

Rise and fall of a spruce bark beetle outbreak – Importance of colonisation density and reproductive success

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ABSTRACT

Tree-killing bark beetles are an important disturbance factor in conifer forests. We studied if bark beetle performance in colonised trees may influence outbreak progression. Trees colonised by the Eurasian spruce bark beetle *Ips typographus* were sampled during an entire outbreak triggered by a storm-felling in southern Sweden. The study was conducted at nine storm gaps where no sanitation cuttings were done. Colonisation density (maternal gallery density) and reproductive success (daughters per mother) of *I. typographus*, and densities of competitors and enemies, were recorded from bark samples collected in the autumn from colonised storm-felled and standing trees during seven years. Yearly colonisation densities were much lower in storm-felled (68 – 103 galleries per m²) than in standing trees (218 – 717 galleries per m²). For standing trees the lowest colonisation densities occurred in the first two years of the outbreak and colonisation density was positively related to tree diameter. Beetle reproductive success was higher in storm-felled (9.4 – 9.6 daughters per mother) than in standing trees (0.4 – 5.7 daughters per mother). In standing trees the highest values occurred in the first two years of the outbreak. Reproductive success was significantly related to colonisation density (negatively), tree diameter (positively), parasitoid density (negatively at high densities) and attack year (negatively). Colonisation density had the largest effect. Our results demonstrate the importance of managing spruce forest in a way that increases tree vitality and minimises the risk for storm-fellings. Timely sanitation cuttings of colonised storm-felled and low-vitality standing trees may reduce the risk for outbreak initiations.

1. Introduction

Tree-killing bark beetles are a major disturbance factors in conifer forests (Raffa et al., 2008; Bentz et al., 2010; Hicke et al., 2016; Hartmann et al., 2022). In Europe the Eurasian spruce bark beetle *Ips typographus* (L.) (Coleoptera, Curculionidae) is the most important tree-killing bark beetle (Christiansen and Bakke, 1988; Grégoire and Evans, 2004; Schelhaas et al., 2003; Seidl et al., 2011) and damages have increased greatly in recent decades (Hlásny et al., 2021; Hartmann et al., 2022). Large-scale storm-fellings and warm and dry summers are known to increase the risk for outbreaks of *I. typographus* (Schroeder and Lindelöw, 2002; Kärvmö et al., 2014; Hlásny et al., 2021; Rousi et al., 2023). But the specific mechanisms behind outbreak initiation are still not fully understood, and we know even less about the outbreak collapse phase (Biedermann et al., 2019; Huang et al., 2020).

Time series analyses of tree mortality or beetle trapping data have been used to explore how population fluctuations of tree killing bark beetles may be related to climatic drivers and population densities of bark beetles and their enemies (Turchin et al., 1991; Berryman, 1999; Reeve and Turchin, 2002; Økland and Berryman, 2004; Washaya et al., 2024). For *I. typographus*, time-series analyses have demonstrated that populations increase after warm and dry summers and storm-fellings, while they decrease when populations are high, i.e., beetle population dynamics exhibit negative density dependence (Marini et al., 2012, 2013, 2017). However, to better understand the mechanisms behind these relationships, studies of bark beetle performance in their breeding material, and factors affecting it, are required for entire outbreak periods.

Two factors that can be expected to influence outbreak progression is between-generation changes in the colonisation density (i.e., how many

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bark beetles that are required to overcome the defences of a tree) and the reproductive success in successfully colonized trees. To our knowledge, no earlier study have investigated the temporal variation in colonisation density, and reproductive success, during an entire large-scale outbreak for a tree-killing bark beetle (but see Turchin et al., 1999). Factors that may influence bark beetle reproductive success are colonisation density, competition with other bark- and wood-boring beetles and enemy pressure. Colonisation density affects reproductive success both by affecting the probability of overcoming tree defences and by leading to strong intraspecific competition at high densities (see below). When bark beetles and their associated microorganisms colonise living conifers they encounter complex tree defences in the form of constitutive and induced mechanisms (Franceschi et al., 2005; Raffa, 2014; Krokene, 2015; Mageroy et al., 2019; Whitehill et al., 2023). Bark beetles may overcome tree defences by mass attacks, coordinated by aggregation pheromones that rapidly attract high numbers of beetles, which increase the probability of overcoming tree defences. Thus, for successful colonisation the density of attacking individuals must exceed a critical threshold (Berryman, 1982; Raffa and Berryman, 1983; Mulock and Christiansen, 1986; Christiansen et al., 1987; Pineau et al., 2017). If the attack density is below the critical threshold, reproduction will be strongly reduced or fail completely. The critical threshold can be expected to be influenced by tree vitality. Bark beetles utilise host tree terpenes for pheromone production and as synergists of attraction to their aggregation pheromones (Birgersson et al., 1984; Blomquist et al., 2010). Thus, during the colonisation phase higher number of beetles are attracted to well-defended trees than to trees of lower vitality (Raffa and Berryman, 1983). In accordance with this, lower colonisation densities can be expected in years when trees are under severe stress.

Intraspecific competition occurs both between bark beetle parents (influencing the length of maternal galleries and thus also the number of eggs laid), and between the larvae feeding on the phloem, resulting in a strong negative relationship between colonisation density and reproductive success (Anderbrant et al., 1985; Anderbrant, 1990; Reeve et al., 1998). Thus, colonisation density could potentially be an important factor influencing the magnitude and development of bark beetle outbreaks.

Also interspecific competition may affect the reproductive success of tree-killing bark beetles. During endemic periods many secondary bark beetles and cerambycid species compete with tree-killing species for weakened or newly dead trees (Schroeder and Weslien, 1994; Göthlin et al., 2000; Ayres et al., 2001). During outbreaks the tree-killing bark beetles have the advantage of generally being the first to colonise trees. However, more secondary species may also colonise the trees after tree defence capacity has been exhausted and thereby influence the reproductive success of the primary colonisers (Coulson et al., 1980).

Many insect species prey on bark beetle developmental stages under the bark (Weslien, 1992; Hedgren and Schroeder, 2004; Kenis et al., 2004; Wermelinger, 2002; Wermelinger et al., 2012). Comparisons of caged and uncaged bark beetle-colonised stem sections have demonstrated a large negative impact of natural enemies on bark beetle reproductive success (Linit and Stephen, 1983; Riley and Goyer, 1986; Weslien, 1992; Weslien and Schroeder, 1999). However, only a few cage studies have explored changes in enemy impact on reproductive success between consecutive bark beetle generations during outbreaks (Turchin et al., 1999; Schroeder, 2007). Time-series analyses of enemy densities estimated from trap catches have also been used but are restricted to clerid predators (Turchin et al., 1991; Marini et al., 2013; Martinson et al., 2013). In addition, a few studies have recorded the densities of enemy larvae under the bark in bark beetle killed trees. However, all these studies are based on relatively low numbers of sampled trees per beetle generation and only include a few years of an outbreak or only small localised outbreaks (McCambridge and Knight, 1972; Berryman, 1973; DeMars et al., 1986; Vanická et al., 2020). Thus, it is still unknown how the enemy complex responds to the increased densities of tree-killing bark beetles during large-scale outbreaks and to what extent

they contribute to outbreak collapse.

In January 2005, the storm Gudrun felled 70 million m³ of forest in southern Sweden of which 80 % consisted of Norway spruces *Picea abies* L. (Karst.) (Anonymous, 2006; Svensson, 2007). About 9 million m³ of wind-felled spruces remained in the forest during the first summer after the storm (Schroeder et al., 2006), providing *I. typographus* with large amounts of breeding material with low defences. This initiated a large-scale *I. typographus* outbreak in the second summer after the storm, resulting in 3.5 million m³ of killed spruce before the outbreak ended after five years (Kärvemo and Schroeder, 2010). This offered a possibility to study the within-tree performance of *I. typographus* during an entire outbreak period, spanning from the initial colonisation of storm-felled trees to the initiation and culmination of killing of standing trees and the subsequent decline. The following questions were addressed: (1) How do *I. typographus* colonisation density and reproductive success vary during outbreak progression? (2) How do densities of competitors and natural enemies under bark vary during outbreak progression? (3) Which are the most important factors influencing *I. typographus* colonisation density and reproductive success?

2. Materials and methods

2.1. Study area

The study was conducted in southern Sweden in the counties of Kronoberg and Jönköping. About 80 % of the study region is covered by forest of which most is managed for timber production. Production stands are even aged and thinned two to three times before final harvest by clear-felling at an age of 60 – 80 years. Norway spruce (hereafter spruce) and Scots pine *Pinus sylvestris* (L.) are the dominant tree species. *Ips typographus*-colonised storm-felled and standing spruces were sampled in and around nine uncleared storm gaps created by the storm Gudrun in January 2005 (Fig. 1). The storm gaps were chosen in protected areas because these were the only areas in which we could be sure that storm-felled and *I. typographus*-killed trees would remain for sampling (Kärvemo et al., 2014). Our study sites were dominated by even-aged spruce forests. Sampling of bark from *I. typographus*-colonised spruces was conducted each autumn from 2005 to the outbreak ended in 2011. Because *I. typographus* generally is univoltine in Sweden (Fritscher and Schroeder, 2022) the data from each year mainly represents one beetle generation (including sister broods).

The number of storm-felled trees ranged from 117 – 1168 and number of *I. typographus*-colonised storm-felled trees from 90 to 818 in the storm gaps (Appendix 1. Table S1). The number of *I. typographus*-killed standing trees in the years 2006 – 2010 (killed trees were not counted in 2011) adjacent to the storm gaps ranged from 418 – 7565 per gap (Appendix 1. Table S1). No standing trees were killed in 2005 (the first summer after the storm-felling). The nine gaps were part of a larger selection of 36 storm gaps for which the proportion of storm-felled trees colonised, and the number of killed trees in the forest surrounding the gaps, were studied in relation to storm gap size and landscape variables (Schroeder, 2010; Kärvemo et al., 2014).

2.2. Collection of bark samples

Ips typographus-colonised storm-felled trees were identified by carefully checking the tree stems for boring dust and entrance and emergence holes. For standing trees also the colour of the tree crown and signs of woodpecker activity was used. Colonised storm-felled trees were sampled in 2005 and 2006, and standing killed trees from 2006 to 2011.

A total of 195 bark samples were collected from 167 storm-felled trees colonised by *I. typographus* in 2005 and 2006 (Appendix 1. Table S2). In 2005 more than one sample (maximum 3) was taken from each storm-felled tree in some cases (69 samples taken from 34 trees) because few trees were colonised in the first summer after the storm (Schroeder, 2010). In 2006, only one sample was taken from each

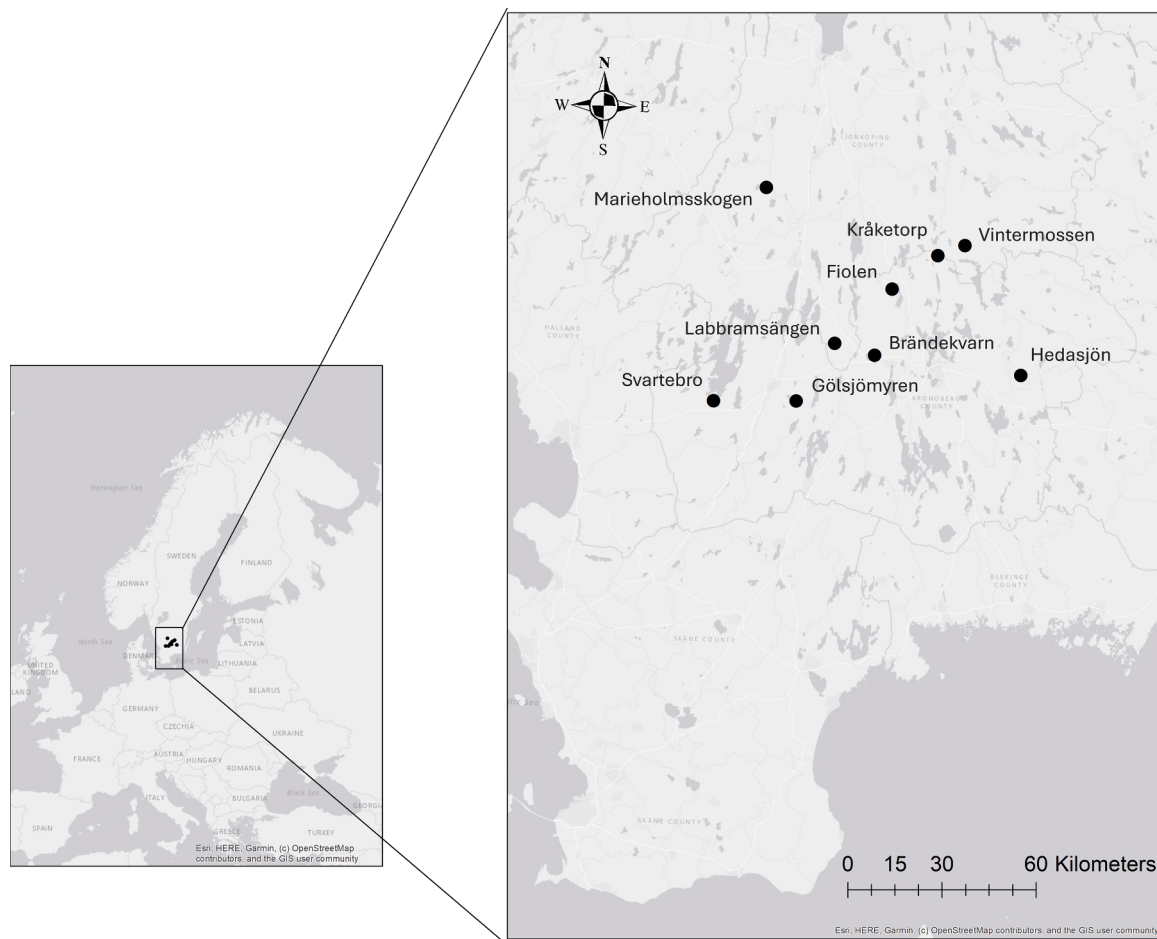


Fig. 1. The geographic locations of the nine storm gap areas sampled in southern Sweden. The storm gap areas included both storm-felled and nearby standing trees colonised by *Ips typographus* and were sampled from 2005 to 2011.

storm-felled tree. A total of 622 standing killed spruce trees adjacent to the storm gaps were sampled and only one sample was taken from each tree (the number of samples from each storm gap and year is given in Appendix 1. Table S2). In the first year of tree killing trees in the gap edges were attacked and in the following years attacks expanded into the adjacent forest (Kärvemo et al., 2014). In the last two years fewer samples were taken because the number of killed trees decreased. The sampling was conducted from August to November on trees colonised the same year. The late sampling ensured that most *I. typographus* offspring had reached the adult stage. Storm-felled trees were sampled along randomly chosen transects across the gaps (Schroeder, 2010) while standing trees were sampled at three or four different sites spread out adjacent to the storm gap if large number of trees were killed.

Bark samples were taken from storm-felled trees at 3 m intervals from the base of the trees to where the stem diameter dropped below 15 cm (mean height of samples = $8.6 \text{ m} \pm 0.3 \text{ m}$ ($\pm \text{SE}$ hereafter)). Standing trees were sampled at a mean height of $6.9 \text{ m} \pm 0.02 \text{ m}$ by using ladder or climbing the trees (Appendix 1. Fig. S1a). One earlier study, and one study initiated at the same time as the present one, have demonstrated that there is no marked difference in *I. typographus* colonisation density and offspring production along this height interval for standing trees (Weslien and Regnander, 1990; Komonen et al., 2011). Bark sample size was $45 \times 15 \text{ cm}$ and longitudinally oriented on the tree stems. Bark samples were stored separately in plastic boxes at $+5^\circ\text{C}$ until analysed.

2.3. Analyses of bark samples

Number of *I. typographus* maternal galleries, emergence holes, adults, pupae and larvae were recorded from the bark samples in the laboratory (see Appendix 1, Fig. S1b for a more detailed description of the procedure). For maternal galleries it was also noted if they were successful (defined as having larval galleries) or unsuccessful (no larval galleries). In the analyses we recalculated numbers to densities (no. per m^2 bark) because bark sample sizes were not exactly the same (mean sample size storm-felled trees 0.0644 ± 0.0006 , standing trees $0.0686 \pm 0.0002 \text{ m}^2$). The number of maternal galleries per m^2 bark corresponds to the density of colonising females (hereafter colonisation density). Because maternal galleries of *I. typographus* are longitudinally oriented along the tree stem (as the bark samples), and much shorter than 45 cm, the $45 \times 15 \text{ cm}$ sample size is appropriate for estimating colonisation densities. In an earlier study conducted on standing trees average maternal gallery length was 6.0 cm (range 5.3 – 6.9 cm) (Hedgren and Schroeder, 2004). The sum of live adults found in the bark sample and the number of exit holes, divided by sample area gives an estimate of the total number of beetles produced per m^2 of colonised bark (hereafter production). Reproductive success was defined as the number of daughters produced per mother [number of beetles produced $\times 0.5$] / [number of maternal galleries] (Hedgren and Schroeder, 2004). Larvae and pupae were not included as they would have suffered some extra mortality before developing into adults (i.e., to avoid over-estimating brood production). Larvae and pupae constituted a minor part of *I. typographus* offspring, making up 11.1 % in storm-felled and 0.7 % in standing trees.

Counts of *I. typographus* emergence holes may underestimate true production, because more than one beetle may use each emergence hole, especially when production is high (Carlsson, 1983; Schlyter et al., 1984). In our study many beetles still remained under the bark at the time of sampling. The mean estimated percentages that had emerged, assuming one beetle used each emergence hole, were 21.9 % in standing trees and 29.2 % in storm-felled trees. In addition, the average density of exit holes was much lower than in the material examined by Schlyter et al. (1984). Carlsson (1983) found that the number of emerging beetles per exit hole in material with similar densities of emergence holes to ours was close to one. Thus, the underestimation of offspring production should have been minor in our study, and mainly affected results for the years 2006 and 2007 when reproductive success and production was high in standing trees.

For the potential bark beetle competitors *Pityogenes chalcographus* (L.) and *Polygraphus poligraphus* (L.) we estimated the coverage of their gallery systems in percentage of the bark sample area. Only *P. chalcographus* was frequent enough to be analysed statistically. The number of cerambycid larvae were counted but not included in the analyses because the density was low.

For bark beetle enemies the number of larvae in the bark samples were counted. Enemy larvae were not identified to species but grouped into the following categories: (i) wasps that are larval ectoparasitoids (hereafter parasitoids), (ii) predatory long-legged flies of the genus *Medetera* (Dolichopodidae) and (iii) predatory beetles of the genus *Thanasimus*. These three groups include the most common insect enemies associated with *I. typographus* (Weslien, 1992; Wermelinger, 2002; Hedgren and Schroeder, 2004; Kenis et al., 2004; Wermelinger et al., 2012). *Thanasimus* could include two species, *T. formicarius* (L.) and *T. femoralis* (Zett.), whereas the parasitoids and *Medetera* groups include several species. The parasitoids were either recorded as cocoon (braconids) or larvae without cocoon (chalcids). Each parasitoid larva consume one bark beetle larva while each *Thanasimus* and *Medetera* larva will kill several bark beetle larvae. At the time of sampling, most *Thanasimus* larvae should already have left the samples while a considerable proportion of parasitoids, and close to 100 % of *Medetera*, hibernates under the bark (Schroeder 1999a; Weslien, 1992; Hedgren and Schroeder, 2004). Thus, our density estimates should be accurate for *Medetera*, somewhat underestimated for chalcid parasitoids (but not for braconids because their cocoons will still remain) and strongly underestimated for *Thanasimus*. Because the sampling was conducted at approximately the same time each year, changes in relative densities among years of the two latter groups could still be evaluated.

2.4. Statistical analyses

Only bark samples from killed standing trees were included in the statistical analyses because the method of sampling differed somewhat between storm-felled and standing trees (see above). Also, the main focus of the study was on changes in colonisation density and reproductive success of *I. typographus* during the outbreak phase (i.e., the period when standing trees were killed). We used generalized additive mixed models (GAMMs; Wood, 2017) to analyse colonisation density and reproductive success. These models allow the expected response to vary smoothly and non-linearly as a function of explanatory variables. All analyses were conducted in R (R Core Team, 2024) using the gam function from the mgcv package, with smoothing penalties estimated using maximum likelihood (ML) and restricted maximum likelihood (REML; Wood, 2017).

2.4.1. Colonisation density

To model colonisation density of *I. typographus*, we used the estimated number of maternal galleries M_i from each sample i as the response with area of the bark sample A_i as an offset under a quasi-Poisson family:

$$M_i \sim \text{quasi-Poisson}(A_i \exp(a + s(d_i) + z_{\text{year}(i)} + w_{\text{location}(i)} + \epsilon_{\text{year}(i)},$$

$$\text{location}(i) + \gamma_{\text{group}(i)}))$$

where a is an intercept, $s(d_i)$ is a smooth function (a reduced rank thin-plate spline with basis dimension 9; Wood, 2017) of the diameter d_i of the sampled tree, $z_{\text{year}(i)}$ is a fixed factor effect for the *I. typographus*-colonisation year of the sample, $w_{\text{location}(i)}$ is a fixed factor effect for the location of the storm gap area of the sample, $\epsilon_{\text{year}(i), \text{location}(i)}$ is a normally distributed random effect for the interaction between year and location, and $\gamma_{\text{group}(i)}$ is a normally distributed random effect for the group of trees within the location from which the samples was taken.

2.4.2. Reproductive success

To model reproductive success of *I. typographus* we used the estimated number of offspring P_i from each sample i as the response with twice the number of maternal galleries M_i as an offset (with the factor two representing the expectation that half of the offspring produced are females), again with a GAMM under a quasi-Poisson family:

$$(1) P_i \sim \text{quasi-Poisson}(2 M_i \exp(a + s(\log(M_i / A_i)) + s(d_i) + s(\log(\text{Med}_i + 1)) + s(\log(\text{Par}_i + 1)) + h(\text{Pc}_i) + z_{\text{year}(i)} + w_{\text{location}(i)} + \epsilon_{\text{year}(i), \text{location}(i)} + \gamma_{\text{group}(i)}))$$

Here, a is again an intercept, $s(\log(M_i / A_i))$ is a smooth function of the (log-transformed) number of maternal galleries per unit area of the sample to account for intraspecific density dependence, $s(d_i)$ a smooth function of the diameter, $s(\log(\text{Med}_i + 1))$ and $s(\log(\text{Par}_i + 1))$ are smooth functions of the (log(x + 1)-transformed) densities of *Medetera* and parasitoids (braconids and chalcids pooled), $h(\text{Pc}_i)$ is a categorical effect of *P. chalcographus* split into three groups (0, 1–25 and >25 % of bark sample covered by *P. chalcographus* gallery systems), $z_{\text{year}(i)}$ a fixed effect for year, $w_{\text{location}(i)}$ a fixed effect for location, $\epsilon_{\text{year}(i), \text{location}(i)}$ is a random effect for the interaction between year and location, and $\gamma_{\text{group}(i)}$ is random effect for the tree group. All smooth functions were modelled as reduced rank thin plate regression splines of dimension 9.

3. Results

3.1. Colonisation density

The mean annual colonisation density of *I. typographus* in storm-felled trees in 2005 and 2006 (68 and 103 maternal galleries per m² bark, respectively) was much lower compared with in the standing trees killed in 2006–2011 (218 – 717 maternal galleries per m²) (Fig. 2a). In 2006, when both storm-felled and standing trees were attacked, colonisation density was about twice as high in standing trees. Colonisation density in standing trees differed strongly between years; being lowest in the first year of tree killing (2006), somewhat higher in the second, and considerably higher in the final four years of the outbreak with a peak in 2008 (Fig. 2a). This pattern over time was rather consistent among individual storm gaps even though the absolute values differed between localities (Appendix 1. Fig. S2).

The GAMMs with ML and REML estimations gave similar results (Table 1; Appendix 1. Table S3). Concurvity of the smooth term was small with the mgcv concurvity index, limited between 0 and 1 with lower values meaning less concurvity, equal to 0.1. The variance inflation factor was smaller than 2 for all predictors. Significant predictors were attack year, tree diameter, location (near significant for REML) and there was a significant interaction between attack year and location. Tree diameter seemed to influence colonisation density in standing trees with a modest predicted increase from 15 – 25 cm, before it leveled out (Fig. 3a).

For storm-felled trees all maternal galleries were successful (i.e., had larval galleries) while for standing trees there was an increase over time in percentage of unsuccessful maternal galleries (except for the last two years): 2006 = 0 %, 2007 = 0.1 %, 2008 = 0.3 %, 2009 = 5.2 %, 2010 = 0.6 % and 2011 = 0 %.

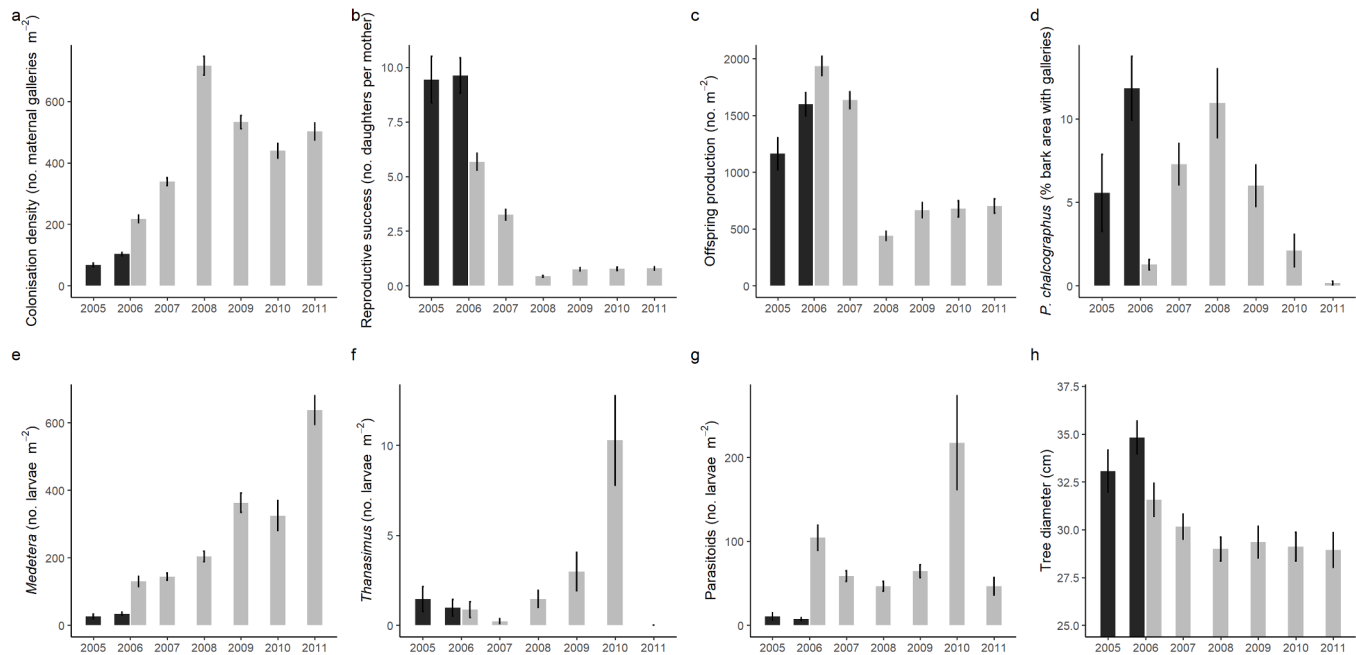


Fig. 2. Yearly mean values for *Ips typographus*-colonised trees in nine storm gap areas for (a) *Ips typographus* colonisation density, (b) *Ips typographus* reproductive success, (c) *Ips typographus* offspring production, (d) percentage of bark sample area covered by *Pityogenes chalcographus* gallery systems, (e) densities of *Medetera* larvae, (f) densities of *Thanasisimus* larvae, (g) densities of parasitoid larvae and (h) mean diameter at 1.3 m of sampled trees. Dark grey bars denote storm-felled trees and light grey bars denote standing trees. Error bars represent $\pm$ SE.

Table 1
Result table for Generalized Additive Mixed Models (GAMMs) with maximum likelihood (ML) estimation, for *Ips typographus* colonisation density and reproductive success. P-values are approximate significance of smooth terms. P/A = presence/absence data, class = data in three classes (0, 1–25 and >25 % of bark sample covered by *P. chalcographus* galleries), and RE = random effects. Δ Deviance (%) is the change in residual deviance when a significant variable of interest was removed from the model. Edf = effective degrees of freedom.

Model	Variable	edf	F	p-value	Δ Deviance(%)
Colonisation density Residual deviance 2901.6	Tree diameter	3.6	4.73	< 0.01	2.4
	Attack year:Location RE	15.7	2.79	< 0.01	-
	Tree group RE	3.3	0.26	0.12	-
	Attack year		32.3	< 0.01	-
	Location		2.98	< 0.01	-
Reproductive success Residual deviance 12468.2	Colonisation density	4.4	80.84	< 0.01	12.6
	Tree diameter	1.0	20.38	< 0.01	0.7
	<i>Medetera</i>	1.0	1.71	0.19	-
	Parasitoid	4.8	12.56	< 0.01	2.3
	Attack year:Location RE	16.3	2.51	< 0.01	-
	Tree group RE	8.0	1.50	< 0.01	-
	<i>Thanasisimus</i> P/A		0.18	0.67	-
	<i>P. chalcographus</i> class		0.29	0.59	-
	Attack year		11.66	< 0.01	-
	Location		0.83	0.57	-

3.2. Reproductive success

The mean annual reproductive success of *I. typographus* in storm-felled trees in 2005 and 2006 (9.4 and 9.6 daughters per mother, respectively) was considerably higher than in the standing killed trees in 2006–2011 (0.4 – 5.7 daughters per mother) (Fig. 2b). Reproductive success in standing trees differed strongly between years; being highest in the first year of tree killing (2006), somewhat lower in the second, and considerably lower in the final four years of the outbreak with a minimum in 2008 (Fig. 2b). This pattern was rather consistent among storm gaps (Appendix 1. Fig. S3).

The GAMMs with ML and REML estimations gave similar results (Table 1; Appendix 1. Table S3). Concurvity of the smooth terms was small to moderate with the maximum mgcv concurvity index equal to 0.53. The largest variance inflation factor among all predictors was 3.

Significant predictors were colonisation density, attack year, tree diameter, density of parasitoids, location, tree group and the interaction between location and tree diameter. The most important factor affecting the reproductive success of *I. typographus* in standing trees was colonisation density, with a predicted strong negative relationship from densities of about 100 maternal galleries per m^2 bark (Fig. 3b). For tree diameter there was a positive relationship with reproductive success up to about 22 cm after which it levelled out, but the effect size was small (Fig. 3c). Among the enemies there was no significant relationship between densities of larvae of *Medetera* (Fig. 3d), or presence/absence of *Thanasisimus* larvae, and *I. typographus* reproductive success. The density of parasitoid larvae was significantly related to the reproductive success of *I. typographus*, with a weak positive relationship up to densities of about 400 larvae per m^2 bark after which it changed to a negative effect (Fig. 3e). There was no significant effect of coverage of gallery system of

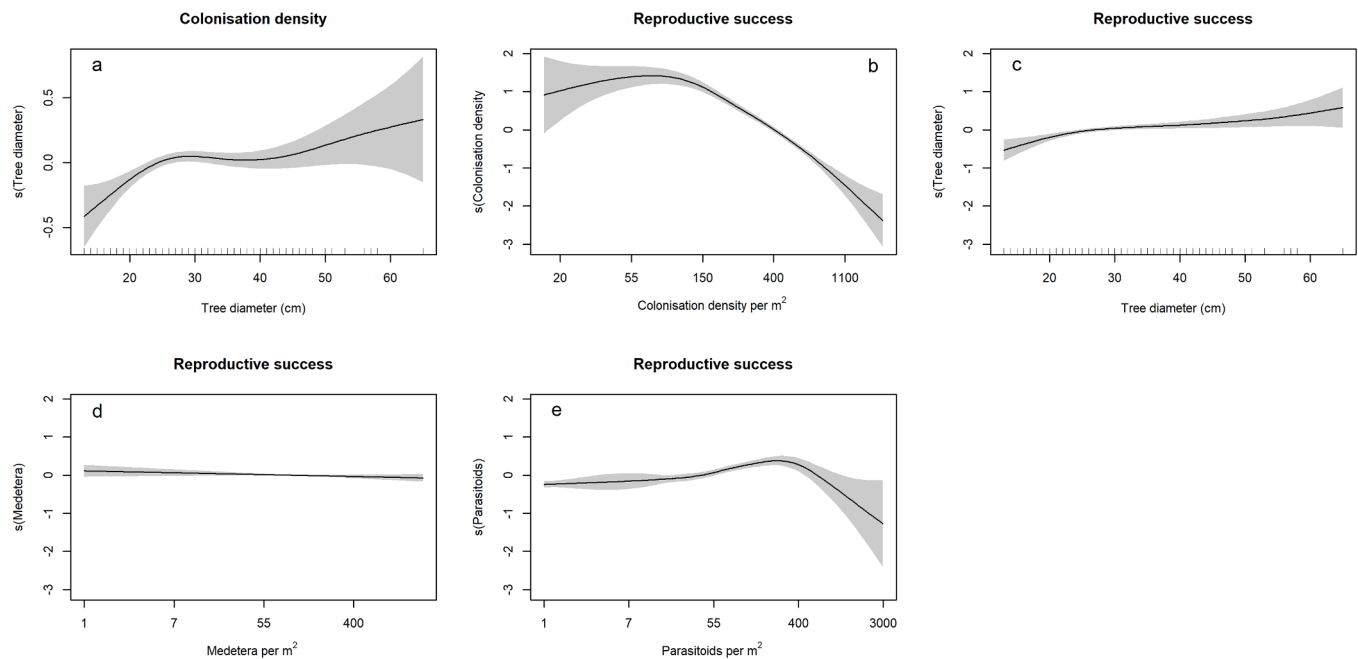


Fig. 3. Predicted relationships (log scale) between (a) *Ips typographus* colonisation density and tree diameter, and between *Ips typographus* reproductive success (no. produced daughters per mother) and (b) colonisation density (maternal galleries), (c) tree diameter, (d) density of *Medetera* larvae and (e) density of parasitoid larvae. Estimated effects are centred around 0. Shaded areas denote the 95 % confidence intervals. Effective degrees of freedom (edf) are given in Table 1.

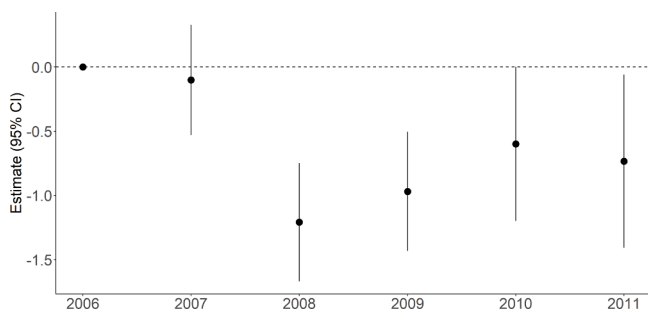


Fig. 4. Predicted change (log scale) in *Ips typographus* reproductive success in standing trees over years relative to 2006 (i.e., estimated year effects). Bars denote 95 % confidence intervals.

the bark beetle *P. chalcographus*. The significant effect of attack year show that considerable variation in reproductive success among years remained after having accounted for the effects of colonisation density, tree diameter, enemies and competitors. Compared with 2006 (the first year of tree-killing) model estimates show that the reproductive success was lower during the years 2008–2011 (Fig. 4). This can also be seen in the raw data where for similar colonisation densities the reproductive success was markedly lower during the years 2008–2011 compared with in 2006 (Appendix 1. Fig. S4).

The mean annual *I. typographus* offspring production in storm-felled trees in 2005 and 2006 (1162 and 1599 adults per m² bark respectively) was similar to the production in standing trees in the first two years of the outbreak in 2006 and 2007 (1935 and 1634 adults per m² bark, respectively) (Fig. 2c). In the four last years of the outbreak production was considerably lower (439–702 adults per m² bark).

3.3. Competitors and enemies

The most common competitor found in the bark samples from *I. typographus*-colonised trees was *P. chalcographus* which was present in 43 % of the samples from storm-felled trees and in 31 % of the samples

from standing trees. The average yearly percentage of the bark area covered by gallery systems of this species in standing trees peaked in 2008 after which it decreased (Fig. 2d). Other bark beetle species were present in less than 10 % of the bark samples from storm-felled trees and less than 5 % of the samples from standing trees and generally with only a few individuals (*Crypturgus* spp. not included). Cerambycid larvae (mainly *Rhagium inquisitor* (L.)) were present in 10 % of the samples from storm-felled trees and in 8 % of samples from standing trees with an average density of 2.5 and 1.9 larvae per m² bark respectively.

The most frequent enemy group in standing trees was *Medetera*, present in 90 % of the samples, and it also occurred in the highest densities. In storm-felled trees *Medetera* was present in 46 % of the samples. Densities of *Medetera* increased over time in both storm-felled and standing trees (Fig. 2e). *Thanosinus* larvae were present in 9 % of the samples from standing trees and there was no significant differences in density between years (except for in the last year when almost no larvae were present) (Fig. 2f). In storm-felled trees *Thanosinus* was present in 6 % of the samples. Parasitoids were present in 74 % of the samples from standing trees and 16 % of the samples from storm-felled trees. Of the parasitoid larvae in standing trees chalcids constituted 66 % (present in 67 % of the samples) and braconids 34 % of the larvae (present in 23 % of the samples). Densities of parasitoids did not increase over time but parasitoids were found in higher densities in standing than in storm-felled trees (Fig. 2g). In the 14 samples from standing trees with parasitoid densities exceeding 400 larvae per m² bark, braconids dominated (71 %).

The annual mean diameter at 1.3 m of sampled *I. typographus*-killed trees varied from 28.9–31.6 cm and did not differ significantly between years (Fig. 2h).

4. Discussion

Our study focus on an *I. typographus* outbreak initiated by a large scale storm-felling in southern Sweden. We provide new knowledge about how *I. typographus* colonisation density and reproductive success may vary from the initial colonisation of storm-felled trees until outbreak collapse, and discuss how these two factors may have contributed to outbreak initiation and decline. We also analyse the

importance of different factors that may influence colonisation density and reproductive success.

4.1. Colonisation density

The lower colonisation density of *I. typographus* in storm-felled trees compared with in standing killed trees is in accordance with earlier studies (Furuta, 1989, Komonen et al., 2011) and is probably a result of the weaker defences of storm-felled trees in combination with the big surplus of suitable breeding material after large-scale storm-fellings. For standing trees the colonisation density was markedly lower in the first year of tree killing compared with in the following years. This indicates that outbreak initiation was not only caused by the population build up in the storm-felled trees, but also by reduced vigour of standing trees resulting in a lower threshold of attack required for overcoming tree defences (Raffa and Berryman, 1983). Tree defences may temporally have been reduced as a result of the exceptionally strong January 2005 storm. Seidl and Blennow (2012) showed that the growth of Norway spruce in the storm-affected region in Sweden was reduced by more than 10 % during a three-year period after the storm and that the negative effect was especially strong in 2006 (i.e., the first year of tree killing). They suggested damages to the root systems and increased allocation of carbohydrates to the below-ground tree parts as explanations for the reduced tree growth, both of which could have negatively affected allocation of resources to tree defences. In addition, the summer of 2006 was unusually warm in the outbreak region in southern Sweden (Swedish Meteorological and Hydrological Institute) which may have further temporally drought stressed the trees and made them more vulnerable for *I. typographus* attacks (Netherer et al., 2015, 2024). In addition, when colonisation densities are low more trees can be killed by a given number of beetles which also may have contributed to the high regional tree mortality during the first year of the outbreak (Fig. 5).

Colonisation density of *I. typographus* increased with tree diameter up to about 25 cm after which it levelled off. This may be due to an increase in bark thickness with tree diameter (Laasasenaho et al., 2005). *Ips typographus* is a rather large bark beetle species and thus needs thicker bark for its galleries. In addition, large diameter trees may have thicker phloem providing more food for the bark beetle larvae (but see Hutchison and Reid, 2022). Furthermore, a considerable proportion of new generation *I. typographus* adults overwinter in the dry outer bark of their brood trees and thus may be favoured by thicker bark (Weslien et al., 2024). Also for *D. ponderosae* a positive relationship between tree diameter and colonisation density has been demonstrated (Graf et al., 2012). This relationship has been suggested to be a consequence of larger tree being better defended than smaller ones (Boone et al., 2011; but see Hutchison and Reid, 2022). Bark beetles utilise terpenes when producing aggregation pheromones and thus a higher production of aggregation pheromones could be expected from better defended trees resulting in increased attraction of colonisers (Raffa and Berryman, 1983).

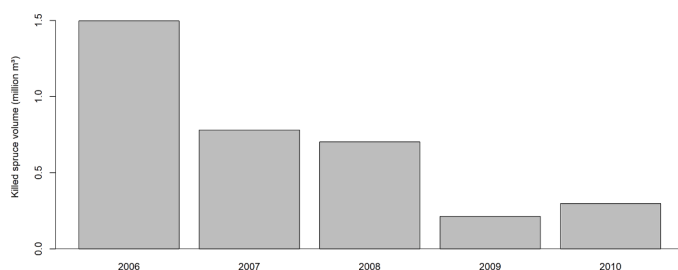


Fig. 5. Volume of Norway spruce killed by *Ips typographus* during the outbreak initiated by the large storm-felling caused by the Storm Gudrun in January 2005. An estimated 40 % of the total killed volume occurred in the provinces of Kronoberg and Jönköping where this study was conducted.

4.2. Reproductive success

Not only the large surplus of storm-felled trees, but also the high reproductive success in them, should have resulted in a rapid population increase of *I. typographus* that contributed to outbreak initiation. A few earlier studies have demonstrated a markedly higher reproductive success in storm-felled trees compared with in standing killed trees (Furuta, 1989, Komonen et al., 2011). In standing trees the reproductive success peaked in the first year of tree killing (2006) after which it decreased, with a minimum in 2008 being one order of magnitude lower than in 2006. During the last four years of the outbreak the reproductive success was below one daughter per mother which will have contributed to outbreak collapse.

Colonisation density was the most important factor influencing the reproductive success of *I. typographus* in standing trees. The strong decline in reproductive success with increasing colonisation density is in accordance with a laboratory study (Anderbrant et al., 1985) and a field study using caged logs that excluded enemies and competitors (Schroeder, 2007). The study by Anderbrant et al. (1985) also showed that increasing colonisation densities (including the range of densities recorded in the present study) resulted in lighter offspring, with a lower fat content. In addition, offspring males obtained from higher colonisation densities also had lower amounts of the pheromone components cis-verbenol and 2-methyl-3-buten-2-ol in the hindguts after monoterpen exposure. Thus, in addition to a reduction of the reproductive success also the quality of the offspring decreased which may result in a lower dispersal capacity and also a reduced ability to overcome tree defences for example. These factors may have contributed to outbreak decline.

Also tree diameter seemed to influence the reproductive success of *I. typographus*. There was a positive relationship with diameter up to about 22 cm after which it levelled off. This may be one explanation for the preference for large-diameter trees that has been demonstrated in earlier studies for this species (Lekander, 1972, Göthlin et al., 2000). There are few earlier studies on bark beetle reproductive success across diameters of standing killed trees (but several on offspring production per m² bark which does not necessarily correspond to reproductive success). In a study on *D. ponderosae* reproductive success was constant across tree diameters but offspring body size increased somewhat with diameter (Graf et al., 2012). Our study supports the hypothesis that large-diameter trees are preferred by *I. typographus* because they result in a somewhat higher fitness.

There was no negative relationship between densities of enemy larvae and reproductive success of *I. typographus* except for at parasitoid densities exceeding 400 larvae per m² bark. There may be several explanations for this. First, the densities of enemy larvae in the autumn (when the sampling was conducted) is the end result of not only consumed preys but also of competition/predation within (Weslien, 1994) and between enemy species (Schroeder, 1996). In addition, in the autumn most *Thanasimus* larvae, and some of the parasitoids, have already emerged from the trees which further increase uncertainty. Thus, densities of enemy larvae in the autumn may be a poor measure of enemy impact. Second, part of the enemy-caused mortality of *I. typographus* larvae may have been compensated for by a reduced intraspecific competition between the bark beetle larvae later on (i.e., bark beetle larvae that were consumed by an enemy would have died anyway as a result of subsequent competition between the *I. typographus* larvae) (Lawson et al., 1997). This phenomenon should have been especially important in the latter years of the outbreak when *I. typographus* colonisation densities were highest. The only significant negative impact of enemies occurred for parasitoids at densities exceeding 400 larvae per m² bark. Especially braconids seemed to contribute to this effect.

Despite several years of a continuous supply of prey in *I. typographus*-killed standing trees at the study localities, as well as in the whole region (Appendix 1. Table S1; Fig. 5), the increase in enemy densities under bark was moderate for *Medetera* and variable for *Thanasimus* while

parasitoids did not seem to respond at all. This was not a result of a dilution effect because the number of *I. typographus*-killed trees peaked at the first year of the outbreak and then decreased over time at the regional level, while in the study localities the decrease started one year later in six of the nine areas. Thus, increased densities of enemies in the killed trees could have been expected even without a numerical response. One explanation for the moderate, or absent, enemy response may be that most of the *I. typographus* enemies are generalists, utilising several bark beetle species (Kenis et al., 2004) differing in their phenology. Thus, the enemies are not able to fully realise their reproductive capacity on a single prey species even though *I. typographus* during outbreaks constitute the major source of bark beetle preys. It could also be that even though most enemies use several host species some prey species are more important than others. A time-series analysis showed that *T. formicarius* densities were not related to fluctuations in *I. typographus* densities but instead seemed to be driven by population levels of the secondary bark beetle *Tomicus piniperda* (L.) which breeds in Scots pine (Marini et al., 2013). *Tomicus piniperda* has an early flight period and is the first bark beetle species that *T. formicarius* adults utilise as prey in the spring (Schroeder 1999b). In addition, *T. formicarius* has a two-year developmental time which will slow down the response to increased prey densities (Schroeder 1999a).

One unexpected result of the study was the considerable drop in *I. typographus* reproductive success in the four last years of the outbreak. This drop remained after accounting for the effect of colonisation density and the other predictors. Interestingly, from 2008 and onwards we also noted that in many bark samples the *I. typographus* larval galleries were narrower than usual indicating that larval growth was not optimal. One contributing factor for the drop in reproductive success may be the general increase in tree vitality that can be expected to have occurred in the years after the storm disturbance and the warm 2006 summer. Also a “vaccination” effect induced by previous unsuccessful *I. typographus* attacks may have negatively affected the reproductive success. In an experimental study in which the stems of Norway spruces were treated with the plant defence hormone methyl jasmonate (MeJA) and subsequently baited with *I. typographus* pheromone lures, the maternal gallery length and abundance of brood (egg, larvae and pupae) was negligible compared to control trees (Mageroy et al., 2019). In our study there was an increased proportion of maternal galleries without larval galleries in the years 2009–2010. Also other factors like changes in the community of symbionts associated with *I. typographus* may have played a role in reducing beetle attack success (c.f. Biedermann et al., 2019). More studies are needed to clarify if the drop in reproductive success observed in this study is a common phenomenon during the collapse phase of bark beetle outbreaks, and if so, what the underlying mechanisms are.

Our study demonstrates that even though *I. typographus* got access to a large source of potential breeding material (i.e., living spruces), when densities exceeded the critical threshold required for tree-killing, a positive feedback did not predominate and the outbreak ended long before regional host tree depletion occurred. The estimated killed volume during the outbreak was 3.5 million m³ in the affected region (Göteborg) which correspond to 1 % of the growing stock of Norway spruce with minimum diameter of 15 cm at 1.3 m (data from 2008 from Swedish National Forest Inventory). If only the hardest hit provinces (Kronoberg and Jönköping) are included the figure increases to only 4 % of the growing stock.

5. Conclusions

Our results suggest that the strength of intraspecific competition plays an important role in *I. typographus* outbreak initiation and decline. Strong intraspecific competition seems to largely be driven by tree resistance, as the beetles need to attack in high densities to overwhelm tree defences. We show that the mean annual reproductive success of *I. typographus* varied with a factor of 24 during an entire outbreak

period. It was highest in storm-felled trees in 2005 and 2006 (9.6 – 9.4 daughters per mother), intermediate in the first two years of tree killing (5.7 – 3.2 daughters per mother) and much lower in the last four years of the outbreak (0.4 – 0.8 daughters per mother). Thus, the high reproductive success in the colonised storm-felled trees contributed to the population increase that triggered the start of large-scale tree killing. In addition, the low colonisation density in the first year of tree-killing indicates that tree defences were reduced, resulting in an enhanced reproductive success which further contributed to outbreak progression. In contrast, during the last four years of the outbreak colonisation density was 2 – 3 times higher indicating that tree defences had recovered. This, in combination with the low reproductive success should have contributed strongly to the decline of the outbreak. The most important factor influencing the reproductive success was its negative relationship with colonisation density, i.e., at higher densities increased intraspecific competition strongly reduced the reproductive success. Our results show that spruce forests should be managed in a way that minimise the risk for storm-fellings and increase tree vitality. After large-scale storm disturbance timely sanitation cuttings of colonised storm-felled spruces and attacked standing trees should be practised to prevent *I. typographus* population increase and thereby reducing outbreak magnitude. The positive relationship between tree diameter and reproductive success indicates that sanitation cuttings should be prioritised for large-diameter stands which generally also are the most valuable.

Author contributions

MS developed research ideas, MS and SK developed study design, SK led the field work, JK led statistical analyses, MS led the writing of the manuscript. All authors were involved in data interpretation, revised drafts and contributed to the final version.

CRedit authorship contribution statement

Schroeder Martin: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Knape Jonas:** Writing – review & editing, Formal analysis. **Kärvemo Simon:** Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis.

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.

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Appendix. A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122695.

Data availability

Data will be made available on request.

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