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Winter mortality of the bark beetle *Ips typographus* in standing trees and in the ground

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Abstract

1. *Ips typographus* is the most important tree-killing bark beetle in Europe. In the north, it overwinters either in the bark of its host tree or in the ground, while in central Europe, overwintering in trees is most common. Few studies have estimated winter mortality of *I. typographus* in northern Europe.
2. Mortality of *I. typographus* adults overwintering in killed trees was estimated by comparing densities per m^2 bark of live (one winter) and dead adults (five winters), and proportion of dead adults (one winter), in bark samples collected before and after winter in Sweden. Densities of live and dead larvae of predatory *Medetera* spp. (Dolichopodidae) were recorded in the bark samples (one winter), as was the amount of bark removed by woodpeckers from *I. typographus*-killed trees during winter foraging (five winters). Mortality of *I. typographus* adults overwintering in the ground was estimated by spring sampling of soil (three winters).
3. The density of *I. typographus* live adults in trees was 3% lower after winter, while densities of dead adults was 6% higher and 5% lower respectively during two different outbreaks (differences after vs. before winters were non-significant). The proportion of dead adults was 4% higher after winter (significant). Winter mortality of adults overwintering in the ground was on average 58%.
4. The density of *Medetera* was 6% and 8% lower after winter for live and dead larvae, respectively (non-significant).
5. The amount of remaining bark on standing killed trees was on average 8% lower after than before winter (significant).

KEYWORDS

climate warming, Eurasian spruce bark beetle, long-legged flies, *Medetera*, natural enemies, Norway spruce, outbreak, overwintering behaviour, winter mortality, woodpecker predation

INTRODUCTION

Tree-killing bark beetles are a major disturbance factors in conifer forests worldwide (Bentz et al., 2010; Hicke et al., 2016; Raffa et al., 2008). In Europe, the Eurasian spruce bark beetle *Ips typographus* (L.) (Coleoptera, Curculionidae) is the most important tree-killing bark beetle (Christiansen & Bakke, 1988; Grégoire & Evans, 2004). Volumes of Norway spruce *Picea abies* L. (Karst.) killed by *I. typographus* have increased in recent decades as a result of large storm-fellings and warm and dry summers (Hlásny et al., 2021;

Schelhaas et al., 2003; Seidl et al., 2011), and this trend is expected to continue due to climate warming. To improve the accuracy of scenarios for future damages, it is important to consider how a warmer climate may affect bark beetle populations. One important factor to consider is mortality during overwintering, which can be high for bark beetles. For the North American mountain pine beetle, *Dendroctonus ponderosae* (Hopkins), which overwinter in pre-imaginal stages in killed trees, mortality rates exceeding 90% have been recorded (e.g., Amman, 1984; Dooley et al., 2015; Langor, 1989).

For *I. typographus*, a warmer climate may affect winter mortality in two ways. First, the number of generations per year will increase in a climate with warmer summers (Bentz et al., 2019; Jakoby et al., 2019; Jönsson et al., 2011). In northern Europe, where univoltine populations are currently most common, a switch to bivoltinism will likely occur. This may result in increased population densities because an increased proportion of adults will reproduce in the same year as they developed (i.e., before affected by winter mortality). Second, some *Ips* species, including *I. typographus* (see below), show a regional differentiation in overwintering behaviour. In North America, *Ips grandicollis* (Eichhoff) spend the winter in the bark of their brood trees in regions with a warmer climate, while in colder regions, they emerge to hibernate in the ground where they are protected from extreme temperatures by a snow cover (Lombardero et al., 2000). Comparisons of *I. grandicollis* populations in reciprocal thermal environments provided evidence that this difference in choice of hibernation site is not a simple response to temperature regime. In central Europe, most *I. typographus* individuals overwinter in the bark of their brood trees. If overwintering as adults, they move to the dry outer bark after they have completed maturation feeding. In contrast, in northern Europe with colder winters a considerable proportion of the adults instead overwinters in the organic layers of the ground (moss layer, litter, decomposed organic layer; hereafter ground) (Annila, 1969; Dworschak, Meyer, et al., 2014; Pettersen & Austarå, 1975; Weslien et al., 2024). Thus, in a climate with warmer winters, an increasing proportion of *I. typographus* may overwinter in the bark of their brood trees in northern regions as an adaptation to the lower risk of cold spells. To quantify how expected changes in voltinism and overwintering behaviour may affect *I. typographus* populations in a warmer climate, we need accurate data on winter mortality in both standing killed trees and in the ground.

Ips typographus generally overwinters as adults because pre-imaginal stages are more susceptible to die from low temperatures (Annila, 1969; Dworschak, Meyer, et al., 2014; Faccoli, 2002; Schopf & Kritsch, 2010). Average supercooling points (i.e., the temperature to which an insect may be cooled before ice nucleation occurs within the body fluids) of adults from central European populations in mid-winter was −20 to −22°C (some individuals reached −27°C), and for adults from northern Europe, it was −29°C (some individuals −32°C) (Annila, 1969; Koštál et al., 2011). There are only a few studies on winter mortality of *I. typographus*, and most of them are based on small sample sizes. For winter mortality in the bark, we are aware of five studies of which only two included mature adults (Annila, 1969 conducted in Finland; Dworschak, Gruppe, & Schopf, 2014 conducted in Germany). The other studies included larvae, pupae, callow adults, or parental adults because the studies were conducted on trees or stem sections that were colonized by *I. typographus* in late summer and the offspring constituting the second or third generations (Austarå et al., 1977; Faccoli, 2002; Schopf & Kritsch, 2010). In addition, none of the above-mentioned studies included winter predation by woodpeckers. Woodpeckers have been suggested to be an important mortality factor for bark beetles (Fayt et al., 2005). Regarding mortality of *I. typographus* adults overwintering in the ground, we are aware of three earlier studies (Annila, 1969 conducted in Finland; Zumr, 1982 conducted in Czech Republic; Austarå & Midtgaard, 1986 conducted in Norway) of which one (Annila, 1969) excluded natural enemies.

Several species of long-legged flies of the genus *Medetera* (Dolichopodidae) often occur in the galleries of *I. typographus* where the larvae prey on the bark beetle brood (Hedgren & Schroeder, 2004; Wermelinger, 2002; Weslien, 1992; Weslien et al., 2024). *Medetera* spp. (hereafter *Medetera*) is also generally the most abundant *I. typographus* natural enemy overwintering in killed trees and unlike many other enemies of *I. typographus*, the entire new generation overwinters in the killed trees in Sweden (Hedgren & Schroeder, 2004; Weslien, 1992). We are aware of only one earlier study on winter mortality of *I. typographus* enemies in the bark of killed trees and it did not include *Medetera* (Faccoli, 2002).

In the present study, we quantified winter mortality of *I. typographus* adults during two outbreaks in Sweden. Both adults overwintering in the bark and in the ground were included in the study. In addition, we estimated winter mortality of *Medetera* larvae overwintering in trees killed by *I. typographus*.

MATERIALS AND METHODS

Study regions

The study included data collected during two *I. typographus* outbreaks, the first initiated by a large storm-felling in January 2005 (hereafter denoted the first outbreak) and the second by the exceptionally warm and dry summer in 2018. During the first outbreak, data were collected in southern Sweden in the province of Småland, while during the second outbreak, localities were distributed along a latitudinal gradient in southern Sweden (Figure 1). Mean elevation of the study sites was 195 m (range 72–295 m). All study sites were protected areas (forest reserves) except for one (Ebbegärde) from the second outbreak that was on forest company land. The use of protected areas ensured that *I. typographus*-killed trees were not removed from the forest during the winter. For both outbreaks, winter mortality of *I. typographus* adults overwintering in the bark and amount of bark removed by woodpeckers were estimated. During the first outbreak, also winter mortality of *I. typographus* overwintering in the ground was estimated, while during the second, also mortality of *Medetera* larvae in the bark was recorded.

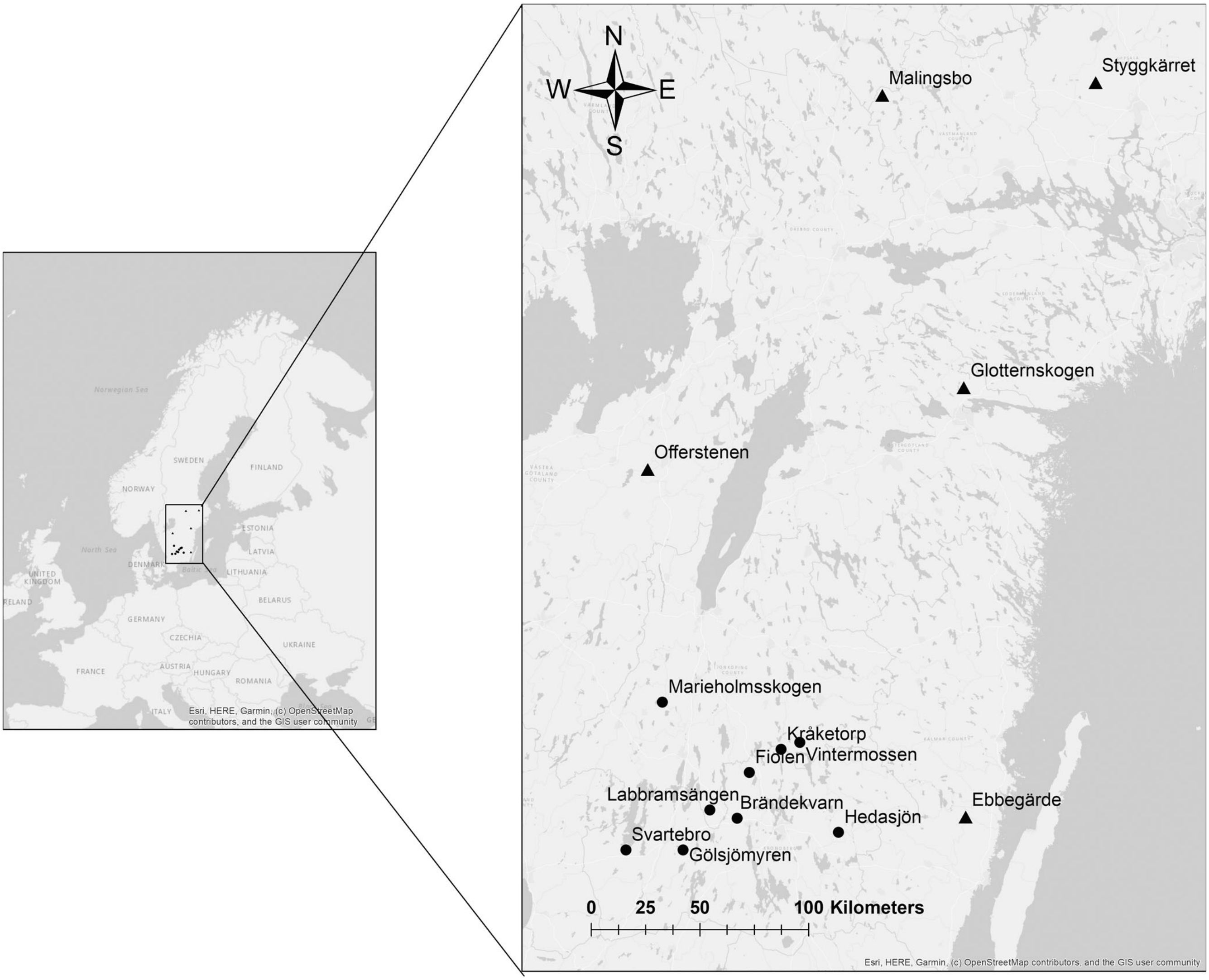

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FIGURE 1 Locations of the study areas in southern Sweden where winter mortality of *Ips typographus* adults and predatory *Medetera* larvae in standing *Ips typographus*-killed Norway spruces was estimated. Circles represent the nine areas studied during the first *I. typographus* outbreak and triangles the five areas studied during the second outbreak.

Winter mortality in trees

Mortality in bark

During the first outbreak mortality of *I. typographus*, adults overwintering in the bark of *I. typographus*-killed Norway spruces were estimated by comparing densities of dead adults before winter (September–November) with densities after winter (March–April). During the second outbreak, winter mortality of *I. typographus* adults in killed trees was estimated by comparing (1) densities of live adults, (2) densities of dead adults, and (3) proportion of dead adults before (December) and after (March) winter. Densities were expressed as number of individuals per m^2 bark area. Proportion of dead adults was calculated as number of dead adults divided by the sum of dead and live adults recorded in each bark sample. In addition, winter mortality of *Medetera* larvae was estimated by comparing densities of live and dead larvae before and after winter. Proportion of dead larvae (no. dead larvae/(no. dead and live larvae)) was not calculated because of low numbers of dead larvae. Bark sample size was 15 × 45 cm during both outbreaks. We used insect densities (instead of number of individuals) because bark sample sizes were not exactly the same: mean sample area first outbreak 0.0697 m^2 ± 0.0003 m^2 (± SE hereafter) and second outbreak 0.0714 m^2 (± 0.0004 m^2). The comparison of live *I. typographus* adults, and proportion of dead individuals, was excluded from the first outbreak because emergence from the trees to the ground had not yet ended in the autumn when the sampling was conducted (see Table S1 for dates of bark sampling and diameter of sampled trees). This means that if densities of live beetles are compared before and after winter, late-emerging adults that have left to overwinter in the ground will be interpreted as missing because of mortality (i.e., mortality will be overrated).

In all years and locations, bark sampling was conducted on trees killed by *I. typographus* in the same year as the sampling before winter was conducted (i.e., on current-year killed trees). During the first

TABLE 1 Densities (per m^2 bark) of live and dead *Ips typographus* adults and predatory *Medetera* larvae in bark samples collected from *I. typographus*-killed Norway spruces before and after winter. In the winters 2006/2007–2009/2010, different trees were sampled before and after winter, while in the winter 2020/2021, the same trees were sampled in both seasons. For dates of sampling, see Table S1.

	No. inspected trees		Densities (per m^2)			
			Before winter		After winter	
Taxa and year	Before winter	After winter	Mean	SE	Mean	SE
Live insects						
Ips typographus						
2020/2021	107	107	509	40	496	42
Medetera						
2020/2021	110	110	181	17	170	13
Dead insects						
Ips typographus						
2006/2007	45	26	82	12	39	9
2007/2008	109	53	60	7	102	16
2008/2009	43	40	85	15	78	17
2009/2010	68	42	201	20	195	23
2020/2021	107	107	106	9	101	9
Medetera						
2020/2021	110	110	12	2	11	1

outbreak, bark samples were collected at a stem height of 7 m, except in spring 2009 when the height was 4 m. During the second outbreak, the sampling height was 4 m. The aspect of the tree stem that was sampled differed between trees because it was chosen to find the safest aspect to use a ladder or for an arborist to climb the tree. All sampled trees were situated within stands (i.e., not in exposed stand edges). During the first outbreak, bark samples were collected from nine areas in southern Sweden (Brändekvarn, Fiolen, Gölsjömyren, Hedasjön, Kråketorp, Labbramsängen, Marieholmsskogen, Svartebro, and Vintermossen) for four winters from 2006/2007 to 2009/2010 (Figure 1). Not all areas were sampled in all winters because of lack of killed trees. Different trees were sampled in autumn and spring (i.e., each tree was only sampled once), resulting in 426 sampled trees (see Table 1 for number of samples per year and season). The trees sampled before and after winter belonged to the same groups of killed trees in each area and had similar average diameters (Table S1). During the second outbreak, five trees were sampled in each of five groups of *I. typographus*-killed trees for each of five regions (Ebbegärde, Billingen, Glotternskogen, Malingsbo, and Styggkärret; a total of 125 sampled trees) in the winter 2020/2021 (Figure 1). The minimum distance between any two sampled tree groups within regions was 300 m and the maximum distance 5 km. In contrast to the first outbreak, sampling before and after winter were conducted on the same tree, on opposite sides of the tree stem (i.e., each tree was sampled twice, one time before and one time after winter). The distance between the edges of the two bark samples was at least 5 cm. When samples were collected before winter, the bark area on the opposite side of each tree, planned for the spring sampling, was covered with chicken wire mesh to prevent woodpeckers from flaking, excavating or removing bark. Due to labelling problems, eight trees were discarded from analyses. For each taxon, that is, *I. typographus* and *Medetera*, trees with no living individuals in both the pre-winter and spring sample were also excluded from the analyses. Thus, for *I. typographus*, 107 trees were included in the analyses and for *Medetera* 110 trees (Table 1).

Bark samples were stored in plastic boxes in +4°C until analysed in the lab. The boxes were regularly dry-wiped to prevent growth of mould. For the first outbreak, the mean storage time of bark samples (from collection to analysis) was 15 days (range between years 12–17 days), while it was 28 days for the second outbreak. There was no correlation between storage time and density of dead *I. typographus* adults for the first outbreak (range between years of $r^2 = 0.004$–0.02) or the second outbreak for live ($r^2 = 0.002$) or dead ($r^2 < 0.001$) *I. typographus*.

Woodpecker removal of bark during winter

The proportion of bark remaining on *I. typographus*-killed Norway spruces was estimated by ocular evaluation before and after winter in the same winters and geographic areas as bark sampling was done. During the first outbreak, different trees were inspected before and after winter, while during the second outbreak, the same trees were inspected. The trees inspected before and after winter during the first outbreak belonged to the same groups of killed trees in each area and had similar average diameters (Table S2). During the first outbreak, 12,387 *I. typographus*-killed trees were inspected and during the second 96 trees (for inspection dates and tree diameters see Table S2). The 96 trees were from four (Ebbegärde, Billingen, Glotternskogen, Malingsbo) of the five regions sampled for *I. typographus* in the bark. For number of inspected trees per season and year, see Table S3.

Winter mortality in ground

Winter mortality of *I. typographus* overwintering in the ground was recorded for three winters during the first outbreak (2007/2008, 2008/2009, and 2009/2010) in the same nine areas that were sampled for mortality in bark. After winter (March–April; Table S1), soil samples were collected close, generally within 1.0 m, to Norway spruce trees killed by *I. typographus* in the previous year. The samples were taken by cutting out soil samples, to a depth of about 10–15 cm, which were placed in plastic boxes and then stored in +4°C until analysed. Each year, between 21 and 46 samples were collected (Table 2). Mean analysed sample sizes were 2008 = 1020 ± 81 mL, 2009 = 976 ± 35 mL, and 2010 = 1509 ± 58 mL of which 401 ± 30 mL belonged to the top and 1108 ± 58 mL to the bottom layer. The top layer consisted of the upper 3–5 cm of the soil samples. The division of the samples in the top and bottom layer was done to see if the proportion of dead individuals was higher in the top layer which may indicate that some of the dead individuals had died already on the trees and fallen to the ground. The soil samples were carefully analysed for numbers of live and dead *I. typographus* adults, including body parts (head with pronotum, abdomen, and elytra divided into left and right). Based on the numbers of different types of body parts, and intact bodies, the minimum number of dead *I. typographus* individuals was calculated for each sample (i.e., based on the highest number of any of the different body parts found). It was also noted if live and dead adults were present in bark pieces in the soil samples. Mean weight of bark pieces in the soil samples were 19.6 ± 2.8 g ($N = 42$), 2009 = 12.6 ± 4.7 g ($N = 20$), and 2010 = 13.1 ± 3.1 g ($N = 10$) of which 9.4 ± 2.0 g ($N = 7$) in top and 7.3 ± 1.9 g ($N = 9$) in bottom layer. Besides *I. typographus* also other species of dead Coleoptera (including body parts) were recorded but not determined to species.

Minimum winter temperature

For each study area, the minimum daily temperature for each winter during the study period (i.e., the period between the samplings of bark conducted before and after the winter) was derived from the closest weather station of the Swedish Meteorological and Hydrological Institute (SMHI). In addition, the mean minimum winter temperature for the 10 preceding years was calculated for each study area to give an indication of how "normal" the study winters were. The minimum daily temperatures were based on measurements taken once a minute. For the first outbreak, the 10-year period preceding the first study winter was used. The mean distance to the weather stations was 20 km (range 8–27 km) for the first outbreak and 16 km for the second outbreak (range 8–28 km). The weather stations and their distances to the closest weather stations are presented in Table S4.

Statistical analyses

Only adult *I. typographus* were included in the analyses of winter mortality in the bark because very few larvae and pupae were recorded in the samples. During the first outbreak 0.4% (85 of 21,631 individuals) of all living *I. typographus* recorded from the bark samples consisted of larvae and pupae (all from the sampling before winter), the rest being adults. During the second outbreak, no larvae or pupae of *I. typographus* (8278 living adults) and no adults or pupae of *Medetera* (2892 living larvae) were found in the bark samples (i.e., only larvae were present).

Analysis of variance (ANOVA) (SAS, Proc. Mixed) was used to analyse the winter morality of *I. typographus* and *Medetera* in the bark of standing trees. Each response variable was analysed and if necessary transformed so that its distribution resembled a normal distribution. Winter mortality of *I. typographus* adults was estimated by three variables: density of dead adults (first and second outbreak), density of live adults (second outbreak), and the proportion of dead adults (second outbreak). Winter mortality of *Medetera* (second outbreak) was estimated by two variables: densities of live and dead larvae. In all analyses, the fixed independent variable was "season" (before or after winter). For the first outbreak, site and sampling winter were included as random variables. For the second outbreak (when the same tree was sampled before and after winter), tree id and site were included as random variables. The dependent variables live and dead *I. typographus* and *Medetera* were log10($x + 1$)-transformed and proportion of dead *I. typographus* arcsine(x0.5)-transformed. F- and p-values are given for fixed variables.

To compare the removal of bark by woodpeckers between autumn and spring for each study season, Wilcoxon tests were used, as the model residuals were not normally distributed. These analyses were performed using R (R Core Team, 2024). As the bark recordings

TABLE 2 Number of live and dead *Ips typographus* adults in soil samples, and in soil plus pieces of bark and cones present in the samples, in early spring for three winters. In 2009/2010, the samples were divided into an upper and lower layer. N = number of samples.

		Only soil			Soil and bark/cones		
Year	N	Sum live	Sum dead	Percent dead	Sum live	Sum dead	Percent dead
2007/2008	46	503	357	42	552	364	40
2008/2009	26	77	126	62	82	126	61
2009/2010	21	132	361	73	138	361	72
Mean				59			58
2009/2010 upper	21	56	143	72	59	143	71
2009/2010 lower	21	76	218	74	79	218	73

from the first outbreak were performed on different trees, and recordings from the second outbreak were conducted on the same trees, the independent Mann–Whitney–Wilcoxon tests were carried out for the first outbreak, while the dependent (paired) Wilcoxon signed-rank test was employed for the second outbreak. Because woodpecker activity can vary spatially based on available resources (Fayt et al., 2005), spatial autocorrelation analyses of removed bark were performed to determine if possible regional differences in woodpecker abundance may have influenced the results of removed bark. These analyses were conducted using the "ape" package in program R (*Moran's I*; Paradis & Schliep, 2019).

RESULTS

Winter mortality in trees

Mortality in bark

During the first outbreak (winters 2006/2007–2009/2010), the mean density of dead *I. typographus* adults was 6% higher after than before winter, 110 ± 10 and 104 ± 8 dead adults per m^2 bark, respectively (means based on pooled samples from all years, for individual winters see Table 1). The difference was not significant (ANOVA, $p = 0.70$, $F_{1,413} = 0.2$). During the second outbreak (winter 2020/2021), the mean density of dead *I. typographus* adults was 5% lower after than before winter: 101 ± 9 and 106 ± 9 dead adults per m^2 bark, respectively (Table 1, means here and below based on pooled samples for all regions, for individual regions see Table S5). The difference was not significant (ANOVA, $p = 0.28$, $F_{1,106} = 1.2$).

During the second outbreak (winter 2020/2021), the mean density of live *I. typographus* adults was 3% lower after than before winter: 496 ± 42 and 509 ± 40 live adults per m^2 bark, respectively (Table 1, for individual regions see Table S5). The difference was not significant (ANOVA, $p = 0.06$, $F_{1,106} = 3.7$).

During the second outbreak (winter 2020/2021), the mean proportion of dead *I. typographus* adults was 4% higher after than before winter: 0.24 ± 0.02 and 0.20 ± 0.02, respectively (for individual regions see Table S6). The difference was significant (ANOVA, $p = 0.04$, $F_{1,106} = 4.29$).

For live *Medetera* larvae (winter 2020/2021), the mean density was 6% lower after than before winter: 170 ± 13 and 181 ± 17 live larvae per m^2 bark, respectively (Table 1). The difference was not significant (ANOVA, $p = 0.34$, $F_{1,107} = 0.9$; Table S7). The mean density of dead *Medetera* larvae was 8% lower after than before winter: 11 ± 1 and 12 ± 2 dead larvae per m^2 bark, respectively (Table 1, for individual regions see Table S7). The difference was not significant (ANOVA, $p = 0.41$, $F_{1,107} = 0.68$).

Woodpecker removal of bark during winter

The mean percentage of bark remaining on *I. typographus*-killed trees in autumn was 91.3 ± 3.1% and in spring 83.3 ± 1.5% (Figure 2). The difference between autumn and spring was significant in all 5 years (Wilcoxon test, $p < 0.001$ in each year). The mean loss of bark until spring was 8% (range 4%–11%). There was no spatial correlation of remaining bark among sites for either the spring (Moran's *I*, $p = 0.65$) or autumn ($p = 0.85$) or when separating the first and second outbreak sites (first: $p > 0.71$, second: $p > 0.68$).

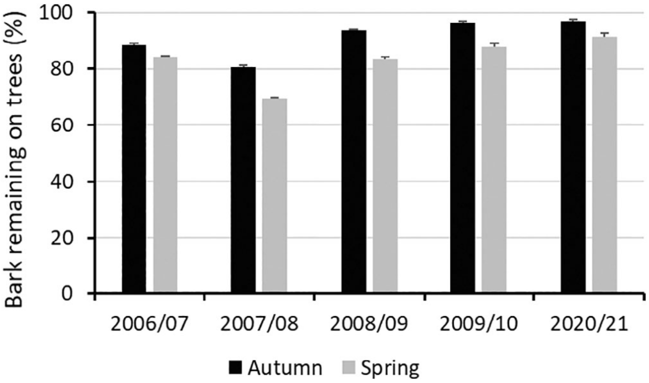

FIGURE 2 Percentage of bark remaining on *Ips typographus*-killed Norway spruces before and after winter in 5 years. In 2006/2007–2009/2010, different trees were inspected before and after winter, while in 2020/2021, the same trees were inspected. Number of inspected trees per season and year is given in Table S3. Error bars = SE.

Winter mortality in the ground

In the three winters, a total of 772 live and an estimated total number of 851 dead *I. typographus* adults were recorded from the soil samples including pieces of bark and cones (Table 2). The mean yearly percentage of dead *I. typographus* adults was 58% (range 40%–72%) (Table 2). In 2009/2010, when the soil samples were divided in an upper and lower layer, the percentage of dead *I. typographus* was 2% lower in the upper layer. Of the 67 adults found in pieces of bark or cones, seven (10%) were dead. Of the 844 dead adults found in soil (excluding bark and cones), 81 (10%) consisted of intact beetles (i.e., not parts of the bodies). A total of 1631 dead intact and parts of *I. typographus* were recorded during the 3 years compared with 259 intact and parts of other beetle species.

Minimum winter temperature

During all winters when sampling was conducted the lowest daily temperature occurred within the study periods, that is, between the autumn and spring sampling for mortality in trees and before spring sampling for mortality in ground. Minimum daily temperatures, ranged from −12.5 to −24.7°C (Table 3). In the winters 2006/2007 to 2008/2009, the minimum temperatures were on average somewhat higher compared with the mean of minimum temperatures for the 10-year period preceding 2006/2007 (3.6, 7.8, and 3.8°C, respectively), while in 2009/2010, it was 3.1°C lower and in 2020/2021 about the same.

TABLE 3 Minimum daily winter temperature during the study winters of the two *Ips typographus* outbreaks and the mean of minimum daily winter temperatures for the 10 winters preceding the start of the studies (first outbreak 1996/1997–2005/2006 and second outbreak 2010/2011–2019/2020).

Winter and study	Min temperature	Min temperature 10-year period (°C)		
Area	Study winter (°C)	Mean	Min	Max
2006/2007				
Brändekvarn	−17.1	−18.0	−19.9	−14.0
Kråketorp	−16.5	−19.0	−21.2	−14.0
Gölsjömyren	−18.2	−23.6	−26.1	−18.5
Svartebro	−18.2	−23.6	−26.1	−18.5
2007/2008				
Kråketorp	−12.5	−19.0	−21.2	−14.0
Labbramsängen	−14.2	−23.6	−26.1	−18.5
Marieholmsskogen	−16.2	−23.8	−27.8	−17.9
2008/2009				
Kråketorp	−14.8	−19.0	−21.2	−14.0
Gölsjömyren	−20.0	−23.6	−26.1	−18.5
Svartebro	−20.0	−23.6	−26.1	−18.5
Labbramsängen	−20.0	−23.6	−26.1	−18.5
2009/2010				
Fiolen	−23.8	−19.0	−21.2	−14.0
Kråketorp	−23.8	−19.0	−21.2	−14.0
Hedasjön	−21.2	−18.0	−19.9	−14.0
Svartebro	−23.8	−23.6	−26.1	−18.5
Vintermossen	−19.5	−16.8	−19.5	−13.3
2020/2021				
Ebbegärde	−19.3	−17.1	−25.6	−9.9
Billingen	−15.4	−15.1	−18.6	−9.9
Glotternskogen	−14.0	−14.6	−20.2	−6.1
Malingsbo	−19.0	−21.8	−28.2	−12.2
Styggkärret	−24.7	−22.4	−30.1	−10.6

The minimum temperatures during the 10-year periods ranged from −19.5 to −27.8°C.

DISCUSSION

Our study demonstrates that winter mortality of *I. typographus* new generation adults overwintering in the bark of standing killed trees is low. The densities of adults after and before winter were almost the same (live adults 3% lower second outbreak; dead adults 6% higher first outbreak, and 5% lower second outbreak) and did not differ significantly. The proportion of dead adults was 4% higher after than before winter, and this difference was significant. In addition, woodpecker removal of bark during winter affected on average only 8% of the stem bark area of killed trees and the resulting mortality of *I. typographus* is probably considerably lower than this figure because of adults surviving in pieces of bark falling to the ground (see below). In contrast, mortality of *I. typographus* overwintering in the ground was considerably higher with an estimated average of 58% for the three studied winters. The higher mortality in the ground compared to in the trees may be an important factor contributing to the dominance of overwintering in trees in the lowlands of central Europe where the risk of lethal winter temperatures is low.

Most earlier studies on mortality of *I. typographus* overwintering in the bark of their brood trees were conducted in central Europe on trees or stem sections colonized late in summer and thus included parental and callow adults as well as pre-imaginal stages. This may explain the much higher mortality recorded in these studies compared to our study, which only included mature adults (Table 4). Two earlier studies including mature adults exposed to minimum winter temperatures of about −10°C, reported a low winter mortality of 2%–7%, which is in accordance with our study (Annila, 1969; Dworschak, Gruppe, & Schopf, 2014). Thus, if the *I. typographus* offspring have time to develop to mature adults and move to the dry outer bark

TABLE 4 Summary of earlier and the present study on winter mortality of *Ips typographus* overwintering in the bark of their brood trees.

Country/region and winter	Developmental stage	Mortality (%)	Min temp	Description	Reference
Southern Norway				Attacked standing trees, second generation brood, two trees cut in autumn and two in spring, bark samples, living and dead progeny recorded	Austarå et al. (1977)
1975/1976	Larvae, pupae, callow adults	88–100	−24°C		
Northern Italy				Attacked standing trees, third generation brood, three trees cut in autumn, bark samples, living and dead progeny recorded	Faccoli (2002)
1997/1998	Larvae, pupae, callow and mature adults	49	−11°C		
Southern Germany				Reared in 24 stem sections, attached to standing trees at three altitudes, in spring reared out and sections debarked	Dworschak, Gruppe, and Schopf (2014)
2007/2008	Mature adults	2	−9 to −12°C		
	Larvae, pupae, callow adults	39			
Southern Finland					Annila (1969)
1966/1967	Eggs, larvae, pupae, above snow	100	−31.1°C	Reared in six stem sections, three placed on ground and 3 at 2 m height, debarked in spring, live and dead progeny recorded	
	Eggs, larvae, pupae, below snow	100	ND		
1964/1965	Mature adults, above snow	58	−29.9°C	Stem sections from attacked trap trees, placed on ground or 2 m height, debarked in spring, live and dead adults recorded	
	Mature adults, below snow	7	ND		
1965/1966	Mature adults, above snow	100	−33.3°C		
	Mature adults, below snow	3	−8.3°C		
1966/1967	Mature adults, above snow	100	−31.1°C		
Eastern Austria				Stem sections from attacked standing trees, third generation brood, bark samples checked monthly, live and dead progeny recorded	Schopf and Kritsch (2010)
2008/2009	Larvae	100	−9.4°C		
	Pupae	100			
	Parental adults	50–60			
2009/2010	Larvae	100	−12.8°C	Reared in stem sections, bark samples checked 27 Oct to 9 Feb, live and dead progeny recorded	
	Parental adults	40–55			
Southern Sweden					Present study
2006/2007–2009/2010	Mature adults	6	−12.5 to −23.8°C	Attacked standing trees, bark samples before and after winter, densities of dead adults compared	
2020/2021	Mature adults	0–4	−14 to −25°C	Attacked standing trees, bark samples before and after winter, densities of live and dead adults, and proportion of dead adults compared	

Abbreviation: ND, no data available.

before winter, mortality in standing killed trees is low if the winter temperature stays above the lethal temperature. Based on the supercooling point of −29°C for *I. typographus* adults in Finland (Annila, 1969), this was the case in our study even though also other factors than the supercooling point may influence the winter mortality. The very low proportion of larvae and pupae found in the bark samples (0.3% of all collected living individuals during the two outbreaks) demonstrates that *I. typographus* in Sweden is generally well adapted to avoid reproducing too late in the season when offspring may not reach the adult stage before winter. The main mechanism for avoiding reproducing too late in the season in *I. typographus* is a photoperiod-induced reproductive diapause, that is, shorter day lengths in late summer induce diapause (Schebeck et al., 2022). An earlier study conducted along a climatic gradient in Sweden showed a positive correlation between latitude of *I. typographus* population origin and proportion of individuals that entered reproductive diapause at given day lengths, which demonstrates local adaptations (Schroeder & Dalin, 2017).

Before winter, on average 91% (range 81%–97%) of the bark surface remained on the *I. typographus*-killed trees. This means that woodpeckers had on average removed 9% of the bark prior to the inspections before winter. During winter, on average an additional 8% (range 4%–11%) of the bark surface was lost due to woodpecker activity. From our data, it is not possible to determine exactly how large mortality this winter foraging by woodpeckers caused to the overwintering population of *I. typographus* in the trees. However, it can be expected to be lower than the percentage of bark removed from the trees. First, mature *I. typographus* adults overwinters inside the outer bark (i.e., not at the phloem-sapwood interface) and are thus well protected in pieces of bark falling to the ground due to woodpecker foraging. Second, winter survival of *I. typographus* adults in pieces of bark lying on the ground was at least 80% in a study of bark strips falling off from *I. typographus*-killed trees during winter logging by harvesters (Weslien et al., 2024). High survival in bark pieces on the ground is also in agreement with a study from Germany demonstrating a positive relationship between amount of bark on the ground (due to woodpecker activity) and number of *I. typographus* emerging from ground in spring (Dworschak, Meyer, et al., 2014). In addition, the number of emerging beetles decreased when the bark pieces were removed from the ground in that study.

Also, *Medetera* larvae experienced a low winter mortality in the bark of *I. typographus*-killed trees. The density of live larvae was 6% lower, and the density of dead larvae was 8% lower, after than before winter and the differences were not significant. In addition, the densities of dead larvae were much lower than densities of live larvae. We are not aware of any studies of woodpecker predation on *Medetera* (or other natural enemies of *I. typographus*), but if woodpeckers eat *Medetera* larvae they may cause a maximum of 8% additional mortality. Winter survival of *Medetera* in pieces of bark lying on the ground was high (93%) in a study of bark strips falling off from *I. typographus*-killed trees during winter logging by harvesters (Weslien et al., 2024). The only earlier study on winter mortality of *I. typographus* enemies overwintering in the bark of killed trees reported a mortality close to 50% for the two parasitoids *Coeloides bostrychorum* and *Roptrocerus xylophagorum* (Faccoli, 2002). This study was based on repeated sampling of living insects in bark from November to April of three *I. typographus*-killed trees felled in November.

The mortality of *I. typographus* adults overwintering in the ground ranged from 40% to 72% during the three studied winters. In an earlier study on winter mortality of *I. typographus* overwintering in the ground in northern Europe (conducted in Norway with a different method, see Table 5), reported a mortality of 40% (Austarå &

TABLE 5 Summary of earlier and the present study on the mortality of *Ips typographus* adults overwintering in the ground adjacent to killed trees.

Country/region and winter	No. adults	Mortality (%)	Min temp	Description	Reference
Southern Finland				Adults in boxes with mesh top and bottom netting, placed in moss layer, examined in spring. Temperature recorded under snow.	Annila (1968)
1964/1965	276	2	ND		
1965/1966	117	4	−1.2°C		
1966/1967	105	5	−2.2°C		
Czech Republic, south Bohemia				Ground samples from three cultivated and three natural stands, collected December to March, living and dead adults recorded.	Zumr (1982)
1977 to 1979	Cultivated stands: 1115	16	ND		
	Natural stands: 511	36			
South-eastern Norway				In August stem sections cut from attacked standing trees, emerging beetles directed into cages including ground soil, in spring fresh stem sections placed in cages and colonizing beetles counted, 10 replicates.	Austarå and Midtgaard (1986)
1982/1983	1441	40	ND		
Southern Sweden				Ground samples from nine stands, collected March–April, living and dead adults recorded	Present study
2007/2008	860	42			
2008/2009	203	62			
2009/2010	493	73			

Abbreviation: ND, no data available.

Midtgaard, 1986). In central Europe, 16%–36% mortality was recorded using a similar method as in our study (Zumr, 1982). One factor that may have contributed to the somewhat lower mortality in the study by Zumr (1982) is that soil sampling was conducted earlier (December–March) compared with our study (March–April). The fact that 90% of the dead individuals recorded in our study consisted of body parts of adults suggests that predation is a major mortality factor. In a study conducted in Finland (Annila, 1969), winter mortality of *I. typographus* adults in boxes with top and bottom nettings and placed in the soil was only 2%–5% (Table 5). There is a risk of underestimating mortality in the ground because beetles that are totally consumed (e.g., by rodents or birds) will not be included in the estimates. On the other hand, it has been proposed that some dead *I. typographus* found in the ground may have died already on the trunk of the attacked tree (and then fallen down), thus resulting in an overestimate of winter mortality in the ground (Zumr, 1982). Our result that mortality in the upper soil layer was about the same as in the lower layer does not support this suggestion. It is also possible that some of the dead *I. typographus* found in the soil samples have died already during previous years, that is, dead adults that have not attacked or developed in the killed trees close to which the soil samples were taken. However, the contribution of dead *I. typographus* adults from previous years can be expected to be small compared to adults originating from the nearby brood trees for two reasons. First, most *I. typographus* that emerge to overwinter in the soil stay close to their brood trees which results in high densities (Austarå et al., 1993; Biermann, 1977). Second, 86% of the recorded dead Coleoptera (i.e., all species and including parts and intact beetles) consisted of *I. typographus*. If a considerable proportion of the recorded dead *I. typographus* originated from previous years, you would expect to find much higher numbers of body parts and intact specimens when summing up all other forest-living beetle species.

Climate change results in warmer summers and winters, and the temperature increase is especially high in the north where also cold spells have become less frequent (IPCC, 2021; Pinto et al., 2024; Rousi et al., 2023). Thus, two behavioural shifts can be expected for *I. typographus* in northern Europe that may reduce the negative impact of winter mortality on populations. First, warmer summers are predicted to increase the occurrence of bivoltinism in regions where univoltinism currently dominates like in northern Europe (Bentz et al., 2019; Fritscher & Schroeder, 2022; Lindman et al., 2023). This means that an increasing proportion of the first generation produced in summer will avoid the considerable winter mortality in the ground by reproducing directly after emergence (i.e., before overwintering). Second, warmer winters may increase the proportion of beetles overwintering in the bark of standing trees and thereby avoiding the higher mortality experienced by beetles in the ground. In southern Sweden, where most *I. typographus* outbreaks have occurred so far (Kärvemo & Schroeder, 2010; Schroeder & Kärvemo, 2022), and where *I. typographus* is mostly univoltine (Fritscher & Schroeder, 2022), around half of the new generation beetles overwinters in the ground in the current climate. Weslien et al. (2024) reported that in the winter 2020/2021, 52% (based on data from the same bark samples as used in this study) and in 2021/2022, 56% of the new generation beetles overwintered in the ground in southern Sweden. The study by Weslien et al. (2024) also showed that there is a gradient with even lower proportion overwintering in trees in harsher climatic conditions further north. In contrast, in central Europe with a warmer climate (where bivoltinism or even three generations per year dominates), most *I. typographus* overwinter in trees (Dworschak, Meyer, et al., 2014). This indicates that in a warming climate, the proportion of *I. typographus* overwintering in the ground in Sweden will gradually decrease over time as an adaptation to a lower risk of cold spells during winter and the considerably higher mortality in the ground than in the bark. Altogether, these two behavioural shifts may increase the risk for damages by reducing the negative effect of winter mortality on population levels of *I. typographus*.

AUTHOR CONTRIBUTIONS

Martin Schroeder: Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; writing – review and editing. **Simon Kärvemo:** Formal analysis; investigation; methodology; writing – review and editing. **Dragos Cocos:** Investigation; methodology; writing – review and editing. **Petter Öhrn:** Investigation; methodology; writing – review and editing. **Jan Weslien:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Dates for bark sampling before and after winter and diameter at 1.3 m of sampled *Ips typographus*-killed Norway spruces. In 2006/2007–2009/2010 different trees were inspected before and after winter while in 2020/2021 the same trees were inspected in both seasons. The sampling dates for soil (conducted in 2007/2008, 2008/2009 and 2009/2010) were the same as for bark samples in the spring.

Table S2. Dates for inspections of proportion of bark remaining on *Ips typographus*-killed Norway spruces before and after winter and diameter of inspected trees at 1.3 m. In 2006/2007–2009/2010 different trees were inspected before and after winter while in 2020/2021 the same trees were inspected in both seasons. ND = No data available.

Table S3. Number of inspected trees per season and year for proportion of bark remaining on *Ips typographus*-killed Norway spruces before and after winter. In 2006/2007–2009/2010 different trees were inspected before and after winter while in 2020/2021 the same trees were inspected in both seasons.

Table S4. Weather stations used for deriving minimum winter temperatures and the distances between study areas and weather stations during the first (2006/2007–2009/2010) and second (2020/2021) *Ips typographus* outbreak.

Table S5. Densities of dead and live *Ips typographus* adults in bark samples collected from *I. typographus*-killed Norway spruces before and after winter. The same trees were sampled in both seasons. Sampling regions listed from south to north. *N* = number of sampled trees.

Table S6. Proportions of dead *Ips typographus* adults in bark samples collected from *I. typographus*-killed Norway spruces before and after winter. The same trees were sampled in both seasons. Sampling regions listed from south to north. *N* = number of sampled trees. Proportions of dead *I. typographus* were calculated as number of dead individuals divided by the sum of live and dead individuals.

Table S7. Densities (per m^2 bark) of dead and live *Medetera* larvae in bark samples collected from *Ips typographus*-killed Norway spruces before and after winter in 2020/2021. The same trees were sampled in both seasons. Sampling regions listed from south to north. *N* = number of sampled trees.

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