



Effects of sanitation logging in winter on the Eurasian spruce bark beetle and predatory long-legged flies

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ABSTRACT

Bark beetles may cause great damage to forests by killing trees over large areas during outbreaks. So-called sanitation logging is frequently used in both Europe and North America. Despite this, there are few evaluations of the efficiency of sanitation logging for reducing bark beetle numbers. The Eurasian spruce bark beetle *Ips typographus* (SBB) has caused unprecedented high tree mortality in Europe during recent years. Much of the sanitation logging is done during winter when SBB are in the adult stage. Sanitation logging may also affect natural enemies of SBB, especially larvae of long-legged flies, *Medetera* spp., that overwinter in the killed trees. The main goal of this study was to quantify how sanitation logging during the winter affects mortality of SBB and *Medetera* compared to leaving the trees in the forest. In one part of the study the proportion of the new generation of SBB that overwintered in 237 trees in two years across a climatic gradient was estimated. Within the area of the latest outbreak that started 2018 in Southern Sweden, the average proportion of SBB overwintering in the tree was 48%. Further north the proportion was significantly lower (mean 27%). In another part of the study, the amount of bark that was stripped off by harvesters during processing of 424 SBB-killed trees at six sites and the survival of SBB and *Medetera* until spring in stripped-off bark was estimated. On average 50% of the bark was stripped off during processing by harvesters. More bark was stripped off when processing trees with thawed (mean 61%) than with frozen bark (mean 37%). The estimated survival of SBB and *Medetera* in stripped-off bark was high (>70%), and consequently the relative reduction of both SBB and *Medetera* by sanitation logging was lower for trees harvested with thawed than with frozen bark. The mean reduction of *Medetera* by sanitation logging was greater than that of SBB (49% vs. 29%) mainly because all *Medetera* stay in the tree during winter while most SBB leave the tree before winter. The limited effect of sanitation logging on SBB reduction during winter, especially if bark is thawed, suggests that as much as possible of SBB-killed trees should be logged during summer. Logging during winter risks hitting *Medetera* proportionally harder than SBB, and this is a factor to consider in the control of SBB.

1. Introduction

Bark beetles (Coleoptera, Curculionidae) cause great damage to coniferous forests across the northern hemisphere by killing trees over large areas during outbreaks. Among different measures to reduce economic losses during bark beetle outbreaks, so-called salvage logging (to save timber values) and sanitation logging (to reduce spreading of infestation) of attacked trees are frequently practiced methods in both Europe and North America (Carroll et al., 2006, Schowalter, 2012, Stadelmann et al., 2013, Fettig and Hilszczanski, 2015, Fettig et al., 2022). Despite this, there are surprisingly few evaluations of the

efficiency of sanitation logging for reducing bark beetle numbers. Knowledge on how much logging reduces bark beetle population density in combination with the timber value and the cost of logging is necessary for estimating cost efficiency of the method. Also, in protected areas (e. g., nature reserves and national parks), where the economic value of the trees is of less concern, but where nature values may be threatened if bark beetle damage becomes too severe, it is important to know how efficient sanitation logging reduces bark beetle numbers. Moreover, it has been shown that sanitation or salvage logging can have unwanted negative impact on other species such as woodpeckers (Basile et al., 2023) and deadwood-dependent beetles (Schroeder, 2007a; Thorn et al.,

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2017). The distinction between salvage and sanitation logging is seldom clear because both saving of timber value and a reduction of bark beetles is usually the aim. Because this study focuses on evaluating the suppressive effect of logging on bark beetle numbers the term sanitation logging is used in the following text.

Among bark beetles that cause serious damage to forests during outbreaks are several species of the genus *Dendroctonus* in North America (e.g., Aukema et al., 2006, Edburg et al., 2012, Hicke et al., 2016, Dodds et al., 2018) and the Eurasian spruce bark beetle *Ips typographus* (L.) in Europe (e.g., Christiansen and Bakke, 1983, Hlásny et al., 2021a). Bark beetle outbreaks are generally triggered by extreme weather events like large scale storm-fellings or exceptionally warm and dry summers, sometimes with a combination of these factors (Berg et al., 2006; Safranyik and Carroll, 2006; Marini et al., 2017, Kärvelo et al., 2014). In both cases large amounts of suitable breeding material with weak defenses (i.e., storm-felled trees or standing drought stressed trees) are created which results in increased bark beetle population growth and tree mortality. In both Europe and North America, the frequency and magnitude of outbreaks have increased and can be expected to further increase in a warmer climate (Bentz et al., 2009, 2010, 2019; Seidl et al., 2014; Hicke et al., 2016),

After an extremely warm and dry summer in 2018, historically high volumes of Norway spruce, *Picea abies* (L.) Karst, were killed by the Eurasian spruce bark beetle (hereafter SBB) in Central Europe and Sweden (Hlásny et al., 2021b; Schroeder and Kärvelo, 2022). Sanitation loggings have been carried out on large scale to reduce populations of SBB (by removing attacked trees with bark beetles from the forest) and thereby decreasing the risk for new attacks. Sanitation loggings are mostly carried out by harvesters in Sweden, and this is also common in other countries. During processing of logs by harvesters varying amounts of bark are stripped off and thus remain in the forest (Delb et al., 2021). If the logging is carried out during the summer, before the bark beetles have completed their development, most of the larvae and pupae in stripped-off bark will not be able to complete development. Despite this knowledge, it was estimated that 75–80% of the killed trees remained in the forest in September during the latest SBB outbreak in Sweden (Wulff and Roberge, 2021a; 2021b). There are several reasons for the low proportion of killed trees harvested during summer. Firstly, during large-scale outbreaks limited logging resources, and market demands for timber, will affect the amounts of killed trees that can be processed during the rather short time before the beetles have completed their development. Secondly, many attacked trees are still green and difficult to detect (Huo et al., 2023). Thirdly, logging during summer is problematic due to the fire hazard and the risk for ignition by forest machines. Lastly, nature protection issues such as protection of nesting birds should be considered (European Commission, 2019). Thus, most of the logging of killed trees occurs during SBBs overwintering phase when they are in the adult stage. It is not known to what extent adults of SBB in stripped-off bark survive until spring flight.

The efficiency of sanitation logging also depends on how many bark beetles remain in the tree till the time of felling. In Central Europe, SBB overwinters to a high degree in the bark of the killed trees in lowland-areas with multivoltine populations, whereas a high proportion of the SBB adults leave the trees before winter in the mountains (Wild, 1953; von Biermann, 1977; Wermelinger et al., 2012; Dworschak et al., 2014; Kasumović et al., 2019). In Fennoscandia, where SBB is mainly univoltine (Annala, 1969; Fritscher and Schroeder, 2022), more than 70% of the new generation SBB adults have been shown to leave the brood tree in autumn (Pettersen and Austarå, 1975; Weslien, 1992; Hedgren and Schroeder, 2004) and overwinter in the ground litter beneath the brood tree (Lindelöv and Weslien, 1986; Austarå et al., 1993). These studies were made at sites close to or north of latitude 60° N. There are no published studies from the more southern parts of Scandinavia, where recent SBB-outbreaks (after 2005) have occurred, regarding the proportion of SBB that overwinter in the trees. Hypothetically, a higher proportion of beetles may overwinter in the trees in southern than in

northern Scandinavia. This is because the risk for lethally low temperatures during winter is greater in the north and thus overwintering in the snow-covered ground is more favorable.

Little is known about how the proportion of SBB overwintering in trees is influenced by tree characteristics such as age, diameter, or bark thickness. Hypothetically, trees with thick bark (offering better overwintering niches than trees with thin bark) and trees that still have green needles in winter (indicating late attack) should have higher proportions of overwintering beetles than brown trees. There is some evidence of a vertical gradient within trees with decreasing proportions of overwintering SBB with increasing height above ground (Komonen et al., 2011), which means that sampling at a reachable height from the ground may overestimate number of SBB present in the tree.

Many enemies of SBB live in the galleries under bark (Kenis et al., 2004). Experiments in which SBB enemies have been excluded by fine-mesh nets show that the enemies can reduce SBB emergence by 25–87% depending on species and densities of enemies (Weslien and Regnander, 1992; Weslien, 1992; Weslien and Schroeder, 1999; Schroeder, 2007b). Sanitation logging conducted during the winter will also affect natural enemies of bark beetles hibernating in the bark. Thus, it is desirable that sanitation logging does not result in substantially greater mortality of enemies than of SBB. If most SBB hibernate in the ground while some enemies mostly hibernate in the trees, sanitation logging in winter may be contra productive from a control perspective. Long-legged flies (Dolichopodidae) of the genus *Medetera*, are abundant enemies of SBB (e. g., Weslien, 1992, Wermelinger, 2002, Hedgren and Schroeder, 2004). *Medetera* spp. (hereafter *Medetera*) adults lay eggs in the bark of SBB-attacked trees and their larvae feed on immature life stages of SBB. Weslien, 1992 found in a controlled cage experiment that predation mainly by *Medetera* larvae at a density of c. 150 larvae m⁻² reduced SBB production by about 50% compared to a control treatment without any enemies. In Scandinavia, *Medetera* that live in SBB galleries are univoltine and unlike many other SBB enemies, the new generation does not leave the trees until the following spring (Weslien, 1992; Hedgren and Schroeder, 2004). The new generation overwinters almost exclusively in the larval stage and the adult flies emerge 1–3 weeks after SBB flight has started (Morén James 2023). There are no previous studies about how winter logging of SBB-killed trees affects *Medetera*.

Overall, there are many uncertainties on the effect of sanitation logging during winter. The main goal of this study was to clarify how sanitation logging of killed trees by harvesters during the winter affects mortality of SBB and *Medetera* compared to leaving the trees in the forest. We asked the following questions:

- 1) What proportion of SBB overwinter in bark on standing spruces along a climatic gradient?
- 2) What tree characteristics affect the proportion of SBB that overwinter in bark on standing spruces?
- 3) Is there any vertical gradient along the tree trunk in the proportion of SBB that overwinter in bark?
- 4) How much bark is stripped off when processing infested trees with harvesters and how is this affected by tree diameter, time of attack and if the bark is frozen or not?
- 5) What proportion of SBB adults are killed during processing by the knives and feed rollers of the harvester head?
- 6) What are the survival rates of SBB and *Medetera* in stripped-off bark lying on the ground until spring?
- 7) How sensitive is the effect of sanitation logging on SBB and *Medetera* to variations in values estimated under questions 1–6?

Field data was collected to answer questions 1–6. To answer question 7, a formula was developed that returns the effect of sanitation logging on survival of SBB and *Medetera*. The output compares the proportion of SBB and *Medetera* that remain in the forest, and that survive the winter, after sanitation logging with the proportion that would have survived the winter if the tree had been left standing (i.e., not harvested).

2. Material and methods

The study was conducted during two SBB outbreaks in southern Sweden. The first was initiated by the large-scale storm-felling caused by the storm Gudrun in January 2005 and the second by the exceptionally warm and dry summer in 2018. The study includes two kinds of surveys. In the first, the proportion of SBB that overwinter in killed trees and the density of *Medetera* larvae in the bark were estimated (hereafter Overwintering study). In the second, SBB-killed trees were sampled before and after processing by harvesters in one winter per outbreak. The proportion of the bark (containing insects) stripped off during the processing and the survival of SBB and its enemies in the stripped-off bark were estimated (hereafter Harvester study).

2.1. Overwintering study

2.1.1. Both winters

The proportion of new-generation-adults of SBB that overwintered in the bark of killed trees was estimated during the winters 2020/2021 and 2021/2022 by counting live SBB adults and exit holes in bark samples (see below). Bark samples from 237 trees, from 15 areas (blocks), were analyzed (103 samples in 2020/2021 and 134 in 2021/2022). The distance between the most southern and most northern block was about 700 km and crossed six climatic cultivation zones (Appendix A). The average number of days during 1991–2020 with minimum temperature in January below -10°C ranged from 2 to 20 within the sampled area (Swedish Meteorological and Hydrological Institute, 2020). The minimum distance between any two sampled tree groups within blocks was 300 m and the maximum distance 5 km (with one exception in 2021/2022 in the block “Torsby”, 40 km). In both winters, bark samples were taken at a height of four meters above ground level, and the diameter at breast height (DBH) and crown color (green or brown) were recorded for each sample tree. Crown color, “brown” or “green”, was used as a proxy for earlier (the whole tree crown brown) or later (whole or parts of the tree crown green) attacked trees. All bark samples were stored separately in plastic boxes at $+4^{\circ}\text{C}$ until analyzed in the lab 1–87 days later (median 44 days). The area of each bark sample was measured and the number of live SBB adults and *Medetera* larvae was counted. The lighter juvenile SBB were separated from the darker parent beetles.

The number of SBB leaving the tree to overwinter in the soil was estimated from the number of exit holes (i.e., each exit hole represents one beetle overwintering in the soil). In Sweden the SBB is mainly univoltine and even during exceptionally warm summers only a minor part of the new-generation beetles will try to reproduce before hibernation (Fritscher and Schroeder, 2022). The proportion of new-generation SBB that overwintered in the bark was calculated by the formula; $(\text{no. live SBB})/(\text{no. live SBB} + \text{no. exit holes})^{-1}$.

2.1.2. Winter 2020/2021

In 2020/2021, standing trees were sampled using a ladder. Bark samples, c. 45 cm long (along the stem) and 15 cm across (c. 675 cm^2), were taken at 4-m-height in December. The sampling point at 4 m was chosen because it was reachable using a ladder and because, in our experience, bark reachable from the ground is often sparsely attacked by SBB. Four of the five blocks were within nature reserves with old trees and one block in production forest. After omitting 22 bark samples, 103 trees remained for analysis (Appendix B). In 2020/2021, also a bark sample, protected from woodpeckers during the winter by a chicken net, was taken in March 2021 close to the December-sample. The objective was to estimate winter survival of SBB and *Medetera* in standing trees which both were found to be close to 100% (Weslien et al., 2022).

2.1.3. Winter 2021/2022

In 2021/2022 ten blocks in production forests owned by forest companies were sampled. Each sample tree was felled and a bark sample about the same size as in 2020/2021 was taken at 4-m-height. After

omitting 13 bark samples, 134 trees remained for analysis (Appendix B). Besides the sample at 4-m-height, two more bark samples, taken at 37.5% and 62.5% of the total tree height were analyzed for 48 trees. The objective was to explore how different variables recorded in the 4-m-samples vary with height within trees and allow adjustment to per-tree-values for variables that showed a significant vertical gradient along the tree trunk. Each tree was divided into four equally long sections from stump to top and each of the three bark samples was assumed to be representative for its' section. The top quarter of the tree was not sampled since it usually contains few SBB. The number of SBB maternal galleries, live SBB adults, SBB exit holes, and *Medetera* larvae per tree were calculated by weighting densities recorded from the bark samples with surface area of each tree section. Comparisons of 4-m-samples between trees with only one sample and trees with three samples indicate that the trees with three samples were representative (Table C.1).

2.2. Harvester study

2.2.1. Proportion of bark stripped off during processing

Studies were conducted during the winters 2007/2008 and 2020/2021. We followed three harvesters operating on 6 sites (Table D.1): South I, II and III (latitude c. 57°N) and North I, II and III (c. $59,5^{\circ}\text{N}$). SBB-killed trees were inspected before and after felling to estimate the proportion of bark still stuck to the trunk after processing by harvester and investigate which factors that affect the degree of bark stripping during processing. The factors included were: 1) the proportion of remaining bark before processing, 2) the color of the tree crown (indication of the time of SBB attack), 3) tree diameter and 4) frozen or thawed bark. For a detailed description of the method see Appendix D.

2.2.2. Proportion of SBB killed during processing by harvester

The proportion of SBB killed during processing was estimated by counting live and newly dead SBB in bark that was stripped off by the knives of the harvester head (hereafter called bark strips) and in small pieces of bark ripped off by the feed-rollers (hereafter called bark crumbs). The area covered by feed rollers was estimated for one of the harvesters. For a detailed description see Appendix E.

Bark crumbs were immediately analyzed (within 48 h) in the lab where live and dead SBB were counted. Bark strips were held separately in plastic boxes at $+4^{\circ}\text{C}$ until they were analyzed within two weeks (median 8 days). Dead beetles were categorized as newly dead (fresh and moist specimens) or since long dead (dry specimens). The proportion of newly dead SBB was calculated for each sample $(\text{no. newly dead SBB})/(\text{no. newly dead SBB} + \text{no. live SBB})^{-1}$.

2.2.3. Winter survival of SBB and *Medetera* in stripped-off bark

The densities of living SBB and *Medetera* larvae in bark strips were compared between two neighboring samples of bark strips from the same tree, one sample analyzed at the time of harvest and the other after having laid on the ground in the cut stand until early spring. The piece taken directly to the lab was stored at $+4^{\circ}\text{C}$ until analyzed 4–18 days later (median 8 days). Bark strips that were left in the forest were positioned so that every second had the outer bark facing the ground. After being collected from the forest in spring, the bark strips were stored at $+4^{\circ}\text{C}$ until they were analyzed 16–65 days later (median 36 days).

The ratio between spring and winter samples regarding the density of new-generation-adults of SBB and of *Medetera* larvae respectively was used as an estimate of winter survival in the bark. After omitting empty bark samples 76 winter-spring pairs for SBB and 73 winter-spring pairs for *Medetera* remained for analysis (Appendix F).

In 2020/2021, also a third bark sample was taken from 48 of the 88 trees and left on the ground at the logging site during the winter. This sample often consisted of bark strips collected from different logs (as there was usually a lack of stripped-off bark in connection with the first two samples) but always from the same tree. In the spring these samples

were laid in emergence boxes for hatching of live insects. The purpose of the hatching was to check that live insects were vital enough to also emerge from the stripped-off bark in spring. This is especially relevant for *Medetera* that overwinter as larvae and must pupate before developing into adults that emerge. The boxes (27 × 27 × 14 cm, with a glass tube) were emptied every three days and were stored in a climate room with a 20-hour day and a temperature of 23 - 27 °C (the temperature varied because the lights heated the room).

2.3. Statistical methods

2.3.1. Overwintering study

ANOVA (SAS, Proc. Mixed) was used when analyzing SBB production and the proportion of SBB overwintering in trees with Block as random effect. The combination of variables that yielded the lowest AIC-value gave the final model. The deviance of the full model was compared with that of the model with only random effect. Differences between variables within trees at different heights were analyzed with tree id. as random effect.

2.3.2. Harvester study

ANOVA (SAS, Proc. GLM) was used when analyzing bark-stripping during processing by harvesters. Relevant independent variables were first tested singly against the response variable, and any statistically insignificant variable (p > 0.05) was excluded from further testing. Variables with p < 0.05 when tested singly but p > 0.05 when tested with other variables were not included in the final model. For included variables, their effect size $\eta^2 = (SS_{Effect})/(SS_{Total})^{-1}$ was calculated.

2.3.3. Calculation of the reduction of SBB and *Medetera* by sanitation logging

The decrease in spring population by sanitation cutting (D) is calculated by the formula $D = (A-B)A^{-1}$, where A is the surviving spring population of SBB and *Medetera* respectively in the case when the tree is left standing and B when the tree is harvested at time T (populations at time T set to 100%). The calculations assume univoltine populations and that the new generations of SBB and *Medetera* overwinter in defined places (hereafter cohorts). The new generation of SBB at time T consists of four cohorts and the new generation of *Medetera* consists of three cohorts (Table 1). The relative size of each cohort is defined by three variables at time T: a=proportion bark on tree before harvest, b= proportion bark on tree after harvest and P = proportion of SBB and *Medetera* overwintering in bark on tree (Table 1, Appendix G). Cohort size at time T and the best available estimate of each cohort's survival rate from time T till spring flight (a value between 0 and 1, hereafter default value) were used to calculate spring populations and D for SBB (Dsbb) and *Medetera* (Dmed) for each harvested tree in the harvester study (Table 1).

Table 1

Definitions of overwintering cohorts of *Ips typographus* (SBB) and *Medetera* with the relative size of each cohort defined by at least one of three variables at time T: a=proportion bark on tree before harvest, b= proportion bark on tree after harvest, and P = proportion of SBB and *Medetera* respectively overwintering in bark on tree. Survival rate for cohort 4 is split in two occasions: s4 = survival during processing by harvester and s5 = survival during winter in bark strips on ground (total survival=s4xs5). Default values for survival rates are given with source. Case A: Trees are left, Case B: Trees are cut at time T.

Cohort	Relative size of cohort	Survival rate SBB Default	Source for survival rate SBB	Survival rate <i>Medetera</i> Default	Source for survival rate <i>Medetera</i>
Cohort 1: in standing tree (A)	aP	s1 = 0.90	Trees from this study 2020/2021, Westien et al., 2022	S1 = 0.90	Trees from this study 2020/2021, Westien et al., 2022
Cohort 2: in ground (A & B)	1-P	s2 = 0.60	Austarå and Midtgaard, 1986, Zumr, 1982	Not applicable	
Cohort 3: in bark on ground lost by woodpeckers (A & B)	P(1-a)	s3 = 0.80	Lack of data, assumed to be lower than in standing trees	s3 = 0.80	Lack of data, assumed to be lower than in standing trees
Cohort 4: in bark stripped off by harvester (B)	P(a-b)	s4 = 0.85, processing s5 = 0.82 winter	Trees from this study	s4 = 0.85, processing s5 = 0.93 winter	Lack of data but assumed to be the same as for SBB Trees from this study

Since the parameter P for SBB (proportion of SBB overwintering in tree) was not measured in the harvester study it was modeled using data from the overwintering study by the following model: $Arcsine(P) = 0.020 * DBH (cm) - 0.16 * (crown\ color\ brown = 1) + 0.14$, ($R^2 = 0.17$). The model is based on bark samples at 4-m-height from trees sampled in 2021/2022 in cultivation zones II, III, and IV, representing managed forests in Southern Sweden (where the harvesting sites were located). The output (arcsine-transformed P), for each harvested tree was retransformed and multiplied by 0.79 according to the relationship between P in 4-m-samples and P in whole tree (Fig. 1), which gave values of P ranging 21% to 70% (mean 44%).

In summary, Dsbb and Dmed were calculated by the formulas below (parameters defined in Table 1):

$$D = (A-B)A^{-1}$$

$$A = s1(aP) + s2(1-P) + s3P(1-a)$$

$$B = s4s5P(a-b) + s2(1-P) + s3P(1-a)$$

Three parameters vary between the harvested trees: a, b, and P (for SBB), of which a and b were measured in the field and P, for SBB, modelled using field data from this study. Parameters that did not vary between trees were P for *Medetera* which was set to 100% (see Introduction) and the default values for the survival rates s1-s5 of which s1, s4 and s5 were based on data from trees in this study (Table 1).

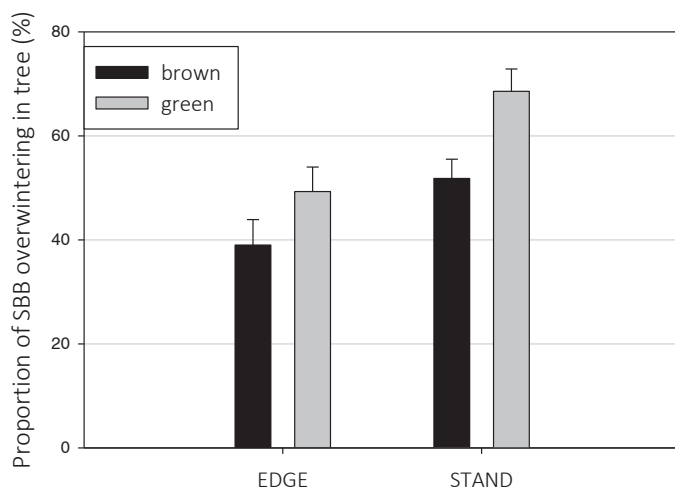


Fig. 1. The proportion of *Ips typographus* (SBB) overwintering at 4-m-height in brown and green trees located at edges or inside the stand. Sample size: edge brown, n = 27, edge green, n = 28, stand brown, n = 41, stand green, n = 38. Data from 2021/2022, means and standard errors.

The sensitivity of Dsbb and Dmed to varying levels of the parameters P and s1-s5 was assessed by linear correlation in which one parameter at a time was varied from 0 to 100% while keeping the others constant. High absolute value of the slope indicated high sensitivity to the parameter. If the relationship between dependent and independent variable was non-linear the slope was approximated within delimited intervals of the parameter where absolute value of the correlation coefficient, $|r|$, exceeded 0.99.

3. Results

3.1. Overwintering study

3.1.1. Proportion of SBB overwintering in trees along a climatic gradient

In 2020/2021, there were no significant differences between the three most southern cultivation zones II, III and IV in the proportion of overwintering SBB in trees at 4-m-height indicated by overlapping 95% confidence intervals (c. i.). In 2021/2022, when trees were sampled in four cultivation zones, II, III, IV, and VI+ (zones V and VII clustered as VI+) there was a significant effect of cultivation zone on the proportion of overwintering SBB in bark at 4-m-height ($p < 0.01$, $F=4.2$, one-way Anova). Zone VI+ had the lowest proportion, $34\% \pm 5.6\%$ compared to $58\% \pm 5.2\%$ for zone II, $54\% \pm 5.1\%$ for zone III and $58\% \pm 2.5\%$ for zone IV. Zone VI+ had a slightly overlapping 95% c.i. with zone III but non-overlapping with the two other zones. With cultivation zone VI+ excluded, all three remaining zones had overlapping 95% c. i. for proportion of SBB overwintering in tree.

3.1.2. SBB production and overwintering in standing trees

Over both winters, 58% of total number of SBB produced (live SBB + exit holes) overwintered in the tree at 4-m-height (Table B.1). There was a strong positive effect of bark thickness on the proportion SBB overwintering in tree. Bark thickness together with crown color explained 30% of the deviance when data from both winters were included in the analysis (Model 1, Table 2). Trees sampled in 2020/2021 compared to 2021/2022 had on average thicker bark and a higher proportion of SBB

overwintering in the tree (Table B.1). Sampling year and DBH were significant ($p < 0.05$) when tested alone against the response variable (proportion SBB overwintering in tree), but the effect disappeared when bark thickness was entered in the model. DBH was correlated with bark thickness ($r = 0.48$, $p < 0.001$).

For 2021/2022, 38% of the deviance in proportion SBB overwintering in tree was explained by the three variables bark thickness, crown color and edge or stand (Model 2, Table 2). The mean proportion of SBB overwintering in the bark was lower for edge trees than for trees inside stand and lower in brown than green trees (Fig. 1). Bark thickness was correlated with DBH ($r = 0.52$, $p < 0.001$) and tree age ($r = 0.40$, $p < 0.001$).

Over both years, SBB production (live adults + exit holes) averaged 870 SBB m^{-2} bark (range: 120 to 2700) and *Medetera* density averaged $210 \text{ larvae m}^{-2}$ bark (range: 0 – 1560). Fourteen percent of the deviance in SBB production was explained by *Medetera* density and DBH (Model 3, Table 2). The estimate for the variable *Medetera* density in model 3 indicated that SBB production decreased by 1.2 SBB m^{-2} as *Medetera* density increased by 1 larva m^{-2} .

3.1.3. Vertical gradients within trees

Bark thickness, SBB production and proportion overwintering in tree, and density of *Medetera* larvae all decreased with increasing sampling height and decreasing diameter (Table 3).

Linear regression with proportion overwintering SBB in bark samples at 4-m-height as independent variable and the per-tree-value for proportion overwintering SBB as dependent variable indicated that the per-tree-value was about 80% of the 4-m-value (Fig. 2).

3.2. Harvester study

3.2.1. Proportion of bark stripped off during processing by harvester

The average proportion of bark on the SBB-killed trees before felling ranged from 61 to 98% (mean 84%) and the proportion of bark after harvester processing from 27 to 64% (mean 43%), for the six different harvesting sites (Table D.2). On average, a higher part of the bark was

Table 2

Results of Anova (mixed model) with Block as random effect. Models 1 and 2 response variable: Proportion *Ips typographus* (SBB) overwintering in trees at 4-m-height (live adults)(live adults + exit holes)⁻¹ from both winters 2020/2021 and 2021/2022 (model 1) and from 2021/2022 (model 2). Model 3 response variable: SBB production (live adults + exit holes)^{m⁻²} from both winters 2020/2021 and 2021/2022. Response variable in model 1 and 2 was arcsine-transformed. Response variable and independent variables in model 3 were log¹⁰-transformed (18 observations with zeroes or missing values excluded). Positive or negative relationship between quantitative variable and response variable indicated with (+) or (-). For qualitative variables the relation is indicated by (+) after the category with positive relationship. Deviance in full model (dev_{full}) was compared with deviance in model with only random effect (dev_{rand}). Explained deviance = $100(\text{dev}_{\text{rand}} - \text{dev}_{\text{full}})/(\text{dev}_{\text{rand}})$ ¹.

Response variable	Independent variables	df	F	p	Explained deviance (%)
Model 1. Proportion SBB overwintering in tree (%). 2020/2021 and 2021/2022	Bark thickness, mm (+)	1/220	12	< 0.001	30
	Crown color green (+) or brown	1/220	9	< 0.01	
Model 2. Proportion SBB overwintering in tree (%). 2021/2022	Bark thickness, mm (+)	1/120	36	< 0.001	38
	Crown color, green (+) or brown	1/120	22	< 0.001	
	Position, stand (+) or edge	1/120	6	< 0.01	
Model 3. SBB production m ⁻² 2020/2021 and 2021/2022	<i>Medetera</i> larvae m ⁻² (-)	1/202	5	< 0.05	14
	Dbh, cm (+)	1/202	4	< 0.05	

Table 3

Means and standard errors of variables from bark samples taken at different heights above ground on 48 trees killed by *Ips typographus* (SBB). P-values refer to Anova with sample (1,2 or 3) as fixed and tree id as random variable. The last column gives the bark area-weighted average per tree.

	Sample 1 (4 m)	Sample 2 37.5% of tree height	Sample 3 62.5% of tree height	p	Weighted average per tree
Diameter at sample height (cm)	25 ± 0.6	21 ± 0.6	16 ± 0.5	< 0.001	-
Bark thickness (mm)	4.7 ± 0.2	4.4 ± 2	3.8 ± 2	< 0.001	-
Proportion SBB overwintering in tree (%)	52 ± 4.3	43 ± 4.5	37 ± 4.8	< 0.01	42 ± 3.9
Production SBB m ⁻²	851 ± 82	763 ± 67	601 ± 58	< 0.05	735 ± 59
<i>Medetera</i> larvae m ⁻²	257 ± 40	146 ± 26	68 ± 16	< 0.001	145 ± 22

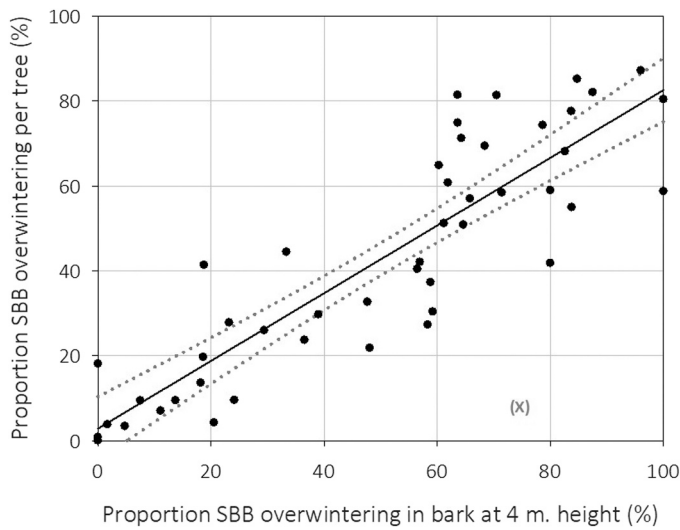


Fig. 2. Linear regression of proportion *Ips typographus* (SBB) overwintering in bark per tree and at 4-m-height (n = 47, one influential outlier (x) excluded from the model). Per-tree values are based on 3 bark samples at different heights. Dotted lines: 95% confidence limits, Equation: (Prop-tree) = 0.79 (Prop-4 m) + 2.8, R² = 0.76.

stripped off when processing trees with thawed (mean 61%) than with frozen (mean 37%) bark (Table D.2).

The strongest factor affecting the proportion of bark after processing was the proportion of bark before processing (Model 1, Table 4) and the strongest factor affecting the proportion of stripped-off bark was if the bark was frozen or thawed (Model 2, Table 4).

3.2.2. Proportion of SBB killed during processing by harvester

The mean proportion of newly dead SBB in bark strips and bark crumbs directly after processing ranged from 9 to 27% (Fig. 3) and there was no significant difference between the 2007/2008 and the 2020/2021 results (t-test, p > 0.1). The mean proportion of newly dead SBB over the two winters was 11% in bark strips and 22% in bark crumbs. The mean proportion of the bark area covered by the feed rollers, from which most bark crumbs originate was 35% (North I. Appendix E).

3.2.3. Survival rate of SBB and Medetera in stripped-off bark

The mean ratio between spring and winter density in the same tree of live SBB adults was 0.82 ± 0.11 and the mean ratio between spring and winter density of live *Medetera* larvae was 0.93 ± 0.11. For SBB, 53 of the 76 bark samples had a ratio below 1.0 and for *Medetera*, 52 of the 73 samples had a ratio below 1.0. There was no apparent pattern for the variation in ratios coupled to the number of days that the bark samples lay on the ground that ranged from 30 to 118 days for the six sites (Table F.1). There was no difference in spring/winter ratio for SBB or *Medetera* between bark samples that were placed with outside bark facing the ground and samples with the outside bark facing the sky (t-

Table 4

Results of Anova (GLM) of bark stripping by harvester during processing of 424 trees killed by *Ips typographus*. Model 1 response variable: Proportion of bark after processing by harvester. Model 2 response variable: Proportion of stripped-off bark (bark before processing - bark after processing)/(bark before processing)⁻¹. Significant (p < 0.05) independent variables and their effect size η², (SS_{Effect})/(SS_{Total})⁻¹. Positive or negative relationship between quantitative variable and response variable indicated with (+) or (-). For qualitative variables the relation is indicated by (+) after the category with positive relationship. Proportions of bark before and after processing and proportion stripped-off bark were all arcsine(x^{0.5})-transformed before analysis.

Response variable	Independent variables	df	F	P	η ² (%)	R ² (%)
Model 1. Proportion of bark after processing (%)	Bark before processing, % (+)	1/421	280	< 0.001	30	55
	Frozen (+) or thawed bark	1/421	133	< 0.001	14	
Model 2. Proportion of stripped-off bark (%)	Frozen or thawed (+) bark	1/421	114	< 0.001	21	24
	Bark before processing, % (-)	1/421	4.8	< 0.05	1	

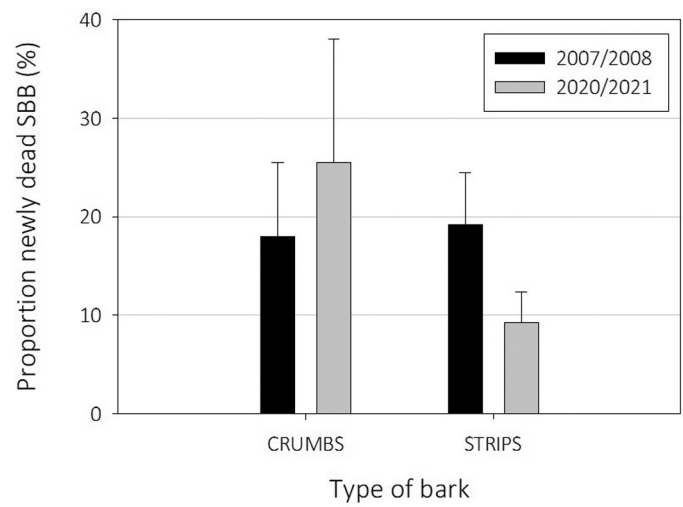


Fig. 3. Proportion of *Ips typographus* (SBB) adults that were judged to have recently died in samples from bark pieces less than 9 cm² in size (bark crumbs) and in stripped-off bark (bark strips) collected from harvester-processed trees. Proportion calculated by: (no. dead)/(no. dead + no. living)⁻¹. Sample size Crumbs: 13 trees in 2007/2008, 10 trees in 2020/2021; Strips: 20 trees in 2007/2008, 88 trees in 2021/2022. Means and standard errors.

test, p > 0,1). In the sub-study with hatching of insects after overwintering in 2020/2021, mean densities of SBB and *Medetera* were similar to or higher than mean densities in the dissected bark samples from winter and spring (Table F.2).

3.3. Calculated reduction of SBB and Medetera by sanitation logging

The calculated reduction of *Medetera* (Dmed) was greater than that of SBB (Dsbb) for almost all 424 trees (Fig. 4) with Dmed ranging from 1.0 to 98% (mean 49%) and Dsbb from 0.6 to 68% (Mean 29%). Mean Dsbb per harvesting site ranged from 17% (South I) to 38% (North II) and mean Dmed from 31% (South I) to 64%. (North I & II). Dsbb and Dmed depended strongly on the proportion of bark after processing (r² Dsbb= 0.88, r² Dmed= 0.98) and were higher for trees with frozen bark than for trees with thawed bark (Fig. 4). Both slope and intercept of the function for the regression between Dmed and Dsbb (Fig. 4) differed significantly (p < 0.001) from the identity line (y = x).

The sensitivity of the reduction of SBB (Dsbb) and *Medetera* (Dmed) by sanitation logging, tested over different levels of each parameter, showed non-linear relationships for all parameters except survival in stripped-off bark. For the non-linear relationships, the sensitivity was higher at low than at high levels, i.e., the rate of change grew as the parameter decreased (Fig. 5). Slopes for Dsbb and Dmed within limited intervals around default values, indicate highest sensitivity of Dsbb to proportion SBB overwintering in tree and of Dmed to survival in standing trees (Table 5). Since the slopes are additive it is possible to calculate the change in mean Dsbb or Dmed for the 424 harvested trees if

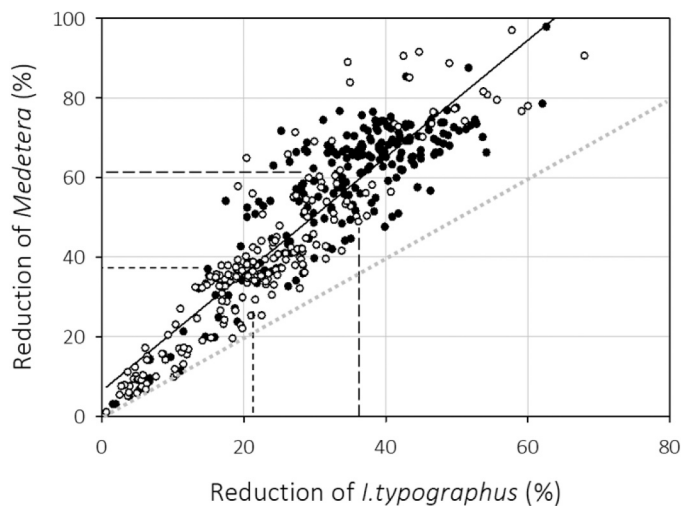


Fig. 4. Linear regression showing the relationship between calculated reduction of *Ips typographus* (Dsbb) and *Medetera* per tree (Dmed) after sanitation logging ($n = 424$) Frozen bark: black dots and mean values indicated by long-dashed-line. Thawed bark: white dots and mean values indicated by short-dashed-line. Dotted line marks the identity line ($y = x$). Equation: $Dmed = 1.5Dsbb + 6.3$.

several parameters diverge from default values. For instance, a 10% higher mean value of proportion SBB overwintering in tree (slope ≈ 0.52), a 10% lower value than default of SBB survival in ground (slope ≈ -0.22) and a 10% higher value than default in stripped-off bark (slope ≈ -0.24) will give a 5% increase in mean Dsbb compared to the default setting ($5.2 + 2.2 - 2.4 = 5.0$).

4. Discussion

4.1. Overwintering study

On average 48% of SBB overwintered in the trees in cultivation zones II, III, and IV when considering both years and calculated for the whole trees. In 2021/2022, when sampled trees were more representative for managed forests in Sweden than the trees sampled in 2020/2021, the mean proportion was 44%. Most SBB outbreaks in Sweden, including the largest one that started in 2018, have occurred in these regions. The study supports the hypothesis that the proportion of SBB overwintering in bark on killed trees is lower in a colder winter climate. In winter 2021/2022 the average overwintering proportion in the northern zones VI and VII was 27%. This may be an adaptation to the higher risk of exposure to lethal winter temperatures in trees compared to in the ground under a snow cover (Annala, 1969).

There was a considerable between-tree variation in proportion of SBB overwintering in the tree. For both winters combined 30% of the deviance was explained by bark thickness and crown color while in 2021/2022, when also the position of each tree (at the edge or inside a stand) was recorded, the explained deviance increased to 38%. Bark thickness was the most important factor and positively related to proportion overwintering in trees. This may be explained by thicker outer bark offering drier overwintering conditions than thin bark. High bark moisture has been found to decrease SBB-survival during winter (Koštal et al., 2011) and SBB movements from moist to dry bark before and during overwintering has been documented (Dworschak et al., 2014). The higher proportion of overwintering SBB in trees with green crowns

(compared with trees with brown crowns) may be a result of green trees being colonized later in summer and thus the offspring have had less time to leave the trees. The lower proportion of overwintering SBB in edge trees may be a result of higher solar insolation than in the interior of stands and thus the SBB development rate will be faster in edges (Lindman et al., 2023).

4.2. Harvester study

The proportion of bark that was lost during harvester processing ranged from 33 to 71%. Temperature was the strongest factor affecting how much bark was lost when processing during winter. When winter temperatures are above zero, and the bark is thawed, which is common for large parts of Europe, including Southern Sweden, much of the remaining bark will be stripped off and remain in the forest.

The survival of SBB during processing was high ($> 70\%$) in our samples of bark strips and bark crumbs. In the study by Delb et al. (2021) the survival of SBB adults was lower, only 34% with the same type of harvester head as used at five of our sites (H415). Possibly, many SBB in the study by Delb et al. (2021), which was conducted in summer, were callow adults under bark and then more sensitive than the mature adults found in the outer bark in our study. In agreement with our results, it showed that the survival of adult SBB in stripped-off bark was high.

The winter survival in stripped-off bark of SBB and *Medetera* was high when estimated by the ratio between living specimens in spring and winter (0.83 for SBB and 0.93 for *Medetera*). Also, the results from the hatching of insects from stripped-off bark that had laid on the ground during winter indicated that both SBB and *Medetera* were vital enough to leave the bark in spring, which in the case of *Medetera* includes completing development from larva to adult. Although high, the winter survival of SBB may be underestimated because some SBB may have left the bark during winter to hibernate in the ground. In central Europe, a large proportion of SBB leave bark that has fallen off the trees for overwintering in the ground (Dworschak et al., 2014). It is probable that this occurs also in Scandinavia given that the temperature is high enough. Mild periods occurred during the time that the bark lay on the ground both in 2007/2008 and 2020/2021 with maximum temperature (taken at the nearest meteorological station) above 10°C in November 2007 (South I) and in March 2020/2021 (South II, III and North I, II, III), which is above the mobility threshold for SBB (Annala, 1969). For *Medetera* there are no records of overwintering outside trees, and it seems unlikely that larvae would have left the bark.

4.3. Impact of sanitation logging

Our study indicates that the reduction of SBB by sanitation logging during winter when the bark is thawed, which is common during large parts of the winter in southern Scandinavia, will be quite low (mean 22%). For sanitation logging to be more effective in reducing SBB the trees should have frozen bark and a high proportion of SBB overwintering in them. While the probability of frozen bark increases with colder winter climate, the probability of a high proportion SBB overwintering in the trees decreases. This paradox may be true also for parts of Europe with great differences in altitude, where close to 100% of the second-generation adults overwinter in trees in the lowlands and considerably less among univoltine populations in the mountains (Wermelinger et al., 2012; Kasumović et al., 2019). The sensitivity analysis indicated that the reduction of SBB and *Medetera* were quite insensitive to moderate variation around default values of the survival rates. Therefore, the estimates of reduction of SBB and *Medetera* presented here should be quite stable.

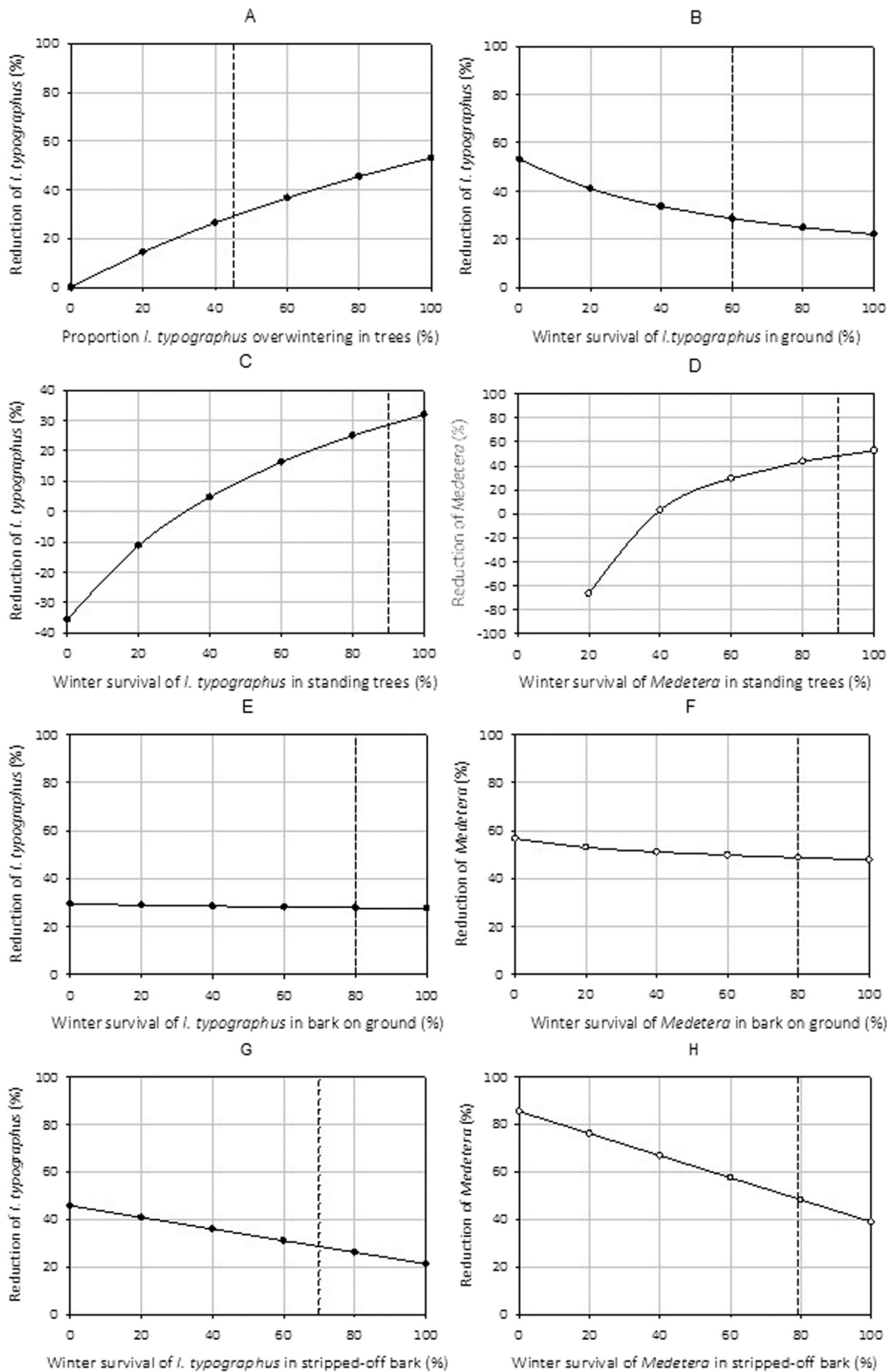


Fig. 5. Sensitivity analysis of the calculated reduction of *Ips typographus* (SBB) and *Medetera* by sanitation logging at six levels (0%, 20%, 40%, 60%, 80%, 100%) of eight parameters. A: proportion of SBB overwintering in tree (P). B: survival rate of SBB overwintering in ground (s2). C and D: survival rate of SBB and *Medetera* overwintering in standing tree (s1). E and F: survival rate of SBB and *Medetera* overwintering in bark on ground lost by woodpeckers (s3). G and H: survival rate SBB and *Medetera* in bark stripped off by harvester during processing (s4) and overwintering (s5), where total survival is the product of s4 and s5. Mean reduction of SBB and *Medetera* were calculated for 424 harvested trees at each of the six levels. The proportion of SBB overwintering in tree (P, pane A), was kept at the mean modelled value (dashed line, 44%), survival rates at default values while the proportion of bark before and after processing varied between the 424 trees. Survival rates (s1-s5, panes B-H) were kept at default value (dashed line) while the proportion of bark before and after processing and the modelled value for P differed between trees.

Table 5

Slopes for reduction of *Ips typographus* (D_{sbb}) and *Medetera* (D_{med}) within delimited intervals of each parameter, where the relationship between D_{sbb} or D_{med} and the parameter was linear or close to linear ($|r| > 0.99$). (See Fig. 5).

Parameter	Default value (%)	Interval for estimated slope (%)	Slope D _{sbb}	Slope D _{med}
Proportion <i>I. typographus</i> overwintering in tree (P)	441	20 - 80	≈ 0.52	-
Survival of <i>I. typographus</i> and <i>Medetera</i> in standing trees (s1)	90	60 - 100	≈ 0.39	≈ 0.58
Survival of <i>I. typographus</i> in ground (s2)	60	40 - 100	≈ - 0.19	-
Survival of <i>I. typographus</i> and <i>Medetera</i> in lost bark on ground lost by woodpeckers (s3)	80	20 - 100	≈ - 0.02	≈ - 0.06
Survival of <i>I. typographus</i> and <i>Medetera</i> stripped-off bark (s4 * s5)	70	0 - 100	= - 0.24	= - 0.46

1 mean modelled value for P

The results from this study indicate that the relative reduction of *Medetera* is much higher than that of SBB after sanitation logging in winter. This may result in a decreased predation pressure by *Medetera* on the following SBB generation. It is hard to predict how much bark beetle production will increase at a given reduction of a specific predator because this relationship is seldom linear. Both bark beetle and enemy reproduction are influenced by competition within (Weslien, 1994) and between enemy species (Schroeder, 1996). Also, predation may relieve competition between SBB larvae (Lawson, 1997; Schroeder, 2007b) which is also dependent on gallery density (Anderbrant, 1990). In a controlled caging experiment (Weslien, 1992), SBB production decreased from c. 2800 to c. 1400 SBB m⁻² mainly due to predation by *Medetera* at a density of c. 150 larvae m⁻², i.e., the rate of decrease was about 9 SBB per *Medetera* larva and the overall suppressive effect by *Medetera* predation c. 50%. In this study, the rate of decrease was 1.2 SBB per *Medetera* larva, corresponding to a suppressive effect of 22% at the average densities of *Medetera* and SBB production (210 m⁻² and 870 m⁻² respectively). It is noteworthy that such an effect of predation by *Medetera* could be detected considering the variation involved. This suggests that the effect of *Medetera* predation on SBB numbers cannot be neglected and that the negative effect on *Medetera* by winter logging of SBB-killed trees may be a factor to consider in the control of SBB.

4.4. Management implications

The limited effect of sanitation logging on SBB reduction during winter suggests that as much as possible of the sanitation logging should be carried out during summer. When prioritizing stands for sanitation logging in winter, stands with thick-barked trees still having lots of bark attached should be given priority since they are likely to contain many SBB. Diameter or stand age may be used as proxies for bark thickness since they are easy to assess and usually documented in forest management plans at the stand level. Brown trees in stand edges are the ones most likely to be spotted first in the autumn but are also the ones that contain the lowest proportion of overwintering SBB. So, when prioritizing stands for sanitation cutting whole stands need to be assessed regarding damage level. If possible, sanitation cutting should be done when bark is frozen to reduce the degree of bark-stripping and the number of SBB left in the forest.

It is important to acknowledge that the relative reduction in SBB population by sanitation logging does not necessarily reflect the risk for continued tree-killing of remaining living spruces in the stands. There are several reasons for this: (1) The risk for continued tree-killing the following year is low if small groups of SBB-killed trees are retained compared to if large groups are retained (Hedgren et al., 2003, Kärvement al., 2014, 2016). (2) The absolute reduction of a local SBB population

by sanitation logging depends on the production of SBB, which can vary much between trees (this study, 4-m-samples range: 120–2600 m⁻²), and stands (this study, 4-m-samples range of means: 360–1600 m⁻²stand⁻¹). (3) The predisposition of trees to SBB-attacks may differ between stands and years and thus also the proportion of the spring population that may be successful in colonizing living trees. Thus, the cost-efficiency of sanitation logging depends also on factors outside the scope of this study. Probably, small groups of SBB-killed trees should be left standing since the cost is high relative to harvested volumes, the reduction in beetle numbers low and the risk for continued attacks by SBB is lower than for large groups.

Finally, logging during winter risks hitting *Medetera* proportionally harder than SBB and, if not motivated by saving timber values and if the reduction of SBB is deemed to be low, based on findings in this study, it should be avoided or postponed until next summer after *Medetera* adults have emerged.

CRedit authorship contribution statement

Weslien: Funding acquisition, Project administration, Conceptualization, Methodology, Formal analysis, Writing – original draft. **Rosenberg:** Funding acquisition, Investigation, Writing – review & editing. **Örhn:** Investigation, Writing – review & editing. **Schroeder:** Funding acquisition, Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A

Map of blocks for sampling in relation to cultivation zones

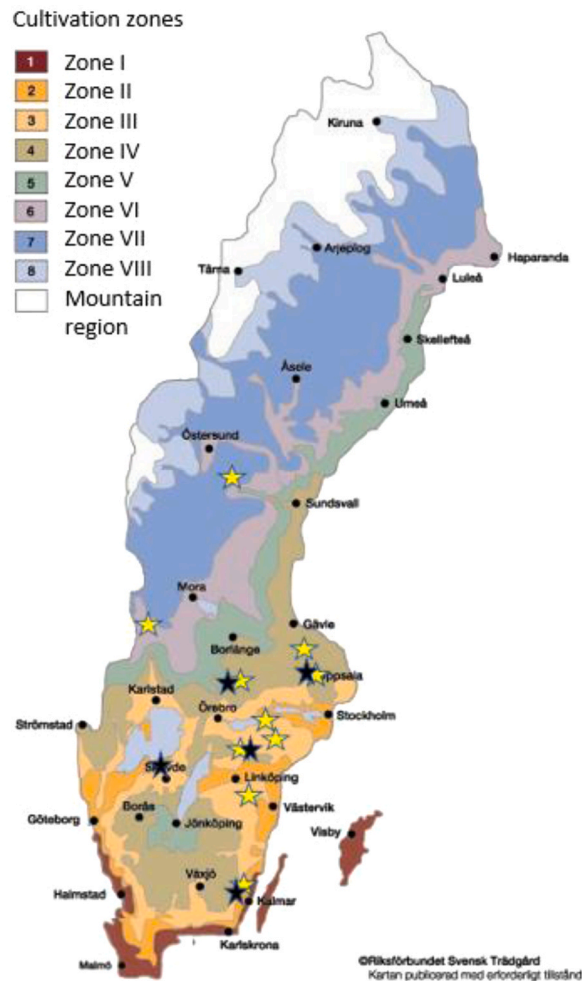


Fig A.1. Locations of 15 blocks in Sweden where bark samples were taken from *Ips typographus* (SBB)-killed trees in winters 2020/2021 (black stars) and 2021/2022 (yellow stars). The map shows the cultivation zones according to The Swedish Horticultural Society with increasingly colder winters with increasing zone number. The three most northern blocks are located north of latitude 60° N. Published with approval of the Swedish Horticultural Society.

Appendix B

Overwintering study – sampling method and overview of collected data Year 2020/2021

In each block, five different groups of at least 10 SBB-killed trees from 2020 were sampled. Bark samples were taken on five trees in each group, during December 1 – 15, 2020. In total, samples were taken from 125 trees (5 blocks x 25 trees). To get reasonably continuous estimate of the proportion SBB hibernating in the bark, 14 samples with less than 10 produced SBB (no. live SBB + no. exit holes) were excluded from analyses. Six samples were excluded because there were ambiguities in the labeling of samples and two because they were probably attacked before 2020 (the bark sample did not contain any SBB or *Medetera* larvae). Thus, 103 trees remained for analysis.

Year 2021/2022

Each sample tree was felled and a bark sample of 600 – 800 cm² was taken at 4-m-height either by peeling the bark off in the field or, when frozen, by cutting a slab of wood with attached bark with the chain saw. In each block, in the standard case, 3 groups of trees were sampled with 4–5 sampled trees per group, which amounted to 147 sampled trees. After excluding 7 trees attacked before 2021 and 6 trees that had less than 10 produced SBB in the bark sample at 4-m-height, 134 trees remained for analysis of which 48 had samples from three different heights.

Table B.1

Means and standard errors for different variables from bark samples at 4-m-height above ground during two winters.

	2020/2021	2021/2022	All
Number of trees	103	134	237
DBH (cm)	29.7 ± 0.5	28.4 ± 0.7	29.0 ± 0.4
Bark thickness (mm)	5.1 ± 0.14	4.6 ± 0.12	4.8 ± 0.09
Bark (%)	96 ± 0.7	93 ± 0.6	94 ± 0.5
<i>Ips typographus</i> overwintering in tree (%)	65 ± 2.2	54.0 ± 2.3	58 ± 1.7
Production SBB /m ²	798 ± 45	934 ± 48	874 ± 33
<i>Medetera</i> larvae/m ²	178 ± 19	236 ± 21	210 ± 15
Proportion green trees (%)	28	49	40

Table B.2Data by block in the overwintering study. Means and standard errors for density of *Medetera* larvae and proportion of *Ips typographus* (SBB) overwintering in bark samples at 4-m-height.

Year	Block	Cultivation zone	Total no. trees	No trees with 3 samples	Prop. green trees (%)	Prop. edge trees (%)	<i>Medetera</i> larvae m ⁻²	Prop. SBB in bark (%)
2020/2021	Ebbegårde	II	23	-	35	-	148 ± 34	55 ± 6.7
2020/2021	Billingen	III	20	-	25	-	230 ± 20	79 ± 3.0
2020/2021	Glottorn	IV	17	-	24	-	256 ± 89	79 ± 4.3
2020/2021	Styggekärret	IV	24	-	40	-	96 ± 18	54 ± 3.8
2020/2021	Malingsbo	IV	21	-	29	-	196 ± 22	64 ± 3.1
2021/2022	Rugstorp	II	14	5	71	79	210 ± 69	49 ± 7.5
2021/2022	Överum	II	11	4	73	9	340 ± 60	68 ± 7.1
2021/2022	Ripsa	III	15	4	40	13	247 ± 66	56 ± 7.1
2021/2022	Värhulta	III	15	3	53	47	366 ± 65	51 ± 7.3
2021/2022	Rejmyre	IV	15	4	60	47	272 ± 91	54 ± 7.6
2021/2022	Ramnäs	IV	14	3	43	7	293 ± 71	66 ± 5.8
2021/2022	Uppsala	IV	18	11	56	47	118 ± 32	55 ± 6.0
2021/2022	Hyttön	IV	13	4	62	77	178 ± 88	57 ± 7.2
2021/2022	Torsby	VI	16	8	19	50	161 ± 57	32 ± 6.3
2021/2022	Bräcke	VII	3	2	33	33	365 ± 65	43 ± 10

Appendix C

SBB and Medetera at 4-m-height in trees with one sample or three samples

Table C.1

Ips typographus (SBB) production and proportion overwintering in tree, and density of *Medetera* larvae at 4-m-height for trees with only one sample (n = 90) and trees with three samples (n = 48). Means ± se.

	n	Production SBB m ⁻²	Proportion SBB in tree (%)	<i>Medetera</i> larvae m ⁻²
One sample (4 m)	90	945 ± 61	54 ± 2.9	226 ± 25
Three samples (4 m)	48	851 ± 82	52 ± 4.3	257 ± 40

Appendix D

Proportion of bark stripped off during processing

A few days before each felling, experimental trees (SBB-attacked in 2007 respective 2020) were marked with numbers. For each tree diameter at breast height (DBH), proportion of bark left on the stem and color of the crown was recorded (Table D.1). The proportion of bark was estimated on two opposite sides of the tree so that the entire perimeter of the trunk was assessed. The color of the crown was classified as “Brown” (the whole tree crown brown) or “Green” (whole or parts of the tree crown green). The driver was instructed to lay the logs in order from root to top next to each other and as far as possible separate them from other experimental trees and trees that were not included in the study (Fig. D.1). Inspection of the logs was done on the same day or the day after they had been processed by the harvester (Table D.2). In 2021 the length and middle diameter were measured on each log and the proportion of attached bark was estimated on two opposite sides so that the entire circumference of the trunk was assessed. The proportion of bark stuck to the tree after processing was calculated by dividing the total calculated bark area (sum of bark area on all logs) by total stem surface, approximating each log as a cylinder. In 2007 the proportion of bark was estimated in the same way for each log but without accounting for differences in length and diameter between logs. Unprocessed tops with limbs, which are left in the forest, were not included in any year. In the morning before the felling of the experimental trees began and a few more times during the day, air temperature was recorded. In 2007 the air temperature was not measured but taken from the nearest meteorological station.

Table D.1

Site, date of logging, mean diameter at breast height (DBH) of harvested trees, stand age, harvester id (A, B, C), harvester and harvester head models and minimum and maximum temperature recorded during harvest of the trees.

Site, Date of logging	Proportion green trees (%)	DBH (cm)	Stand age (yrs.)	Harvester id.	Harvester, harvester head	Temperature (°C) min/max
South I, 22–23 Oct, 2007	26	25.3 ± 0,6	ND	A	Rottne H8, EGS 402	+ 2 /+ 7
South II, 20–21 Jan, 2021	20	31.4 ± 1,0	130	B	JD 1470 G, H415	+ 2 /+ 3
South III, 1 Feb, 2021	41	33.4 ± 1,1	105	B	JD 1470 G, H415	-10/– 7
North I, 27 Jan, 2021	51	26.4 ± 0,7	55	C	JD 1270 G, H415	-10/– 6
North II, 9 Feb, 2021	41	29.1 ± 0,6	65	C	JD 1270 G, H415	-19/– 14
North III, 24 Feb, 2021	11	26.5 ± 0,7	55	C	JD 1270 G, H415	+ 3/+ 6

Table D.2

Site, harvester id, number of processed trees, proportion of tree bole surface covered by bark before and after processing and the proportion of the bark cover before processing that was stripped off by the harvester. Means ± standard errors.

Site	Frozen or thawed bark	Harvester id	n	Bark before processing (%)	Bark after processing (%)	Stripped-off bark (%)
South I	thawed	A	82	61 ± 4.0	27 ± 2.0	56 ± 2.6
South II	thawed	B	79	84 ± 2.5	39 ± 3.1	56 ± 2.9
South III	frozen	B	63	79 ± 2.8	50 ± 3.5	38 ± 3.4
North I	frozen	C	61	92 ± 2.0	60 ± 1.3	33 ± 1.8
North II	frozen	C	76	98 ± 0.7	59 ± 0.9	40 ± 0.8
North III	thawed	C	63	98 ± 0.6	29 ± 0.5	71 ± 0.5
All			424	84 ± 1.1	43 ± 1.1	50 ± 1.2



Figure D.1. Field measurements of logs processed by the harvester.

Appendix E

Proportion of Ips typographus killed during processing by harvester

The harvester head consists of knives, used for debranching the trunks, and feed rollers, used for moving the trunk through the harvester head. The feed rollers often rip small pieces of bark off the tree (Fig E.1), hereafter called bark crumbs, while the knives strip off larger bark pieces, hereafter called bark strips. Bark strips were collected from 20 trees in 2007/2008 and from 88 trees in 2021/2022 (see Table F.1). Bark crumbs were collected from 13 trees in 2007/2008, on a cotton sheet placed under the tree after felling and before processing with the harvester head. At North I, where felling took place during a very cold period, similar bark crumbs were still stuck to the tree after processing and were collected by peeling them off from 10 trees with a knife the day after felling (28 Jan. 2021). The proportion of bark that was covered by the feed rollers at North I was calculated by dividing the total width of the feed rollers tracks by the circumference of the tree at one sampling point per log. The mean proportion covered by feed roller tracks was 35% (range 28 - 42%).



Fig E.1. Log with diameter 29.5 cm processed with frozen bark and with harvester head H415. Note feed roller tracks with ripped-off bark.

Appendix F

Winter survival of SBB and *Medetera* in stripped-off bark

Bark samples of stripped-off bark were collected on the same day as the trees were processed. Two bark strips (mean size $7.5 \pm 0.2 \text{ dm}^2$, range 1–14 dm^2) from the same part of the tree were taken. Almost always they consisted of a larger piece of bark divided into two parts of similar size. Among the 108 bark sample pairs (Table F.1), there were many samples without any SBB or *Medetera* in both winter and spring samples (below referred to as “zero-samples”). All zero samples were excluded before calculating the ratio between spring and winter sample regarding living SBB and *Medetera*, leaving 76 paired observations for SBB and 73 for *Medetera*. Among the 32 omitted zero-samples for SBB, 15 were common for both winter and spring, 7 were only winter and 10 were only spring. The corresponding values for the 35 omitted zero-samples for *Medetera* were 16, 8 and 11. Thus, the number of excluded zero-samples was quite balanced between winter and spring and did not seriously affect the relationship between winter and spring densities (compared to keeping zero-samples).

Table F.1

Number of trees from which bark samples were taken, harvest date, date when samples were taken, date when they were placed on the ground and number of days that they lay on the ground before taken to the lab. in spring.

Site	n	Harvest Date	Bark samples taken	Samples placed on ground	Number days on ground
South I	20	22-23 Oct., 2007	22-23 Oct., 2007	23 Oct., 2007	118
South II	18	20–22 Jan., 2021	22 Jan., 2021	22 Jan., 2021	61
South III	22	1–3 Feb., 2021	4 Feb., 2021	4 Feb., 2021	48
North I	7	27 Jan., 2021	9 Feb., 2021	13 Feb., 2021	41
North II	25	10-11 Feb., 2021	10 Feb., 2021	13 Feb., 2021	41
North III	16	24 Feb., 2021	24 Feb., 2021	24 Feb., 2021	30

Table F.2

Density of *Ips typographus* and *Medetera* spp. in bark samples gathered from 48 trees in 2020/2021. Means \pm standard errors.

	Winterbark dissection	Springbark dissection	Springhatching
n	48	48	48
<i>I. typographus</i> m^{-2}	160 \pm 30	91 \pm 19	70 \pm 11
<i>Medetera</i> m^{-2}	112 \pm 16	61 \pm 14	117 \pm 19

Appendix G

Cohort size of *Ips typographus* (SBB) overwintering in ground and in lost bark

The relative sizes of overwintering SBB cohorts 2 (in ground) and 3 (in bark lost by woodpeckers) are difficult to define because woodpecker activity may occur during the period when the bark beetles exit the tree to overwinter in the ground. To keep formulas simple, a choice between two extreme assumptions was made. We chose the assumption that all SBB had exited the tree before any bark was lost, i.e., cohort 2 = (1-P) and cohort 3 = P(1-a) where “a” is the proportion of bark on tree and “P” the proportion of SBB overwintering in bark on tree at time T. We judged this alternative to be more realistic than the other extreme assumption that no SBB exited the tree before the bark was lost, i.e., cohort 2 = a(1-P) and cohort 3 = (1-a). The true mean value of the relative cohort sizes should be between the mean values calculated by the two alternative assumptions (Table G.1). The sum of the relative sizes of cohorts 2 and 3 were 62,5% in both alternatives which had similar output values of Dsbb, indicating that Dsbb was not sensitive to which alternative that was used (Table G.1).

Table G.1

Calculation of relative size of overwintering cohorts of *Ips typographus* (SBB) in ground (cohort 2) and in bark lost by woodpeckers (cohort 3) for 424 harvested trees and the relative reduction of SBB by the harvest (Dsbb) under two alternative assumptions: Alternative 1: all SBB had exited the tree before any bark was lost by woodpeckers. Alternative 2: no SBB had exited the tree before the bark was lost by woodpeckers.

	Alternative 1: all SBB exits occur before bark is lost	Alternative 2: no SBB exits occur before bark is lost
Mean relative size of cohort 2 (%)	55.7	46.9
Mean relative size of cohort 3 (%)	6.8	15.6
Mean Dsbb (%)	28.8	28.5

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