

Microclimatic Conditions Mediate The Effect of Deadwood and Forest Characteristics On a Threatened Beetle Species, *Tragosoma Depsarium*

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1 **Microclimatic conditions mediate the effect of deadwood and forest characteristics on a**
2 **threatened beetle species, *Tragosoma depsarium***

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6

7 **Abstract**

8 While climate change has increased interest in the influence of microclimate on many organisms,
9 species inhabiting deadwood have rarely been studied. Here we explore the relationships between
10 characteristics of forest stands, deadwood and microclimate, and analyse how the microclimate inside
11 deadwood affects the occurrence of wood-living organisms, exemplified by the red-listed beetle
12 *Tragosoma depsarium*. Some of the measured deadwood and forest variables explain much of the
13 variation in temperature, but little of humidity aspects of the microclimate within deadwood. Several
14 variables known to influence habitat quality for deadwood-dependent species were found to correlate
15 with microclimate *viz.*: warmer conditions in standing deadwood and open canopy than in downed logs
16 and under a closed canopy; higher humidity and more stable daily temperatures in shaded habitats and
17 in downed and large-diameter wood, than in sun-exposed locations and standing, small-diameter wood.
18 *T. depsarium* occupancy and abundance were negatively correlated with daily temperature fluctuations,
19 and positively related to spring and summer temperature and humidity. This can explain why the species
20 occurred more frequently in deadwood items with characteristics associated with these microclimatic
21 conditions, i.e. downed large-diameter logs occurring in open conditions. Since microclimatic
22 conditions are important for *T. depsarium* and related to several habitat characteristics, we expect the
23 effects of these characteristics to interact with each other, and for species' habitat requirements to vary
24 due to local and regional climate conditions, and to changes due to climate warming.

25

26 **Keywords:** data-logger, habitat, humidity, saproxylic, temperature

27

28 **Introduction**

29 Microclimates, by definition, can vary widely within small geographical areas. This has consequences
30 for species distributions at multiple spatial scales, including their response to climate change (Thomas
31 et al. 1999; Suggitt et al. 2011). Modern low-cost data-loggers have made microclimatic data easier and
32 cheaper to collect in the field (Terando et al. 2017) thus enabling studies to demonstrate the existence
33 of strong links between microclimate and local biodiversity (De Frenne et al. 2021) as well as how
34 microclimate is affected by topography (Gillingham 2010; Seidelmann et al. 2016), vegetation (Ohler
35 et al. 2020), and land-use (Gillingham 2010).

36 Individual insect species typically flourish with optimal performance (survival, growth, fecundity, and
37 dispersal) within a well-defined temperature range (Chown and Nicolson 2004). Outside the tropics,
38 there is usually a part of the year when the temperature is too low for insect activity (Wolda 1988).
39 Microclimate conditions then become important influences on the development times of insect life-
40 stages and consequently their population dynamics (Johnson et al. 2016; Rebaudo et al. 2016); similarly
41 the spatial distribution of microclimatically suitable habitats affects patterns of occurrence (Sillett et al.
42 2000).

43 Approximately one third of all forest insect species are saproxylic, i.e. dependent on dying or dead trees
44 (Ulyshen and Šobotnik 2018). Many of these species are now in decline because forestry practices
45 decrease the amount and quality of deadwood (Siitonen 2001; Stokland et al. 2012); managed forests
46 have far less deadwood than natural forests, especially items of larger dimensions and in later stages of
47 decay (Siitonen 2001; Gossner et al. 2013). Saproxylic species are often specialized on deadwood with
48 certain qualities; wood diameter, canopy openness where the deadwood is situated, tree species from
49 which it is derived, whether standing or downed, and stage of decay are all important characteristics
50 (Siitonen et al. 2000; Stokland et al. 2012; Ranius et al. 2015). Several of these characteristics are likely
51 to influence the microclimatic conditions inside deadwood, but this has never been tested (Müller et al.
52 2020).

53 We hypothesize that the fundamental microclimatic conditions of temperature and humidity inside
54 deadwood are linked to characteristics of both the deadwood items and the surrounding forest and that
55 this in turn can explain the occurrence patterns of saproxylic species. We used the red-listed beetle,
56 *Tragosoma depsarium* (Linnaeus, 1767), as a study species because field observations indicate that it
57 favours sun-exposed conditions (Wikars 2004; Swedish Species Information Centre 2020). We thus
58 hypothesize that the preferred conditions of *T. depsarium* in its microhabitat of deadwood are largely
59 microclimatic, i.e. that both species' abundance and occurrence patterns as well as habitat
60 characteristics that explain these patterns are strongly correlated with microclimatic variables within.
61 The aim was to answer the following questions:

- 62 (i) What are the relationships between the microclimatic conditions in deadwood, and those
63 properties of deadwood and forest characteristics that are known to affect saproxylic
64 insects?
- 65 (ii) Which microclimatic variables within deadwood explain the occurrence and abundance of
66 *T. depsarium*?
- 67 (iii) Which deadwood properties and forest characteristics explain the occurrence and
68 abundance of *T. depsarium* and are they associated with favourable microclimatic
69 conditions within deadwood?

70

71 **Material and methods**

72 *Study species*

73 *T. depsarium* is a 20-35 mm long saproxylic longhorn beetle. It is a boreo-montane species with
74 fragmented distribution in the mountain regions of southern and central Europe and in boreal forests in
75 eastern Europe and Fennoscandia (Mannerkoski et al. 2010). In Fennoscandia, the larvae develop
76 mainly in large-diameter, bark-free, and sun-exposed logs of Scots pine (*Pinus sylvestris*), or rarely
77 Norway spruce (*Picea abies*) (Palm 1951; Wikars 2004), and the development takes four years or more
78 (Palm 1951). When an adult emerges, it creates an easily identifiable exit-hole (Ehnström and Axelsson
79 2002). It is reported to develop in quite recently dead trees, but also in very old logs which may have

80 been dead more than 100 years (Palm 1951). As the species is dependent on deadwood in open habitats,
81 it is threatened by industrial forest management and effective fire-fighting practices, which are causing
82 the forests to become younger and denser, and with less deadwood (Swedish Species Information
83 Centre 2020). The species is classified as Near Threatened (NT) according to European Red List of the
84 IUCN (Nieto and Alexander 2010) and as Vulnerable (VU) according to the Swedish national Red-List
85 (Swedish Species Information Centre 2020).

86 ***Study area and design***

87 We conducted the study in south-eastern Sweden around 20 km northwest of Uppsala (Fig. 1). The
88 study landscape is around 250 km² in size and is dominated by coniferous forests (Länsstyrelsen i
89 Uppsala län 2017). It contains large areas dominated by old pine forests that are only partly affected by
90 clear-felling forestry.

91 We studied the microclimate inside standing (*snag*) and downed (*log*) deadwood items of pine (*P.*
92 *sylvestris*) with *T. depsarium* present or absent. The deadwood items studied were identified by using
93 data from a survey conducted in 2015 by Olof Hedgren (Länsstyrelsen i Uppsala län 2017), who
94 reported the coordinates of 62 pine logs with recent exit-holes of the species. We visited the locations
95 of these logs in August and September 2019, searching for fresh exit-holes. New exit-holes are
96 identifiable by their light creamy-white colour, like freshly cut wood; old exit-holes are dark and grey
97 inside (Online Resource 1). New exit-holes were from individuals that had emerged from the deadwood
98 items in 2019 and 2020, while old exit-holes could be of individuals that had emerged many years
99 previously, but not later than 2018. When a deadwood item with a fresh exit-hole was found, a *site* was
100 identified, defined as the item with a fresh exit-hole together with the three or four closest deadwood
101 items of pine (*snag* or *log*), which never occurred farther away than 15 m. Our intention was to include
102 items which potentially varied in their internal microclimatic conditions, but to minimize differences in
103 colonization rate caused by differences in spatial location. We identified 19 such *sites*. Additionally, we
104 included four *sites* where the species was absent as control *sites*, where four or five nearby deadwood
105 pine items (not farther away than 15 m from each other) were defined as a *site*. We only included

106 deadwood items with diameter ≥ 8 cm, because the species rarely uses smaller items (Wikars 2004). In
107 total, 23 *sites* with 98 deadwood items were included in the study. For each deadwood item, we
108 measured deadwood properties and forest characteristics at the location and counted the number of new
109 and old exit-holes of *T. deparium*.

110 We used iButton Hygrochron DS 1923 (Maxim/Dallas Semiconductor Corp., USA) data-loggers to
111 record temperature and humidity inside each deadwood item during the four seasons of a year (from
112 October 2019 to September 2020). The loggers were placed inside deadwood items, on the south-facing
113 side, either close to a new exit-hole or, if new exit-holes were absent, close to the old exit holes or, if
114 no exit-holes were present, in the middle of *logs* or 50 cm above the ground of *snags* (Fig. 2). In
115 September 2019, we made holes 5 cm deep and 22 mm wide, placed loggers inside, and isolated them
116 from the outside air with a wine cork and apple tree wax. Additionally, to measure local air temperature,
117 we placed Lascar EL-USB-1 (Lascar Electronics, UK) temperature data-loggers in the middle of the
118 *sites*, attaching them on the north side of trees at breast height (1.3 m from the ground). We used data
119 from October 2019 (autumn), January 2020 (winter), April 2020 (spring) and July 2020 (summer).

120 The winter temperature in 2020 was considerably higher, at 3.3 °C, than the average temperature during
121 the last 30 years, which was -2.6 ± 5.6 SD °C, while during other seasons the temperature was closer to
122 the average (autumn 2019: 6.1 °C, 30-year average: 6.1 ± 4.4 SD °C; spring 2020: 5.7 °C, 30-year
123 period: 5.3 ± 5.2 SD °C; summer 2020: 15.5 °C; 30-year period: 17.3 ± 4.7 SD °C; data from the
124 closest weather station; SMHI 2021a).

125 ***Deadwood and forest characteristics***

126 For each deadwood item, we measured characteristics, which have been previously described as
127 important for *T. deparium* (Palm 1951; Wikars 2004) or which we assumed could influence
128 microclimate (Online Resource 2). All deadwood variables were measured either within a buffer zone
129 of 2 m around the new exit-holes, or, if new exit-holes were absent, within a buffer zone of 2 m around
130 the old exit holes or, if no exit-holes were present, in the middle of the deadwood items. Forest variables
131 were measured while standing above the downed *logs* and next to the *snags*.

132 *Deadwood characteristics*

133 We recorded whether the deadwood item was standing (*snag*) or downed on the forest floor (*log*).
134 *Diameter* was measured with a calliper. The *length* (or *height*) was measured with a measuring tape if
135 the item was shorter than 2 m, while for longer/higher items it was estimated with 1 m accuracy. *Ground*
136 *contact*, *bark cover* and *vegetation cover* of deadwood items were estimated as percentages of how
137 much of the whole deadwood item was in contact with the ground, or covered by bark or vegetation,
138 respectively.

139 For *softness*, we pressed a knife into the deadwood and measured the blade length that penetrated wood.
140 This was done three times for each item and the average penetration was recorded. *Decay stages* were
141 classified depending on an item's penetrability according to a published classification system
142 (Larjavaara and Muller-Landau 2010), and placed in one of five classes: 1) recently dead tree: wood
143 still hard, knife blade penetrates a few millimetres, bark normally intact; 2) weakly decayed wood: knife
144 blade penetrates 2 cm, loose bark; 3) medium decayed: knife blade penetrates 2-5 cm, usually without
145 bark; 4) very decayed wood: knife blade penetrates all the way; and 5) almost decomposed wood: breaks
146 up easily by hand, often overgrown by lichens, mosses, and dwarf shrubs.

147 *Forest characteristics*

148 To estimate *canopy openness*, photographs were taken with a fisheye lens ca 30-40 cm above the
149 ground, placing the camera above *logs* or next to *snags*. The photos were analysed with a Gap Light
150 Analyzer (Frazer et al. 1999). The variable expresses the percentage of the area not covered by canopy.

151 *Basal area* – the area (m²) of the cross-sections of the tree trunks at breast height (1.3 m) per hectare, -
152 commonly used as an indicator of stand density – was measured with a relascope while standing next
153 to (or above if possible) each deadwood item. The value was estimated for each deadwood item because
154 conditions may differ considerably within a *site*. The ratio between the chain length and the width of
155 opening of the relascope was 1:35, to calculate *basal area*, the relascope counts were therefore
156 multiplied by two (Järvis 2013).

157 The *vegetation types* were divided into three classes (Wikars 2004): dry (dominated by *Vaccinium vitis-*
158 *idaea* L. and lichens on the ground); mesic (*V. myrtillus* L. and pleurocarpous mosses); and wet
159 (Sphagnum-mosses in the bottom layer). However, no deadwood item was located in wet conditions.

160 We divided the *sites* into four *stand types*: 1) young clear-cut aged up to around 10 years, or a glade
161 (diameter > 30 m), due to a thin soil layer – tree height usually ≤ 3 m; 2) old clear-cut aged around 11-
162 24 years – tree height of 3 m to 15 m; 3) young forest aged around 25-75 years – tree height > 15 m,
163 and average diameter < 20 cm; 4) mature forest aged > 75 years – tree height > 15 m, and average
164 diameter > 20 cm.

165 Although topography has been found to be an important factor affecting microclimate (Gillingham
166 2010; Seidelmann et al. 2016), we did not include that variable in our analyses since our study sites
167 were located in a topographically homogenous landscape with only small differences in average air
168 temperature between the warmest and coldest sites being between 0.8 °C (in autumn) and 2.7 °C (in
169 spring and summer).

170 ***Statistical analysis***

171 We used hourly-recorded microclimatic data inside deadwood from October, January, April, and July,
172 to represent autumn, winter, spring, and summer, respectively, from which we calculated mean
173 temperature and humidity, daily temperature fluctuations (as a difference between daily minimum and
174 maximum), minimum temperature of the coldest, and maximum temperature of the warmest month.
175 These microclimatic variables were first analysed in relation to deadwood properties and forest
176 characteristics. To analyse the effect of forest and deadwood characteristics (Online Resource 2) on
177 internal microclimatic variables, we analysed each of the variables described above as response
178 variables in relation to i) deadwood properties; ii) forest characteristics; and iii) deadwood and forest
179 characteristics combined. We used Mixed ANOVA (linear mixed models) and included *site* as a random
180 factor. Average relative humidity values were transformed with Tukey transformation, analysed with
181 linear models, and back-transformed when presenting the results.

182 To understand which variables explain the occurrence (presence/absence) and abundance of
183 *T. depsarium*, we used four data sets: two for occurrence and two for abundance. One of them reflected
184 the current occurrence or abundance, and the second the occurrence or abundance over a longer time
185 span. The current occurrence was obtained by including all examined deadwood items, and considering
186 the presence of new exit-holes. Long-term occurrence was the presence of all exit-holes (new and old)
187 in all examined deadwood items. The current abundance was obtained by including only those
188 deadwood items with new exit-holes present, and assessing the number of new exit-holes. Long-term
189 abundance was obtained by assessing the number of exit-holes excluding the deadwood items with exit-
190 holes absent.

191 We analysed the four response variables of current and long-term occurrence and abundance of
192 *T. depsarium* in relation to deadwood and forest characteristics and microclimatic variables separately
193 and together in order to find out which groups of variables best explain the patterns of *T. depsarium*.
194 More precisely, we analysed these four response variables in relation to i) deadwood characteristics; ii)
195 forest characteristics; iii) deadwood and forest characteristics combined; iv) internal microclimatic
196 variables (temperature and humidity); v) deadwood and forest characteristics and microclimatic
197 variables combined. Occurrence was analysed using binomial logistic regression with presence (1) or
198 absence (0) as the response variable. Abundance was analysed using a generalized linear model with
199 Poisson distribution. *Site* was included as a random factor in all models.

200 Due to the relatively high number of potential predictors ($4 \leq k \leq 24$, depending on the analysis), in all
201 analyses we performed a first selection of the variables, analysing one variable at a time, using second-
202 order Akaike's information criterion corrected for small sample size (AICc; R package *AICcmodavg*
203 (Mazerolle 2019)), as recommended when N (*sample size*) $\times k$ (*number of predictors*)⁻¹ < 40 (Burnham
204 and Anderson 2002). We selected all variables that decreased the AICc value in comparison to the null
205 model. Thereafter, we built multivariate models by testing all possible combinations of selected
206 variables together, using the R package MuMIn (Bartoń 2019). For each model, we compared its AICc
207 value with the best-fitting model ($\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\min}$); we considered all plausible models with
208 $\Delta\text{AICc} < 2$ (Burnham and Anderson 2002), and present them below. Correlated variables (like the

209 deadwood variables *decay class* and *softness*, and several internal microclimatic variables; $-0.43 < r$ or
210 $r > 0.43$) were never included in the same model.

211 As an absolute value for goodness-of-fit for the models of temperature variables, we report *marginal* R^2
212 (describing the proportion of variance explained by the fixed factor(s) alone) and *conditional* R^2
213 (describing the proportion of variance explained by both the fixed and random factors, i.e. the variance
214 explained by the whole model). For relative humidity, *adjusted* R^2 values are presented for models of
215 transformed data. Therefore, these were not included in comparisons with other microclimatic variables.
216 To assess the predictive performance of our models of occurrence and abundance of *T. depsarium*, and
217 to understand which variables are better at explaining the patterns of *T. depsarium*, we used
218 *Nagelkerke's pseudo-R-squared* (R^2_N) and coefficient of determination based on the *likelihood-ratio*
219 *test* (R^2_{LR}) values, calculated separately for models with deadwood characteristics, forest characteristics,
220 combination of deadwood and forest characteristics, microclimatic variables, and a combination of all
221 the variables.

222

223 **Results**

224 ***Effect of deadwood and forest characteristics on the internal microclimate of deadwood***

225 In comparison to the local air temperature, it was slightly warmer inside deadwood in autumn
226 (5.7 ± 0.4 SD °C vs. 5.2 ± 3.7 °C) and summer (15.9 ± 1.2 °C vs. 15.7 ± 4.9 °C), while it was slightly
227 colder in winter (1.7 ± 0.6 °C vs. 2.2 ± 2.8 °C) and spring (6.0 ± 1.2 °C vs. 6.1 ± 5.8 °C). The daily
228 temperature fluctuations were always lower inside wood compared to the air (autumn: 3.2 ± 0.9 °C vs.
229 5.7 ± 3.0 °C; winter: 1.7 ± 0.7 °C vs. 4.0 ± 2.3 °C; spring: 8.4 ± 2.7 °C vs. 12.4 ± 6.5 °C; summer:
230 8.3 ± 3.0 °C vs. 10.7 ± 6.3 °C).

231 Deadwood and forest characteristics combined explained a considerable part of the average temperature
232 ($0.33 \leq R^2_c \leq 0.72$), temperature fluctuations ($0.34 \leq R^2_c \leq 0.56$), and temperature extremes
233 ($0.41 \leq R^2_c \leq 0.46$; Table 1; Online Resource 3). In autumn and winter, deadwood characteristics
234 explained average temperature and temperature fluctuations better than forest characteristics (Online
235 Resource 4). By contrast, forest characteristics were better at explaining all temperature variables in

236 summer, and temperature fluctuations in spring (Online Resource 5). Average humidity was poorly
237 explained ($-0.02 \leq R^2_{adj} \leq 0.14$) by deadwood and forest characteristics (Table 2).

238 Five deadwood characteristics (especially *log*, but also *diameter*, *length*, *vegetation cover*, and *decay*
239 *stage/softness*) and three forest characteristics (especially *canopy openness*, but also *basal area*, and
240 *vegetation type*) occurred frequently in the models predicting climate variables (Tables 1 and 2). In
241 comparison to *logs*, the average temperature was higher in *snags* (*snags*: autumn 5.9 ± 0.5 SD °C;
242 winter 2.0 ± 0.6 °C; *logs* autumn 5.6 ± 0.4 °C; winter 1.5 ± 0.5 °C), the daily temperature fluctuations
243 were wider (Online Resource 6), the summer maximum temperature higher (*snags*: 20.5 ± 2.8 °C; *logs*:
244 20.3 ± 2.6 °C) and the humidity lower (*snags* autumn 97.2 ± 7.5 SD %; summer 88.4 ± 15.1 %; *logs*
245 autumn 101.5 ± 8.3 %; summer 98.5 ± 23.8 %). In deadwood items with larger *diameters*, daily
246 temperature fluctuations were lower, but winter minimum temperatures (Table 1) and humidities were
247 higher (Table 2). Deadwood items that were longer and with higher *vegetation cover* had higher
248 humidity. In later *decay stages*, the daily temperature fluctuations were narrower, while with increased
249 *softness* the humidity was higher.

250 Average temperature (Fig. 3), daily temperature fluctuation, and summer maximum temperature
251 increased with increasing *canopy openness*, while humidity decreased (Tables 1 and 2). The average
252 and minimum temperatures in winter increased with higher *basal area*. Average temperature was higher
253 in dry (autumn 5.8 ± 0.5 SD °C, summer 16.3 ± 1.3 °C) than in mesic *vegetation type* (autumn
254 5.6 ± 0.3 °C, summer 15.5 ± 0.9 °C), but daily temperature fluctuations (in spring, in dry 8.7 ± 3.0 °C
255 versus in mesic 8.0 ± 2.4 °C) and humidity were lower in dry *vegetation type* (in spring, in dry
256 93.5 ± 24.2 SD % versus in mesic 98.8 ± 14.9 %).

257 ***Occurrence and abundance of T. depsarium***

258 We observed 472 exit-holes of *T. depsarium*. Among these, 100 exit-holes were new, distributed among
259 28 logs, while the 372 old exit-holes were distributed among 40 logs. The species inhabited only
260 downed *logs* and never *snags*.

261 The combination of deadwood and forest characteristics and microclimatic variables was almost always
262 better ($0.71 \leq R^2_N \leq 0.99$) at explaining occurrence and abundance of *T. depsarium* (Fig. 4) than only
263 deadwood characteristics ($0.34 \leq R^2_N \leq 0.65$; Online Resource 7), only forest characteristics
264 ($0.17 \leq R^2_N \leq 0.72$; Online Resource 8), deadwood and forest characteristics combined
265 ($0.43 \leq R^2_N \leq 0.89$; Table 3), or only microclimatic variables ($0.63 \leq R^2_N \leq 0.99$; Table 4). The
266 combination of deadwood and forest characteristics ($0.70 \leq R^2_N \leq 0.78$) explained occurrence equally
267 well as microclimatic variables ($0.62 \leq R^2_N \leq 0.70$), but microclimatic variables were better at
268 explaining abundance of *T. depsarium* ($0.82 \leq R^2_N \leq 0.99$) than the combination of deadwood and forest
269 characteristics ($0.37 \leq R^2_N \leq 0.89$).

270 In comparison to unoccupied deadwood items, occupied items had larger *diameter* (current:
271 26.7 ± 4.4 SD cm vs. 22.3 ± 8.3 cm; long-term: 26.5 ± 6.4 cm vs. 22.2 ± 8.2 cm), and were situated in
272 stands with smaller *basal area* (current: 6.4 ± 4.7 SD m² ha⁻¹ vs. 16.9 ± 10.3 m² ha⁻¹; long-term:
273 6.9 ± 4.7 m² ha⁻¹ vs. 16.6 ± 10.4 m² ha⁻¹; Table 3). Currently occupied logs were longer
274 (1460 ± 593 SD cm vs. 850 ± 684 cm), and long-term occupancy was higher in items of later *decay*
275 *stages*.

276 The average temperatures in currently occupied deadwood items were slightly lower in autumn
277 (5.6 ± 0.4 SD °C vs. 5.7 ± 0.5 °C), fluctuated less in winter (1.2 ± 0.5 °C vs. 1.9 ± 0.7 °C) and had higher
278 summer maximum (20.9 ± 2.5 °C vs. 20.1 ± 2.6 °C; Table 4). In comparison to unoccupied deadwood
279 items, in long-term occupied items, the average temperatures were slightly higher in spring (6.2 ± 1.4 °C
280 vs. 5.8 ± 1.0 °C), and the humidities were lower in winter (88.3 ± 23.5 SD % vs. 90.2 ± 20.0 %) and
281 summer (92.0 ± 27.9 % vs. 100.9 ± 12.7 %).

282 Current *T. depsarium* were more abundant in *logs* with lower average and maximum temperatures in
283 the summer, and with a narrower range of temperature fluctuations in autumn. Furthermore, abundance
284 increased with higher average humidities in winter, spring, and summer. The long-term abundance
285 increased with higher average temperature in spring and humidity in winter, and lower humidity in
286 autumn (Table 4).

287 **Discussion**

288 During the last two decades, a large number of studies have revealed that different deadwood and forest
289 characteristics (wood diameter, canopy openness, whether standing or downed, and decay stage) affect
290 occurrence patterns of saproxylic species (Siitonen et al. 2000; Stokland et al. 2012; Ranius et al. 2015).
291 We have shown for the first time that these deadwood characteristics are driving microclimatic
292 conditions inside deadwood. Furthermore, we have shown that deadwood and forest characteristics
293 combined, explain the occurrence of *T. depresso* as well as microclimatic variables, while the
294 abundance of the species is explained better by microclimatic variables than deadwood and forest
295 characteristics. This supports the view that the species is directly affected by the microclimatic
296 conditions in deadwood.

297 ***Importance of deadwood and forest characteristics for microclimate***

298 The microclimate inside deadwood was affected by both deadwood and forest characteristics. The most
299 important factors affecting microclimate in deadwood items in the present study (Table 1) have all been
300 found to be important for species inhabiting deadwood: habitat openness (*canopy openness* and *basal*
301 *area*) (Müller et al. 2015; Seibold et al. 2016), whether the item is standing or downed, and the
302 dimension of the item (*diameter*: Siitonen et al. 2000; Ranius et al. 2015; and *length*: Haeler et al. 2021).

303 During the warmer part of the year, a higher degree of *canopy openness* implied higher average and
304 maximum temperature as well as larger daily fluctuations, and lower humidity. In contrast, during
305 winter time it was warmer where the *basal area* was higher. This is similar to observations of near-
306 ground microclimate (Greiser et al. 2018), and can be explained by the fact that the canopy has a
307 buffering effect on temperature (De Frenne et al. 2019) by reducing incoming solar radiation during the
308 day and heat loss overnight (Geiger et al. 2012; Gaudio et al. 2017). Additionally, the deadwood was
309 drier with increasing *canopy openness*. This can be due to both higher temperatures and increased wind
310 speed (Renaud et al. 2011).

311 The average temperature was higher and fluctuated more in *snags* than in *logs* and they were also drier.
312 This can be because in downed *logs* the moisture content is buffered by the ground and the *vegetation*

313 often covering the downed log protects them from direct sunlight (Talley et al. 2002; Bässler et al.
314 2010). Higher water content, in turn, tends to give more stable temperatures. The microclimatic
315 differences may affect organisms both directly, but also indirectly by, for instance, affecting the rate of
316 decay of deadwood (Eichenberg et al. 2017).

317 Larger deadwood items – principally with a higher *diameter*, but to some extent also greater *length* –
318 had more stable temperatures, higher winter minimum temperature and higher humidity. The higher
319 moisture could be explained by a larger volume in relation to the surface area, and hence lower
320 evaporation. The more stable temperatures could be due to the wood buffering temperature changes
321 (Walczyńska and Kapusta 2017); higher humidity also contributes to the decrease of temperature
322 fluctuations. The more stable microclimatic conditions could be one reason why many wood-living
323 species prefer deadwood of larger dimensions, although, inter alia, large diameter deadwood also
324 persists longer (Hyvönen et al. 2000).

325 The decomposition stage of the deadwood items explained part of the microclimatic variability; the
326 daily temperature fluctuation decreased with *decay stage* in spring, while humidity increased with
327 *softness* in autumn. Pouska et al. (2016) also found that as the state of decay progressed the water
328 content of the wood and its temperature stability increased. This may be because the water holding
329 capacity of wood increases as it decays (Harmon and Sexton 1995) and higher humidity buffers
330 temperature fluctuations (Davis et al. 2019).

331 The difference in average temperature between the warmest and coldest deadwood items was between
332 2.2 °C (in autumn) and 5.7 °C (in summer). This is comparable with the predicted effect of climate
333 warming in Uppsala (where this study was done), which is between 2.3 °C and 4.4 °C in the next 40
334 years according to an ensemble of nine climate scenarios based on RCP8.5, a scenario with emissions
335 considerably higher than those laid down under the current Paris agreement (SMHI 2021b). It is also
336 comparable with temperature differences between southernmost (Sturup, latitude 55.52) and
337 northernmost (Latnivaara, latitude 67.25) parts of Sweden, a distance of about 1750 km, over which the
338 difference in annual average temperature has been 9.6 °C over the last 30 years (SMHI 2021a). Thus,

339 the observed difference between deadwood items corresponds to differences between sites situated 400-
340 1000 km from each other in a south-north direction. This implies that in a topographically homogenous
341 area, deadwood and forest characteristics have a lesser effect on the microclimate inside deadwood than
342 climatic differences might have over north-south distances exceeding 1000 km, and be of the same
343 magnitude as that predicted under climate warming during an intermediate time scale. Thus, species are
344 probably able to compensate for less favourable regional climatic conditions and changes over time by
345 using different types of deadwood. However, the variation between northern and southern Sweden is
346 too large for *T. depsarium* to compensate for it by selecting different types of deadwood. Indeed, *T.*
347 *depsarium* is absent from the coldest, northwestern part of Sweden (Swedish Species Information
348 Centre 2020), probably because it is too cold.

349 ***Occurrence and abundance of T. depsarium***

350 Microclimatic variables were as good as the deadwood and forest characteristics combined at explaining
351 the occurrence of *T. depsarium*, but better at explaining their abundance. The strong relationship
352 between microclimatic variables and the occurrence and abundance of the species is consistent with
353 several field studies on insects in other habitats showing a similarly strong effect of microclimate on
354 occurrence and abundance (e.g. Eilers et al. 2013; Righi et al. 2018), but this has until now not been
355 documented for any saproxylic insects in deadwood.

356 *T. depsarium* occurred more often and at higher abundance in deadwood items with narrow temperature
357 fluctuations and high average temperatures in spring, and, to some extent, with high summer
358 temperatures, and cooler temperatures during winter and autumn. Higher humidity in spring and
359 summer was also favourable for the species. High temperatures and narrow temperature fluctuations
360 are also important for other species, e.g., a moth (Moore et al. 2021), and higher humidity for, e.g., dung
361 beetles (Righi et al. 2018). The microclimatic preferences we observed agree with the habitat
362 requirements of *T. depsarium* reported elsewhere (Palm 1951; Wikars 2004). In our study we also found
363 the species to occur more often and more abundantly where the canopy was more open, where the spring
364 and summer temperatures were higher; they were also more abundant in well-decayed wood, and where

365 the temperature fluctuations in spring were narrow. The negative relationship with autumn and winter
366 temperatures was unexpected, but an explanation could be that with decreasing autumn and winter
367 temperatures, daily temperature fluctuations during these seasons decreased, and average temperature
368 during spring and maximum in summer increased. Greiser et al. (2018) have observed similar seasonal
369 patterns. Especially if the relationships are non-linear, autumn and winter climate may be included in
370 the models, even if their direct effect on insects are only weak or even absent.

371 Although microclimate is clearly important, other factors undoubtedly affect the species. For example,
372 the state of decaying wood for saproxylic beetles (Müller et al. 2020), such as *T. depsarium* affects the
373 availability of nutrients (Laiho and Prescott 2004). Furthermore, since *T. depsarium* has a development
374 time of around four years (Palm 1951), our data, based on emergence holes, might also explain why we
375 rarely found the species in wood in its earliest stages of decay. The higher frequency of occurrence and
376 abundance in larger logs could, except of more narrow temperature fluctuations, also be explained by
377 more resources available.

378

379 **Implications for conservation**

380 We have shown a correlation between internal microclimatic conditions in deadwood and the
381 occurrence patterns of *T. depsarium*. This has consequences for our understanding of the habitat
382 requirements of saproxylic species. First, the microclimatic conditions within deadwood are affected
383 by a hierarchy of interacting influences. These range from certain properties of the deadwood itself;
384 characteristics of the forest from which it is derived; and by regional and local climatic conditions,
385 which in turn are affected by, e.g. topography and distance to water bodies (De Frenne et al. 2021). The
386 microclimatic conditions within deadwood are the results of all these factors interacting, and thus, we
387 should expect species to live in different types of deadwood in different parts of their distribution areas.
388 Second, we should expect that climate change will have a large impact on saproxylic organisms. They
389 may not only change their distribution areas, but they could also remain within their current areas by
390 using different types of deadwood, with different microclimatic conditions.

391 Forestry has a large effect on saproxylic insects, since it decreases the amount and quality of deadwood
392 (Stokland et al. 2012). Our study indicates that other consequences of forestry may also be important.
393 Intensive forest management generates both more dense forests (Swedish Species Information Centre
394 2020) and, after clear-cutting, very sun-exposed conditions. These dynamic changes affect
395 microclimatic conditions (Greiser 2020), which in turn affect saproxylic species. Thus, modifying
396 forestry practices could mitigate some of the negative consequences of climate change on saproxylic
397 insects.

398

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402

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406 **Ethics approval** All applicable national guidelines for the care and use of animals were followed.

407 **Consent to participate** Not applicable.

408 **Consent for publication** Not applicable.

409 **Availability of data and material** Available from the corresponding author on reasonable request.

410 **Code availability** Available from the corresponding author on reasonable request.

411 **Authors' contributions** TR originally formulated the idea. All co-authors developed and planned the
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413 with active support from TR, and all co-authors contributed to the final version of the manuscript.

414

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557 **Table 1.** Plausible candidate models ($\Delta\text{AICc} < 2$) explaining (1) average temperature; (2) temperature fluctuations in (a) autumn, (b) winter, (c) spring, and (d)
558 summer; (3) temperature extremes in (a) winter and (b) summer, in relation to deadwood and forest characteristics. *Site* as a random factor is included in all
559 models. Sample size (N), intercept (Int.), number of parameters (k), model weight (w_i), *marginal* R^2 (R^2_m) and *conditional* R^2 (R^2_c) are presented

N	Int.	log	dia- meter	ground contact	decay stage 2	decay stage 3	decay stage 4	decay stage 5	canopy	basal area	veget. type	k	LogLik	ΔAICc	w_i	R^2_m	R^2_c
1. Average temperature																	
a) in autumn																	
77	5.93	-0.350										4	-43.61	0.00	0.70	0.12	0.35
	6.01	-0.343									-0.205	5	-43.29	1.66	0.30	0.17	0.36
b) in winter																	
78	1.43	-0.408							0.082			5	-39.18	0.00	1.00	0.56	0.72
c) in spring																	
77	4.55							0.025				4	-117.21	0.00	1.00	0.13	0.33
d) in summer																	
77	13.44							0.044				4	-106.62	0.00	0.72	0.44	0.46
	13.73							0.041		-0.288		5	-106.43	1.91	0.28	0.45	0.47
2. Temperature fluctuations																	

a) in autumn

76	2.75		-0.049					0.027		5	-91.71	0.00	0.66	0.39	0.43
	3.08	-0.300	-0.054					0.027		6	-91.21	1.36	0.34	0.41	0.48

b) in winter

78	3.06	-0.390	-0.032	-0.009						6	-68.28	0.00	1.00	0.35	0.56
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c) in spring

77	4.27				0.037	0.085	-0.210	-1.897	0.080		8	356.5	0.00	0.47	0.34	0.53
	3.71				-0.093	0.091	-0.033	-1.869	0.085	0.584	9	357.3	0.81	0.31	0.40	0.46
	4.17	-0.214			-0.078	-0.035	-0.336	-1.977	0.080		9	358.0	1.54	0.22	0.39	0.52

d) in summer

77	2.44								0.104		4	-183.57	0.00	0.46	0.33	0.34
	2.12	0.423							0.104		5	-182.87	0.89	0.30	0.33	0.34
	2.36								0.105	0.066	5	-183.07	1.30	0.24	0.32	0.35

3. Temperature extremes

a) min in winter

78	-0.03		0.020						0.061		5	-40.90	0.00	0.62	0.42	0.46
	0.50								0.055		4	-42.52	0.96	0.38	0.31	0.41

b) max in summer

14.57		0.101		4	-164.73	0.00	0.53	0.43	0.43
14.87		0.098	-0.302	5	-164.33	1.50	0.25	0.43	0.43
14.60	-0.042	0.101		5	-164.49	1.80	0.22	0.43	0.43

561 **Table 2.** Plausible candidate models ($\Delta AICc < 2$) explaining average humidity in (a) autumn, (b) winter, (c) spring, and (d) summer in relation to deadwood
 562 and forest characteristics. Sample size (N), intercept (Int.), number of parameters (k), model weight (w_i), *adjusted R*² (R^2_{adj}) are presented

N	Int.	log	dia- meter	length	ground cont.	bark	veget. cover	soft- ness	canopy	veget. type	k	LogLik	$\Delta AICc$	w_i	R^2_{adj}
a) in autumn															
76	99.10	88.06					51.44	64.99	-49.88		6	-2946.30	0.00	0.40	0.14
	99.85	87.48						66.49	-50.31		5	-2947.59	0.23	0.35	0.12
	128.97	89.05	56.22				50.85	63.39	-49.84		7	-2945.53	0.90	0.25	0.15
b) in winter															
78	104.33								-48.20		3	-3160.66	0.00	0.33	-0.01
	101.43		60.84						-48.70		4	-3159.90	0.70	0.24	-0.01
	103.08			34.74					-45.74		4	-3160.28	1.45	0.16	-0.02
	104.71				-47.94				-47.15		4	-3160.42	1.74	0.14	-0.02
	104.26					49.49			-49.20		4	-3160.46	1.82	0.13	-0.02
c) in spring															
77	98.35		63.02	39.27					-55.09		5	-3263.62	0.00	0.36	0.08
	102.29			39.28					-54.83		4	-3265.02	0.50	0.28	0.05

97.89	62.08	39.62	54.06	-54.90	6	-3263.04	1.19	0.20	0.08
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96.39	63.18	39.21		-52.91	80.30	6	-3263.21	1.53	0.16	0.07
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d) in summer

77	98.76	83.09	50.10	-50.90	5	-2708.20	0.00	0.31	0.08
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93.74	84.91	55.16	49.16	-51.06	6	-2707.13	0.21	0.28	0.09
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100.16	81.86			-50.92	4	-2710.03	1.35	0.16	0.05
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97.69	80.36	28.20	50.46	-50.38	6	-2707.87	1.69	0.13	0.08
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102.19				-50.93	3	-2711.40	1.88	0.12	0.03
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564 **Table 3.** Plausible candidate models ($\Delta\text{AICc} < 2$) explaining current (1a) and long-term (1b) occurrence; and current (2a) and long-term (2b) abundance of
565 *Tragosoma depsarium* in relation to deadwood and forest characteristics. Sample size (N), intercept (Int.), number of parameters (k), model weight (w_i), a
566 coefficient of determination based on the likelihood-ratio test (R^2_{LR}) and Nagelkerke's pseudo-R-squared (R^2_N) are presented

N	Int.	log	dia- meter	length	soft- ness	decay stage2	decay stage3	decay stage4	decay stage5	canopy	basal area	veget. type	k	LogLik	ΔAICc	w_i	R^2_{LR}	R^2_N
1. Occurrence																		
a) current																		
98	-25.07	20.35	0.207	0.0011							-0.371		5	-26.15	0.00	0.52	0.49	0.70
	-24.98	20.80	0.225	0.0009	-0.145						-0.396		6	-25.65	1.27	0.27	0.50	0.71
	-25.86	20.83	0.228	0.0010							-0.353	-0.575	6	-25.91	1.79	0.21	0.50	0.71
b) long-term																		
98	-26.33	6.30	0.235			16.79	18.18	16.89	18.49		-0.390		8	-24.96	0	0.7	0.58	0.77
	-25.95	6.20	0.229			16.83	18.13	16.64	18.35		-0.361	-0.716	9	-24.62	1.75	0.3	0.58	0.78
2. Abundance																		
a) current																		
29	-1.10		0.073		0.076								3	-75.46	0.00	0.28	0.43	0.43
	-1.26		0.059	0.0003	0.088								4	-74.11	0.00	0.28	0.48	0.48

-1.02	0.082							2	-77.00	0.58	0.21	0.37	0.37
-0.84	0.058	0.087					0.247	4	-74.91	1.60	0.12	0.45	0.45
-1.29	0.076	0.068				0.043		4	-75.06	1.91	0.11	0.45	0.45

b) long-term

43	0.033	0.017	0.0002	0.121		0.020	-0.081	6	-204.89	0.00	1.00	0.89	0.89
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568 **Table 4.** Plausible candidate models ($\Delta\text{AICc} < 2$) explaining current (1a) and long-term (1b) occurrence; and current (2a) and long-term (2b) abundance of
569 *Tragosoma depsarium* in relation to microclimatic variables (t °C – average temperature, t °C fluct. – daily temperature fluctuations, max t °C – maximum
570 temperature, RH % – relative humidity). Sample size (N), intercept (Int.), number of parameters (k), model weight (w_i), a coefficient of determination based on
571 the likelihood-ratio test (R^2_{LR}) and Nagelkerke's pseudo-R-squared (R^2_N) are presented

N	Int.	t °C	max	RH %	RH %	RH %	RH %	k	LogLik	ΔAICc	w_i	R^2_{LR}	R^2_N					
		autumn	winter	spring	summer	fluct.	fluct.	t °C	autumn	winter	spring	summer						
1. Occurrence																		
a) current																		
77	6.95	-1.915						-2.330	0.323				4	-33.74	0.00	0.51	0.49	0.62
	7.70	-1.846						-2.33	0.325			-0.013	5	-33.24	1.30	0.27	0.49	0.63
	6.76	-2.011						-2.41	0.318		0.010		5	-33.43	1.69	0.22	0.49	0.63
b) long-term																		
77	3.31		-3.14	0.743								-0.03	5	-34.72	0.00	0.28	0.57	0.69
	2.94		-2.91	0.638								-0.022	4	-36.04	0.35	0.23	0.55	0.67
	1.77		-2.99	0.495									3	-37.29	0.62	0.20	0.54	0.65
	2.03		-3.14	0.811			-0.325					-0.03	6	-34.10	1.13	0.16	0.58	0.70

-0.9	-2.82	0.635		0.040	-0.03		5	-35.51	1.60	0.13	0.56	0.68
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2. Abundance

a) current

22	3.25		-1.199		0.011		3	-63.23	0.00	0.11	0.83	0.83	
	1.89			-0.089		0.011	3	-63.25	0.03	0.10	0.83	0.83	
	2.00			-0.080			0.009	3	-63.30	0.14	0.10	0.83	0.83
	2.81		-0.173			0.012	3	-63.33	0.19	0.10	0.83	0.83	
	2.86		-0.157				0.010	3	-63.34	0.21	0.10	0.83	0.83
	2.11			-0.096		0.010	3	-63.35	0.23	0.09	0.83	0.83	
	1.02		-0.258				0.010	3	-63.55	0.64	0.08	0.83	0.83
	0.80			-0.37			0.009	3	-63.60	0.73	0.07	0.83	0.83
	0.81		-0.273			0.012	3	-63.71	0.96	0.07	0.82	0.82	
	0.97		-0.289			0.010	3	-63.90	1.33	0.05	0.82	0.82	
	2.85	-0.505				0.011	3	-64.00	1.53	0.05	0.82	0.82	
	2.18	-0.329					0.009	3	-64.09	1.71	0.04	0.82	0.82
	0.74		-0.05				0.009	3	-64.21	0.96	0.04	0.82	0.82

b) long-term

35 3.52

-0.78 0.122

-0.023 0.013

5 -144.44 0.00 1.00 0.99 0.99

Figure legends

573 **Fig. 1.** Location of study sites (black filled symbols) of *Tragosoma depsarium*, located close to four
574 nature reserves (surrounded by dark grey line) and one conservation area (surrounded by light grey line)

575 **Fig. 2** A schematic drawing of an identified study *site*, including four *logs* and one *snag*, with locations
576 of new (triangles) and old (squares) exit-holes and data-loggers (circles)

577 **Fig. 3** Average temperature in: (A) autumn in *snags* and *logs* in dry (black boxplots) and mesic (grey
578 boxplots) vegetation types; (B) winter in *snags* (black symbols) and *logs* (grey symbols) in relation to
579 basal area; (C) spring in relation to canopy openness; (D) summer in dry (black symbols) and mesic
580 (grey symbols) vegetation types in relation to canopy openness, expressing the main results of the first
581 order models

582 **Fig. 4** Predictive performance of models of current and long-term occurrence and abundance of
583 *T. depsarium* in relation to deadwood characteristics, forest characteristics, the combination of
584 deadwood and forest characteristics, microclimatic variables, and the combination of deadwood and
585 forest characteristics and microclimatic variables

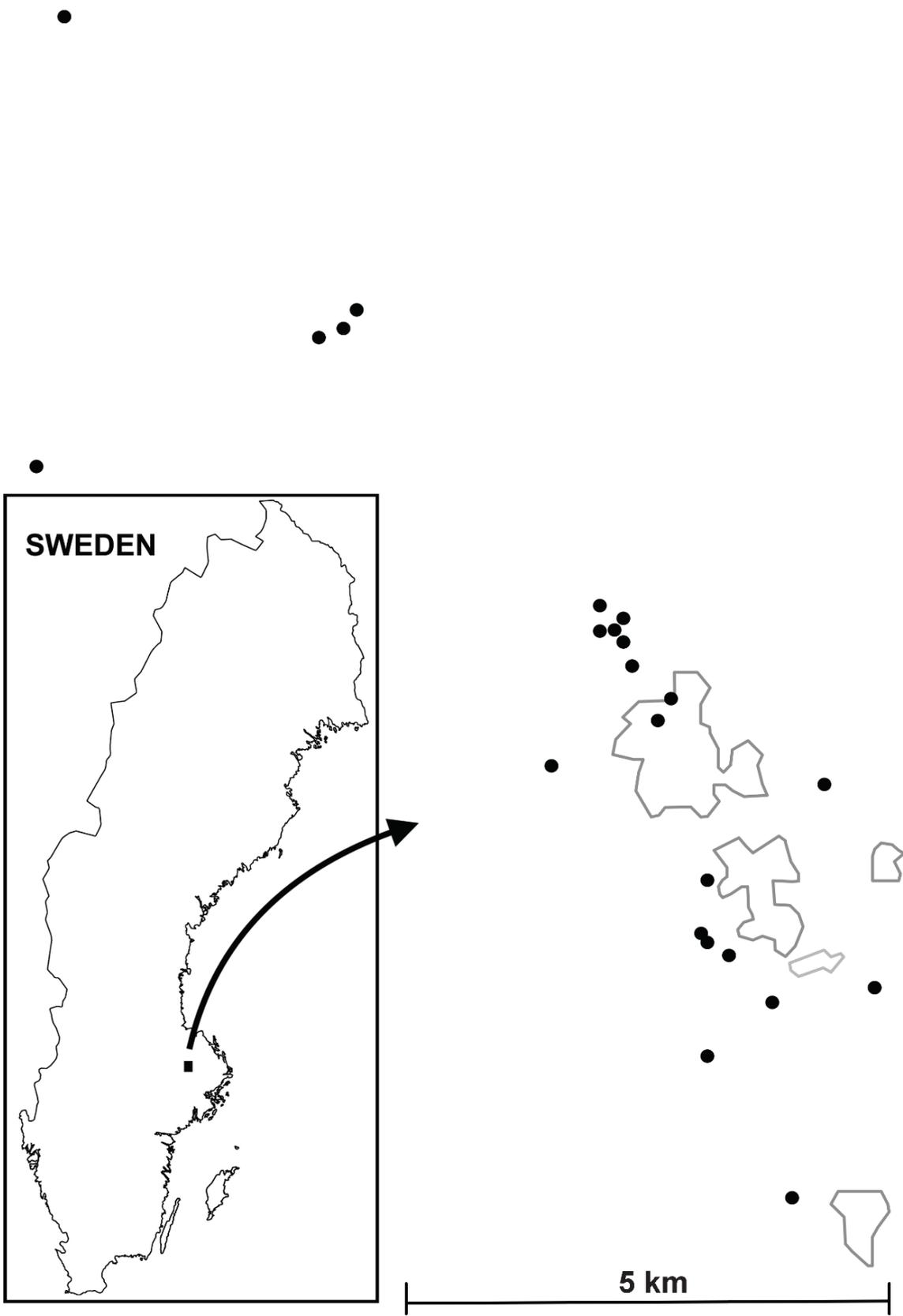


Fig. 1

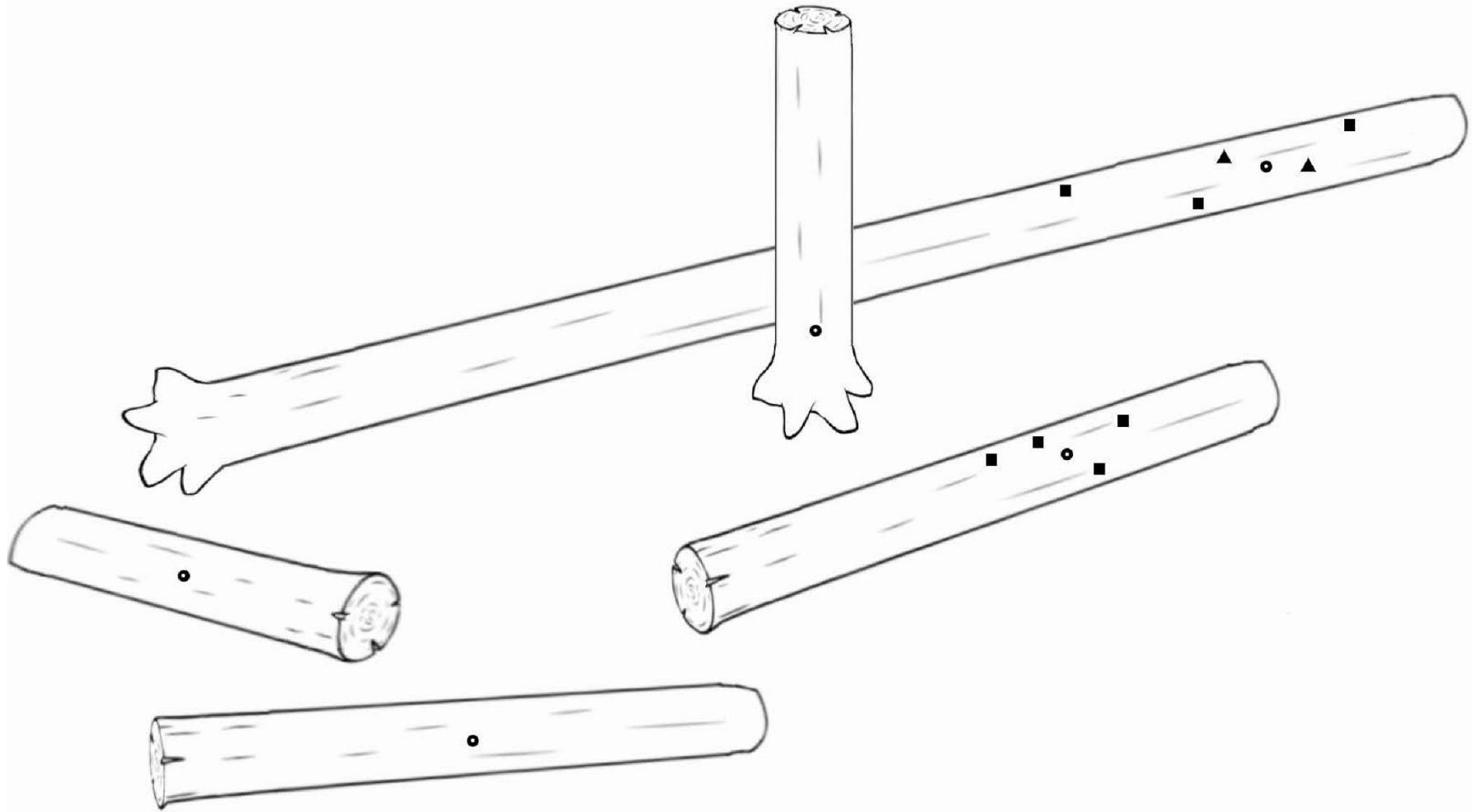


Fig. 2

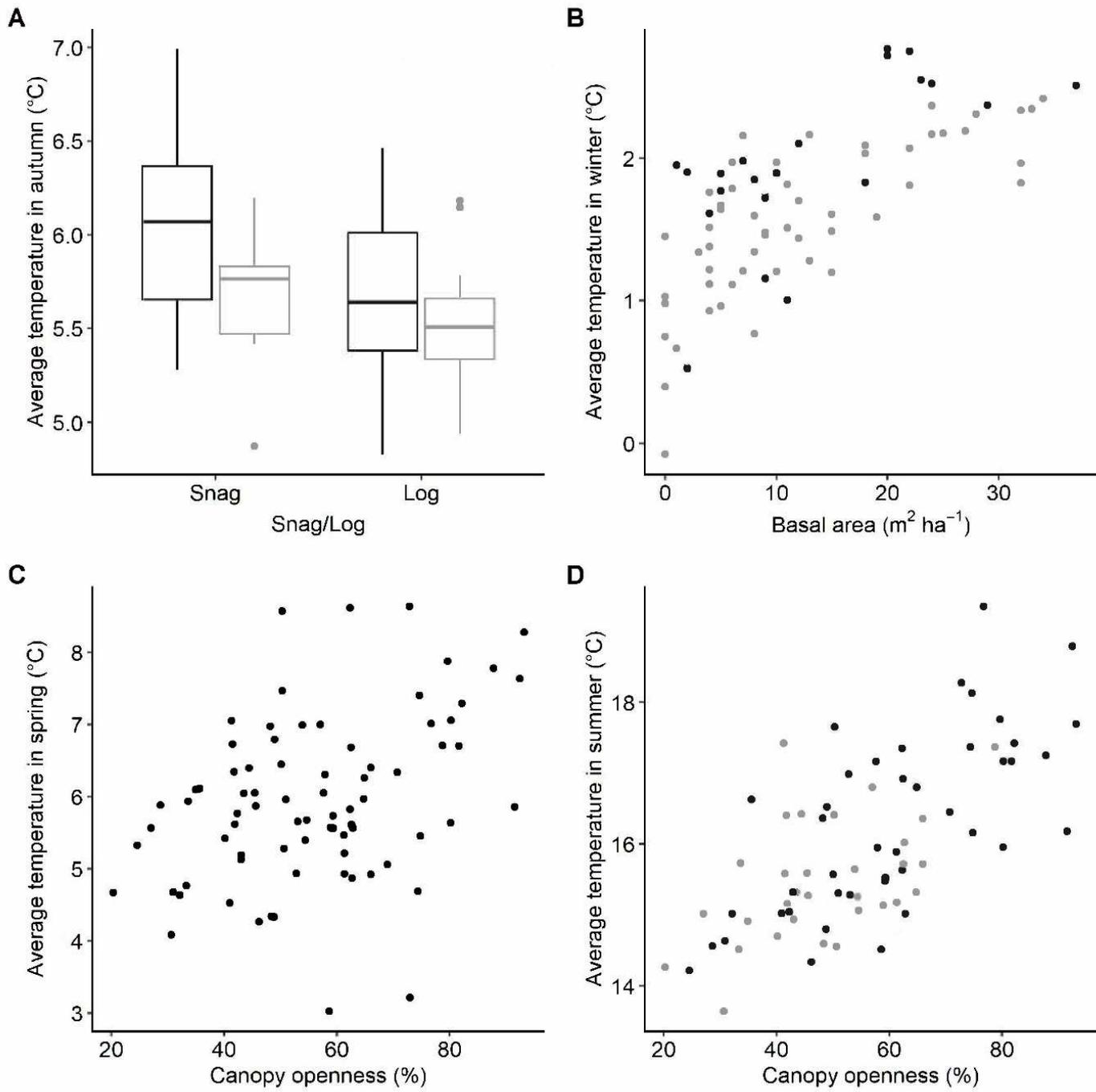


Fig. 3

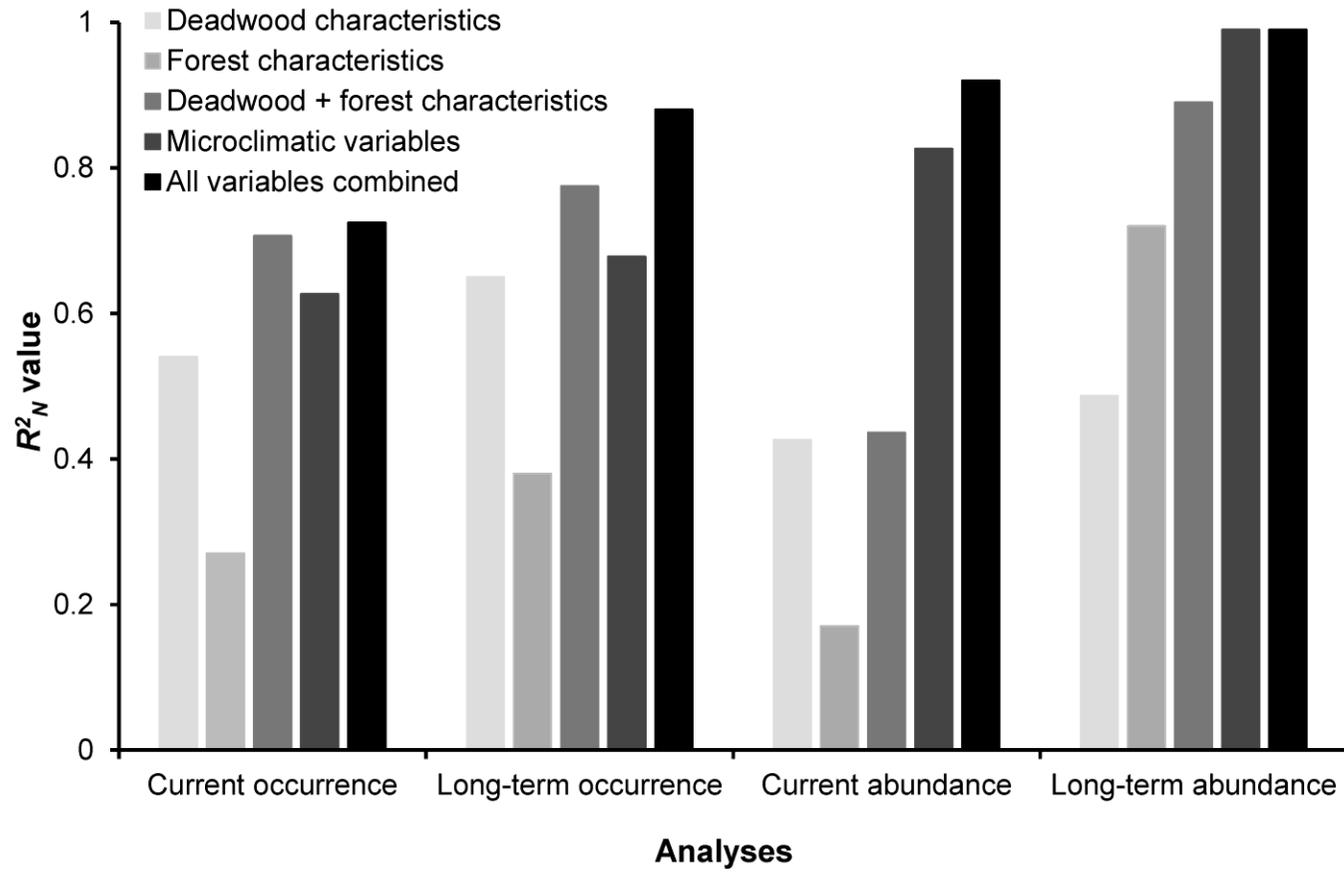


Fig. 4

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