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Microclimate in hollow trees and how it affects an inhabiting beetle species, *Osmoderma eremita*

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Abstract

1. Studies of species' responses to microclimatic conditions have increased our understanding of their habitat requirements and possible responses to climate warming. However, little is known about the role of microclimate for insects inhabiting hollow trees.
2. We explored the relationship between tree characteristics and microclimate, and analysed how the microclimate in tree-hollows affects the occurrence and body size of an endangered beetle species, *Osmoderma eremita*.
3. We placed temperature data-loggers in wood mould (= loose material in tree-hollows) and surveyed *O. eremita* in 47 hollows in oak pastures in south-eastern Sweden. We found that tree characteristics previously known to be associated with occurrence of beetle species confined to tree-hollows (larger diameters, more wood mould, entrances higher up, and not directed upwards) tend to decrease moisture and moisture variation, while their effects on temperature and temperature fluctuations differ during different seasons. This indicates that microclimatic conditions are important for beetles in hollow trees, and many specialised species seem to avoid conditions that are too moist.
4. *O. eremita* occurred more frequently in trees with a warmer and more stable microclimate, while adult body size decreased with a warmer microclimate. A positive effect of a warmer microclimate was expected, since the study was done near the northern margin of the species' range.
5. *O. eremita* is confined to living in hollow trees, which may be due to the microclimate there being more stable in comparison to both the ambient climate and the microclimate in standing and downed dead wood.

KEYWORDS
body length, capture-mark-recapture, cavity, data-loggers

INTRODUCTION

With a warming climate, the importance of microclimate for an organism's performance is increasingly recognised, since macroclimate affects organisms through the microclimatic conditions (Greiser et al., 2020). Microclimate is the temperature and humidity in a small space (Geiger et al., 2012), which is continuously modified by solar radiation and wind (Willmer, 1982). It is affected both by natural

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variation in vegetation and topography, and by land use and management (Greiser et al., 2020). Studies on the effect of microclimate on organisms should preferably be based on direct measurements of the microclimate. However, many studies only consider habitat characteristics assumed to be microclimate proxies (Seibold et al., 2016; Siitonen, 2001), probably because it can be difficult to collect microclimatic data directly. With the development of low-cost data-loggers it has become easier and cheaper to collect microclimatic data in the field (Terando et al., 2017). This has recently resulted in many studies demonstrating strong links between microclimatic conditions and biodiversity (De Frenne et al., 2021).

Insect species have well-defined temperature ranges, within which their performance is optimal (Chown & Nicolson, 2004). It is assumed that insects select habitats based on their intrinsic quality, including microclimatic conditions, to maximise fitness (Eilers et al., 2013; Morris, 2003). Temperature affects the survival of insects (Andrewartha & Birch, 1954), but also development time and body size according to the '*temperature-size rule*', which proposes that ectotherms that develop at higher temperatures will grow faster but be smaller as adults (Atkinson, 1994; Kingsolver & Huey, 2008). In turn, adult body size influences population dynamics, since individuals with larger body size tend to have greater performance and fitness than smaller individuals within a population (Kingsolver & Huey, 2008). Thus, climatic conditions are important for the persistence of populations (Kiritani, 2013).

Knowledge about microclimatic requirements is important in nature conservation, since conservation management can help to generate required microclimatic conditions. Saproxylic (i.e., deadwood-dependent) insects inhabiting old trees are one of the most endangered invertebrate groups due to a severe loss of habitat worldwide (Seibold et al., 2015). Many saproxylic insects are positively affected by keeping trees free-standing, which may affect the microclimatic conditions inside the trees (Ranius & Jansson, 2000). A large number of saproxylic beetles (Ranius & Jansson, 2000) and other invertebrates are specialised to tree hollows (Siitonen & Ranius, 2015). While the microclimatic conditions in tree hollows have been shown to be important for nesting birds and mammals (e.g., Maziarz & Wesołowski, 2013; Sedgeley, 2001; Wiebe, 2001), this has been poorly studied for invertebrates (see, however, Gouix et al. (2012) and Chiari et al. (2012), who both related a qualitative categorisation of moisture of hollow trees to the occurrence of certain beetle species). For beetles associated with other types of deadwood, only recently have microclimatic variables and species' data been analysed together (Lettenmaier et al., 2022; Lindman et al., 2022; Müller et al., 2020).

Among saproxylic insects confined to tree hollows, *Osmoderma eremita* (Scopoli 1763) is the most widely studied species. Microclimate is thought to be an important factor explaining the suitability of hollow trees for *O. eremita*, but it might have different effects at different latitudes (Chiari et al., 2012; Ranius & Nilsson, 1997). Several studies have explored the characteristics of hollows inhabited by *O. eremita* in south-eastern Sweden and found that habitat openness (Ranius & Nilsson, 1997), the volume of wood mould (i.e., the mixture of organic detritus formed in the tree hollows which includes rotten wood, dead invertebrates, fungi, and old bird nests etc.; Ranius et al., 2005, 2009; Lindman et al., 2020), and the size of the entrance hole (Lindman et al., 2020) are the most important characteristics explaining the patterns of species' occurrence. It has been suggested that these characteristics reflect suitable microclimatic conditions (Ranius, 2002); however, this has never been confirmed by combining direct measures of microclimatic conditions with observations of insect species inhabiting wood mould in tree hollows. Furthermore, it has been observed that the adult body size of *O. eremita* differs among trees, and this is probably related with the suitability of trees (Hedin & Smith, 2003).

The aim of the present study is to reveal the relationships between characteristics of hollow trees, the microclimate for invertebrates living in the wood mould, and the occurrence and body size of *O. eremita*. More precisely, we aim to answer the following questions:

i. How is the microclimate inside hollows affected by tree characteristics?
ii. To what extent are the occurrence and body size of *O. eremita* related to the microclimate in tree hollows?
iii. How are the occurrence and body size of *O. eremita* related to tree characteristics?

We explore microclimatic conditions directly by placing temperature data-loggers in the wood mould of tree hollows. This is a novel approach to analyse wood mould microclimate in relation to tree characteristics. We hypothesise that microclimatic variables are important for *O. eremita* and thus explain to a large extent the observed patterns of occurrence and body size. Thus, we further hypothesise that the species' occurrence is positively related, but its body size is negatively related, to a warmer microclimate. This is because our study area is close to the northern limit of the distribution range of *O. eremita*, which can imply that a warm microclimate is more important for the occurrence of the species, while body size is affected by temperature according to the '*temperature-size rule*' (Atkinson, 1994). We hypothesise also that those tree characteristics that relate to occurrence of *O. eremita* also explain microclimatic variables related with a high frequency of occurrence of *O. eremita*. Since body size might be related to the population size, we assessed the population size and included it in the analyses.

MATERIAL AND METHODS

Study species

O. eremita is approximately 3 cm long Scarabaeid beetle, exclusively inhabiting hollows of deciduous trees. Both larvae and adults live mainly in the wood mould (Ranius et al., 2005). In Sweden, *O. eremita* primarily inhabits oak (*Quercus robur*) hollows containing large volumes of wood mould (Ranius et al., 2009). The development time of *O. eremita* larvae is usually 3 or 4 years, while the adults live for a few weeks (Ranius et al., 2005). In Sweden, adults emerge in July and August. They typically remain in the same tree hollows throughout

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their lifetime, but a small fraction (15%) of individuals disperse to other trees (Ranius & Hedin, 2001). Females have slightly longer bodies than males (Svensson et al., 2011).

Study area and sampling design

This study was conducted in 2019 at two areas in south-eastern Sweden, Bjärka-Säby (58°16′ N, 15°46′ E) and Brokind (58°12′ N, 15°40′ E), where *O. eremita* has been studied since 1995 (Lindman et al., 2020). The study areas contain a high density of hollow oaks. Together with the surrounding region, they harbour the highest concentration of known localities of *O. eremita* in the world (Ranius et al., 2005). The two study areas include 47 sampled hollows clustered in five sites (Figure 1).

We included all standing hollow trees with cavities in which it was possible to place a pitfall trap. We excluded the trees where the entrance hole of hollows was higher than 5 meters above the ground (length of the ladder), hollows which were too narrow to access, had too little accessible wood mould in which to place a pitfall trap, or where the wood mould was inaccessible (i.e., too far from the entrance hole to be reached). In each hollow, we placed a pitfall trap, which was an empty jar with a top diameter of 7 cm, and placed it in the wood mould with the opening at the level of the wood mould surface (Ranius, 2001). The traps were emptied every second day from early July to mid-August. Each trapped beetle was measured, sexed, given an individual mark on the elytra and then released on the surface of the wood mould.

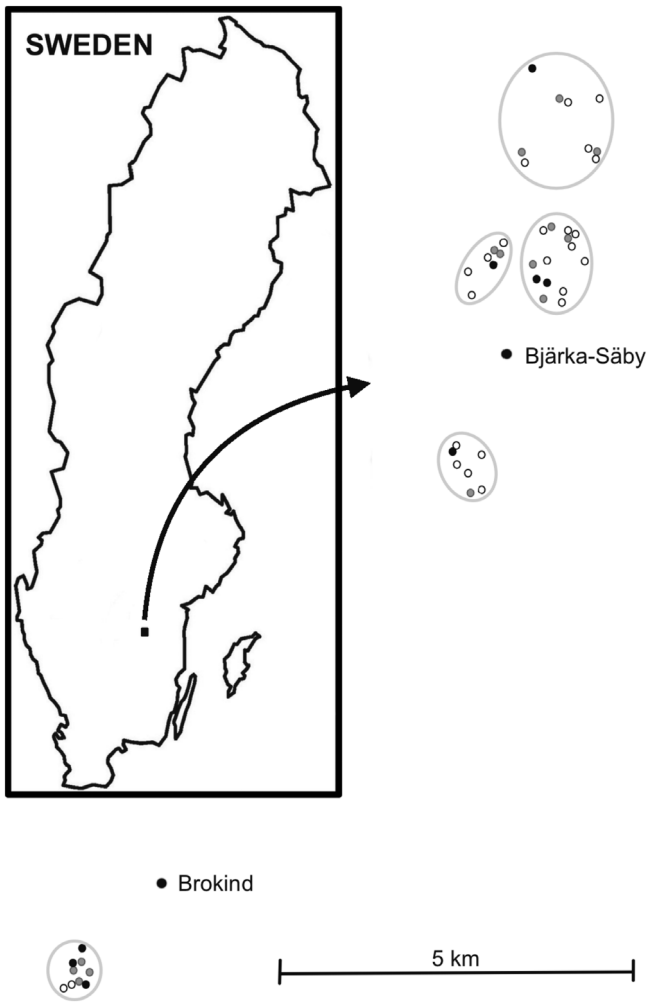

FIGURE 1 Location of the studied hollow trees of *Osmoderma eremita* clustered in five sites (surrounded by light grey line) in Bjärka-Säby and Brokind (Östergötland, Sweden) with population size >10 (black filled circles), > 0 and ≤10 (grey filled circles), and 0 (open circles)

Microclimatic variables

To record internal temperature, we placed one Lascar EL-USB-1 (Lascar Electronics, UK) temperature data-logger 15 cm below the wood mould surface inside each tree hollow being sampled with a pitfall trap. In addition, one logger *per* site was attached to the northern side of a tree 2.5 m above the ground to record the ambient temperature. The ambient temperature was found to differ between sites (average temperature *per* season differed by 0.26°C–1.02°C between the coldest and the warmest sites), but we assumed it to be more similar within each site. This was because several characteristics known to affect microclimate (distance to watersheds, forest and agricultural fields) differed between sites but were similar within sites, although vegetation and altitude were similar for all. The loggers were set to record temperature every hour and were left there for a year (from July 2019 to August 2020). We received temperature data from 38 of 47 loggers placed in the wood mould, since 9 loggers did not work. We divided the temperature data into four seasons due to distinct weather patterns during these periods: summer (June, July, August), autumn (September, October, November), winter (December, January, February), and spring (March, April, May), and calculated *average temperature* and *average daily temperature fluctuations* (as a difference between daily minimum and maximum) for each season. This was done for both temperatures recorded in the wood mould and for the ambient air.

During 1 month (from 10th of July to 8th of August), we measured volumetric water content of the wood mould in each tree every second day with a GS3 sensor (Decagon Devices) at a depth of 5 cm. We calculated the *mean moisture* and the *moisture variation* (as a coefficient of variation of moisture = SD/mean for each tree) over the measured period.

Tree characteristics

Tree characteristics known to be important to *O. eremita* (Ranius, 2002; Ranius & Jansson, 2000; Ranius & Nilsson, 1997) were measured in 2019 (Table 1).

We recorded whether a hollow tree was *alive* or *dead*, and calculated its *diameter* from the circumference measured at 1.3 m above

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TABLE 1 Estimates of microclimatic variables and tree characteristics used in the study

Variables	Min	Max	Mean	SD
1) Difference between internal and ambient microclimatic variables				
Difference between mean daily internal and ambient temperature, ΔTemp				
a) Summer	−3.70	2.05	−1.02	1.23
b) Autumn	−0.24	3.25	1.02	0.71
c) Winter	−0.96	1.15	0.10	0.36
d) Spring	−2.50	1.85	−0.76	0.78
Differences between internal and ambient daily temperature fluctuations, B_{Fluct}				
a) Summer	0.74	0.97	0.88	0.05
b) Autumn	0.70	0.95	0.84	0.06
c) Winter	0.62	0.95	0.79	0.07
d) Spring	0.65	0.98	0.87	0.07
2) Internal microclimatic variables				
Average internal temperature				
a) Summer	14.25	19.66	16.9	1.11
b) Autumn	7.23	10.95	8.52	0.73
c) Winter	2.14	4.15	3.16	0.38
d) Spring	5.04	9.17	6.66	0.73
Internal temperature fluctuations				
a) Summer	0.42	2.41	1.26	0.51
b) Autumn	0.30	1.63	0.85	0.31
c) Winter	0.23	1.63	0.87	0.33
d) Spring	0.28	3.66	1.36	0.71
Moisture				
a) Mean	0.39	18.29	4.39	4.49
b) Variation	0.13	1.06	0.48	0.2
3) Tree characteristics				
Alive/dead	0	1	0.8	0.4
Diameter	52.2	208.8	132.7	34.8
Entrance height	0	417	140.4	130
Area of entrance hole	0.5	166	27.9	43.8
Wood mould volume	0.6	305.0	58.5	63.2
Direction of entrance	1	3	2.0	0.9
Angle of entrance	−39	10	−10.3	11.4
Canopy cover	1	3	1.7	0.7

Note: (1) Differences between internal and ambient microclimatic variables calculated from data of temperature data-loggers placed inside and outside hollows (°C). (2) Internal microclimate: temperatures—calculated values using data from temperature data-loggers placed inside hollows (°C); moisture content—volumetric water content of wood mould (%), measured by GS3 sensor. (3) Tree characteristics used in the analyses: *alive/dead*, 1 = alive with green leaves, 0 = dead; *diameter of trees*, calculated from the measured circumference (cm); *entrance height*, measured distance between the ground and the lower point of hollow (cm); *area of entrance hole*, calculated hollow opening area (cm^2); *wood mould volume*, calculated volume from surface area and the depth of cavity (dm^3); *direction of entrance*, categorised direction according to the distance from south, 3 classes (nr); *angle of entrance*, angle between the upper and lower edge of a hollow entrance (degrees); *canopy cover*, categorised estimation of how much of 2 m around the tree cover is covered by branches of other trees, 3 classes (nr). For measurement and calculation details, see Section 2.

the ground. We measured the *entrance height* as the distance from the ground to the lower part of the entrance hole.

The *area of entrance hole* and wood mould surface in hollows were measured on the basis of the shape they most resembled (ellipse, circle, triangle, or rectangle). The wood mould surface area (S) and the estimated depth of the cavity from the surface (measured three times for each hollow with a wooden ruler, using the largest value) were used for calculating *wood mould volume* (V = [depth of cavity × surface area S]/3).

The *Direction of entrance* was categorised according to the sun-path diagram, considering the intensity of the sun's irradiation. We divided the circle (360°) into four sections which were numbered

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according to the distance from south (180°), resulting in three categories: 1 (136°–225°) being the most southerly, 2 (46°–135° and 226°–315°) east and west, and 3 (316°–45°) the most northerly direction.

Angle of entrance is the angle between the upper and lower edge of a hollow entrance: the angle was negative when the upper edge was less protruding than the lower edge (generating a higher probability to get wet from rainwater) and positive when not. Thus, an entrance directed totally upwards has an angle of −90°, and an entrance directed totally downwards +90°.

Canopy cover was estimated based on the percentage of the area of 2 m around the cover of a focal tree that was covered by branches of other trees. We divided the estimates into three categories: 1 (<25%), 2 (25–75%), and 3 (>75%).

Occurrence, body length, and population size

Surveyed trees were classified as occupied or unoccupied by *O. eremita* according to the adults caught in 2019. Eight trees, where only one individual was found and was never recaptured in the tree, were categorised as unoccupied to avoid false positives due to immigration. Each captured individual was sexed and its body length from the front of the head (i.e., the labrum) to the tip of the abdomen (i.e., the pygidium) was measured with 1 mm accuracy as a proxy for body size.

To estimate population size from capture-mark-recapture data, we used Craig's (1953) model: $log\ n - log\ (n - r) = s \times n^{-1}$, in which n is the population size, r is the number of captured individuals, and s is the number of captures. Although different models based on the Jolly-Seber method (Jolly, 1965) have recently been used more often to estimate population size (Madon et al., 2011; Schwarz, 2001), we used Craig's model, since it requires less data and has been shown to result in fairly accurate estimates of population size (Matter & Roland, 2004; Ranius, 2001). However, even with this method it was not possible to calculate the population size for each tree separately, as many trees had no recapture events. Therefore, we divided the trees into two groups: (i) trees with >10 captured individuals, and (ii) trees with ≤10 captured individuals. For the first group, we used Craig's model for each tree separately. For the second group, we used Craig's model to estimate the total population size in all studied trees. This estimate was divided by the number of captured individuals to give a 'catchability' rate. The population size in each tree was estimated by multiplying this rate by the number of captured individuals in each tree. Due to the small number of occupied trees ($N = 13$) in our study, we only explored the relationships between microclimatic variables, presence/absence, and body size, but not the population size of *O. eremita*.

Statistical analysis

To understand how microclimatic conditions inside hollows are related to tree characteristics, while considering the difference in ambient air temperature between sites, we calculated (i) the mean internal-ambient temperature difference (ΔTemp = average internal temperature – average ambient temperature), and (ii) a variable reflecting the capacity to buffer temperature fluctuations, B_{Fluct} where:

B_{Fluct} = 1 – (average internal fluctuations × average ambient fluctuations^{-1}).

The calculated variables *mean moisture* and *moisture variation* were log-transformed, analysed, and back-transformed when presenting the results. Temperature and moisture variables described above were analysed as response variables in relation to tree characteristics (Table 1), using linear models for ΔTemp and moisture variables, and generalised linear models (beta regression with the *betareg* package; Cribari-Neto & Zeileis, 2010) for B_{Fluct}.

To test which microclimate and tree variables explain occurrence (presence/absence) and body size of *O. eremita*, we used two data sets. First, for analysing occurrence, we used a data set that included all surveyed trees. Second, for analysing the body size, we used a data set of all captured individuals. Due to unbalanced data, we used a Welch two-sample t-test to see whether body size differed between sexes and locations. Tree characteristic *alive/dead* was excluded from these analyses as *O. eremita* only occurred in living trees.

We analysed species' presence/absence and body size, in relation to tree characteristics and microclimatic variables recorded in hollows (Table 1), separately and together, in order to find out which group of variables best explain the patterns of *O. eremita*. More precisely, we analysed these two response variables in relation to (i) tree characteristics; (ii) microclimatic variables (temperature and moisture); and (iii) tree characteristics and microclimatic variables combined. Occurrence was analysed using binomial logistic regression with presence (1) or absence (0) as the response variable. Body size was analysed using linear mixed models with location (binary: Bjärka-Säby, Brokind) as a random factor; the variables *population size* and *sex* were included in all models.

Due to the high number of potential predictors ($k \leq 21$, depending on the analysis), 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)* × *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 ΔAICc <2 to be plausible (Burnham & Anderson, 2002).

As we did not usually find a single best model, we performed model averaging to circumvent the problem of competing models. We extracted all possible models from a global model with a ΔAICc <7 (Burnham et al., 2011) and performed multimodel inference (with the

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R package *MuMIn* (Bartoń, 2019)) to calculate standardised averaged parameter estimates of all variables and estimated their relative importance based on the sum of Akaike weights of all candidate models containing the variable. We considered relative variable importance >0.5 important. Correlated variables (like several microclimatic variables; $r < -0.43$ or $r > 0.43$) were never included in the same model.

As an absolute value for goodness-of-fit for the models of ΔTemp, *adjusted* R^2 (R^2_{adj}) values are reported, and for B_{Fluct} *pseudo-R-squared* (squared correlation between a linear predictor and a link-transformed response variable; R^2_{beta}) values. For moisture variables, *adjusted* R^2 (R^2_{adj}) values are presented for models of transformed data. These were therefore not included in comparisons of models of other variables. To assess the predictive performance of our models of *O. eremita* occurrence, and to understand which variables are better at explaining the patterns of *O. eremita*, we used *Nagelkerke's pseudo-R-squared* (R^2_N) and the coefficient of determination based on the *likelihood-ratio test* (R^2_{LR}) values, calculated separately for models with tree characteristics, with internal microclimatic variables, and with these variables combined. To assess the predictive performance of our models of *O. eremita* body size, and to understand which variables are better at explaining the size of adults, *marginal* R^2 (R^2_m, describing the proportion of variance explained by the fixed factor[s] alone) and *conditional* R^2 (R^2_c, describing the proportion of variance explained by both the fixed and random factors, that is, the variance explained by the whole model) are reported.

RESULTS

Effect of tree characteristics on the internal microclimate of hollows

The temperature inside hollows was slightly warmer than the external ambient air in autumn (inside hollows: 8.52 ± 0.73 SD°C vs. ambient air: 7.50 ± 0.13°C) and winter (3.16 ± 0.38°C vs. 3.06 ± 0.08°C), while it was slightly colder in spring (6.66 ± 0.73°C vs. 7.41 ± 0.11°C) and summer (16.90 ± 1.11°C vs. 17.92 ± 0.37°C). Internal temperature varied daily following changes of the ambient temperature, but the range of the daily temperature fluctuations was always narrower inside hollows compared to the ambient air (summer: 1.26 ± 0.51°C vs. 10.73 ± 1.13°C; autumn: 0.85 ± 0.31°C vs. 5.56 ± 0.33°C; winter: 0.87 ± 0.33°C vs. 4.24 ± 0.22°C; spring: 1.36 ± 0.71°C vs. 10.66 ± 1.43°C; Figure S1). The highest temperature in hollows in summer was 26°C and the lowest in winter −3°C, while the corresponding ambient temperatures were 41.5°C and −7°C, respectively.

Tree characteristics explained a considerable part of the ΔTemp variation in spring and summer ($0.47 \le R^2_{adj} \le 0.51$), but less of its variation in autumn and winter ($0.21 \le R^2_{adj} \le 0.28$). Tree characteristics explained the variation of B_{Fluct} poorly in spring and summer ($0.01 \le R^2_{beta} \le 0.12$), but slightly better in autumn and winter ($0.19 \le R^2_{beta} \le 0.27$). Mean moisture and moisture variation were poorly ($-0.02 \le R^2_{adj} \le 0.11$) explained by tree characteristics (Table S1).

Five tree characteristics (*diameter*, *entrance height*, *wood mould volume*, *direction of entrance*, and *angle of entrance*) occurred frequently in the models predicting microclimatic variables (with the order reflecting their importance, *diameter* and *entrance height* being the most important; Table 2). With larger *diameters*, the temperature was cooler in summer but warmer in autumn and winter (Figure 2a-c). Furthermore, with larger *diameters*, B_{Fluct} was higher in summer, indicating narrower internal fluctuations in summer in larger trees. With increasing *entrance height*, it was warmer in spring and summer but colder in autumn and winter. With increasing *wood mould volume*, the temperature was lower in summer, winter and spring (Figure 2i-k). With increasing *direction of entrance*, ΔTemp decreased in spring (Figure 2d), and B_{Fluct} increased in autumn and winter, implying that hollows with north-facing entrances were colder and with narrower temperature fluctuations. With decreasing *angle of entrance* (negative value implies that the entrance is directed more upwards) moisture was higher and B_{Fluct} in autumn was greater, indicating narrower temperature fluctuations.

Occurrence and body length of *O. eremita*

O. eremita was found in 13 (28%) of 47 sampled hollows. We captured 256 individuals of *O. eremita*, and made 234 recaptures in total.

A combination of tree characteristics and internal microclimatic variables explained the occurrence and body size of *O. eremita* better (Table S2) than only tree characteristics (Table S3) or only microclimatic variables (Table S4). Microclimatic variables were better at explaining the occurrence compared to tree characteristics. Conversely, body size was better explained by tree characteristics than microclimatic variables (Figure 3).

The species occurred more frequently in hollows with a higher mean summer temperature, and lower summer temperature fluctuations and moisture variation (Figure 4a-c). Occupied trees had entrance holes higher up compared to unoccupied hollow trees (Table 3; Figure 4d).

We measured the size of 82 females and 174 males. Males tended to be smaller than females, but the difference was not significant ($t = -1.59$; $df = 172.8$; $p = 0.114$). Average body length for females was 29.3 (± 2.2 SD) mm, and for males 28.8 (± 2.4) mm. Individuals were longer ($t = 6.08$; $df = 245.7$; $p < 0.0001$) in trees in Bjärka-Säby than in Brokind (Figure 4e). The population size between individual trees differed considerably (Table S5).

Individuals were bigger in hollows with south-facing entrances that had lower and more stable temperatures in spring, and narrower moisture variation (Table 3; Figure 4f–i). Wider winter fluctuations appeared in some microclimatic models, associated with larger body

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TABLE 2 Model averaged parameter estimates (Est.), standard errors (SEs), and relative variable importance (RVI) of tree characteristics explaining (1) daily average temperature ΔTemp (ΔTemp = average internal temperature—average ambient temperature); (2) buffering of fluctuations B_{Fluct} (B_{Fluct} = 1 – (average internal fluctuations × average ambient fluctuations^{-1}) in (a) summer, (b) autumn, (c) winter, and (d) spring; and (3a) mean moisture, and (3b) moisture variation (as a coefficient of variation of moisture = SD/mean for each tree), based on models with ΔAICc <7

Variables	Est.	SE	RVI	Est.	SE	RVI	Est.	SE	RVI	Est.	SE	RVI
1. ΔTemp		**a) Summer**			**b) Autumn**			**c) Winter**			**d) Spring**	
Alive/dead	−0.012	0.064	0.19	0.011	0.078	0.15	−0.038	0.114	0.24	0.001	0.054	0.14
Diameter	−0.458	0.129	**1.00**	0.367	0.203	**0.89**	0.259	0.202	**0.76**	−0.011	0.055	0.16
Entrance height	0.612	0.134	**1.00**	−0.306	0.227	**0.77**	−0.160	0.186	**0.56**	0.470	0.124	**1.00**
Area of entrance hole	0.050	0.110	0.31	0.099	0.173	0.38	0.071	0.144	0.34	0.023	0.078	0.21
Wood mould volume	−0.127	0.147	**0.57**	−0.097	0.166	0.38	−0.149	0.184	**0.54**	−0.351	0.138	**0.97**
Direction of entrance 2	0.011	0.056	0.08	−0.036	0.112	0.15	−0.147	0.203	0.44	−0.015	0.136	**1.00**
Direction of entrance 3	−0.006	0.044		0.012	0.074		−0.119	0.174		−0.507	0.128	
Angle of entrance	0.021	0.073	0.22	−0.006	0.062	0.13	−0.020	0.082	0.20	−0.002	0.049	0.14
Canopy cover 2	0.001	0.034	0.06	−0.155	0.215	0.43	0.001	0.057	0.11	0.024	0.086	0.39
Canopy cover 3	−0.008	0.048		−0.131	0.186		−0.026	0.095		−0.092	0.140	
2. B_{Fluct}		**a) summer**			**b) autumn**			**c) winter**			**d) spring**	
Alive/dead	0.054	0.129	0.30	0.006	0.070	0.16	0.022	0.095	0.21	0.013	0.083	0.19
Diameter	0.145	0.181	**0.53**	0.026	0.087	0.22	0.009	0.067	0.16	0.011	0.075	0.18
Entrance height	0.022	0.093	0.22	−0.016	0.075	0.18	−0.017	0.078	0.18	0.031	0.101	0.24
Area of entrance hole	−0.090	0.158	0.39	−0.012	0.073	0.16	−0.003	0.066	0.15	−0.027	0.099	0.23
Wood mould volume	0.032	0.102	0.24	−0.003	0.061	0.14	0.006	0.067	0.15	0.011	0.077	0.18
Direction of entrance 2	0.022	0.088	0.16	0.319	0.186	**0.91**	0.234	0.203	**0.74**	0.046	0.123	0.20
Direction of entrance 3	0.045	0.124		0.411	0.202		0.313	0.235		0.053	0.133	
Angle of entrance	−0.077	0.145	0.37	−0.197	0.187	**0.66**	−0.060	0.126	0.32	−0.062	0.132	0.32
Canopy cover 2	−0.019	0.079	0.11	−0.011	0.061	0.05	−0.071	0.154	0.23	−0.034	0.108	0.16
Canopy cover 3	0.012	0.071		−0.001	0.039		−0.003	0.083		0.002	0.067	
3. Moisture		**a) Mean**			**b) Variation**							
Alive/dead	0.004	0.073	0.20	−0.021	0.086	0.23						
Diameter	−0.094	0.144	0.45	−0.012	0.073	0.20						
Entrance height	−0.084	0.140	0.41	−0.023	0.088	0.24						
Area of entrance hole	0.024	0.092	0.24	−0.020	0.084	0.22						
Wood mould volume	−0.044	0.106	0.30	<−0.001	0.067	0.19						
Direction of entrance 2	0.055	0.124	0.26	−0.016	0.072	0.11						
Direction of entrance 3	0.065	0.137		−0.023	0.086							
Angle of entrance	−0.176	0.175	**0.65**	−0.006	0.070	0.20						
Canopy cover 2	−0.026	0.088	0.14	0.046	0.119	0.18						
Canopy cover 3	−0.020	0.078		0.009	0.073							

Note: For direction of entrance and canopy cover, the first categories (direction 1, canopy cover 1, respectively) are taken as references. Variable importance >0.5 is in bold font.

size. In all cases, body size decreased with increasing population size (Figure 4j).

DISCUSSION

Using temperature loggers inside tree hollows, in combination with detailed surveys of occurrence and measurements of body size, we assessed the importance of microclimate for the quality of the habitat for a specialised beetle species. We found that tree characteristics indeed influenced the microclimate in tree hollows, and that microclimatic variables improved the predictability of occurrence and body size of *O. eremita* compared to models with tree characteristics alone. Species' occurrence was better explained by microclimatic variables than tree characteristics, while conversely, body size was better explained by tree characteristics than microclimatic variables.

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Ecological Entomology

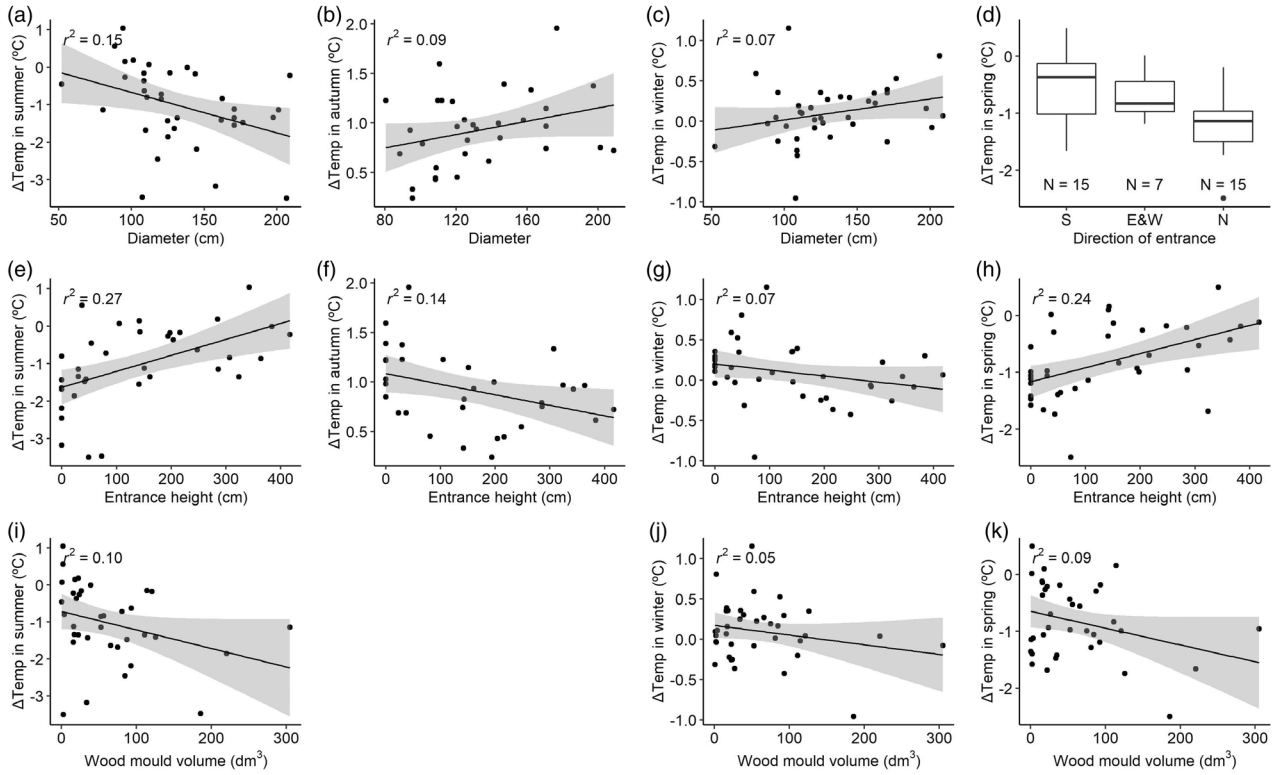

FIGURE 2 Relationships between relatively important tree characteristics (RVI >0.5) and ΔTemp. Relationships between diameter and ΔTemp in (a) summer, (b) autumn, and (c) winter; (d) direction of entrance (S—south, E & W—east and west, N—north) and ΔTemp in spring; entrance height and ΔTemp in (e) summer, (f) autumn, (g) winter, and (h) spring; wood mould volume and ΔTemp in (i) summer, (j) winter, and (k) spring. Either sample size (*N*) or correlation coefficient ($r^2 \pm$ SE as the grey area) is presented accordingly

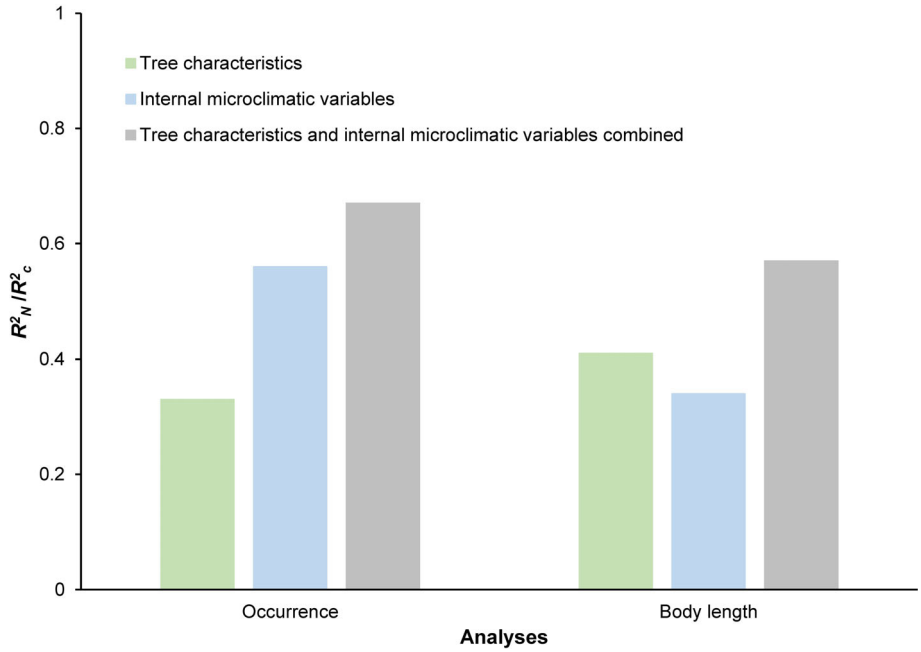

FIGURE 3 Predictive performance (R^2_N/R^2_c) of models of occurrence and body size of *O. eremita* in relation to tree characteristics, microclimatic variables measured inside tree hollows, and the combination of tree characteristics and microclimatic variables

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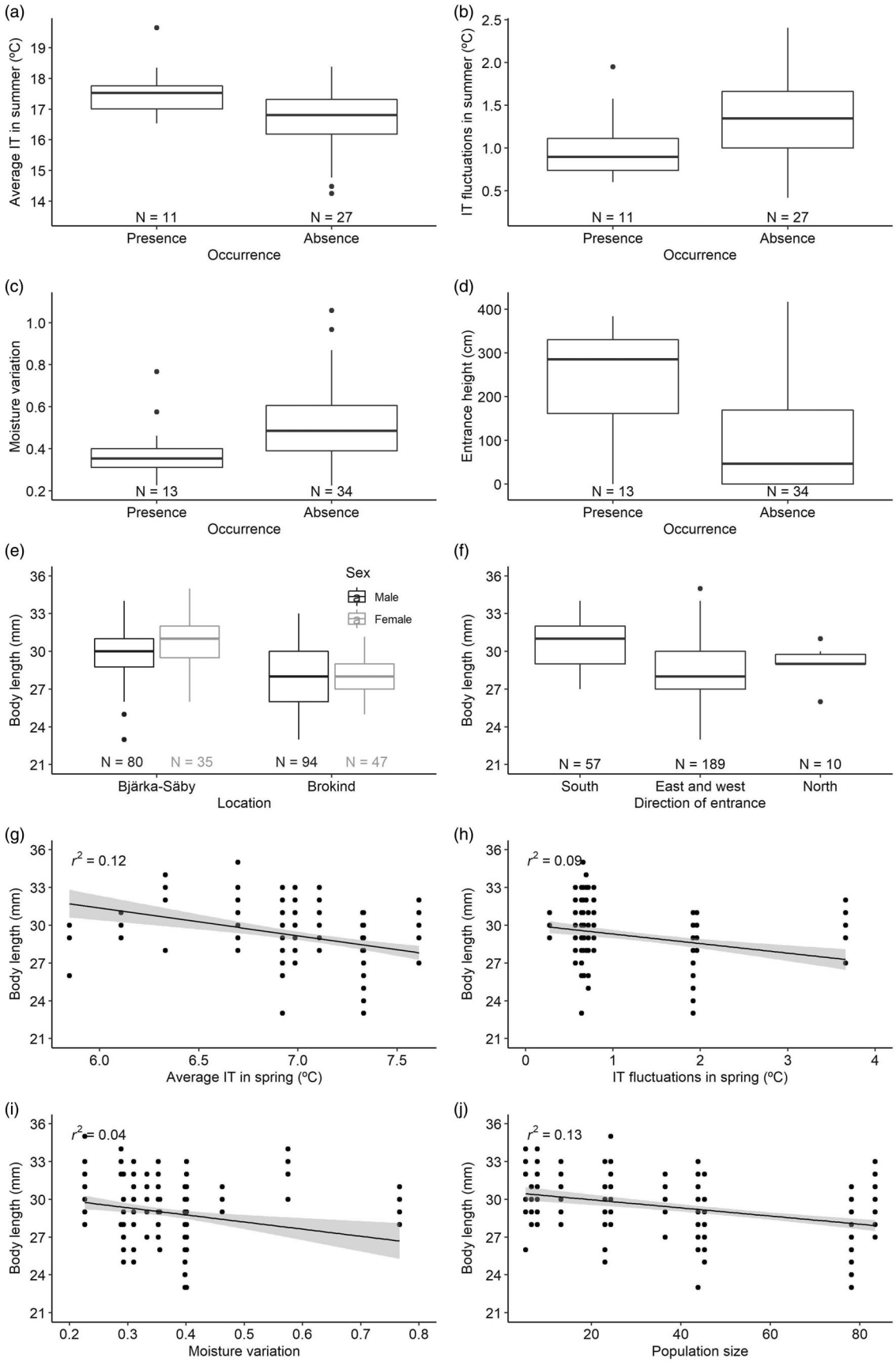

FIGURE 4 Legend on next page.

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Importance of tree characteristics for microclimate

Several tree characteristics have been suggested to affect the microclimate inside tree hollows (Ranius, 2002; Schauer et al., 2018). We found that tree characteristics are indeed driving the microclimatic conditions in the wood mould, which is the habitat for many specialised invertebrate species (Siitonen & Ranius, 2015). In particular, two tree characteristics—tree diameter and entrance height—were important, while wood mould volume, angle of the entrance (upwards or downwards), and direction of the entrance (as distance from the south) were also included in several models explaining microclimatic variables. The first four characteristics—diameter, entrance height, wood mould volume, and angle of entrance—clearly decreased the mean moisture and moisture variation, while these characteristics had various effects on average temperature and temperature fluctuations during different seasons.

Hollows in trees with larger diameters were cooler in summer but warmer in autumn and winter, and had narrower temperature fluctuations in summer. Thus, our study together with some others (Paclik & Weidinger, 2007; Sedgeley, 2001; Wiebe, 2001) provide evidence that tree diameter is an important governor of the internal thermal conditions of hollows, but there are also studies that have found no relationship between tree diameter and microclimate (Clement & Castleberry, 2013; Coombs et al., 2010; Rhodes et al., 2009). That a larger diameter buffers temperature fluctuations has also been found for standing and downed deadwood (Lindman et al., 2022), probably because wood buffers the changes in temperature and moisture (Walczyńska & Kapusta, 2017). Many beetles that specialise on hollow trees occur more frequently in trees with larger diameters (Ranius & Jansson, 2000). This could be because larger trees provide a larger amount of habitat, and that such habitat patches are, on average, older. However, the strong relationship between tree diameter and microclimatic variables is also an explanation, since saproxylic insects often require certain particular microclimatic conditions (Gimmel & Ferro, 2018; Graham, 1924).

Hollows with entrances located higher up on the trunks were warmer in spring and summer, and colder in autumn and winter. A warmer microclimate in higher located hollows during the warm part of the year has also been found by Maziarz and Wesołowski (2013). The explanation may be that during the warmer part of the year, most of the solar energy is absorbed within the top canopy, so the temperature is higher at the height of the tree crown compared to further down the tree trunk (De Frenne et al., 2021). In turn, during the colder part of the year, after the seasonal reduction in canopy cover, the stronger wind speed higher up (De Frenne et al., 2021) cools the microclimate when solar radiation has little warming effect on it (Lindman et al., 2022).

A large wood mould volume clearly decreased the mean temperature, especially in spring, but also in summer and winter. *O. eremita* and several other beetles specialised in tree hollows occur more frequently in hollows with large amounts of wood mould (Ranius et al., 2009, 2010). It has been suggested that larger amount of wood mould contribute to more stable thermal and moisture conditions (Ranius & Nilsson, 1997), but these relationships were only weakly present in our study. However, a larger volume of wood mould also means a larger amount of habitat, and potentially a larger variation of microclimatic conditions; these factors might be more important than the temperature *per se*.

Hollows with south-facing entrances tended to be warmer in spring with wider temperature fluctuations in autumn and winter. Warmer temperatures in south-facing than in north-facing cavities have also been reported previously (Paclik & Weidinger, 2007; Schwartz et al., 2020; Wiebe, 2001). South-facing entrances receive more solar radiation (Koyamatsu et al., 2015) and may therefore warm up faster.

That higher moisture was observed with decreasing angle of entrance (i.e., directing more upwards) was expected due to the higher probability of rainwater entering these hollows. Such a negative effect of upward-facing entrances has been observed for many beetles specialised to tree hollows (Ranius et al., 2010), probably because they avoid too moist conditions. Furthermore, we found that a decreasing angle of entrance was associated with narrower temperature fluctuations in autumn, possibly because the high humidity in moist hollows buffers temperature fluctuations (Davis et al., 2019).

Although canopy cover appeared in a few of our models, its relative importance was always <0.5. This was surprising, as in other microclimatic studies (De Frenne et al., 2021) this variable has been one of the most important by reducing incoming solar radiation during the day and heat loss overnight (Gaudio et al., 2017; Geiger et al., 2012). Furthermore, canopy cover has been reported as having a strong effect on the humidity in cavities (Clement & Castleberry, 2013), although we found no evidence to support that. One explanation may be that our study was conducted in half-open conditions in wooded pastures, and thus the variation in canopy cover may be lower than in some other environments.

We found that the internal temperature varied daily following changes of the ambient temperature, but the range of the daily temperature fluctuations was always narrower inside hollows compared to the ambient air. This agrees with earlier studies of tree hollows (Maziarz & Wesołowski, 2013; Sedgeley, 2001). Our study also confirms that, relative to the ambient temperature, the temperature within hollows is cooler during warmer seasons but warmer during colder seasons (Maziarz & Wesołowski, 2013; Paclik & Weidinger, 2007; Sedgeley, 2001).

FIGURE 4 Relationships between *O. eremita* (presence/absences and body length) and relatively important (RVI >0.5) tree characteristics and microclimatic variables. Occurrence of *O. eremita* in relation to (a) average internal temperature (= "IT") in summer, (b) temperature fluctuations in summer, (c) moisture variation, and (d) entrance height. Differences in the body length of *O. eremita* individuals (e) by location and sex; and in relation to (f) direction of entrance, (g) average internal temperature, (h) internal temperature fluctuations in spring, (i) moisture variation, and (j) population size. Either sample size (*N*) or correlation coefficient ($r^2 \pm$ SE as the grey area) is presented accordingly

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TABLE 3 Model averaged parameter estimates (Est.), standard errors (SE), and relative variable importance (RVI) of: (1) tree characteristics; (2) internal microclimatic variables; and (3) tree characteristics and internal microclimatic variables combined explaining (a) occurrence, and (b) body length, based on models with ΔAICc <7

Variables		Est.	SE	RVI	Est.	SE	RVI
1. Tree characteristics			**a) Occurrence**			**b) Body length**	
Diameter		−0.003	0.009	0.30	0.009	0.017	0.21
Entrance height		0.010	0.003	**1.00**			
Area of entrance hole		−0.001	0.006	0.21			
Wood mould volume		0.001	0.003	0.23			
Direction of entrance 2		0.054	0.334	0.09	−2.015	1.062	**0.79**
Direction of entrance 3		0.077	0.375		−3.136	1.724	
Angle of entrance		0.000	0.015	0.20			
Canopy cover 2		−0.118	0.439	0.16	0.204	0.420	0.21
Canopy cover 3		−0.273	0.824		0.113	0.341	
2. Internal microclimatic variables			**a) Occurrence**			**b) Body length**	
Average temperature	Summer	1.536	0.956	**0.87**			
	Autumn	0.053	0.304	0.08			
	Winter	−0.126	0.826	0.19	0.110	0.336	0.11
	Spring	0.240	0.692	0.13	−0.647	0.293	**0.89**
Temperature fluctuations	Summer	−1.027	1.451	0.43			
	Autumn	−0.329	1.042	0.13			
	Winter	−0.422	1.140	0.17	2.663	0.506	**1.00**
	Spring	−0.075	0.301	0.10			
Moisture	Mean	−0.007	0.054	0.17			
	Variation	−6.136	4.466	**0.86**	−10.84	1.754	**1.00**
3. Tree and microclimatic variables			**a) Occurrence**			**b) Body length**	
Diameter		−0.001	0.007	0.08			
Entrance height		0.002	0.005	0.21			
Area of entrance hole		0.000	0.003	0.05			
Wood mould volume		0.001	0.003	0.09			
Direction of entrance 2		0.025	0.269	0.02	−2.888	0.311	**1.00**
Direction of entrance 3		0.020	0.227		−5.484	0.810	
Angle of entrance		0.039	0.073	0.33			
Canopy cover 2		−0.028	0.314	0.02			
Canopy cover 3		−0.014	0.207				
Average temperature	Summer	1.709	1.459	**0.76**			
	Autumn	0.060	0.332	0.06			
	Winter	−0.035	0.513	0.07			
	Spring	0.098	0.433	0.07	−0.349	0.258	**0.71**
Temperature fluctuations	Summer	−2.162	2.894	**0.55**			
	Autumn	−0.235	0.935	0.09			
	Winter	−0.309	1.068	0.12			
	Spring	−0.025	0.179	0.03	−0.841	0.142	**1.00**
Moisture	Mean	−0.001	0.033	0.06			
	Variation	−6.989	5.018	**0.89**	−4.322	1.982	**0.96**

Note: For direction of entrance and canopy cover, the first categories (direction 1 and canopy cover 1, respectively) are taken as references. Variable importance >0.5 is in bold font.

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Thus, our results support the hypothesis that tree hollows buffer daily temperature fluctuations (Clement & Castleberry, 2013), so providing more stable microclimatic conditions inside than outside (Maziarz & Wesołowski, 2013; Rhodes et al., 2009; Schwartz et al., 2020).

Occurrence and body size of *O. eremita*

Including microclimatic variables into models, together with tree characteristics, improved the predictability of the occurrence and adult body size of *O. eremita*, thus suggesting that the species is indeed affected by the microclimatic conditions inside hollow trees. We only measured microclimatic conditions during 1 year, whereas the observed adults have been affected by the microclimate during their whole larval development time of 3–4 years. Despite this, the microclimatic variables to a high extent explained occurrence patterns of *O. eremita*. This is probably because characteristics of tree hollows are only changing slowly (Lindman et al., 2020), and even though the weather changes between years, the differences in microclimatic conditions among trees are probably far smaller.

We found support for our hypotheses (1) that the occurrence of *O. eremita* at the northern margin of its range is positively related to a warmer microclimate; and (2) that favourable microclimatic conditions explain its habitat. *O. eremita* occurred more frequently in hollows with a warm and stable microclimate, that is, where the average temperature was higher in summer, and the temperature fluctuations in summer and moisture variation were lower. High temperatures and narrow temperature fluctuations have also been found to be important for other insects, for example, a moth (Moore et al., 2021), and a beetle: (Lindman et al., 2022) but we have not seen this documented for any insect species associated with tree hollows.

Regarding tree characteristics, we confirm what has been found in earlier studies: that *O. eremita* occurs more often in hollows with entrances higher from the ground (Chiari et al., 2012; Hedin & Mellbrand, 2003; Ranius et al., 2009). This is directly linked to the favourable microclimatic conditions of the species: we found hollows with higher entrances to be warmer in summer and with a more stable level of moisture. Preference of higher entrances is found also for several other beetle species inhabiting hollows in Sweden (Ranius et al., 2010); however, a negative relationship between entrance height and saproxylic beetle richness has been found in Germany (Henneberg et al., 2021). One explanation for this is that in northern areas the warmer and drier conditions in higher hollows are more suitable, while in warmer, more southerly climates, hollows higher up might be too warm and dry. Note also that Ranius et al. (2010) studied beetles confined to tree hollows, while Henneberg et al. (2021) studied any saproxylic beetles found in tree hollows, and they may have different habitat requirements.

We also found support for our hypothesis that adult body size is negatively related to temperature, confirming the validity of the '*temperature-size rule*' for this species. Body size tended to increase with cooler average temperature and narrower temperature fluctuations in spring, and more stable moisture. It implies that, for *O. eremita*, warmer temperatures have a stronger effect on development rate (differentiation or changes in life stage) than on growth rate (i.e., an increase in size). All relationships were not clearly linear (Figure 4), but the dataset is too small to analyse that more in depth. Although most (>70%) of the studies supporting the "*temperature-size rule*" have been done on insects or other arthropods, exceptions to the rule are common in several insect orders, including Orthoptera and Lepidoptera (Atkinson, 1994; Mousseau, 1997). We found an inverse relationship between adult body size and population size. A large body size may, on one hand, indicate good conditions for the individuals, which generates faster larval growth (Du Plessis et al., 2020). However, on the other hand, the observed negative effect of population size indicates that a smaller body size may reflect stronger intraspecific competition; for instance, density-dependent competition for food (Mock & Parker, 1997). Negative relationships between body size and abundance or density have also been found for other insect species (e.g., Gillespie et al., 2017; Kalinkat et al., 2015) and may be even clearer in populations restricted to more isolated habitat patches, such as tree hollows.

CONCLUSIONS

We found that tree characteristics that explained the occurrence patterns of beetles associated with tree hollows also explained microclimatic variables. Many beetles confined to tree hollows with wood mould tend to occur more frequently in trees with larger diameters, entrances higher up on the trunks, more wood mould, and entrances not opening upwards (Ranius, 2002; Ranius et al., 2010). All these characteristics tend to decrease the mean moisture and moisture variation, while conversely, these variables have various effects on mean temperature and temperature fluctuations. This indicates that it is important for these species to avoid conditions that are too moist, while it is not clear which thermal conditions are the best for the species.

We have shown that *O. eremita* occurs more frequently in trees with a warmer and more stable microclimate. Body size decreased with a warmer microclimate, when controlling for the negative effect of the population size, indicating that body size is not useful as an indicator of good habitat quality for the species. As our study was conducted near the northern margin of *O. eremita*'s range, seeking out a warm microclimate might be particularly important. Since climate differs markedly across the species' distribution area, other microclimatic aspects might be more important further south, such as stable moisture (cf. Chiari et al., 2012). *O. eremita* is still confined to living hollow trees all over its distribution range, which may be due to the fact that these hollows consistently have a more stable microclimate compared with both the ambient microclimate and the microclimate in downed and standing deadwood (Lindman et al., 2022).

AUTHOR CONTRIBUTIONS

Thomas Ranius originally formulated the idea. Ly Lindman and Thomas Ranius developed and planned the project. Ly Lindman

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conducted the fieldwork and analysed the data. Ly Lindman wrote the first draft and all co-authors contributed to the final version of the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in "Data on Microclimate in hollow trees and how it affects an inhabiting beetle species, Osmoderma eremita" in Swedish National Data Service. (Ly Lindman. Sveriges lantbruksuniversitet (2022). Data on Microclimate in hollow trees and how it affects an inhabiting beetle species, Osmoderma eremita. Svensk nationell datatjänst. Version 1. https://doi.org/10.5878/856g-v725).

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Figure S1. Supporting Information

Table S1. Supporting Information

Table S2. Supporting Information

Table S3. Supporting Information

Table S4. Supporting Information

Table S5. Supporting Information

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