaging to circumvent the problem of competing models. We then built multivariable models by testing all possible combinations of the variables selected at the first step. For models with a $\Delta AICc < 7$ (Burnham et al., 2011), we performed multimodel inference with the R package *MuMIn* (Bartoń, 2019) to calculate standardized averaged parameter estimates of all variables and estimated their relative importance (RVI) based on the sum of Akaike weights of all candidate models containing the variable. We considered variables with a relative variable importance > 0.5 as important. Correlated variables (like several microclimatic variables; $r < -0.43$ or $r > 0.43$) were never included in the same model.

3. Results

3.1. Microclimate vs habitat characteristics

Our hourly measurements of temperature from April to September confirmed that, for logs that are sun-exposed or intermediately shaded, ambient and internal mean temperatures were higher and fluctuations wider than for totally shaded logs (Appendix D). Furthermore, in more south-facing stands, ambient and internal mean temperature and temperature fluctuations were higher. With greater log diameter, internal temperature was higher, and internal fluctuations were narrower (Appendix D).

3.2. Frequency of colonisation

Colonisation of logs by *I. typographus* was more likely in regions with warmer climate, and in sun-exposed logs in comparison to totally shaded logs (Table 1). The habitat preferences of *I. typographus* differed along the regional climate gradient: in regions with cooler climate, *I. typographus* was almost absent in totally shaded conditions, while in regions with warmer climate the species colonised such logs to a considerable extent (Fig. 2). This resulted in a statistically significant effect of the interaction between annual temperature and shade level on the probability of colonisation ($z = 3.036$, $p < 0.001$).

3.3. Development

The development time was longer in regions with a colder climate (Appendix E). Despite this, *I. typographus* reached the adult stage in all logs in all regions and shade levels. In all regions, except the two most northern (Vindeln and Ätnarova), adults also started to emerge from all logs at all shade levels in the first summer. In Ätnarova, adults started to emerge from 40 % of the totally shaded, 60 % of the intermediately shaded and 80 % of the sun-exposed logs. In Vindeln, the corresponding values were 20 %, 80 % and 100 %, respectively. The probability of *I. typographus* completing development in the first summer (recorded as presence of emergence holes) was higher at sites with characteristics reflecting a warmer climate: in regions with higher mean annual temperatures and sites with a lower basal area and the edge facing a more southerly direction (Table 2, Fig. 3). The internal thermal sum needed for completion of development differed between study regions (One-way ANOVA; $F4{,}52 = 6.25$; $p < 0.001$; Table 2, Fig. 3, Appendix F). For both the 5 °C and 8.3 °C LDT models, the average thermal sums were highest for the region with the warmest climate (Asa) and decreased with cooler regional climate, except for Järpen. The thermal sums

Table 1
Model averaged parameter estimates (Est.), standard errors (SE), and relative variable importance (RVI) of habitat characteristics explaining colonisation frequency of *Ips typographus* on Norway spruce logs, based on models with $\Delta AICc < 7$. For shade level, the first category (sun-exposed) is taken as a reference and the presented RVI value is valid for all shade levels (sun-exposed, intermediately and totally shaded). Variable importance > 0.5 is in bold font.

Variables	Est.	SE	RVI
Intermediately shaded log	0.0646	0.357	**1.00**
Totally shaded log	−1.9699	0.428	
Geographical region	0.3002	0.120	**0.96**
Diameter of log	0.0271	0.046	0.46
Direction of forest edge	−0.0007	0.003	0.17

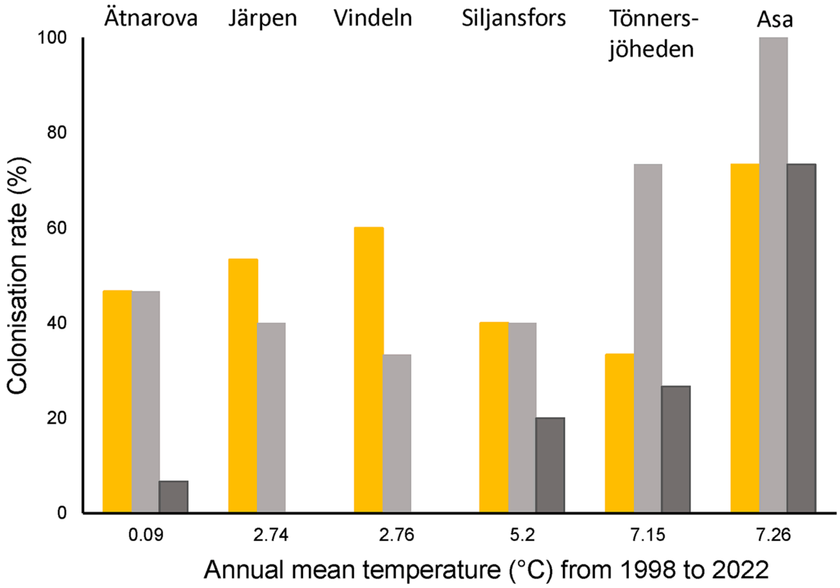

Fig. 2. Frequency of colonisation of *Ips typographus* at three shade levels: sun-exposed (orange), intermediately shaded (light grey), and totally shaded conditions (black) in the six study regions. The study regions are ordered by the average annual temperature over 25 years (1998–2022), starting from the coldest region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Model averaged parameter estimates (Est.), standard errors (SE), and relative variable importance (RVI) of habitat characteristics explaining (1) presence/absence of *Ips typographus* emergence holes (indicating that development has been completed) and (2) internal (measured inside the phloem) thermal sums (5 °C lower developmental threshold) required for development, based on models with ΔAICc < 7. For *location*, the warmest location Asa is taken as a reference and the presented RVI value is valid for all locations. Variable importance > 0.5 is in bold font.

Variables	Est.	SE	RVI	Est.	SE	RVI
	1. Emergence holes			**2. Thermal sums**		
Direction of forest edge	−0.002	0.005	0.33	−0.138	0.227	0.42
Altitude				−0.011	0.074	0.02
Basal area of forest stand	−0.169	0.052	**1.00**	−3.552	1.421	**1.00**
Geographical region	0.985	0.278	**1.00**			
Location: Siljansfors				−81.258	35.839	**0.98**
Location: Vindeln				−27.693	38.480	
Location: Järpen				−165.687	41.579	
Location: Ätnarova				−81.652	36.920	

required for development decreased with increasing stand basal area and with increasing values as for the stand edges facing progressively less southerly directions.

Estimates of the internal thermal sum needed for completing development of two generations of *I. typographus* (based on thermal sums required in 2020 for completing one generation) revealed that, in the region with the warmest climate (Asa), the thermal sum needed for two generations was accumulated in all three shade levels, while that was only the case for some of the logs in the second warmest region (Siljansfors) (Fig. 4). In the three colder regions, two generations were possible in sun-exposed and intermediately shaded logs (Järpen), or only in some of the sun-exposed logs (Ätnarova and Vindeln). In all regions and at all shade levels, the thermal sum was sufficient for development of one generation (Fig. 4).

4. Discussion

4.1. Frequency of colonisation

We found that for *I. typographus*, habitat preferences differ along a south-north gradient: in cooler regions, beetle colonisations were clearly more frequent in sun-exposed logs in comparison to the shaded ones, while that difference was much smaller in warmer regions. Our results are in compliance with earlier observations in Sweden, where *I. typographus* colonised both sun-exposed and shaded wind-felled trees in the south (Göthlin et al., 2000), while at high altitude in central Sweden, only sun-exposed trees were utilised (Schroeder & Lindelöw, 2003). Such preferences can be explained by the great influence of microclimate on insects, and the fact that the microclimate is the result of both regional climate and local habitat characteristics. It is sometimes suggested that habitat preferences differ between regions due to their climate (e.g. Gibbons & Lindenmayer, 2002; Chiari et al., 2012). To disentangle effects of climate from other possible factors varying between regions (cf. Greiser et al., 2021), standardized experiments such as ours are needed, including direct measurements of microclimatic temperature in various habitats as well as regional climate. However, such studies are rare, and to our knowledge the present study is the first of its kind on forest insects.

4.2. Development

In 2020, which had temperatures close to the 25-year average, the new generation of *I. typographus* started to emerge from all logs in the three warmest regions, demonstrating full development (i.e. including maturation feeding of adults). In contrast, in the two most northern regions (Vindeln and Ätnarova) the development was not completed (i.e. the adults did not start to emerge) in many logs in more shaded conditions, although also in these logs specimens had reached the adult stage. This result is in agreement with the low colonisation probability of totally shaded logs we observed in these regions. The development experiment only included logs colonised early in the season, which means that the development success would be even lower for colonisation occurring later.

Our calculations, based on the seasonal thermal sums for 2020 and thermal sums required for complete development of two generations,

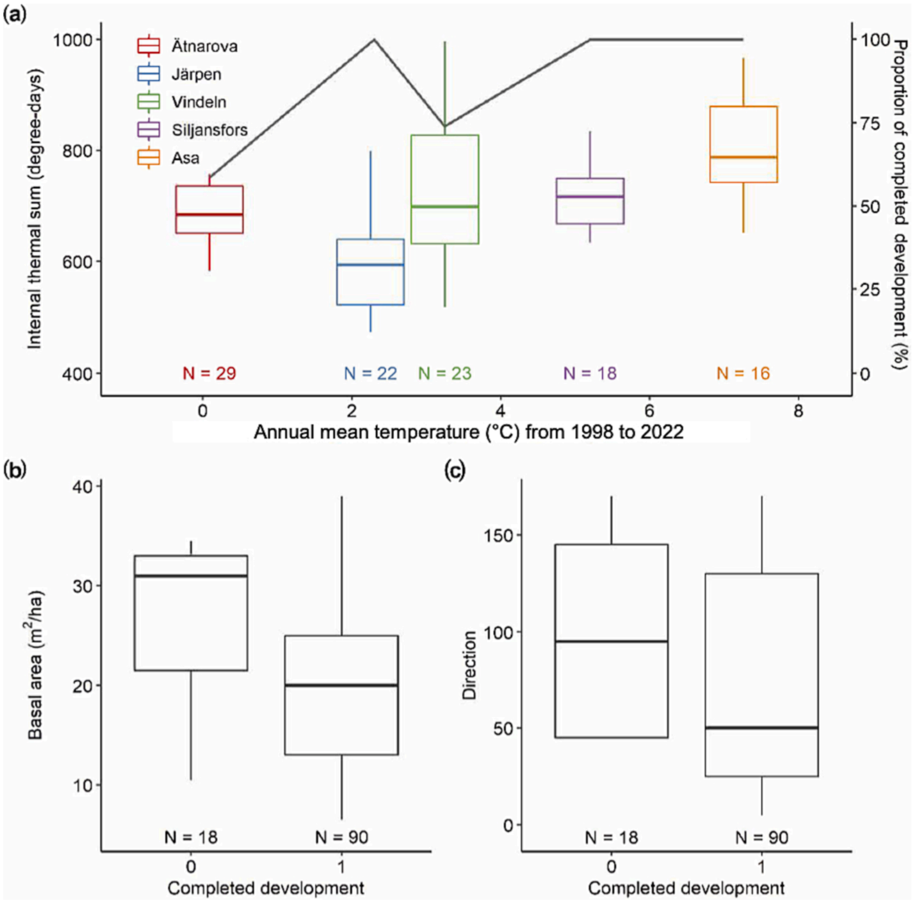

Fig. 3. (a) Internal thermal sums (under bark, 5 °C lower developmental threshold) needed for completed development of *Ips typographus* (i.e. when the first emergence holes appeared) in different study regions (boxplots); proportion of logs with completed development (grey line); and proportion of logs with completed development in relation to (b) stand basal area, and (c) direction of the forest edge (transformed to a linear scale by taking the absolute value of 180° – direction, thus the smaller is the number the more southern direction). The geographical region Tönnersjöheden was not included because the pheromone-baited logs used for the development experiment were not colonized by *Ips typographus*. N is the number of logs.

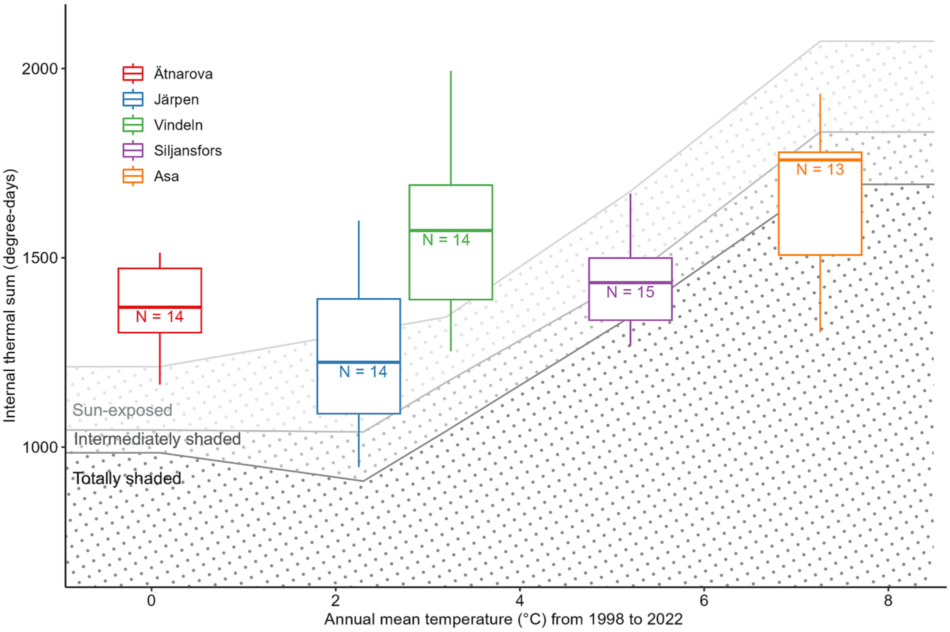

Fig. 4. Calculated internal thermal sums (under bark, 5 °C lower developmental threshold) required for development of two generations of *Ips typographus* in different geographical regions (boxplots) in relation to internal thermal sums over one season (from the first day with 16.5 °C until December 31) for sun-exposed (light grey dotted area), intermediately shaded (medium grey dotted area), and totally shaded (dark grey dotted area) conditions. The geographical region Tönnersjöheden was not included because the pheromone-baited logs used for the development experiment were not colonized by *Ips typographus*. N is indicating the number of internal loggers that were used for calculations. Note that the Y-axis does not start at zero.

reveal that the opportunities for bivoltism is better in southern than in northern Sweden and in sun-exposed than in shaded conditions in the northern regions. In accordance with this, a prior study (conducted in Tönnersjöheden, Siljansfors and Vindeln) demonstrated that a considerably larger proportion of *I. typographus* seasonal trap catches consists of new-generation beetles (i.e. beetles that have developed in the same season) in the southern region compared with the two northern regions (Fritscher & Schroeder, 2022). A limiting factor for bivoltinism is that *I. typographus* must reach the adult stage before hibernation to ensure high winter survival. Thus, when a second generation is initiated, it is important that the remaining seasonal thermal sum is high enough for the brood to reach the adult stage before winter. As an adaptation to this requirement, the proportion of *I. typographus* new generation adults that enter reproductive diapause is affected by the day length. In addition, in northern Sweden a considerable proportion of the new generation has an obligate reproductive diapause (Schroeder & Dahlin, 2017; Schebeck et al., 2022).

We found that the thermal sum under bark needed for development decreased with a cooler regional climate. This is the first study comparing the thermal sums in the substrate where *I. typographus* develops for several regions along a climatic gradient. Earlier studies have mostly been conducted in one region at a time (but see Fritscher & Schroeder, 2022, who however did not measure thermal sums in the substrates used for development) and with different methods, such as rearings in constant temperatures in the lab (Wermelinger & Seifert, 1998) or inspections of trap trees in the field and emergence from stem sections in climate chambers or outdoor photoeclectors (Baier et al., 2007; Ogris et al., 2019). Thus, comparisons between regions have been difficult. The intraspecific variation demonstrated in the present study may be the result of selection pressure for decreasing the thermal sum in cool regions, since there it is difficult for *I. typographus* to complete development, especially in cooler summers. The migration rate of *I. typographus* between regions might be considerable (Jacobsen Ellerstrand et al., 2022), which tends to mitigate the effect of the selection pressure.

4.3. Conclusions

Our study reveals two factors that may contribute to higher outbreak risk in a warmer climate, for instance in southern in comparison to northern Sweden, but also when the climate is warming over time. First, in a warmer climate, *I. typographus* can, to a higher extent, reproduce in shaded as well as sunny conditions, and therefore more habitat is available in spruce dominated forest landscapes in the south compared to the north. This means that in the south, the initial population that is able to take advantage of a disturbance is larger and that more suitable breeding material will be available after storm-felling. Second, in the south, the population growth after a disturbance can be faster since two generations *per* year can develop successfully. Indeed, outbreaks of *I. typographus* have been more frequent and severe in southern than in northern Sweden (Kärvemo & Schroeder, 2010; Schroeder & Kärvemo, 2022). Finally, a warming climate is expected to increase both the frequency and severity of *I. typographus* outbreaks as a result of an increased frequency of exceptionally warm and dry summers (Seidl et al., 2014; Bentz et al., 2019; Wilcke et al., 2020). Projections of how *I. typographus* responds to a warming climate also need to make assumptions about the extent to which regional populations adapt to a new warmer climate by a changed selection pressure or increased immigration from other regions.

We found that the habitat preferences of *I. typographus* differ with regional climate. This has consequences for forestry, since the recommendation is that wind-felled trees are removed before *I. typographus* reproduces in them to decrease the outbreak risk (Schroeder & Lindelöw, 2002). The difference in habitat preferences means that, in the north, it is enough to remove recently wind-felled spruces that are sun-exposed, such as along edges, while in the south, also trees in more shaded conditions inside forests are a suitable substrate for *I. typographus*.

In Northern Europe, forestry has favoured Norway spruce due to its potential for high productivity of cellulose fibre (Schlyter et al., 2006). In a warming climate, the increased risk and severity of *I. typographus* outbreaks makes Norway spruce less attractive. So far, *I. typographus* outbreaks have mainly occurred in the south, but in the future they will probably also be more frequent further north. This should be taken into account in forestry.

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CRediT authorship contribution statement

Ly Lindman: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft. **Thomas Ranius:** Funding acquisition, Project administration, Supervision, Writing – original draft. **Martin Schroeder:** Conceptualization, Methodology, Supervision, Writing – original draft.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Thomas Ranius reports financial support provided by Carl Tryggers Foundation. Ly Lindman reports financial support provided by Brattåsstiftelsen Foundation.

The remaining author declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data available: https://snd.gu.se/sv/catalogue/study/2022-260

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Appendix A. Supplementary data

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