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Drivers of primary bark beetle (Coleoptera: Curculionidae, Scolytinae) infestations in even-aged, uneven-aged, and unmanaged Norway spruce forests in central Sweden

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ABSTRACT

Bark beetle outbreaks are an increasingly important disturbance in boreal forests, yet empirical evidence is limited on how management systems influence stand- and tree-level susceptibility to bark beetle infestation. We quantified infestation patterns of *Ips typographus*, *Pityogenes chalcographus*, and *Polygraphus* spp. across 29 spruce-dominated forest stands in central Sweden representing mature even-aged, uneven-aged, and unmanaged forests. Using GLMs and GLMMs, we evaluated how management type, stand structure, and tree characteristics influenced stand- and tree-level infestation probability. Stand-level predictors provided limited support for explaining infestation probability. For *I. typographus* and *Polygraphus* spp. the measured stand-level variables did not explain infestation probability better than intercept-only models. In contrast, *P. chalcographus* showed a more consistent stand-level response, with infestation probability decreasing with increasing spruce density. At the tree level, both *I. typographus* and *P. chalcographus* showed higher infestation probability in even-aged stands, independent of diameter, sun exposure, and tree condition. *Ips typographus* preferentially colonized larger and more sun-exposed trees, whereas *P. chalcographus* favoured smaller trees. *Polygraphus* spp. showed no detectable response to tree size or sun-exposure. Our results suggest that, under endemic conditions, bark beetle infestation could not be inferred from management category alone. Instead, infestation probability depended on beetle species and was more clearly related to individual host-tree characteristics than to broad stand-level differences among management types.

1. Introduction

Natural disturbance impacts on European forests have increased substantially over recent decades, driven in part by climate change, but also by forest management practices (Hartmann et al., 2022; Patacca et al., 2023; Seidl et al., 2011). Management strategies affect forest composition and structure, which in turn affect the forest's susceptibility to biotic and abiotic disturbances (Felton et al., 2016; Jactel et al., 2009). Among the main disturbance agents in boreal forests are bark beetles, which between 1950 and 2019 caused approximately 17% of the total timber volume disturbed in European forests (Patacca et al., 2023). Only a few bark beetle species are identified as being primary bark beetles, meaning that they can damage and kill living trees, in contrast to secondary bark beetles that utilize dying or recently dead trees. Although bark beetles play a key ecological role in forest succession and nutrient cycling, they also pose a risk to forest owners as outbreaks can result in severe economic losses, with additional negative impacts on ecosystem services (Ahtikoski et al., 2023; Hlásny et al., 2021; Raffa et al., 2015).

The most economically damaging species of bark beetle found throughout Eurasia is the European spruce bark beetle (*Ips typographus* (L.)). In Sweden, this species has killed trees amounting to approximately 34 million m^3 of timber—equivalent to the loss of 2.5% of the total growing stock—between 2018 and 2023 (Carlén et al., 2024). The

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2018 outbreak is the largest ever recorded in Sweden, triggered by an exceptionally warm and dry summer (Schroeder and Kärvemo, 2022). Other important primary bark beetle species found in Northern Europe are the six-toothed spruce bark beetle (*Pityogenes chalcographus* (L.)) and the four-eyed spruce bark beetle (*Polygraphus poligraphus* (L.)), which are also capable of attacking and killing weakened living trees (Eidmann, 1992). In recent years, damage to production forests by *P. poligraphus* has increased in Sweden, with particularly high levels recorded during the 2008–2011 outbreak in central Sweden (Wulff and Hansson, 2013). Furthermore, although *I. typographus* was the dominant damage-causing agent during the 2018 outbreak, *P. poligraphus*, and to a lesser extent *P. chalcographus*, both contributed to the observed tree mortality in production forests (Schroeder, 2023).

Bark beetle voltinism (number of annual broods or generations) varies depending on temperature and length of the reproductive season (Schebeck et al., 2017). Although Sweden currently hosts mostly univoltine populations of *I. typographus* and other bark beetles, climate warming may shift this balance (Fritscher and Schroeder, 2022; Hofmann et al., 2025; Jönsson et al., 2011). Rising temperatures also increase the risk of drought and tree stress, which increases the availability of hosts for bark beetles and amplifies the risk of infestation (Jakoby et al., 2019; Marini et al., 2017). Given the impact of bark beetle infestation and the increasing risk associated with climate change, there is a growing demand for strategies to mitigate and reduce the likelihood and severity of future outbreaks. Because stand structure and composition (e.g., tree species composition, deadwood availability and tree age distribution) influence the susceptibility of a forest patch to disturbances, and different management strategies produce varying stand structures and compositions, it is important to determine whether some strategies are more prone to bark beetle damage than others (Felton et al., 2024; Seidl et al., 2014).

Since the first half of the 20th century, forest management in Sweden has increasingly been defined by even-aged forestry, to the extent that today the vast majority of productive forest area is allocated to clear-cutting with retention of small amounts of living trees, soil scarification and replanting, followed by regular thinning operations to create even-aged stands dominated by Norway spruce (*Picea abies* (L.) Karst) or Scots pine (*Pinus sylvestris* (L.)) (Felton et al., 2020; Kuuluvainen et al., 2012; Lundmark et al., 2013). While this intensive approach to forestry has been highly successful at producing large amounts of wood per hectare, growing concerns suggest that these stands may be more susceptible to bark beetle infestations due to the high concentration of suitable host trees (Kärvemo et al., 2016; Müller et al., 2022). Host tree suitability is influenced by tree size and varies by beetle species, e.g., *I. typographus* is known to prefer larger diameter spruce trees while the opposite has been shown for *P. chalcographus* (Göthlin et al., 2000). The availability of suitable host trees also depends on the stage of rotation, with early phases in the rotation typically lacking appropriate host trees among the production stems, particularly for *I. typographus* that prefers larger host trees.

In uneven-aged forestry, 20–30% of the standing volume may be harvested at a given time through selective or group cutting (Ekholm et al., 2023). This method produces stands with multiple age classes and small-diameter openings, resulting in greater structural complexity than even-aged forestry (Aalto et al., 2023; Stiers et al., 2020). Such stands have fewer large trees relative to mature even-aged stands on soils of similar productivity, which could potentially reduce the density of suitable host material for *I. typographus* (Klapwijk et al., 2016). Despite this potential advantage, uneven-aged stands maintain some large-diameter trees throughout their rotation, which means that while the stem density is lower compared to even-aged stands, suitable host tree material is always available.

Current literature addressing the effects of uneven-aged forestry on the susceptibility of production stands to bark beetle damage has so far been mostly theoretical (e.g. Björkman et al., 2015; Klapwijk et al., 2016; Nevalainen, 2017), or based on remote sensing or simulations (Jönsson et al., 2015; Seidl et al., 2008), with little evidence from field experiments. Therefore, there is a need for empirical studies focusing on uneven-aged forestry and the associated risks of bark beetle damage.

Here we assess whether stand susceptibility to focal bark beetle infestation varies with forest management strategy, specifically by comparing even-aged and selectively cut uneven-aged forests, with unmanaged stands included as an additional reference. The study was conducted under endemic bark beetle population levels. More specifically, we ask: (1) whether management type (even-aged, uneven-aged, unmanaged) and stand characteristics (spruce density, pine and broadleaf basal area and structural heterogeneity) are associated with the stand-level probability of sampled dead or dying spruce showing signs of infestation, and (2) whether tree characteristics (diameter at breast height (hereafter diameter), condition, sun exposure), in combination with stand management type, are associated with the probability that an individual dead or dying spruce shows signs of infestation.

2. Material and methods

2.1. Study area and sites

The experimental sites used in this study were located in the boreal zone of central Sweden, in the counties of Jämtland and Västernorrland (Fig. 1). The study included 29 stands for tree-level analyses and 28 stands for stand-level analyses. Average monthly temperatures in the region vary from –8°C in January to 16°C in July, while the annual precipitation averages 600 mm yr^{-1} (SMHI, 2025). Norway spruce (*P. abies*) dominated the stands (>75% of basal area) with birches (*Betula pendula* and *B. pubescens*), smaller proportions of Scots pine (*P. sylvestris*) and other broadleaf species also present. Stand size varied between 2 and 11 ha, with an average size of 6.6 ha. Ground vegetation was dominated by bilberry (*Vaccinium myrtillus*). The study included three stand types: (1) mature even-aged stands, of approximately 60 years of age that underwent commercial thinning 18 ± 5 years ago (n = 9 for tree-level analyses; n = 8 for stand-level analyses), (2) mature uneven-aged stands that underwent selective felling 14 ± 5 years ago (n = 10), and (3) mature unmanaged stands without a recent (~50 years) history of management (n = 10).

2.2. Bark beetle sampling

The bark beetle sampling was done in August 2023 in 9 even-aged, 10 uneven-aged and 10 unmanaged stands. In each stand we surveyed three randomly selected 1000 m^2 transects for bark beetle damage. The transects extended from one edge of the stand to the opposite edge, oriented either north–south or east–west, with a 10 m buffer from the stand boundary. We chose the transect direction so that they ran perpendicular to old harvesting tracks, to avoid having transects that entirely followed the old tracks as these more open parts of stands would not be representative of the stand. In stands without old harvesting tracks transects stretched across the narrow part of the stand. Within each transect we visually surveyed every standing (≥ 9 cm in diameter) and fallen (≥ 20 cm diameter) dead or dying spruce tree for larval galleries of bark beetles, which usually required partial removal of bark. We classified trees as 'dead' when all needles were brown or had fallen off, and as 'dying' when most needles were brown, but some green needles remained. Due to variable tree conditions, with some trees recently dead with all bark remaining, and others highly decayed with hardly any bark left, it was not possible to remove a predetermined, standardized amount of bark from all trees. Instead, we removed bark until we could determine whether the focal bark beetle species were present, although with the limitation of not being able to reach or see the highest parts of standing trees. For each tree sampled, we removed bark from within an area reachable without a ladder (up to approximately 2.5 m). In the case of uncertainty in beetle identification, we collected bark samples and identified adult insects in the laboratory using a microscope. For each

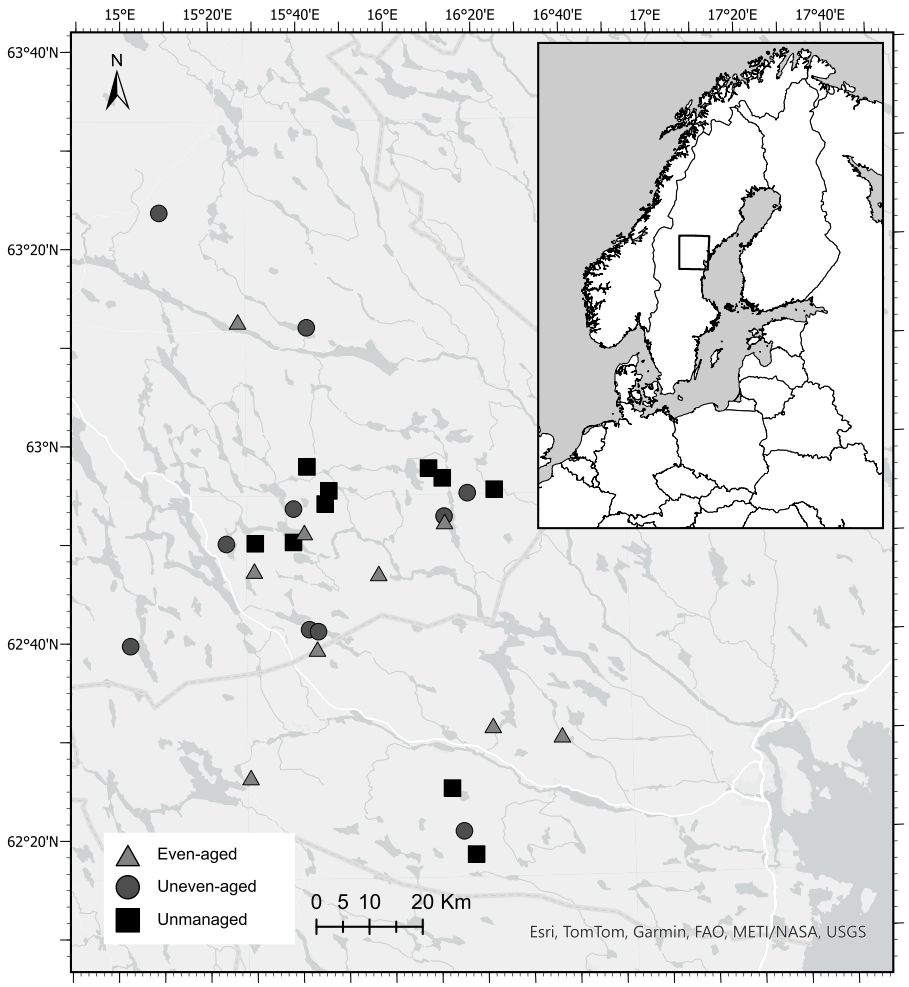

Fig. 1. Map with the location and the distribution of the forest stands used in this study.

species, only presence or absence was recorded. We selected three focal bark beetle species for this study: *Ips typographus, Polygraphus poligraphus* and *Pityogenes chalcographus.* All three species utilize spruce as their main host tree and can co-occur in the same tree. *I. typographus* typically colonizes the thicker bark of the lower bole and mid-stem of mature spruce trees and is the largest of the three species considered here (4.2–5.5 mm long; Heliövaara et al., 1998). In contrast *P. chalcographus* is smaller (1.6–2.9 mm long) and mainly infests the thin-barked upper part of mature spruce trees, although on younger trees it can colonize the entire tree (Grunwald, 1986). *Polygraphus poligraphus* (1.7–3.1 mm long) is known to colonize spruce trees of all sizes (Lekander, 1959). In Sweden, three species occur in the genus *Polygraphus* (*P. poligraphus*, *P. subopacus* and *P. punctifrons*), all of which use spruce as their host and have largely indistinguishable galleries. As such, we pooled observations of *Polygraphus* and treated them as *Polygraphus* spp. in all analyses.

For each inspected tree we noted diameter, sun exposure (shade, semi-shade, semi-open or open) and tree condition (fallen broken, uprooted, standing broken, standing unbroken) and decay stage. The sun exposure levels were based on the observers' (author IR) subjective assessment of the local canopy and light conditions rather than on quantified measures of canopy openness. In general, trees classified as open were fully exposed to direct sunlight for most of the day (e.g., standing in gaps), while semi-open trees received substantial but intermittent sunlight. Semi-shaded trees experienced limited direct sunlight due to partial canopy cover, and shaded trees were located beneath dense canopy where direct sunlight was largely absent. These categorizations reflect field judgments made at the time of survey rather than strict numerical thresholds. The grouping of tree conditions emphasized structural characteristics most relevant to bark beetle colonization, particularly degree of stem breakage and prolonged root contact. For standing trees, the decay stages were: (1) declining, (2) recently died, (3) dead with loose bark $>$ 50%, (4) no or nearly no bark, no branches, (5) broken or (6) broken and decomposed. For fallen trees, the decay stages were: (1) fresh bark: 100% coverage, (2) bark has partly fallen: a knife pushed hard against the trunk penetrates about 1 cm into the wood, (3) bark mainly fallen: a knife penetrates 2–3 cm into the wood, (4) wood can be torn with knife, or (5) wood can be torn with hands (Thomas, 1979).

2.3. Forest structure

Measurements of stand structure were conducted from June to September 2024 in the same stands as the bark beetle sampling the previous year, except that one even-aged stand was clear-cut between sampling years and was therefore excluded, leaving 8 even-aged stands for this sampling. We used one sample plot (10 m radius) per ha in each stand, with a maximum of five plots per stand. Plots were randomly selected from a pre-established grid within each stand. The grid contained 8–20 plots, with 40–60 m between plots, depending on stand size. Within each plot, we measured all standing trees with diameter $\geq$ 5 cm. Fallen trees were measured if their diameter was $\geq$ 20 cm and their point of origin, defined as the root base or stump location, was located within the plot boundary. Thus, fallen trees originating inside the plot were included even if they extended beyond the plot, whereas trees originating outside the plot but extending into the plot were excluded. For all trees, both standing and fallen, we noted species, decay stage,

diameter and tree condition. Decay stages for conifers were the same as mentioned above, while for deciduous trees they were based on the Swedish NFI classification system: 1) living, 2) fresh wood, 3) hard deadwood, 4) somewhat decayed wood, 5) decayed wood and 6) very decayed wood (Sandström et al., 2007). Based on the data collected, we calculated tree species composition, stems per ha, diameter distribution, basal area and the Gini-coefficient. Deadwood basal area was calculated from both standing and fallen deadwood and included all stages of decay. The Gini-coefficient describes the inequity of the diameter distribution and can be used to distinguish between even-aged and uneven-aged forests (Lexerød and Eid, 2006; Peck et al., 2014). The values range between 0 and 1, where low values describe high equality, or homogeneity, in diameter distribution, and high values indicate low equality, or heterogeneity, in diameter distribution. We used the R package "ineq" (Zeileis, 2014) to compute the Gini-coefficient.

2.4. Statistical analysis

All statistical analyses were done using the statistical software R (version 4.5.2; R Core Team, 2025). The applied explanatory variables were not substantially correlated based on a Pearson's correlation matrix. For pairs of variables with $r > 0.7$, one variable was removed, retaining the variable considered most ecologically meaningful. In all analyses, we checked model fit using the "DHARMa" package (Hartig et al., 2024), tested fixed effects using Type II likelihood ratio chi-square tests from the "car" package (Fox and Weisberg, 2019) and ran post-hoc comparisons using the "emmeans" package (Lenth et al., 2025). Results were considered statistically significant at $\alpha = 0.05$.

2.4.1. Stand structure

To analyse similarities in stand structure among management types, we used generalised linear mixed models (GLMMs) with different error distributions depending on the response variable, all fitted using the "glmmTMB" package (Brooks et al., 2017). We analysed basal-area related variables (basal area of living and dead trees, and species-specific basal area for spruce, pine, and broadleaf trees) using GLMMs with Gamma error distributions for strictly positive data, and Tweedie distributions where plots contained zero values. We analysed stand level inequality and size metrics, including the Gini-coefficient and overall stand size, using Gaussian GLMMs. We modelled tree size (average diameter by species group) and tree density variables (total living tree density and diameter class specific densities) using Gamma or Tweedie GLMMs. We fitted the stand-size model at stand level while fitted all other models at the plot level, with stand as a random effect. An overview of the models can be found in Table S1.

2.4.2. Stand susceptibility

To analyse how bark beetle infestation was associated with stand characteristics, we modelled infestation probability at the stand level using generalized linear models (GLMs). For this analysis, we pooled bark beetle infestation data from the three transects at the stand level to align with the stand structure data ($n = 28$). For each bark beetle group, we modelled the proportion of infested dead trees among surveyed dead trees using a two-column response matrix containing the number of infested trees and the number of non-infested trees. Models were fitted separately for each beetle group. For *I. typographus* and *Polygraphus* spp., we used beta-binomial models with a logit link, fitted using the "glmmTMB" package, to account for overdispersion. For *P. chalcographus*, we used binomial GLMs with a logit link, fitted using the base R "glm" function. All continuous predictor variables were scaled prior to analysis. Predictor variables included were (1) spruce density (stems/ha), (2) pine basal area, (3) broadleaf basal area, (4) Gini-coefficient and (5) management type. For each beetle group, we fitted the same set of six candidate models: (1) a null model with no predictors, (2) an additive model including all predictors, (3) a full model including all predictors and interactions between broadleaf basal area and spruce density and between broadleaf basal area and the Gini coefficient, (4) a model excluding management type to test whether infestation patterns were driven primarily by stand structure and composition rather than management, (5) a tree species composition model including spruce density and basal area of pine and broadleaved trees, and (6) a stand-structure model including spruce density and the Gini coefficient. Model assumptions and residual diagnostics were evaluated using simulated residuals from the "DHARMa" package, and overdispersion was assessed using Pearson residuals. We compared candidate models using Akaike Information Criterion for small sample sizes (AICc) and based the model selection on the relative support (ΔAICc and Akaike weights) of competing models (Burnham and Anderson, 2002). Model fit was additionally summarized using Nagelkerke's R^2, computed using the "performance" package (Lüdecke et al., 2021). We included interaction terms based on exploratory visual inspection of the data, which suggested potential non-additive relationships.

2.4.3. Tree level drivers of bark beetle infestation

We analysed the association between tree characteristics, management type, and the probability of bark beetle infestation at the tree level ($n = 938$) using a GLMM with binomial error distribution and fitted using the "glmmTMB" package. Fixed effects included management type, tree diameter (scaled), sun exposure class, and tree condition, together with beetle species and all interactions. We treated stands as a random effect nested within management type, with plots nested within stands. We initially included tree identity as a random effect but excluded it due to negligible variance.

3. Results

We surveyed a total of 938 dead or dying spruce trees, out of which 548 were infested by either one or more of the focal bark beetle species. Among the infested trees, 28% (155 trees) were infested exclusively by *I. typographus*, 41% (227 trees) by *Polygraphus* spp., 9% (50 trees) by *P. chalcographus*, and 22% (116 trees) by a combination of the focal bark beetle species (Table S2). Even-aged stands had a total of 133 dead trees (71% infested), uneven-aged stands had a total of 286 dead trees (57% infested) and unmanaged stands had a total of 519 dead trees (56% infested) (Table S3).

3.1. Stand structure

Deadwood basal area, average spruce diameter, density of small-diameter trees (5–10 cm), and the Gini-coefficient differed significantly between stand types (Table 1, S1). Deadwood basal area was higher in unmanaged stands than in even-aged stands. Average spruce diameter was higher in even-aged stands compared to both other stand types while the density of small diameter trees and the Gini-coefficient were lower in even-aged stands compared to both other stand types (Table S4).

3.2. Stand level susceptibility

AICc-based model selection indicated that, for both *I. typographus* and *Polygraphus* spp., the null model received the strongest support, suggesting that the measured stand-level predictors did not explain variation in infestation probability better than an intercept-only model (Table 2). These results indicate limited evidence that infestation probability of *I. typographus* or *Polygraphus* spp. was associated with the stand-structure or tree-species composition variables included in the candidate model set.

For *P. chalcographus*, model selection was less conclusive. Two models received similar support, with $\Delta AICc < 2$: model 4, which included spruce density, pine basal area, broadleaf basal area, and the Gini coefficient, and model 2, which included the same variables plus

Table 1
Tree and stand structure variables for each management type (mean ± SD is provided). Generalized linear mixed models were used to test for similarities between stand types. The letters after the mean values denote significant differences in the post-hoc test ($P < 0.05$, as indicated in bold).

	Unit	Even-aged	Uneven-aged	Unmanaged	P-value
Nr of stands	n	8	10	10	
Stand size	ha	6.42 (±2.17)	6.46 (±2.14)	6.85 (±3.14)	0.920
Basal area living trees	m^2/ha	27.5 (±7.9)	29.0 (±8.77)	31.3 (±11.2)	0.633
Basal area spruce	m^2/ha	23.6 (±7.55)	22.7 (±8.76)	25.3 (±9.67)	0.463
Basal area pine	m^2/ha	1.55 (±3.05)	1.3 (±3.05)	2.78 (±5.01)	0.708
Basal area broadleaf	m^2/ha	2.34 (±3.11)	4.96 (±6.4)	3.26 (±4.11)	0.398
Basal area deadwood	m^2/ha	2.59 (±3.15) b	5.36 (±5.07) ab	10.1 (±8.46) a	**< 0.001**
Average DBH spruce	cm	19.1 (±7.34) a	14.7 (±8.47) b	15.6 (±8.85) b	**< 0.001**
Average DBH pine	cm	22.5 (±7.53)	29.5 (±5.21)	33.3 (±9.19)	0.696
Average DBH broadleaves	cm	14.6 (±6.6)	18.6 (±9.82)	13 (±6.96)	0.113
Density living trees	n/ha	873 (±341)	1169 (±407)	1222 (±643)	0.078
Density 5–10 cm DBH	n/ha	140 (±127) b	448 (±289) a	449 (±405) a	**< 0.001**
Density 11–20 cm DBH	n/ha	398 (±289)	406 (±191)	460 (±314)	0.812
Density 21–30 cm DBH	n/ha	283 (±154)	242 (±114)	218 (±120)	0.233
Density > 30 cm DBH	n/ha	51.6 (±65.6)	73.2 (±68.4)	94.1 (±80.3)	0.111
Gini-coefficient		0.227 (±0.05) b	0.304 (±0.03) a	0.298 (±0.02) a	**< 0.001**

management type (Table 2). This indicates some model-selection uncertainty, suggesting that model 4 should not be treated as unambiguously better supported than model 2. Across both supported models, however, spruce density was consistently retained and was negatively associated with *P. chalcographus* infestation probability (Fig. 2). This suggests that, among the measured predictors, the most consistent result was a negative association between spruce density and *P. chalcographus* infestation probability. Other predictors showed less consistent support. In model 4, pine basal area and the Gini coefficient were negatively associated with infestation probability, whereas broadleaf basal area was not significant. In model 2, spruce density was the only continuous stand variable that remained clearly significant. Management type showed only weak support as a predictor: the overall Type II likelihood-ratio test was nearly significant ($p = 0.054$), although pairwise comparisons of estimated marginal means suggested higher *P. chalcographus* infestation probability in even-aged than unmanaged stands ($p = 0.048$, Table S5). Because models 4 and 2 had similar AICc support, and because the supported predictors differed between them, the associations with pine basal area, the Gini coefficient, and management type should be interpreted cautiously.

Model diagnostics further supported a cautious interpretation. For *P. chalcographus*, diagnostic results differed between the two top-ranked models: model 4 showed poor residual diagnostics, whereas model 2 had acceptable model fit. Among the lower-ranked *P. chalcographus* models, model 5 showed evidence of dispersion problems, and model 6 showed deviations from the expected residual distribution. Residual diagnostics were generally acceptable for most *I. typographus* models, although model 5 showed deviations from the expected residual distribution. For *Polygraphus* spp., model 3 showed convergence problems and poor residual diagnostics, suggesting overfitting, and models 5 and 6 showed

Table 2
Model selection results for all candidate models fitted for Ips typographus, Pityogenes chalcographus and Polygraphus spp. Models are ranked by Akaike's Information Criterion corrected for small sample size (AICc). For each model, degrees of freedom (df), log- likelihood (logLik), AICc, ΔAICc, and Akaike weight are reported. The lowest AICc model for each species is marked in bold.

Species	Model ID	Model terms	df	logLik	AICc	ΔAICc	weight	Nagelkerke's R2
I. typographus	**1**	**Intercept**	**2**	**−75.32**	**155.1**	**0.00**	**0.84**	**0**
	6	Sprtuce density + Gini	4	−74.68	159.1	3.97	0.12	0.045
	5	BA broadleaf + BA pine + Spruce density	5	−74.39	161.5	6.39	0.03	0.064
	4	BA broadleaf + BA pine + Spruce density + Gini	6	−73.55	163.1	7.99	0.02	0.119
	2	BA broadleaf + BA pine + Gini + Spruce density + Management	8	−73.28	170.1	15.02	0.00	0.136
	3	BA broadleaf + BA pine + Gini + Spruce density + Management + BA broadleaf*Spruce density + BA broadleaf*Gini	10	−73.14	179.2	24.12	0.00	0.144
Polygraphus spp.	**1**	**Intercept**	**2**	**−69.33**	**143.1**	**0.00**	**0.76**	**0**
	5	BA broadleaf + BA pine + Spruce density	5	−66.96	146.6	3.51	0.13	0.066
	6	Spruce density + Gini	4	−69.15	148.0	4.89	0.07	0.184
	4	BA broadleaf + BA pine + Spruce density + Gini	6	−66.75	149.5	6.35	0.03	0.216
	3	BA broadleaf + BA pine + Gini + Spruce density + Management + BA broadleaf*Spruce density + BA broadleaf*Gini	10	−59.59	152.1	8.99	0.01	0.633
	2	BA broadleaf + BA pine + Gini + Spruce density + Management	8	−66.22	156.0	12.88	0.00	0.499
P. chalcographus	**4**	**BA broadleaf + BA pine + Gini + Spruce density**	**5**	**−55.20**	**123.1**	**0.00**	**0.52**	**0.669**
	2	**BA broadleaf + BA pine + Gini + Spruce density + Management**	**7**	**−52.27**	**124.1**	**1.02**	**0.31**	**0.733**
	5	BA broadleaf + BA pine + Spruce density	4	−58.10	125.9	2.81	0.13	0.591
	6	Spruce density + Gini	3	−60.81	128.6	5.50	0.03	0.503
	3	BA broadleaf + BA pine + Gini + Spruce density + Management + BA broadleaf*Spruce density + BA broadleaf*Gini	9	−52.23	132.5	9.34	0.01	0.734
	1	Intercept	1	−70.50	143.2	20.03	0.00	0

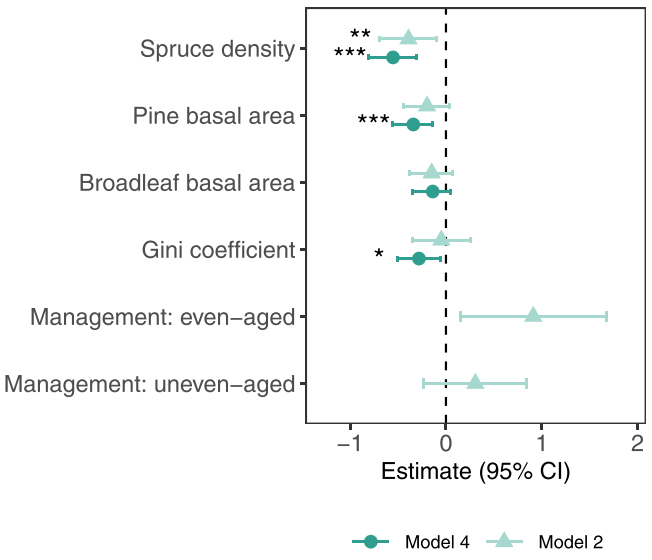

Fig. 2. Generalized linear model coefficient estimates for the relationship between stand characteristics and probability of *Pityogenes chalcographus* infestation. The two best-supported models with ΔAICc < 2 are shown. (Table 1). Whiskers denote 95% confidence intervals of the coefficient estimates. Asterisks indicate statistical significance based on Type II likelihood-ratio tests for each model term (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$).

deviations from the expected residual distribution.

3.3. Tree level drivers of bark beetle infestation

The predicted probability of infestation by *I. typographus* increased significantly with tree diameter (Fig. 3, Table S6). Infestation probability differed among management types, with higher predicted probabilities in even-aged stands compared to unmanaged stands (Fig. 4a, Table S7). Infestation probability decreased with increasing shade, with the lowest probabilities observed under fully shaded conditions (Fig. 4b, Table S8). Predicted *I. typographus* infestation probability differed also among tree condition categories, with significantly higher probability for fallen broken trees than all other categories. In addition, unbroken standing trees had significantly higher probability of infestation than broken standing and uprooted trees (Fig. 4c, Table S9).

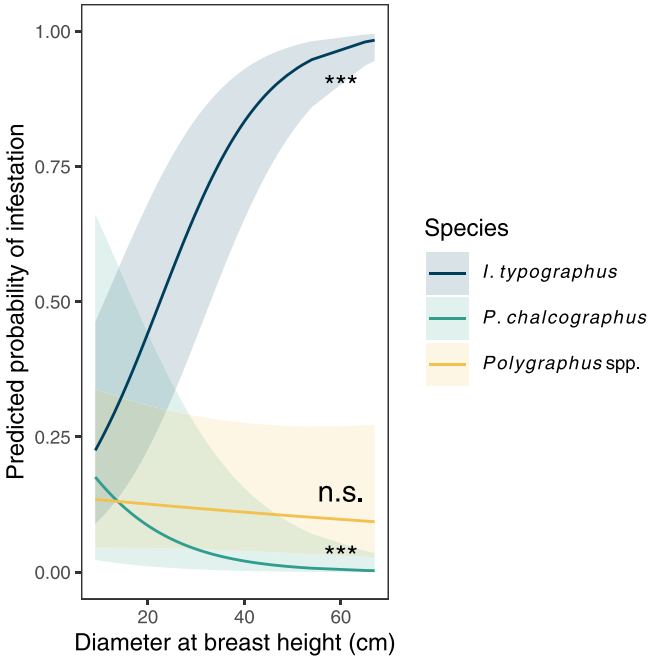

Fig. 3. Model-predicted probability of bark beetle infestation in relation to tree diameter at breast height. Curves represent fitted probabilities for Ips typographus (blue), Pityogenes chalcographus (green), and Polygraphus spp. (yellow), with shaded areas indicating 95% confidence intervals.

The predicted probability of infestation by *P. chalcographus* was negatively associated with tree diameter (Fig. 3, Table S6). Infestation probability differed among management types, with higher predicted probabilities in even-aged stands compared to unmanaged and uneven-aged stands (Fig. 4a, Table S7). Predicted infestation probability was significantly correlated with sun exposure, with higher probabilities in semi-open and semi-shaded trees compared to fully shaded trees (Fig. 4b, Table S8). Infestation probability differed among tree condition categories with higher predicted probabilities in fallen broken trees compared to unbroken standing trees (Fig. 4c, Table S9).

The predicted probability of infestation by *Polygraphus* spp. differed significantly among tree condition categories with higher probabilities in unbroken standing trees compared to all other categories. Standing broken trees had higher infestation probabilities than fallen broken and uprooted trees and fallen broken trees showed higher infestation probabilities than uprooted trees (Fig. 4c, Table S9). No significant effects of tree diameter, sun exposure, or management type were detected.

4. Discussion

4.1. Stand level susceptibility

Contrary to our expectation that stand-level susceptibility would be broadly explained by stand structure or management type, support for stand-level predictors was limited and species-specific. For *I. typographus* and *Polygraphus* spp., null models received the strongest support, indicating that the measured stand-level variables did not explain infestation probability better than an intercept-only model. The clearest exception was *P. chalcographus*, for which spruce density was consistently negatively associated with infestation probability.

The lack of support for stand-level predictors in *I. typographus* and *Polygraphus* spp. should not be interpreted as evidence that stand structure is irrelevant to bark beetle infestation. Previous studies have shown that stand structure can influence bark beetle susceptibility, for example through host-tree availability (Kärvemo et al., 2016; Netherer and Nopp-Mayr, 2005; Stadelmann et al., 2014), presence of non-host trees (Kärvemo et al., 2016), deadwood availability (Joensuu et al., 2008; Martikainen et al., 1999) and stand density (Netherer, 2003). The discrepancy between those findings and our results may reflect differences in population phase, spatial scale, or the specific structural variables measured. Because our study was conducted under endemic conditions, where beetles primarily exploit weakened, stressed, or recently dead trees (Lindgren and Raffa, 2013), infestation may have depended more on the availability and characteristics of suitable individual host trees than on broader stand-level variables such as tree-species composition or stand structure. This interpretation is supported by our tree-level results, where infestation probability showed clear associations with tree diameter, sun exposure, and tree condition. In addition, the sampling intensity used to characterize stand structure may have limited our ability to detect stand-level effects. Although one 10-m radius plot per hectare provided a standardized and spatially distributed estimate of stand conditions, it may not have fully captured fine-scale heterogeneity in variables such as tree-species composition, stem density or diameter distribution. This could have weakened the association between measured stand-level predictors and the local conditions experienced by beetles. Therefore, the lack of support for stand-level predictors should be interpreted with caution, as it may partly reflect limited resolution in the stand-structure data rather than an absence of stand-level patterns.

In contrast, *P. chalcographus* showed some evidence of stand-level

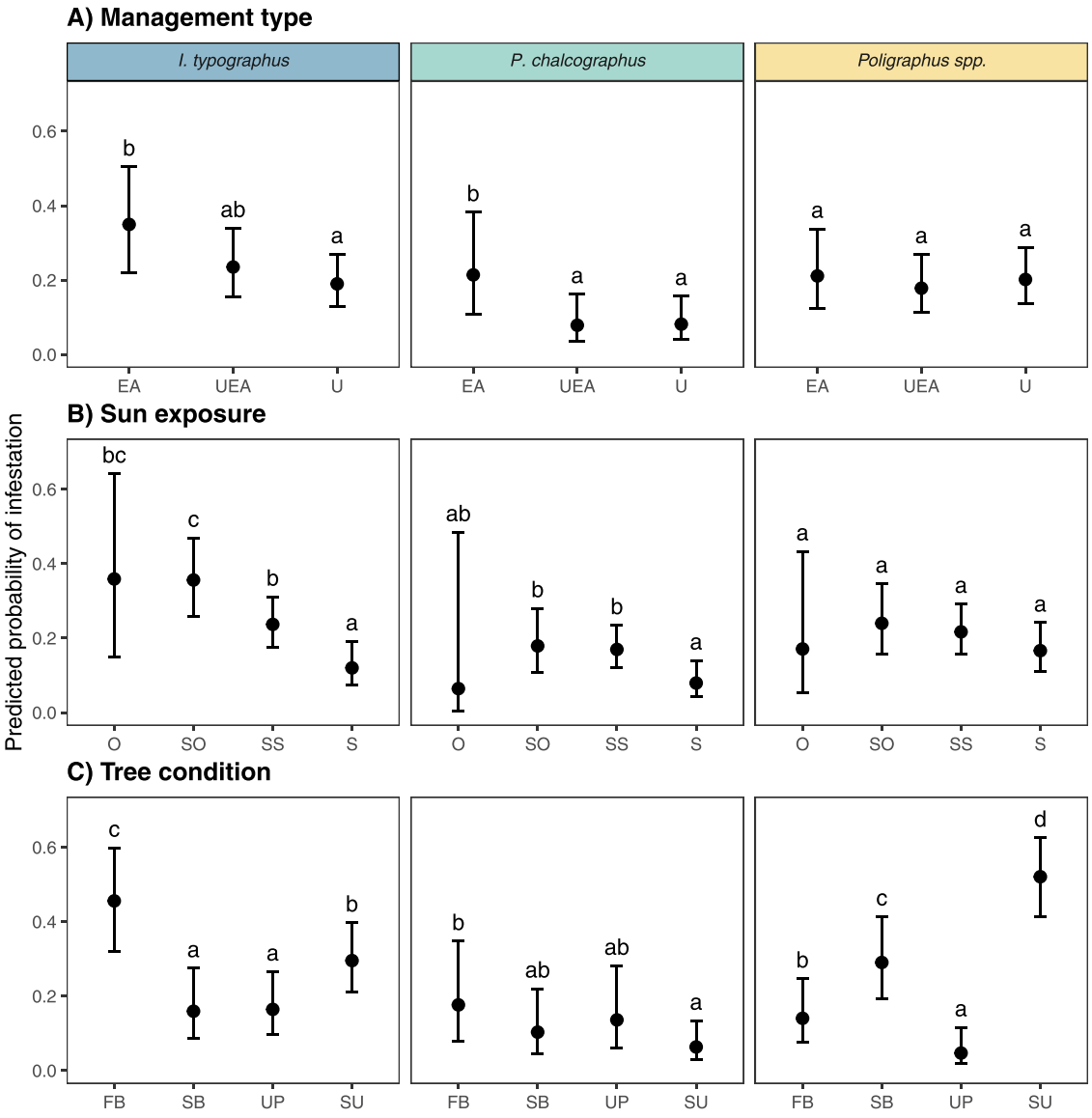

Fig. 4. Predicted probability of infestation (±95% confidence intervals) of individual spruce trees by Ips typographus, Pityogenes chalcographus and Polygraphus spp. across (A) forest management type, (B) sun exposure levels, and (C) tree condition categories. Management types include even-aged (EA), uneven-aged (UEA) and unmanaged (U) stands. Sun exposure levels are open (O), semi-open (SO), semi-shaded (SS) and shaded (S). Tree condition categories are fallen broken (FB), standing broken (SB), uprooted (UP) and standing unbroken (SU). Different letters above points indicate statistically significant differences among factor levels within species (Tukey-adjusted comparisons, $p \leq 0.05$).

sensitivity, with spruce density emerging as the most consistent predictor across the supported models. Infestation probability decreased with increasing spruce stem density, which was somewhat unexpected given that spruce is the main host tree for this species. One possible explanation is that denser spruce stands create cooler and shadier microclimatic conditions, which may reduce beetle activity or limit the suitability of host material despite greater host availability (Netherer and Nopp-Mayr, 2005). Thus, spruce density may reflect not only host availability, but also microclimatic conditions that influence colonization. Alternatively, under endemic conditions when beetle populations are low, higher spruce density might dilute beetle pressure, resulting in fewer detectable colonisations at the stand level. The fact that this structural variable influenced *P. chalcographus,* but not the other taxa, highlights that stand susceptibility is not uniform across bark beetle species, even when they occupy similar host trees and co-occur in the same stands. In addition to the association with spruce density, there was a weak trend toward higher probability of *P. chalcographus* infestation in even-aged stands compared with unmanaged stands. This result should be interpreted cautiously due to model uncertainty and low level of significance, however it is worth noting that the direction of the trend is consistent with our tree-level results, where *P. chalcographus* also showed higher infestation probability in even-aged stands.

Although the three management types differed in some structural attributes, variation within management type was substantial. This combination of overlap among types and large within-type variability likely explains why management type generally did not emerge as an important predictor of infestation intensity at the stand level. Several stand characteristics commonly proposed to mediate bark beetle susceptibility were weakly aligned with management categories. For example, uneven-aged management has been suggested to reduce susceptibility by maintaining a lower density of large spruce, as selective harvesting of dominant trees should limit the availability of preferred hosts (large-diameter spruce) for *I. typographus* (Klapwijk et al., 2016). However, we found no consistent differences in the density of

large-diameter spruce among stand types.

4.2. Tree level drivers of bark beetle infestation

Management appeared significant in our tree-level analysis, with higher probability of *I. typographus* and *P. chalcographus* infestation in even-aged stands than in other stand types. Because our analysis accounted for diameter, sun exposure and tree condition, the influence of management likely reflects additional tree-level attributes or micro-habitat conditions that differ consistently among management types but were not captured in our study. Even-aged stands are typically more homogeneous with respect to tree genetics, age, size and spacing than uneven-aged forests (Hanewinkel, 2004), creating a more uniform canopy and a more continuous distribution of similar host trees. Such structural uniformity could increase host apparency, making trees in even-aged stands easier for dispersing bark beetles to detect and thereby increase colonization pressure. The modest but consistent influence of management therefore suggests that even-aged management can shape fine-scale host conditions in ways that favour colonization by some bark beetle species, a pattern that is further supported by the stand-level trend shown for *P. chalcographus*.

At the tree level, infestation probabilities also varied in relation to species-specific responses to tree diameter, sun exposure and tree condition. For *I. typographus*, higher probabilities on larger trees align with results from previous studies and with its preference for hosts that provide sufficient phloem resources for bark beetles (Göthlin et al., 2000; Lekander, 1972; Vodde et al., 2025). In contrast, *P. chalcographus* showed the opposite pattern, consistent with its suggested specialisation for small-diameter trees, or the upper parts of trees where the bark is thinner, likely to avoid niche competition with *I. typographus* (Göthlin et al., 2000). Sun exposure also influenced the probability of infestation for *I. typographus*, indicating a preference for more sun-exposed trees, which also agrees with previous studies (Kautz et al., 2013). Because we recorded both new and older infestations, the tree condition categories do not necessarily represent the condition of the tree at the exact time of colonization. We therefore interpret the relationship between infestation probability and tree condition with caution, as some trees may have changed condition after colonization. Differences among tree condition classes showed the highest probability of *I. typographus* infestation in fallen broken trees. This category includes any fallen tree without remaining root contact, regardless of whether the stem failed at the base or higher up. Because our survey was conducted under endemic beetle populations, when the beetles mainly exploit weakened or recently dead hosts (Boone et al., 2011), it is more likely that most infestations occurred after the trees had already broken. Although older attacks were also recorded, there have been no known outbreaks in these specific stands, and most infestations were found in trees of early decay stages (Table S10). Together, this suggests that most colonization took place following mechanical damage caused by, for example, storm or snow, when these trees would have been physiologically compromised and easier to exploit. The second-highest infestation probability for *I. typographus* was found in standing unbroken trees. Since their vitality at the time of infestation is unknown, this class likely contains a mixture of trees that were weakened or dying before beetles arrived, and trees that were colonized while still alive. This pattern indicates that *I. typographus* targets a range of suitable substrates, from easy hosts such as newly fallen trees to potentially higher-quality, still-standing hosts, reflecting a trade-off between ease of colonization and host quality (Lindgren and Raffa, 2013). In contrast, *P. chalcographus* showed no strong preferences among our categories of tree condition, while *Polygraphus* spp. displayed a tendency to colonize standing trees, consistent with the anecdotal observations of Ehnström and Axelsson (2002). Overall, although we cannot determine the exact timing of colonization relative to tree death, the patterns across tree condition classes provided insights into which substrates are most likely to be colonized by each species under endemic conditions.

4.3. Conclusions and implications for management

Stand-level predictors provided limited and species-specific support for explaining bark beetle infestation probability. For *I. typographus* and *Polygraphus* spp., the measured stand-level variables did not explain infestation probability better than null models, whereas *P. chalcographus* showed a more consistent negative association with spruce density. This suggests that stand-level susceptibility was not uniformly determined by either management category or the measured structural variables. Instead, infestation patterns were more clearly expressed at the tree level, where host tree diameter, sun exposure, tree condition, and, for *I. typographus* and *P. chalcographus*, management context were associated with infestation probability.

From a management perspective, these findings suggest that bark beetle activity under endemic conditions cannot be inferred from management category alone. Although even-aged, uneven-aged, and unmanaged stands differed in some structural attributes, the overlap among stand types and the weak support for stand-level models indicate that broad management categories alone did not reliably capture variation in infestation probability. Management may instead influence infestation risk indirectly by shaping the availability and characteristics of suitable host trees, local microclimatic conditions, and the spatial distribution of weakened or recently dead spruce.

Because this study was conducted under endemic conditions, the observed patterns should not be extrapolated directly to outbreak scenarios, during which host selection and the relative importance of stand structure and management may differ substantially. Nevertheless, this study adds field-based empirical evidence to the limited literature on bark beetle infestation in uneven-aged forests. Rather than providing a simple ranking of management systems by susceptibility, our results suggest that future assessments should consider beetle species identity, local host-tree characteristics, stand structure and population phase when evaluating bark beetle risk.

CRediT authorship contribution statement

Ida Rönnqvist: Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Anne-Maarit Hekkala:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Jörgen Sjögren:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Matti Koivula:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Maartje Klapwijk:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Felton Annika:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Adam Felton:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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

During the preparation of this work, author IR used ChatGPT (OpenAI) for language editing and readability improvements. After using this tool, the author reviewed and edited the content as needed and take full responsibility for the content of the publication.

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.2026.124065.

Data availability

Data will be made available on request.

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