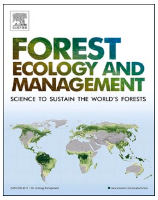
Forest Ecology and Management 578 (2025) 122424

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Peeking under the bark: Within-tree densities of the spruce bark beetle (*Ips typographus*) and its enemies in forest conservation areas

Simon Kärvemo [*], Dragoş Cocoş, Evelina Andersson, Joachim Strengbom

Swedish University of Agricultural Sciences, Department of Ecology, Box 7044, Uppsala 750 07, Sweden

ARTICLE INFO

Keywords:
Infestations
Nature reserves
Outbreak
Reproductive success
Plegaderus
Predators

ABSTRACT

The European spruce bark beetle *Ips typographus* is a major forest pest in Europe, with outbreaks intensifying due to climate change-induced weather events. In this study, we evaluated within-tree densities of the spruce bark beetle and its natural enemies during an outbreak in northern Europe. Densities were compared across different forest management types: managed forests and two conservation areas (woodland key habitats and nature reserves). We assessed beetle colonization density, production, reproductive success, predator abundance, and forest characteristics through bark sample analysis during four years. Our results indicate that spruce bark beetle densities were positively associated with surrounding tree mortality, with no significant differences in within-tree densities across forest types. Instead, variations in density were more pronounced across different outbreak phases and forest conditions, derived from remote sensing data. Enemy abundance, particularly *Plegaderus* spp. and two fungivorous insect groups, were generally higher in nature reserves compared to managed forests. We conclude that complex interactions between forest conditions, outbreak phases, and the occurrence of some specific predators play more crucial roles in bark beetle dynamics than whether a forest is a conservation area or not. For example, in wetter forests, more beetles are needed to overcome defences, while in deciduous forests, non-host volatiles may inhibit pheromones. Specifically, we highlight the less known clown beetle *Plegaderus* spp. as an important predator, negatively affecting bark beetle reproductive success. These findings emphasize the importance of local forest characteristics in managing bark beetle infestations, suggesting that infestation risk assessments should focus on these variables rather than on forest conservation status, though potential variations at larger scales are beyond the scope of our study.

1. Introduction

Tree-killing bark beetles are one of the most important disturbance agents in the northern forested hemisphere, and due to extreme weather events driven by climate change, outbreaks have intensified in recent decades (Jaime et al., 2024). In Europe, the spruce bark beetle (*Ips typographus* L.), is the main forest pest species, killing Norway spruce (*Picea abies* Karst.) during outbreaks. In the last decades, this species has doubled the impact of tree mortality, mainly triggered by recent drought events (Patacca et al., 2023). Sweden experienced similar impacts, with a drought event in 2018, resulting in 34 million m^3 of bark-beetle infested trees, accounting for approximately 70 % of the spruce forest lost to outbreaks over the last 50 years (Schroeder and Kärvemo, 2022).

During past and recent outbreaks, controversies have arisen regarding the management of bark-beetle infestations in conservation areas, such as nature reserves, national parks and voluntary set-asides, and their role in large-scale bark-beetle dynamic, as such areas are typically excluded from bark beetle control measures (e.g. Müller, 2011; Grodzki, 2016; Kulakowski, 2016; Potterf et al., 2023). Differences in management practices, forest structure and infestation history may lead to varying conditions that affect the population dynamics of the spruce bark beetle and their natural enemies (Wermelinger, 2004). Results from previous studies on spruce bark beetles in conservation area are ambiguous. Some studies indicate higher population densities of bark beetle in conservation areas compared to the managed forest (Schlyter and Lundgren, 1993; Grodzki, 2016; Mezei et al., 2017), while other found no significant difference (Weslien and Schroeder, 1999; Vanická et al. 2020), or higher densities in the managed forest compared to nature reserves (Markovic and Stojanovic, 2010; Potterf et al., 2023). Although presence of natural enemies may influence population

---

[*] Corresponding author.
E-mail addresses: Simon.karvemo@slu.se (S. Kärvemo), dragos.cocos@slu.se (D. Cocoş), evelina_98_@hotmail.com (E. Andersson), joachim.strengbom@slu.se (J. Strengbom).

https://doi.org/10.1016/j.foreco.2024.122424
Received 26 September 2024; Received in revised form 21 November 2024; Accepted 22 November 2024

dynamics of bark beetles, only a few studies have investigated the natural enemies of the spruce bark beetle between managed forests and reserves (Hilszczański et al., 2007; Vanická et al. 2020).

Among the approximately 170 enemy species of the genus *Ips* (Wegensteiner et al., 2015), clerid beetles (*Thanasimus* spp) and fly larva (*Medetera* spp.) are the most important predators, with the potential to control bark beetle populations in northern Europe (Weslien and Schroeder, 1999; Weslien et al., 2024) and elsewhere (e.g., Reeve, 1997; Wermelinger, 2002).

As outbreak intensities are increasing with climate change, there is a growing interest in a deeper understanding of factors that drive and control bark beetle dynamics, including factors such as presence of natural enemies and which forest characteristics that can predict bark beetle population densities across spatial and temporal scales. For these purposes, within-tree densities of the spruce bark beetle, including reproductive success, can be used to evaluate whether these trees contribute to population growth - potentially leading to the surpassing of key thresholds resulting in local outbreaks (Raffa et al., 2008).

In this study, we aim to compare within-tree colonisation densities, production and the reproductive success of the spruce bark beetle and densities of associated insects, i.e. predators and parasitoids (hereafter predators) and predators and potential competitors (hereafter enemies; see Table S1 for clarifications) between high conservation value forests, specifically nature reserves (hereafter NR) and voluntary set-asides (woodland key habitats; hereafter WKH) and managed production forests (hereafter M). In addition, we analyzed various local forest characteristics and conditions in relation to different forest types, bark beetle dynamics, and potential predators that could serve as pest control agents.

2. Methods

The study was conducted by annual surveys during the autumns (Oct-Nov) between 2020 and 2023 in Southern Sweden (Fig. 1). We collected 222 bark samples from M (N=71), WKH (N=72) and NR (N=79), typically in spatial triplets (blocks). In total we used 49 sites in this study (M=16, WKH=15, NR=18; Fig. 1). Our objective was to collect five bark samples per site, but due to a limited number of infested trees available in some of the sites, the mean number of sampled trees was 4.53 (SD±1.16). The forested area in the NR varied from 5 to 375 ha (mean of 99 ha, excluding one extreme case of 1149 ha at Sydbillingen). Each reserve contained at least one hectare of 200 m^3 of Norway spruce. NR and WKH are conservation areas with relatively high levels of structural complexity and are exempted from production oriented management to promote biodiversity. NRs, often characterized by their large area, are established to protect specific habitats and species. WKHs, on the other hand, represent smaller-sized set-asides for biodiversity (often 3–5 ha), and are not formally protected, but are considered to be biodiversity hot spots based on their management history and forest composition. Both types of set-asides have higher share of old trees and harbour larger amounts and a more diverse (trees species and decay stages) types of dead wood than the average production forest (Timonen et al., 2011; Wijk, 2017). Sanitation cuttings (removal of infested trees) are performed to a large scale in the M sites, while it is a rare event in the WKHs and NR. However, we did not observe any harvesting in the nearby surroundings of the study sites included in this study.

Each of the 49 sites was visited once during the periods of 5–15 Oct in 2020, 6–29 Oct in 2021, 14–18 Nov in 2022 and 8–17 Nov in 2023 (Fig. 1.). At each site, bark was commonly sampled from two different infested patches located within 100 m. The sampled trees were randomly chosen from infested patches with red/brown crown colour and/or observation of live beetles. The samples consisted of a piece of bark, approximately 45 ×15 cm, carefully cut from a height of 2–3 m height with the help of a ladder. Each sample was then placed in a plastic box and transported to the laboratory for further examination. In the lab, we thoroughly counted the egg galleries, emergence holes, adult spruce bark beetles, and their natural enemies both within and under the bark. The colonisation density was estimated from the number of egg-galleries (maternal galleries) under the bark, while the production of beetles was determined by summing the emergence holes and adult bark beetles. The reproductive success was estimated as the number of daughters per female, i.e. the number of (beetle production/2)/egg galleries (Hedgren and Schroeder, 2004; Komonen et al., 2011). The division by two accounts for the 50 % female-to-male sex ratio (Annila, 1971).

The genus *Ips* has approximately 170 identified predator and parasitoid species (reviewed in Wegensteiner et al., 2015) of which at least 60 are found to attack *I. typographus* in Sweden (Weslien, 1992). Yet their difference in occurrence between managed forest and conservation areas and impact on beetle populations remains poorly understood. Eleven enemy groups are included in this study, of which nine are considered as predators/parasitoids – hereafter predators (Appendix 1. Table S1). The species groups of predators and enemies identified in the bark samples were long-legged flies *Medetera* spp., parasitoid wasps (e.g. Pteromalidae and Braconidae), clerid beetles *Thanasimus* spp., clown beetles *Plegaderus* spp., root-eating beetles *Rhizophagus* spp., rove beetles (Staphylinidae), snake flies (Raphidiidae), soldier flies (Stratiomyidae), lance flies (Lonchaea), fungus gnats (Sciaridae) and gall midges (Cecidomyiidae). Species from the first nine groups are classified as predators (Wegensteiner et al., 2015) and were pooled to separate analysis.

The number of bark samples included in the models was dependent on the variables used in the model. For example, attack year was uncertain for 20 bark samples and were consequently removed from models with year included as a variable, and 11 bark samples had no egg galleries and were removed from the bark-beetle population density models. See Appendix 1. Table S2 for a compilation of the models and the samples sizes included in this study.

To estimate the associations between within-tree dynamics and neighboring infestations in the stands, data of beetle pressure (the noticeable number of recently killed trees in the field) were visually counted within a 150-m radius from the main sampling point. Due to time constraints, this was only conducted in 27 of the 49 sites were evident signs of bark-beetle killed trees were observed. The distance range examined was based on the observed attacked patches and what was feasible for each sampling patch.

To understand the potential impact of structural factors on the population densities of spruce bark beetle and its natural enemies, various forest characteristics were considered in this study. With the exception of host-tree diameter, the local variables considered were soil moisture, total spruce and deciduous forest coverage, which were calculated within a 100-meter radius around the main sampling location for each site. This distance was selected because previous studies have observed that 100 m is a common dispersion distance for the spruce bark beetle during outbreaks (Wichmann and Ravn, 2001; Kautz et al., 2011).

For the existing forest cover around our sampled locations, we utilized data from the National Land Cover Database (Swedish Environmental Protection Agency, 2020). The database categorizes Sweden into various land cover classes with a 10-meter resolution. Among these classes, pixels identified as spruce, defined as areas with trees exceeding 5 meters in height and consisting of over 70 % spruce, were utilized as a variable. This variable is important as it signifies the amount of habitat that may support bark beetle populations (Kärvemo et al., 2016). Connectivity and colonization probability of local populations tend to increase with area of spruce in the landscape, while the extinction probability decrease (Kärvemo et al., 2014, 2016). Mean soil moisture was extracted from a national-scale raster mapping (ranging from 0 to 100, dry to wet, 10-meter resolution), based on digital terrain indices and ancillary environmental information (Ågren et al., 2021). However, values exceeding 98 were excluded as they commonly indicate open fens or bogs and, thus, are non-forest areas. This variable has been observed to negatively affecting bark-beetle attacks at regional scales (Kärvemo et al., 2023; Müller et al., 2022). In addition, the diameter of all sampled

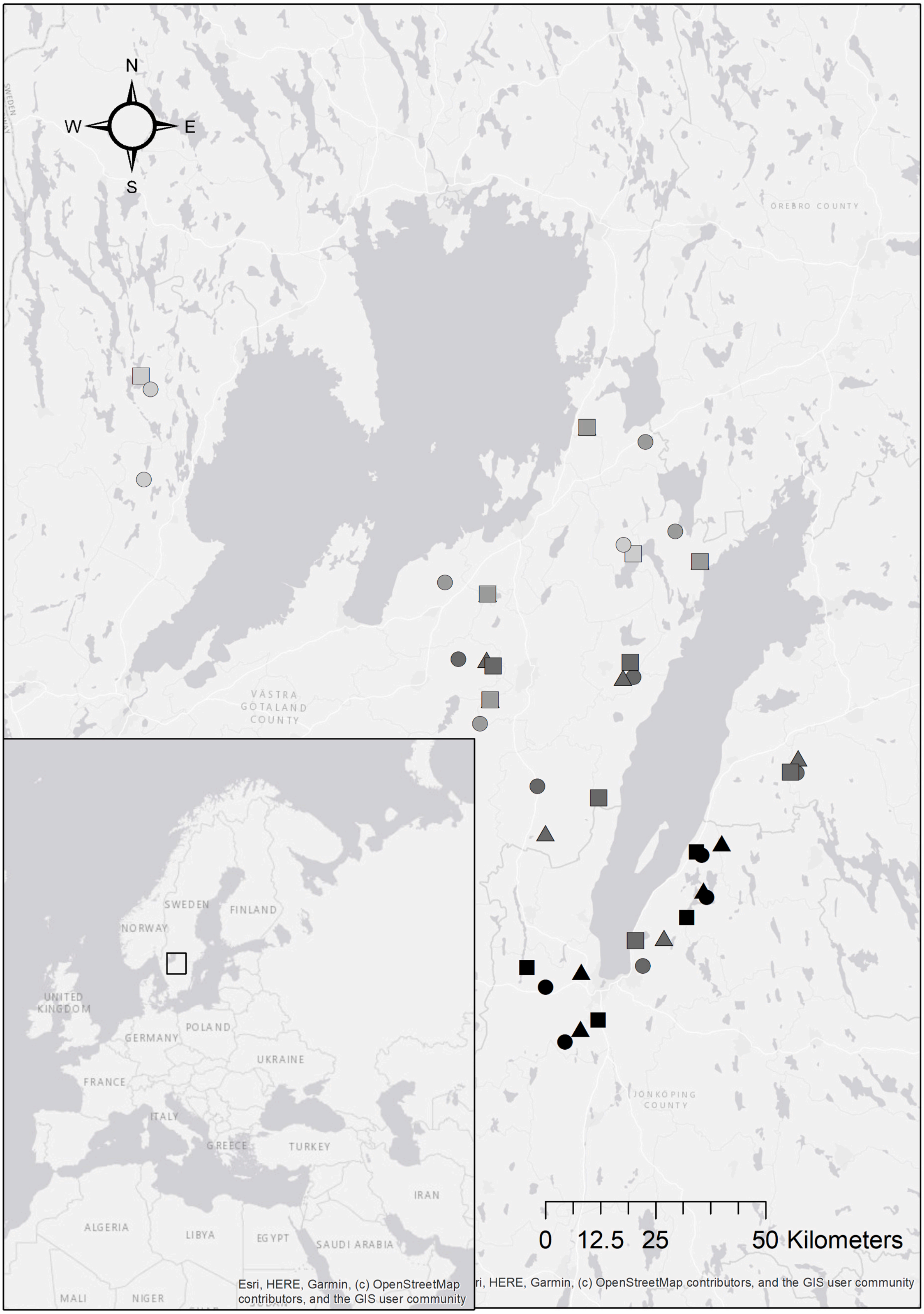


Fig. 1. The 49 study sites with nature reserves (triangles), woodland key habitats (squares) and managed forest (circles). The study period are denoted chronologically from black (2020), dark grey (2021), grey (2022) and white (2023).

trees was measured at breast height with the help of a caliper.

2.1. Statistical analyses

All statistical analyses were performed using the program R ver. 4.3.3 (R Core Team, 2024).

2.1.1. Spruce bark beetle densities

Within-tree colonisation densities, beetle production and reproductive success of the spruce bark beetle were compared between management types: i.e., managed forest (M), woodland key habitats (WKH) and nature reserves (NR). Data were analysed with generalized linear mixed models (GLMM) for colonisation densities and production, while a linear mixed model (LMM) was used for reproductive success. For all models of the population densities in conservation areas, forest management type was included as an interaction term with *year* to elucidate variations across outbreak phases. Moreover, bark sample *size* were included as an offset. *Site* was not included as a random factor in these models since controlling for these variations might reduce the variability, hindering the exploration of management type differences. Instead, when applicable, a *block* triplet including all three management types in close proximity, was used as a random factor to control for spatial variations (93 % of the sites were included in a triplet). Since colonisation densities and production of beetles in the GLMMs are counts, but varied too much to be adequately described by a Poisson distribution, negative binomial distributions were used. For the reproductive success model, the response were log transformed to meet normality and homogeneity of variance assumptions, i.e., LMM. The package multcomp (Hothorn et al., 2008) was used for Tukey's pairwise comparisons. See Appendix 1. Table S2 for a compilation of the models included in the study.

For a subset of the sites, we tested the relationship between the population densities in trees and infestations in the nearby surrounding. GLMs with negative binomial distributions were used including the total number of neighbouring attacked trees as the response variable and colonisation densities, production of beetles and reproductive success as explanatory variables in separate models. No random factors were used for modelling a subset of the sites.

2.1.2. Natural enemies

GLMMs with a negative binomial distribution were employed to analyze the total abundance of natural enemies and additionally predators separately, considering forest management and year, and their interaction as explanatory variables. In addition, the analysis included bark sample size as an offset and block as a random factor to account for these variations. A similar model structure was replicated for each specific species group. However, as these models commonly resulted in singular fits or did not converge (i.e. overfitted models); we chose to exclude the random effect from the separate analyses of species groups. *Thanasimus* spp., Raphidiidae and *Rhizophagus* spp. were not analysed separately because of too few recordings. The predatory species groups showing significant difference between forest types were included as explanatory variables in additional models to understand their influence to reproductive success and production of the spruce bark beetle.

Principal coordinate analysis (PCoA) and permutation-based multivariate analysis of variance (PERMANOVA), were used to test for natural enemy and predator composition among forest types. Both abundance and presence of enemies and predators were evaluated. PERMANOVA was statistically analysed using the pairwise Adonis package of R. Because PERMANOVA is sensitive to variation in multivariate dispersion among groups, we additionally performed a test for the homogeneity of multivariate dispersion using the betadisper function within the R vegan package (Oksanen et al., 2022). To account for bark sample size in the species abundance models, the number of individuals was standardized to a per square meter basis.

2.1.3. Forest variables

The spruce bark beetle dynamics, enemies and predators were additionally analysed including four explanatory forest variables. i.e., host-tree diameter, soil moisture and area of mature spruce forest, as well as area of deciduous forest, all crucial for tree defence and increment of bark beetle populations (e.g., Kärvemo et al., 2014; Müller et al., 2022). For soil moisture, we used the mean value, while for spruce and deciduous forests, area sums were used; all within a 100-meter radius from the main sampling point. The same type of models (GLMM and LMM) were used with bark sample size included as an offset. However, as the same data of soil moisture, spruce and deciduous forest area are used for all sampled trees within each location. *Site* instead of *Block* was used as a random factor (a nested random factor including *Block* did not converge). We could not elucidate correlations between forest variables and bark-beetle densities within each forest type, as the majority of the models did not converge. The forest variables were continuous and standardized to a mean of 0 and standard deviation of 1.

Forest characteristics were also compared between the three different forest management types. Analysis of variance (ANOVA) was applied for host-tree diameter, and normalization of the model residuals was achieved through log transformation. Due to non-normality of residuals, Kruskal-Wallis analyses were conducted to compare soil moisture, spruce, and deciduous forest across forest management types.

3. Results

3.1. Spruce bark beetle densities

The spruce bark beetle dynamics (colonisation densities, production and reproductive success) did not differ statistically between management types (nature reserves (NR), woodland key habitats (WKH) and managed forest (M)). However, there were some differences observed across outbreak phases (years; Appendix 1. Table S3). A general pattern of low colonization densities across forest types in 2021 were found, while the reproductive success was marginally higher in 2021, compared to the other years (Appendix 1. Table S3). WKHs in 2021 and NRs in 2022 had significantly higher colonisation densities during those specific years (Appendix 1. Table S3; Fig. 2).

Since *Plegaderus* spp., Stratiomyidae and parasitoids were the only predatory species groups showing a significant difference between forest types (see 3.2), abundance of these groups was the primary focus in models with predators and production and reproductive success as the response. The reproductive success was negatively associated with *Plegaderus* spp. (Estimate: -0.178; $p<0.001$; Fig. 3b), and positively associated for both Stratiomyidae (Estimate: 0.102; $p=0.005$) and parasitoids (Estimate: 0.07; $p=0.039$). However, no significances for Stratiomyidae was found when removing one outlier (Estimate: 0.057; $p=0.207$), indicating a false positive. In contrast, removing two outliers for parastoids or *Plegaderus* spp. did not affect the significance considerable. The outliers were visually identified from boxplots. No associations were found between production of bark beetles and abundance of *Plegaderus* spp. (Estimate: 0.036; $p=0.506$), Stratiomyidae (Estimate: 0.015; $p= 0.762$) or parasitoids (Estimate: 0.051; $p=0.380$).

The total number of infested trees in neighbouring clusters (counted in a subset of the sites, M=7, WKH=9 and NR=11) was positively related with the production of beetles ($p<0.001$, Estimate: 0.57, AIC: 206; Fig. 4), as well as the reproductive success ($p=0.02$, Estimate: 0.38, AIC: 214), while colonisation densities were not associated with infested trees ($p=0.897$, Estimate: 0.57, AIC: 219).

3.2. Natural enemies

In total, 17,307 enemies were identified and counted, which of 9153 were classified as predators and 8154 were fungivorous (Appendix 1. Table S1). The individuals were mainly found in the larval or pupae stage, except for all rove beetles, 15 clown beetles, six fungus gnats and

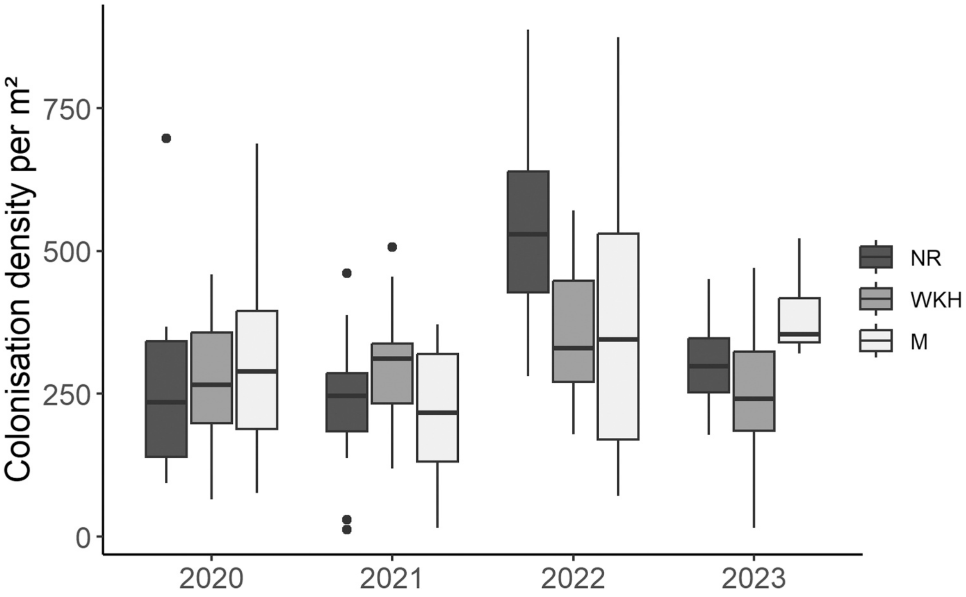


Fig. 2. The number of maternal galleries (colonisations density) across years and different forest management types. The central lines of the box plot represent the median, the box indicates lower (25th) and upper (75th) quartiles and the whiskers represent the largest and smallest observations that fall within 1.5 times the box size from the nearest quartile. For statistical results including random factors (spatial blocks) and interactions between year and forest type; see Table S3.

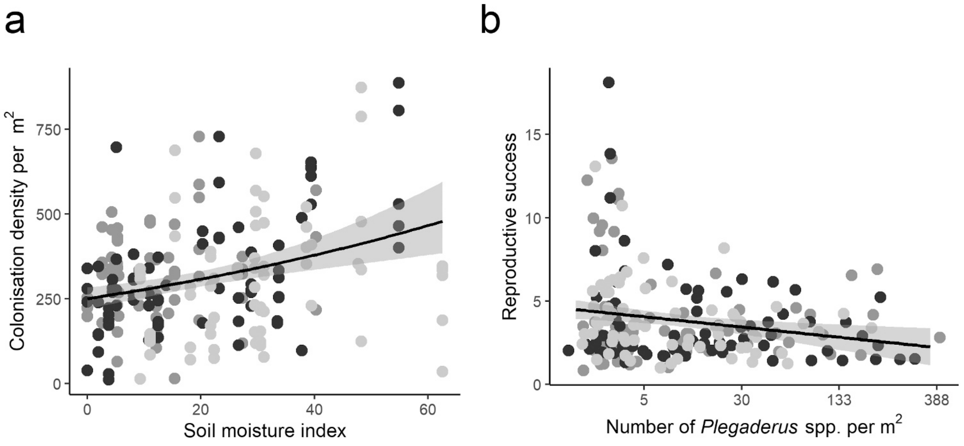


Fig. 3. The relation between a) soil moisture and colonisation density (number of bark beetle maternal galleries) per m^2 and b) number of predatory Clown beetles *Plegaderus* spp. and reproductive success of the spruce bark beetle. The black dots indicate nature reserves (NR) and grey and light grey denote woodland key habitats (WKH) and managed forests (M), respectively.

three parasitoid wasps which were imago. Of the observed Parasitoid wasps, 58 % were in the pupal stage, while the remaining individuals were in the larval stage. Of the 17,307 recorded enemies, the most abundant species group were Sciaridae and Medetera spp. accounting for 6454 and 5438 recordings, respectively (Appendix 1. Table S1). The least abundant species groups were *Thanasimus* sp. (N=33), Raphidiidae (N=15) and *Rhizophagus* spp. (N=96) and were not analysed separately. The total abundance of natural enemies (including 11 sp. groups) was higher in NR than in M (Appendix 1. Table S4; Fig S1) and a significant peak of abundance was observed in 2021 and 2022. The enemy abundance was strongly correlated with species group richness (Estimate: 22.517; p<0.001). When exclusively analysing predatory species groups (N=9), there were no difference between management types, but still a peak in 2021 (Appendix 1. Table S5; Fig. S1).

In comparison to M, NR had significantly higher abundances of *Plegaderus* spp., parasitoids, Sciaridae and Cecidomyiidae (Appendix 1. Table S6; Fig. S1), of which only the first two are considered as true predators/parasites, with possibilities to directly reduce bark beetle populations. WKHs had also more Cecidomyiidae individuals compared to M, while more parasitoids were found in NR compared to WKH. In contrast, both WKH and M (marginally) had a higher abundance of Stratiomyidae compared to NR, but there was no difference between WKH and M. Excluding apparent outliers from Stratiomyidae and *Plegaderus* spp. did not change the difference between the forest types, while for the parasitoids, all significant results disappeared when two outliers were excluded (visually identified from boxplots).

The Permanova analyses indicated that the composition of enemy species groups in NR was significantly different from that in M and WKH, whereas there was no significant difference in the composition of predatory species (Appendix 1. Table S7; Fig S2).

Neither natural enemies nor predators were significantly associated with different forest characteristics, although natural enemy abundance increased marginally with tree diameter and deciduous forest (Appendix 1. Table S8).

Fig. 4. The estimated production of spruce bark beetles per m^2 bark and the total number of infested trees in neighbouring patches.

3.3. *Forest variables*

The size of the sampled spruce trees (dbh) was significantly larger in the conservation areas (NR and WKH) compared to M (WKH-M: $p=0.01$; NR-M: $p<0.001$; Fig. 5a). There was less soil moisture in the M sites compared to WKHs ($p=0.002$), while NR did not differ from either M ($p=0.095$) or WKH ($p=0.0267$; Fig. 5b). The area of Norway spruce surrounding the sampling points where higher in NR compared to WKH ($p=0.038$; Fig. 5c). In contrast, deciduous forest was less abundant in WKHs compared to M ($p=0.047$; Fig. 5d). Analyses of general forest characteristics showed that higher soil moisture (wetter) significantly increased the colonisation densities (Fig. 3a), while deciduous forests decreased it (Table 1). Neither the area of spruce forest nor spruce diameter were found to have a significant association with colonisation densities, production or reproductive success.

4. Discussion

The within-tree population densities of the spruce bark beetles did not differ statistically between forest types (nature reserves (NR), woodland key habitats (WKH) and managed forest (M)). Since tree diameter in conservation areas were generally larger than those in managed forests, it might be expected that more beetles would be needed to overcome the tree defences in conservations areas (Hutchison and Reid, 2022), which would increase colonisation densities and thus affect other density patterns. On the other hand, the generally drier soil moisture in the conservation areas, suggests a higher tree stress level, which may potentially reduce and even out beetle densities. Due to large forest variations also within each forest type (e.g. protected areas; Mujezinović et al. 2023), differences in within-tree densities of bark beetles directly linked to conservation areas are difficult to find, though it may potentially occur at larger scales, such as at the stand or landscape level.

Instead of forest types, more of the bark-beetle variations were explained by outbreaks phases (i.e. years) and forest conditions. Colonization densities were generally lowest in 2021, probably due to an

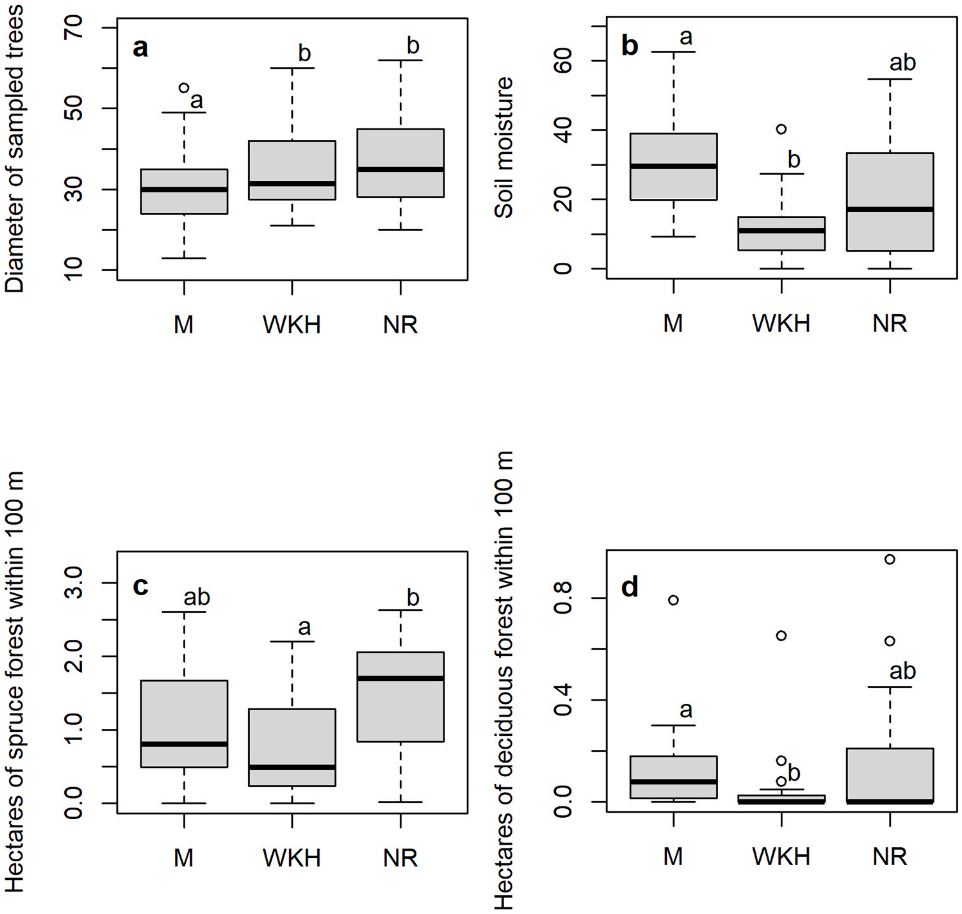


Fig. 5. Difference in a) tree diameter (cm) b) soil moisture, c) area of adjacent spruce forest and d) deciduous forests in managed forest (M), woodland key habitats (WKH) and nature reserves (NR). Letters denote significant differences ($p<0.05$).

Table 1

Spruce bark beetle population variables (colonisation densities, production and reproductive success) from bark samples and associations with forest conditions: spruce diameter of samples trees, and soil moisture index, area of spruce and deciduous forest (> 5 m) within 100 m from the main sampling point. Significant p-values are highlighted in bold.

	Colonisation densities			Beetle production			Reproductive success		
	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
Tree diameter	−0.029	0.037	0.440	0.057	0.059	0.331	0.062	0.040	0.127
Soil moisture	0.143	0.047	**0.002**	−0.050	0.073	0.492	−0.091	0.060	0.135
Spruce forest	0.015	0.049	0.755	−0.091	0.076	0.234	−0.032	0.063	0.610
Deciduous forest	−0.103	0.049	**0.037**	−0.065	0.075	0.390	0.025	0.062	0.694

unusually warm attack period this year, which occurred later than usual (e.g., the end of May and June, with a maximum temperature of 34.6°C in Southern Sweden—the highest since 1947; Swedish Meteorological and Hydrological Institute). This heat may have stressed the trees and lowered the colonization density required to overcome tree defences. The reproductive success were marginally higher in 2021 compared to the other years, which may be caused by the lower colonisation density resulting in a relaxation from intraspecific competition (Anderbrant et al., 1985; Schroeder et al. in prep).

Higher soil moisture increased the colonisation density (Fig. 3a), while deciduous forest reduced it. These findings are consistent with other studies indicating that factors associated with water deficits (e.g., aridity, slope, soil type, elevation, and solar radiation) increase the risk of attacks (e.g. Blomqvist et al., 2018, Netherer and Nopp-Mayr, 2005, Stadelmann et al., 2014), while soil moisture per se, decrease infestation risks (Müller et al., 2022; Netherer et al., 2015). The reasoning is that increased water availability boosts the tree's defence capacity by enhancing resin flow and induced defences, requiring a higher colonization rate of beetles to overcome these defences. In this study, a difference in moisture from dry to mesic-moist (Ågren et al., 2021) doubled the colonisation rates from 250 to 500 maternal galleries per m^2, which may reduce the reproductive success (Anderbrant et al., 1985). Such relationship was observed in 2021, with a general lower colonisation density and almost significant higher reproductive success. Unpublished results indicate that the relations between soil moisture and colonisation densities from NR were the main driver of these results, indicating that the results are context dependent. Bark-beetle colonisation densities related to water availability have been poorly studied at the scale of individual trees. In addition, the area of deciduous trees in the study sites seem to reduce the colonisation density. For spruce bark beetles, green-leaf volatiles have been found to inhibit pheromone attractions (e.g. Byers et al., 1998; Zhang and Schlyter, 2004) which potentially could reduce colonisation densities and risks of tree mortality. However, it could alternatively be related to an interspecific competition between spruce (*Picea* sp.) and birch (*Betula* sp.), which has been observed to reduce the growth and vitality of spruce in Canada (Green and Hawkins, 2005), and thus the number of bark beetles needed to overcome tree host defences.

In this study, 83 % (583 out of 700) of the infested neighbouring trees were attacked within the same year as the studied trees. Therefore, we do not believe that beetle pressure from the previous years influenced the population density at this scale, as the infestation risk during outbreaks is commonly within 100 m from the previous year (Wichmann and Ravn, 2001; Kautz et al., 2011). Interestingly, the number of infested trees within the same year was correlated with beetle production and reproductive success, suggesting that these within-tree metrics can serve as a proxy for infestation risk at a larger scale. These results may additionally be associated with higher beetle performance at a stand scale, influenced by an interplay of climatic factors (Mezei et al., 2017), nutrient content of the spruce phloem (Reid and Robb, 1999), and a dilution of natural enemies (Aukema and Raffa, 2004). Meanwhile, colonization densities in the trees are to some extent controlled by anti-aggregation pheromones to minimize intraspecific competition (Byers et al., 1984).

This study included eleven groups of natural enemies, of which two may be potential competitors (fungivores), leaving nine species classified as predators, pooled to separate analyses. The abundance of natural enemies was higher in NR compared to WKH. The enemy species composition in NR were additionally different from M. In contrast, the overall abundance and composition of the predators were consistent among the different forest types. Previous studies have found that the number of bark-beetle predators can vary across forest types depending on the predator species, with some being more abundant in managed forests (Schlyter and Lundgren, 1993; Hilszczański et al., 2007; Vanická et al. 2020) and others in unmanaged forests (Weslien and Schroeder, 1999; Johansson et al., 2007), suggesting that the total abundance from different predator species may balance each other out. Similarly, as an example from this study, clown beetles (*Plegaderus* spp. and parasitoids were more abundant in unmanaged than in managed forest, whereas soldier flies (Stratiomyidae) exhibited the opposite trend. Additional studies have found that some predators are increasing with higher densities of bark beetles (e.g. Martikainen et al., 1999; Johansson et al., 2007), which did not differ between the forest types included this study. Except for the clown beetles (*Plegaderus* spp.) and parasitoids also two fly families: Sciaridae and Cecidomyiidae had higher abundances in NR compared to M. Many species of Sciaridae and Cecidomyiidae are fungivorous and the larvae of these conifer-associated species commonly occur under the bark (Skuhravá et al., 2006). However, the biology and habitat preferences of these species-rich fly families (580 vs. 639 recorded species in Sweden) are poorly understood, and the reasons for their preferences for NR are unknown. Since the species are fungivorous and often relatively abundant in bark-beetle attacked trees (e.g. Hedgren and Schroeder, 2004), there may be interspecific competition with the spruce bark beetles, which may also feed to some extent on fungi (e.g. Tanin et al., 2021). However, since these species, included in natural enemy analyses, were more abundant in NR, while no reduction in bark-beetle densities were observed, we do not believe that these non-coleopteran competitors have a strong impact on bark-beetle densities.

In contrast to the numerous fly species included in the study, there are only six *Plegaderus* species found in Sweden. The most common species, *P. vulneratus* feed on both bark beetle larvae and eggs (Amett and Thomas, 2000; Pelto-Arvo, 2020 and references therein) and can respond quickly to infested trees as a response to bark beetle pheromones (Dixon and Payne, 1979; Pelto-Arvo, 2020). Accordingly, *Plegaderus* was found to be negatively associated with the bark-beetle reproductive success (Fig. 3). However, when zeros were excluded, no significant correlation was observed, suggesting that the mere presence of *Plegaderus* is more important than its abundance. The mean reproductive success in bark samples with *Plegaderus* was 1.79 (SD±1.62) daughters per mother, compared to 2.99 (±3.34) in samples without *Plegaderus* (Wilcoxon test: W = 6540, p-value = 0.035). Both the abundance and occurrence model indicated significant reproductive reductions with ~40 %. These results are similar to a study by Shepherd and Goyer (2005) in Lousianna (USA) who reported that *Plegaderus* sp. can reduce survival of *Ips calligraphus* with about 30 %. This is additionally comparable to the impact of the more well-known clerid beetle, *Thanasimus formicarius*, and long-legged flies *Medetera* spp., which have been documented to reduce the reproductive success of the spruce bark beetle by approximately 45 % (Weslien and Regnander, 1992) and 50 % (Weslien, 1992), respectively. Also in the present study, there was a negative correlation between *Medetera* spp, and the reproductive success of the bark beetles (Estimate: −0.003; p=0.044), though its effect was weaker compared to that of *Plegaderus*.

The results highlight *Plegaderus* as an additional candidate for controlling local bark beetle populations, particularly in NR, where it not only had a higher abundance but also had a 25 % higher occurrence per bark sample; 60 % in NR compared to 44–46 % in WKH and M. Accordingly, a three-fold higher abundance of *P. vulneratus* in unmanaged vs. managed stands has been observed in a previous study (Weslien and Schroeder, 1999).

In contrast to *Plegaderus*, parasitoids had a positive association with the reproductive success of the spruce bark beetle. The lack of a negative correlation with the reproductive success is that parasitoids have a limited effect on bark beetle populations, as each parasitoid developing in or on a host results in the death of just one bark beetle (Wegensteiner et al., 2015). Additionally, adult parasitoids do not feed on bark beetles. The positive correlation between parasitoids and the bark beetle reproductive success may be due to their synchronized response to bark beetle population fluctuations. (Wermelinger et al., 2013).

4.1. Conclusions

The within-tree colonisation densities, production or reproductive success of the spruce bark beetle did not differ significantly between nature reserves, set-asides and managed forest. Since there is a higher possibility that tree-mortality at larger scales occur when key thresholds at tree-levels are surpassed (Raffa et al., 2008), this information is important to understand infestation dynamics and risks in general, and particularly in conservation areas - often accused to act as bark beetle population sources. However, differences in population densities between forest types at larger scales may occur, but were not sufficiently evaluated in the present study. More general drivers for population densities in host trees include outbreak phases, forest characteristics per se, and the occurrence of predators. In wetter forests, more bark beetles are required to overcome tree defences, whereas in deciduous forests, pheromone responses might be inhibited by non-host volatiles or reduced tree vitality due to interspecific competition. Deciduous forests, along with large sized host trees, may also somewhat support the occurrence of natural enemies, such as the parasitoid wasps and clown beetles *Plegaderus* spp. of which the latter one may be important for controlling bark beetle populations. Consequently, when planning for forest management and maintaining predator populations, it is important to consider forest conditions such as ground moisture, the proportion of deciduous trees, and tree size related to rotation periods.

Funding sources

This work was supported by Skogssällskapet (2020–774), Formas – the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (2021–01610) and SLU Forest Damage Centre at the Swedish University of Agricultural Sciences (SLU) (2022–51–06).

CRediT authorship contribution statement

Simon Kärvemo: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Dragoş Cocoş:** Writing – review & editing, Methodology, Investigation, Data curation. **Evelina Andersson:** Writing – review & editing, Methodology, Investigation, Data curation. **Joachim Strengbom:** Writing – review & editing, Methodology, Investigation, Conceptualization.

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.

Acknowledgements

This study was funded by Skogssällskapet 2020–774, Formas – a Swedish Research Council for Sustainable Development 2021–01610 and SLU Forest Damage Centre at the Swedish University of Agricultural Sciences (SLU) 2022–51–06. We are also grateful to the Horizon project RESDINET. We also thank Pontus Eriksson and Hanna Jonsell for assistance in the field and in the lab and Anders Wiborg, Peter Post, Kristina Johansson and Kjell Mohlin for help with locating infestations. Finally, we thank Janne Weslien for commenting on an early draft of the manuscript. Approval for sampling infested trees in the nature reserves were received from the administrative county boards of Västra Götaland, Jönköping and Östergötland.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve readability and grammar of some sentences. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122424.

Data Availability

https://doi.org/10.5061/dryad.hhmgqnks1

References

Ågren, A.M., Larson, J., Paul, S.S., Laudon, H., Lidberg, W., 2021. Use of multiple LIDAR-derived digital terrain indices and machine learning for high-resolution national-scale soil moisture mapping of the Swedish forest landscape. Geoderma 404, 115280 https://doiorg/101016/jgeoderma2021115280.

Amett Jr., R.H., Thomas, M.C., 2000. American Beetles, Volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Florida.

Anderbrant, O., Schlyter, F., Birgersson, G., 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus.* Oikos 44, 89–98.

Annila, E., 1971. Sex ratio in *I typographus* L (Col, Scolytidae). Ann. Entomol. Fenn. 37, 7–14.

Aukema, B.H., Raffa, K.F., 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. Ecol. Entomol. 29, 129–138.

Blomqvist, M., Kosunen, M., Starr, M., Kantola, T., Holopainen, M., Lyytikäinen-Saarenmaa, P., 2018. Modelling the predisposition of Norway spruce to *Ips typographus* L infestation by means of environmental factors in southern Finland. Eur. J. For. Res. 137, 675–691.

Byers, J.A., Wood, D.L., Craig, J., Hendry, L.B., 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter-and intraspecific competition. J. Chem. Ecol. 10, 861–877.

Byers, J.A., Zhang, Q.H., Schlyter, F., Birgersson, G., 1998. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. Sci. Nat. 85, 557–561.

Dixon, W.N., Payne, T.L., 1979. Sequence of arrival and spatial distribution of entomophagous and associated insects on southern pine beetle infested trees. Tex. Agric. Exp. Stn. Misc. Publ. 1432 (No).

Green, D.S., Hawkins, C.D., 2005. Competitive interactions in sub-boreal birch–spruce forests differ on opposing slope aspects. For. Ecol. Manag. 214, 1–10.

Grodzki, W., 2016. Mass outbreaks of the spruce bark beetle *Ips typographus* in the context of the controversies around the Białowieża Primeval Forest. For. Res. Pap. 77, 324–331.

Hedgren, P.O., Schroeder, L.M., 2004. Reproductive success of the spruce bark beetle *Ips typographus* (L) and occurrence of associated species: a comparison between standing beetle-killed trees and cut trees. For. Ecol. Manag. 203, 241–250.

Hilszczański, J., Gibb, H., Bystrowski, C., 2007. Insect natural enemies of *Ips typographus* (L) (Coleoptera, Scolytinae) in managed and unmanaged stands of mixed lowland forest in Poland. J. Pest. Sci. 80, 99–107.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363.

Hutchison, I.K., Reid, M.L., 2022. Phloem and defence traits in relation to tree size and age: implications for host selection by bark beetles. For. Ecol. Manag. 513, 120183.

Jaime, L., Batllori, E., Lloret, F., 2024. Bark beetle outbreaks in coniferous forests: a review of climate change effects. Eur. J. For. Res. 143, 1–17.

Johansson, T., Gibb, H., Hjältén, J., Pettersson, R.B., Hilszczański, J., Alinvi, O., Danell, K., 2007. The effects of substrate manipulations and forest management on predators of saproxylic beetles. For. Ecol. Manag. 242, 518–529.

Kärvemo, S., Van Boeckel, T.P., Gilbert, M., Grégoire, J.C., Schroeder, M., 2014. Large-scale risk mapping of an eruptive bark beetle–importance of forest susceptibility and beetle pressure. For. Ecol. Manag. 318, 158–166.

Kärvemo, S., Johansson, V., Schroeder, M., Ranius, T., 2016. Local colonization-extinction dynamics of a tree-killing bark beetle during a large-scale outbreak. Ecosphere 7, e01257. https://doi.org/10.1002/ecs2.1257.

Kärvemo, S., Huo, L., Öhrn, P., Lindberg, E., Persson, H.J., 2023. Different triggers, different stories: Bark-beetle infestation patterns after storm and drought-induced outbreaks. For. Ecol. Manag. 545, 121255.

Kautz, M., Dworschak, K., Gruppe, A., Schopf, R., 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. For. Ecol. Manag. 262, 598–608 https://doiorg/101016/jforeco201104023.

Komonen, A., Schroeder, L.M., Weslien, J., 2011. *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. J. Appl. Entomol. 135, 132–141.

Kulakowski, D., 2016. Managing bark beetle outbreaks (Ips typographus, Dendroctonus spp) in conservation areas in the 21st century. Lesn Pr. Badaw. 77, 352–357.

Markovic, C., Stojanovic, A., 2010. Differences in bark beetle (Ips typographus and Pityogenes chalcographus) abundance in a strict spruce reserve and the surrounding spruce forests of Serbia. Phytoparasitica 38, 31–37.

Martikainen, P., Siitonen, J., Kaila, L., Punttila, P., Rauh, J., 1999. Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. For. Ecol. Manag. 116, 233–245.

Mezei, P., Jakuš, R., Pennerstorfer, J., Havašová, M., Škvarenina, J., Ferenčík, J., Netherer, S., 2017. Storms, temperature maxima and the Eurasian spruce bark beetle Ips typographus—An infernal trio in Norway spruce forests of the Central European High Tatra Mountains. Agric. For. Meteorol. 242, 85–95.

Mujezinović, O., Zahirović, K., Pernek, M., Vesnić, A., Ivojević, S., Dautbašić, M., 2023. Influence of forest type and climate factors on the number of caught Ips typographus (Coleoptera, Curculionidae) bark beetles in pheromone traps in protected areas of Bosnia and Herzegovina. SEEFOR 14, 171–182.

Müller, M., 2011. How natural disturbance triggers political conflict: bark beetles and the meaning of landscape in the Bavarian Forest. Glob. Environ. Change 21, 935–946.

Müller, M., Olsson, P.O., Eklundh, L., Jamali, S., Ardö, J., 2022. Features predisposing forest to bark beetle outbreaks and their dynamics during drought. For. Ecol. Manag. 523, 120480.

Netherer, S., Nopp-Mayr, U., 2005. Predisposition assessment systems (PAS) as supportive tools in forest management—rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. For. Ecol. Manag. 207, 99–107.

Netherer, S., Matthews, B., Katzensteiner, K., Blackwell, E., Henschke, P., Hietz, P., Schopf, A., 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? New. Phytol. 205, 1128–1141.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., et al., 2022. Package 'vegan' Community ecology package. R package version 26-4. ⟨https://CRANR-projectorg/package=vegan⟩.

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., et al., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Glob. Change Biol. 29, 1359–1376.

Pelto-Arvo, M., 2020. The impact of forest health status on natural enemies and associates of the European spruce bark beetle *Ips typographus* (L.). Master thesis. University of Helsinki.

Potterf, M., Svitok, M., Mezei, P., Jarčuška, B., Jakuš, R., Blaženec, M., Hlásny, T., 2023. Contrasting Norway spruce disturbance dynamics in managed forests and strict forest reserves in Slovakia. Forestry 96, 387–398.

R Core Team, 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517.

Reeve, J.D., 1997. Predation and bark beetle dynamics. Oecologia 112, 48–54.

Reid, M.L., Robb, T., 1999. Death of vigorous trees benefits bark beetles. Oecologia 120, 555–562.

Schlyter, F., Lundgren, U., 1993. Distribution of a bark beetle and its predator within and outside old growth forest reserves: no increase of hazard near reserves. Scand. J. For. Res. 8, 246–256.

Schroeder, M., Kärvemo, S., 2022. Rekordstort utbrott av granbarkborre–orsaker och vad man kan göra. Kungl Skogs-och Lantbruksakad. Tidskr. 7 [In Swedish].

Shepherd, W.P., Goyer, R.A., 2005. Impact of Platysoma parallelum and Plegaderus transversus (Coleoptera: Histeridae) predation on developing Ips calligraphus and Ips grandicollis (Coleoptera: Scolytidae) brood. J. Entomol. Sci. 40, 80–87.

Skuhravá, M., Skuhravý, V., Jørgensen, J., 2006. Gall midges (Diptera: Cecidomyiidae) of Denmark. Entomol. Medd. 72, 1.

Stadelmann, G., Bugmann, H., Wermelinger, B., Bigler, C., 2014. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. For. Ecol. Manag. 318, 167–174.

Swedish Environmental Protection Agency, 2020. Swedish national land cover database. ⟨https://www.naturvardsverket.se/en/services-and-permits/maps-and-map-services/national-land-cover-database/⟩.

Tanin, S.M., Kandasamy, D., Krokene, P., 2021. Fungal interactions and host tree preferences in the spruce bark beetle *Ips typographus*. Front. Microbiol. 12, 695167.

Timonen, J., Gustafsson, L., Kotiaho, J.S., Mönkkönen, M., 2011. Hotspots in cold climate: Conservation value of woodland key habitats in boreal forests. Biol. Conserv. 144, 2061–2067.

Vanická, H., Holuša, J., Resnerová, K., Ferenčík, J., Potterf, M., Véle, A., Grodzki, W., 2020. Interventions have limited effects on the population dynamics of *Ips typographus* and its natural enemies in the Western Carpathians (Central Europe). For. Ecol. Manag. 470, 118209.

Wegensteiner, R., Wermelinger, B., Herrmann, M., 2015. Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega, F., Hofstetter, R. (Eds.), Bark beetles: Biology and Ecology of Native and Invasive Species. Academic press, Amsterdam, pp. 247–304.

Wermelinger, B., 2002. Development and distribution of predators and parasitoids during two consecutive years of an *Ips typographus* (Col., Scolytidae) infestation. J. Appl. Entomol. 126, 521–527.

Wermelinger, B., 2004. Ecology and management of the spruce bark beetle Ips typographus—a review of recent research. For. Ecol. Manag. 202, 67–82.

Wermelinger, B., Obrist, M.K., Baur, H., Jakoby, O., Duelli, P., 2013. Synchronous rise and fall of bark beetle and parasitoid populations in windthrow areas. Agric. For. Entomol. 15, 301–309.

Weslien, J., Regnander, J., 1992. The influence of natural enemies on brood production in *Ips typographus* (Col. Scolytidae) with special reference to egg-laying and predation by *Thanasimus formicarius* (Col.: Cleridae). Entomophaga 37, 333–342.

Weslien, J., 1992. The arthropod complex associated with *Ips typographus* (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity. Entomol. Fenn. 3, 205–213.

Weslien, J., Öhrn, P., Rosenberg, O., Schroeder, M., 2024. Effects of sanitation logging in winter on the Eurasian spruce bark beetle and predatory long-legged flies. For. Ecol. Manag. 554, 121665.

Weslien, J., Schroeder, L.M., 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. For. Ecol. Manag. 115, 267–275.

Wichmann, L., Ravn, H.P., 2001. The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. For. Ecol. Manag. 148, 31–39.

Wijk, S., 2017. Biologisk mångfald i nyckelbiotoper: resultat från inventeringen. Uppföljning av biologisk mångfald 2009–2015. Report 2017/4. Swedish Forest Agency, Jönköping [In Swedish].

Zhang, Q.,H., Schlyter, F., 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. Agric. For. Entomol. 6, 1–20. https://doi.org/10.1111/j.1461-9555.2004.00202.x.