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Bark beetles on logging residues of European larch: Effects of shading and diameter of logging residues on infestation density

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Abstract

1. *Ips cembrae*, an important pest of European larch (*Larix decidua*), has caused local outbreaks in the last two decades and is becoming increasingly important as the proportion of European larch in forests increases.
2. In 2021–2023, larch logs and piles of branches were placed into shaded forest and sunlit areas every month to study bark beetle species on logging residues. After adult emergence, the logs and branches were debarked, and the infestation density of bark beetles was analysed. The results indicate that shading, log diameter and top/bottom parts of log had a significant effect on infestation density of *I. cembrae* on logs. The infestation density of *I. cembrae* was higher on logs felled between December and June than on logs felled between July and November.
3. Shading of branches was the most significant variable affecting the bark beetle species composition on branches. All four of the bark beetle species recorded were affected by diameter of the branches. *Ips cembrae* primarily infested sunlit branches while *Cryphalus intermedius* preferred shaded branches. In contrast, the infestation densities of *Pityogenes chalcographus* and *Pityophthorus pityographus* seemed to be affected primarily by moisture content of the branches.

KEYWORDS
Cryphalus intermedius, *Ips cembrae*, *Larix decidua*, thinning

INTRODUCTION

Bark beetles are among the most common and abundant forest pests of Eurasia and America (Bentz et al., 2010; Marini et al., 2017; Thom et al., 2013). Some species of conifer bark beetle can produce outbreaks during favourable environmental conditions, causing large-scale dieback of forest stands (Biedermann et al., 2019; Raffa et al., 2008). Bark beetles of the genera *Ips* and *Dendroctonus* have destroyed millions of hectares of coniferous forests in the Americas and Europe over the past few decades (Hicke et al., 2015; Seidl et al., 2014). Following the outbreak of the spruce bark beetle (*Ips typographus* L.) in the Czech Republic, European larch is being studied as a suitable tree species for reforestation of clear-cut areas (Kulla & Sitková, 2012; Zeidler et al., 2022). Planting European larch in a mixture reduces the probability of infestation by bark beetles (Berthelot et al., 2021). Over the last 50 years, the area reforested with larch in Europe has increased, particularly in the last few decades (Lindelöw et al., 2015).

Thinning is the silvicultural reduction of tree density and management of stand structure, resulting in increased resistance and resilience to drought (D'Amato et al., 2013; Zhang et al., 2024) and increased forest growth (Ara et al., 2023; Roberts & Harrington, 2008). Thinning is usually conducted during periods of reduced beetle activity (Fettig et al., 2007). Thinning increases trees' resistance to bark beetle attack (Brandt et al., 2019; Fettig et al., 2012; Hood et al., 2016). Sanitation logging is the harvesting of trees for the purpose of removing insects or diseases, and salvage logging is the practice of harvesting dead, dying, damaged or weakened trees to recover economic losses from natural disturbances (Hlásny et al., 2019). Sanitation logging is one of the most widespread methods of mitigation of forest disturbances (Leverkus et al., 2018; Müller et al., 2018). Logging residues (logging residues) are the parts of trees left in the forest after thinning and felling and extraction of marketable timber. They include branches, tree tops, technically damaged trunks and stumps (Achat et al., 2015; Foit, 2015a; Ranius et al., 2018). Logging residues can be burned in the forest, chipped and left in the forest or used to produce bioenergy (Mott et al., 2021; Rautiainen et al., 2018; Yan et al., 2017). Leaving logging residues in the forest decreases nutrient depletion from the forest (Ranius et al., 2018; Špulák & Kacálek, 2020; Wall, 2008), particularly as logging residues have higher concentrations of nutrients compared to concentrations in stems (Klockow et al., 2014) logging residues.

The presence of dead wood in a forest increases its biodiversity (Floren et al., 2014; Lassauce et al., 2011; Seibold et al., 2016). Host volatiles emitted from logging residues in clear-cut areas increases the attraction of bark beetles (Müller et al., 2022). For secondary bark beetle species, such as *Ips* spp., logging residues or stressed host trees are important for the growth of populations (Gomez et al., 2023). Foit (2015c) states that logging residues play a minor role in the conservation of saproxylic beetles, but their presence increases the risk of certain pest outbreaks, for example, of bark beetles, as they can rapidly multiply to outbreak proportions on logging residues (Fiala & Holuša, 2022). Some bark beetle species prefer to attack logging residues scattered in the forest rather than in piles (Kacprzyk, 2012; Six et al., 2002). Removal of potential breeding material and infested trees is one of the most effective methods of mitigating bark beetle outbreaks (Dobor et al., 2020; Grégoire & Evans, 2004; Wermelinger, 2004). In removal operations, potential breeding substrate in storm gaps and on stand edges should be given higher priority than material within stands (Göthlin et al., 2000). In the last few decades, several studies on the importance of *Ips cembrae* (Heer) have been published (Arač & Pernek, 2014; Grodzki, 2008; Holuša et al., 2014; Resnerová et al., 2020; Špoula & Kula, 2023a; Špoula & Kula, 2023b). Grodzki (2008) recorded an outbreak of *I. cembrae* in Poland caused by leaving logging residues from thinning and windthrown trees in the forest. *Ips cembrae* is widespread in the Europe, even outside its natural range (Lindelöw et al., 2015). In the Czech Republic, *I. cembrae* is widespread (Grucmanová et al., 2014), and 47,000 m^3 of larch wood infested with *I. cembrae* was logged between 2016 and 2020 (Špoula & Kula, 2023b). *Ips cembrae* usually produces two generations per year (Grucmanová et al., 2014; Holuša et al., 2014). The flight activity begins in April and ends in late summer (mid-September), and the population density of the summer generation is usually lower (Arač & Pernek, 2014; Špoula & Kula, 2023a).

Studies have been published on the effect of logging residues from various tree species on cambio- and xylophagous and saproxylic insects (Foit, 2015a, 2015b, 2015c; Jonsell et al., 2007; Lassauce et al., 2012; Maňák & Jonsell, 2016; Six et al., 2002), but no author has published a study on logging residues from thinning and felling of European larch. The increasing area forested with larch in Europe has acted as an impetus for us to study the potential risk of leaving larch logging residues in the forest.

The aims of this study were to: (i) assess the effects of logging residues variables (shading, moisture content [MC] of the phloem and attractiveness of top/bottom part of larch logs) on *I. cembrae* infestation density (ID) on larch logs from thinning (Experiment 1) and (ii) identify the bark beetle species that infest larch branches as breeding material and investigate the effects of shading, MC of the phloem and branch diameter on bark beetle species composition (Experiment 2).

MATERIALS AND METHODS

Study sites

The experiments were conducted in European larch monocultures or coniferous forests with the presence of European larch in Northern Bohemia and Southern Moravia (Figure 1). Both experiments took place in study sites ranging in altitude from 340 to 595 m a.s.l. and ages from 21 to 120 years. The sites encompassed a range of different site characteristics in order to suppress pseudoreplication and evaluate the results under different environmental conditions (Table 1). The branch pile study sites were selected based on the source of fresh branches from logging to be used in the study. We hypothesized that the different proportions of larch in the stands would have no effect on bark beetle preference for shaded/sunlit branch piles or branch diameter. However, by placing the branches in different stands with different conifer tree species, we aimed to test whether larch branches are attacked by bark beetles that mainly infest tree species of the genera *Pinus*, *Picea*, and so forth.

Experiment 1: Logs study

From January 2022 to August 2023 (Table 2), two trees were felled at each of the three study sites, to simulate breeding material (i.e. logs) from thinning. We assumed that the trees at the sites in Nort Bohemia (Tisá and Železná cesta) are genetically similar to each other, and that the trees at the sites in South Moravia (Soběšice) are genetically similar to each other. We were able to assume this because, since 1940, there has been a law in the Czech Republic stating that trees planted in a province must be grown from seeds collected in that province. The sites in North Bohemia and South Moravia are in different provinces, as well as being a considerable distance apart, they are likely to be genetically different. After felling, branches were removed from the trees and the tree length was measured. The trees were then cut into 2-m logs, their diameter was measured at the centre and logs from one tree were placed in the sunlit area and logs from the other tree were placed in the shade of the forest. The logs were placed onto the logs of deadwood so that they did not touch the ground and the bark beetles could infest the bottom part of the logs (Figure 2).

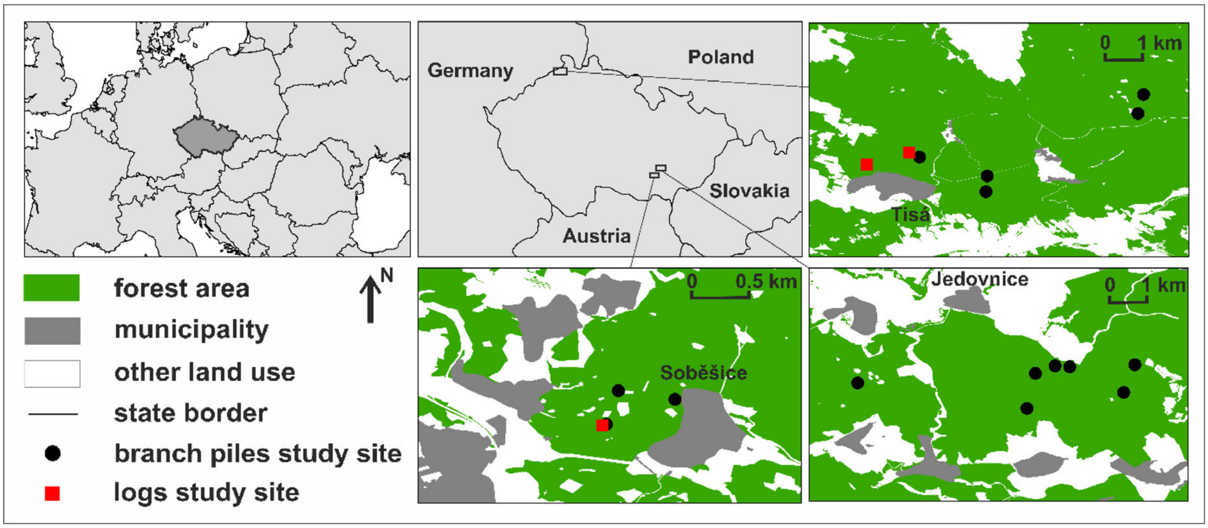

FIGURE 1 Location of the study sites (data: ESRI, 2023).

Subsequently, a mark was spray-painted on the top of the logs to differentiate the bottom from the top of the logs. The average diameter (mean ± SE) of the logs was 7.24 ± 0.09 (2022: 7.92 ± 0.13; 2023: 6.62 ± 0.12). The laying out of replicates ceased in August 2023 as the logs would only be infested in spring 2024 after completion of the experiment.

Experiment 2: Branch piles study

From December 2021 to August 2023 (Table 3), piles of branches of various diameters were placed at 15 study sites. Branches were cut from multiple felled trees, and each pile consisted of at least 15 branches. At each study site, one pile was placed in a sunlit area and the other within the shade of the forest stand. The branches were placed in such a way that they touched the ground as little as possible.

Infestation density

Logs and branches were checked at 14-day intervals for the presence of frass. The infested logs and branches were analysed after adult emergence of the offspring generation and again after adult emergence of the summer generation. For assessment of the infestation of logs, a 5 dm long section was marked in the middle of the log around the circumference of the log and was debarked with a drawknife. The numbers of nuptial chambers and maternal galleries on the upper and lower side of the log were then recorded. Log area was calculated using the formula: $S = (\pi \times \text{diameter of log} \times 5)$. The ID (number of adults/dm^2) was calculated using the formula: ID $=$ (number of nuptial chambers $+$ number of maternal galleries)/log area.

After the infestation of branches was confirmed by frass, two to four infested branches were taken from the pile and cut into 5 dm long sections. Before debarking, the diameter of each section was measured in the centre. The entire 5 dm long sections were debarked with a knife, and the numbers of nuptial chambers and maternal galleries of *I. cembrae*, *Pityogenes chalcographus* L. and *Pityophthorus pityographus* Ratz. were recorded. Only the numbers of nuptial chambers were recorded for *Cryphalus intermedius* Ferrari. The area of the branch sections was calculated using the formula: $S = (\pi \times \text{diameter of log} \times 5)$. The ID on branches was calculated in the same way as for logs.

Moisture content

For experiment 1, the log study, a minimum of 1 dm^2 of phloem was collected from each log using a saw and axe. Phloem samples were taken from logs felled between April and August immediately after felling. Phloem samples from logs felled between September and March were collected in April, before bark beetle flight activity, to determine the current MC. After collection, the phloem was immediately placed in a plastic bag and a portable cooler. For experiment 2, the branch pile study, a branch was selected from the pile and six pieces of phloem were taken from it, which together covered at least 1 dm^2. The samples were taken in the same way as the log samples. In the laboratory, for both log and branch studies, the samples were weighed, dried at 80°C and weighed again to obtain the dry weight. The water content was then calculated using the following formula: MC $=$ (wet weight $-$ dry weight) $\times$ 100. The six samples of phloem from each branch were weighed separately, and the values were then averaged to give a single value.

DATA ANALYSIS

Experiment 1

We used a generalized linear mixed model (GLMM) with a log link function to test the effects of phloem MC, log diameter (LD), log

TABLE 1 Characteristics of the study sites.

Logs	GPS	Forest type	Age	Altitude (m.s.l.)	Avg. temp. in April (°C)	Avg. temp. in July (°C)
Soběšice	49.2552222 N, 16.6045711 E	Dominant *Pinus* in mixture with *Larix* and *Quercus*	41–60	340	8–9	18–19
Tisá	50.7935353 N, 14.0138308 E	Dominant *Larix* in mixture with deciduous tree species	21–40	550	4–6	15–16
Železná cesta	50.7952753 N, 14.0324789 E	*Larix* monoculture	41–60	570	4–6	15–16
Piles of branches						
Jedovnice A	49.3079589 N, 16.7679217 E	*Picea* monoculture	81–100	560	7–8	17–18
Jedovnice B	49.3206528 N, 16.7707111 E	Dominant *Picea* in mixture with *Larix*	101–120	545	7–8	17–18
Jedovnice C	49.3156819 N, 16.7933678 E	Dominant *Larix* in mixture with *Picea*	101–120	530	7–8	17–18
Jedovnice D	49.3226300 N, 16.7802142 E	Dominant *Larix* in mixture with *Picea*	81–100	545	7–8	17–18
Jedovnice E	49.3225197 N, 16.7965783 E	Dominant *Picea* in mixture with *Larix*	41–60	570	7–8	17–18
Jedovnice F	49.3184061 N, 16.7249981 E	*Picea* monoculture	81–100	510	7–8	17–18
Jedovnice G	49.3225086 N, 16.7755122 E	Dominant *Picea* in mixture with *Larix*	101–120	510	7–8	17–18
Kristin Hrádek A	50.8200194 N, 14.1249622 E	*Larix* monoculture	21–40	510	6–7	16–17
Kristin Hrádek B	50.8124936 N, 14.1226286 E	*Larix* monoculture	41–60	450	6–7	16–17
Soběšice A	49.2609028 N, 16.6097044 E	Mixture of *Larix* and *Pinus*	81–100	345	8–9	18–19
Soběšice B	49.2595519 N, 16.6160506 E	Dominant *Larix* in mixture with *Pinus*	81–100	380	8–9	18–19
Soběšice C	49.2553739 N, 16.6064092 E	Dominant *Pinus* in mixture with *Larix*	41–60	335	8–9	18–19
Tisá A	50.7869758 N, 14.0624106 E	Dominant *Larix* in mixture with deciduous tree species	21–40	595	4–6	15–16
Tisá B	50.7805842 N, 14.0613119 E	*Larix* monoculture	21–40	590	4–6	15–16
Tisá C	50.7945719 N, 14.0343828 E	*Larix* monoculture	41–60	570	4–6	15–16

shading (SH), the top/bottom part of the log (TB), locality and tree felling month, on ID of *I. cembrae*. Locality and tree felling month were considered random factors whereas MC, LD, SH and TB were considered fixed factors. The model was made in RStudio (version 2023.12.0 + 369) using the glmer.nb function with a negative binomial distribution from R package lme4 (Bates et al., 2015). IDs of *I. cembrae*, MC and LD were treated as continuous variables, and SH, TB, locality and tree felling month were treated as categorical variables. A pairwise post hoc test on the significant categorical fixed effect factors was conducted using the function lsmeans from the R package lsmeans (Lenth, 2016). Functions kruskal.test from package stats (R Core team, 2023) and dunn_test from package rstatix (Kassambara, 2023) with Bonferroni's *p* value adjustment were used to find differences in ID month. A generalized linear model (GLM) with Gaussian distribution was made to find relationships between the number of maternal galleries and the diameter of logs. The goodness of fit was assessed with the lrtest function from package lmtest (Zeileis & Hothorn, 2002). The marginal and conditional R^2 were computed with function r2_nakagawa (Nakagawa et al., 2017). All analyses were performed at the confidence interval of $\alpha = 0.05$.

Experiment 2

Canonical correspondence analysis (CCA) was used to evaluate the effects of branch microhabitat characteristics on bark beetle species.

TABLE 2 Number of *Larix decidua* trees felled per year and site.

Year	Locality	January	February	March	April	May	June	July	August	September	October	November	December	Trees
2022	Tisá	×	×	×	×	×	×	×	×	×	×	×		22
	Železná											×		2
	Soběšice		×	×	×	×	×	×	×	×	×	×	×	22
2023	Tisá	×	×	×	×	×	×	×	×					16
	Železná	×	×	×	×	×	×	×	×					16
	Soběšice	×	×	×	×	×	×	×	×					16

Note: The '×' denotes months in which two trees were felled at a given site and year.

FIGURE 2 Logs placed in forest shade.

The IDs of *I. cembrae*, *C. intermedius*, *P. chalcographus* and *P. pityographus* were used as species, and MC, LD and SH were used as effects. A Monte Carlo permutation test with 999 permutations was used to calculate the significance of branch microhabitat factors on bark beetle species. The test was computed using the forward selection method on all axes. The test was performed at the confidence interval of $\alpha = 0.05$.

RESULTS

Experiment 1

A total of 550 logs were assessed for infestation by *I. cembrae*, which led to a total of 1100 observations. Overall 57% (45.9% shaded and 68.2% sunlit) of logs were infested by *I. cembrae*. The average ID (nuptial chambers and maternal galleries/per dm^2) was 0.41 ± 0.02. The GLMM with pseudo-R^2 fit (0.62) indicated that MC (average 54.1 ± 6.5%) had no effect on ID of *I. cembrae* ($p = 0.76$). The diameter, side of the log and shading had a highly significant ($p < 0.001$) effect on the ID (Table 4). The ID increased as the diameter of larch logs increased (Figure 3).

Post hoc tests indicated significant differences in ID on shaded/sunlit and bottom/top parts of logs. ID reached higher values on sunlit top parts of logs (Figure 4). The GLM indicated that the number of females in galleries decreased as the diameter of the log decreased. This means that the number of maternal galleries was lower in the thinner logs than in the thicker ones (GLM: $\chi^2 = 1830$, $p < 0.001$; Figure 5).

TABLE 3 Replicates of branch piles per year and site.

		January	February	March	April	May	June	July	August	September	October	November	December
2021	Tisá A				x								
	Kristin Hrádek A				x								
	Kristin Hrádek B				x								
	Jedovnice A												x
2022	Jedovnice B		x										
	Jedovnice C	x											
	Jedovnice D			x									
	Jedovnice E			x									
	Jedovnice F				x								
	Jedovnice G						x	x	x	x	x	x	x
	Tisá B	x	x				x	x	x	x			
	Kristin Hrádek B			x	x	x	x						
	Soběšice A		x										
	Soběšice B				x								
	Soběšice C					x							
2023	Tisá A	x	x										
	Tisá C		x										
	Kristin Hrádek A				x	x	x	x	x				
	Jedovnice G	x	x	x	x	x	x	x	x				

Note: The ‘x’ denotes months in which branch piles were put at a given site and year.

TABLE 4 Results of the generalized linear mixed model model describing the relationship between *Ips cembrae* infestation density on logs and fixed effect factors.

Fixed effects	Estimate	SE	*z* Value	*p*
Intercept	−1.43599	0.61172	−2.347	**0.0189**
Moisture content	−0.00367	0.00933	−0.394	0.6937
Log diameter	0.10095	0.01225	8.237	**<0.001**
Shading	0.76514	0.06727	11.373	**<0.001**
Top/bottom part	0.71007	0.06668	−10.649	**<0.001**

Note: All analyses were performed at the confidence interval of $\alpha = 0.05$.

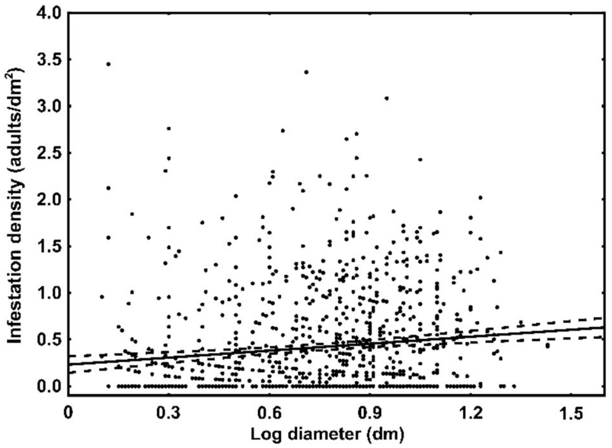

FIGURE 3 The relationship between infestation density of *Ips cembrae* and diameter of larch logs. Solid line indicates regression equation, and dashed lines indicate confidence interval.

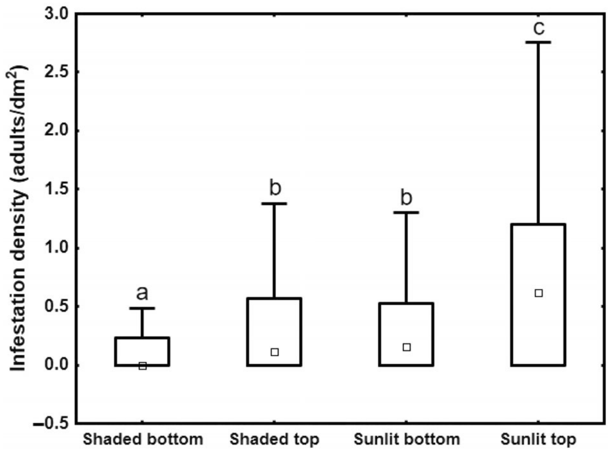

FIGURE 4 Effect of shade and part of log on infestation density of *Ips cembrae*. Significant differences ($p < 0.001$) in the infestation density of groups are labelled with letters. Datasets labelled with the same letter do not differ significantly. Squares indicate medians, rectangles indicate interquartile range and whiskers indicate minimum and maximum values.

Significant differences in ID were found on logs felled in different months (Kruskal–Wallis: $\chi^2 = 302.79$, df $= 11$, $p < 0.001$). The ID of *I. cembrae* was higher on logs felled between December and June than on logs felled between July and November (Figure 6). The logs felled in September and October were not infested by *I. cembrae* at any of the study sites.

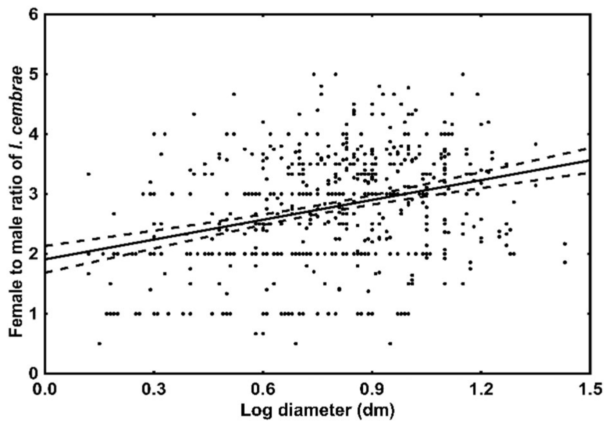

FIGURE 5 Relationship between female to male ratio (i.e. maternal galleries/nuptial galleries) of *Ips cembrae* adults and diameter of logs.

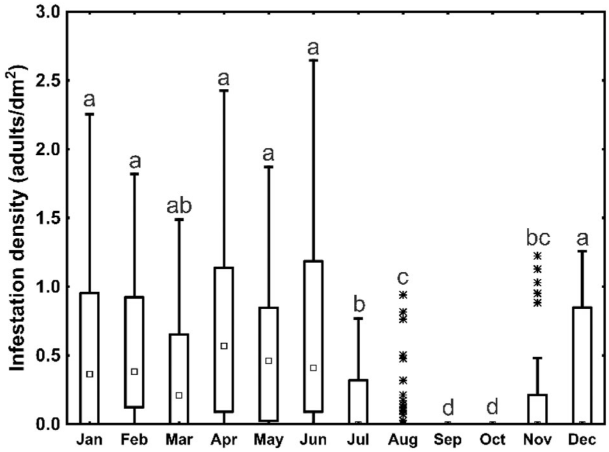

FIGURE 6 Effect of date of felling on infestation density of *Ips cembrae*. Post hoc Dunnett's test significant differences in infestation density of groups are labelled with letters (see Figure 4, stars indicate extremes).

Experiment 2

A total of 1055 branch sections ($d = 5$ dm) were analysed between 2021 and 2023. Four species of bark beetles were recorded. Species preference for branches depended on their diameter and shading (Table 5).

All recorded branch characteristics had a significant effect on bark beetle species composition, and together these habitat variables explained 18.8% of the observed variance in species ID. Shading of branches was the most significant effect affecting species composition (Table 6). The triplot indicated that all four bark beetle species were affected by the diameter of branches. *Ips cembrae* primarily

TABLE 5 Percentage of infested branches and average (mean ± SE) diameters and infestation densities by shading.

	Ips cembrae	*Cryphalus intermedius*	*Pityogenes chalcographus*	*Pityophthorus pityographus*
Percentage of infested branches (%)	46.3 ± 1	21 ± 1	11.9 ± 0.9	15 ± 0.1
Shaded	5.7 ± 5	15.4 ± 3	5.8 ± 0.9	4.9 ± 0.9
Sunlit	51.1 ± 2	5.8 ± 0.9	9.6 ± 0.1	10.2 ± 1
Diameter of infested branches (cm)	3.5 ± 0.1	3.1 ± 0.2	2.9 ± 0.1	2.7 ± 0.9
Shaded	3.9 ± 0.2	3 ± 0.4	2.9 ± 0.2	2.2 ± 0.2
Sunlit	3.4 ± 0.1	3.4 ± 0.2	3 ± 0.2	3 ± 0.1
Infestation density on branches (dm^2)	4.6 ± 0.2	1.8 ± 0.1	1.8 ± 0.1	1.5 ± 0.1
Shaded	3.2 ± 0.6	2 ± 0.3	1.6 ± 0.1	1.6 ± 0.1
Sunlit	4.7 ± 0.2	1.1 ± 0.2	1.9 ± 0.1	2.2 ± 0.1

TABLE 6 Results of canonical correspondence analysis analysis: (a) tests on all axes, (b) factor effects and (c) tests of significance.

(a)

Axes	1	2	3	4
Eigenvalues	0.4216	0.082	0.0088	0.903
Explained variation (cumulative)	15.48	18.49	18.81	51.96
Pseudo-canonical correlation	0.6776	0.3029	0.0981	0
Explained fitted variation (cumulative)	82.28	98.29	100	

(b)

Factor	Explains %	Contribution %	pseudo-F	*p*
Shaded branches	13.4	71.3	83.1	**0.001**
Sunlit branches	13.4	71.3	83.1	**0.001**
Diameter	4	21.4	26.1	**0.001**
Moisture content	1.4	7.3	9	**0.001**

(c)

Test of significance of first canonical axis:	pseudo-$F = 97.8$
	$p = 0.001$
Test of significance of all canonical axis:	pseudo-$F = 41.2$
	$p = 0.001$

Note: All analyses were performed at the confidence interval of $\alpha = 0.05$.

infested sunlit branches, and *C. intermedius* preferred shaded branches. *Pityogenes chalcographus* and *P. pityographus* differed from the other bark beetle species by having IDs on branches probably determined by MC (Figure 7).

DISCUSSION

The preference–performance hypothesis states that insects oviposit in hosts that are well suited to their offspring and thus give them the best chance of completing development (Gripenberg et al., 2010). However, before oviposition, adult bark beetles must successfully overcome the defensive mechanisms of host trees. In bark beetles, before offspring development can begin in the phloem and wood, adult bark beetles must successfully overcome the defensive mechanisms of host trees (Eidson et al., 2018). These defensive mechanisms are disrupted after tree felling, the host trees begin to emit primary volatiles and lose its natural defences, which in conifers are predominantly related to the intensity of resin exudation, viscosity and content of terpenoids (Boone et al., 2011; Lieutier, 2004). The content of terpenoids is influenced by the environment, temperate season and tree chemotype, thus genetically different trees can respond differently to identical environmental stresses (Arrabal et al., 2013; Llusià & Peñuelas, 2000; Malik et al., 2023). Our results may be affected by the study design, where trees in different provinces (Northern Bohemia and Southern Moravia) are genetically different. Although the trees in these provinces are genetically different, the pattern of ID on logs was similar in both provinces, indicating that it is dependent on shading rather than tree genotype. The study found no significant relationship between ID and phloem MC in logs. It may be that the attractiveness of breeding material for *I. cembrae* is influenced more by the composition of emitted volatiles, which varies according to the

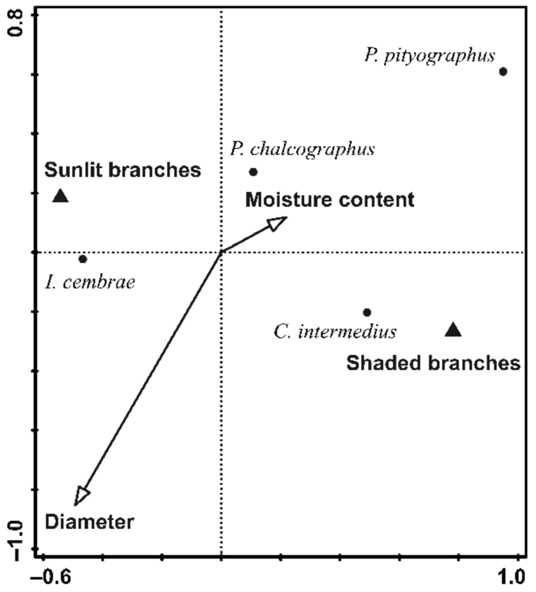

FIGURE 7 Canonical correspondence analysis analysis graph of bark beetle species composition in relation to effects. *C. intermedius*, *Cryphalus intermedius*; *I. cembrae*, *Ips cembrae*; *P. chalcographus*, *Pityogenes chalcographus*; *P. pityographus*, *Pityophthorus pityographus*.

month of felling (i.e. season; Helmig et al., 2013) and phloem quality (Kula & Ząbecki, 2006), than by the MC of the phloem.

Trees are probably most attractive to bark beetles in spring due to the higher water, nutrient and volatile emissions content (Baier et al., 2002; Kopaczyk et al., 2020), which explains the high IDs on logs felled in winter through early summer. Conversely, logs felled during the summer were less attractive to bark beetles, assumedly, because the higher temperatures in summer influenced the composition and concentration of monoterpenes released from the breeding material (Hietz et al., 2005), leading to a decrease in attractiveness for bark beetles (Faccoli et al., 2008). The logs felled in late summer and autumn may not have been infested due to reduced bark beetle flight activity (Holuša et al., 2014; Špoula & Kula, 2023a) and reduced seasonal emissions of host volatiles from the logs. Higher solar radiation and temperature (i.e. warmer breeding substrate) trigger and accelerate the development of bark beetles (Hinze & John, 2020; Mezei et al., 2019; Sproull et al., 2015). Our results show that *I. cembrae* mainly infests sunlit breeding material, which is also true of *I. typographus* (Kautz et al., 2013; Mezei et al., 2019).

Most species of the genus *Ips* are polygamous, although they differ in the number of females associated with a male (Schlyter & Zhang, 1996). Grucmanová et al. (2014) did not find any significant differences in the numbers of captured males and females of *I. cembrae* in slot traps baited with Cembräwit. However, Raffa et al. (2016) found that the number of males in galleries on logs was lower than number of females, probably due to high mortality of pioneer males in search of suitable hosts. The bark beetles in the thinner logs would have experienced increased competition for food because the phloem is thinner. To reduce this intraspecific competition and provide sufficient food for the larvae, females in the thinner logs lay fewer eggs at greater intervals, resulting in longer maternal galleries (Holuša et al., 2014).

Some secondary bark beetles do not produce aggregation pheromones and are attracted by primary host volatiles (Gomez et al., 2023; Kalinová et al., 2014). There are no studies on pheromones of *C. intermedius*. *Cryphalus intermedius* was thought to occur only in northern Moravia (Pfeffer, 1955), but its occurrence was recently recorded in the central and southern parts of the Czech Republic (AOPK, 2024; Fiala & Knížek, 2020). Our study showed its occurrence in southern Moravia and northern Bohemia. Little is known about the bionomy of *C. intermedius*. Pfeffer (1955) states that *C. intermedius* prefers thicker larch branches for breeding and assumes two generations per year. In our study, *C. intermedius* mainly infested shaded branches. This preference is similar to another species in the genus *Cryphalus*, *Cryphalus asperatus* (Ratz.), which prefers to breed in the shaded branches of spruces (Fiala & Holuša, 2022; Pfeffer, 1955). Although not a major pest, populations of *C. asperatus* have increased on logging residues and outbreaks and infestations of seedlings and trees have been recorded (Benz, 1985; Fiala & Holuša, 2021). Thus, although we assume that *C. intermedius* has no economic significance as no outbreaks of this species have yet been recorded, it likely has the logging residues potential to cause outbreaks.

This study confirmed that *I. cembrae* is able to breed not only larch stems but also branches (Grodzki, 2008; Holuša et al., 2014). Our study design, which involved placing branch piles in different study sites having different proportions of larch, allowed us to capture various bark beetle species, not only the species that infest larch. Our results indicate that *I. cembrae* prefers to breed in sunlit logs and branches. *Pityogenes chalcographus* and *P. pityographus* both also preferred sunlit branches for development. These species are polyphagous bark beetles with development on conifer tree species (Bertheau et al., 2009; Mayer et al., 2015; Pfeffer, 1955). Fiala and Holuša (2022) reported an outbreak of *P. chalcographus* and *P. pityographus* on spruce logging residues left near a nursery, which lead to dieback of seedlings. Kacprzyk (2014) found that the position of branches is a factor significantly contributing to the infestation intensity by *P. chalcographus*, which reaches a higher ID on branches placed disorderly on the forest floor than on branches collected in piles. We confirmed that larch is suitable for the development of *P. chalcographus* and *P. pityographus*. We assume that the risk of infestation of larch branches depends on the presence of spruce logging residues from felling, as *P. chalcographus* and *P. pityographus* mostly infested branch piles at study sites located near spruce forests with outbreaks of *I. typographus*.

Our results indicate that trees felled in all months except September and October were favourable for attack by *I. cembrae*. After thinning, we recommend the removal of felled trees or their use as trap trees to control populations of *I. cembrae*. However, trap trees should not be left in the forest or near the stand edge, as healthy larch trees could be infested if trap trees are in the vicinity (Špoula & Kula, 2023b). The trap trees should be sanitated before the new generation of bark beetles emerges (Holuša et al., 2017). Larch branches can cause outbreaks of *I. cembrae*, *P. chalchographus* and

P. pityographus, especially branches in sunlit areas. Chipping of larch branches seems to be the most effective method of logging residues management to prevent bark beetle outbreaks (Gomez et al., 2023). However, there is a risk that the high concentration of terpenoids released during chipping may increase the risk of healthy trees being attacked by bark beetles (Fettig et al., 2007).

CONCLUSIONS

During a 3-year study, ID of bark beetles on larch logging residues from thinning and logging was analysed. *Ips cembrae* preferred the sunlit top part of logs and its ID increased with increasing LD. The number of *I. cembrae* maternal galleries (i.e. females) decreased in thinner logs. ID of *I. cembrae* was highest in logs felled in the spring and winter months. Shading of branches was the most significant effect affecting the bark beetle species composition on branches. Bark beetle species composition on branches was also affected by the diameter of branches. *Ips cembrae*, *P. chalcographus* and *P. pityographus* infested mostly sunlit branches, and *C. intermedius* preferred shaded branches. We conclude that *C. intermedius* is an abundant bark beetle species of no economic importance infesting shaded larch branches. We recommend that trees from thinning operations should be removed from the forest to prevent *I. cembrae* outbreaks. Additionally, branches of thicker diameters should be chipped to prevent general outbreaks of bark beetles.

AUTHOR CONTRIBUTIONS

Jakub Špoula: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; visualization; writing – original draft. **Emanuel Kula:** Conceptualization; funding acquisition; investigation; methodology; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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