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Factors affecting the occurrence of bark- and wood-boring beetles on Scots pine logging residues from pre-commercial thinning

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A total of 480 Scots pine (*Pinus sylvestris* L.) trees felled during pre-commercial thinning in a single stand in the Drahanská Highlands in the Czech Republic were examined for the occurrence of bark- and wood-boring beetles. Thinning was performed on different dates during 2006 and 2007 (February, May, August and November). Half of the felled trees were cut into 1 m-long sections, and the rest were left whole. The fauna inhabiting the logging residues were investigated by peeling off the bark of the felled trees during the first six months of the vegetative period following felling. The studied logging residues hosted species-rich assemblages of bark- and wood-boring beetles (28 species identified), including numerous populations of several pest species (*Pityogenes chalcographus*, *Tomicus minor* and *Tomicus piniperda*). The occurrence of species was significantly affected mainly by the part of the tree and its diameter and bark thickness and by the felling date and post-felling cutting of the trees.

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1. Introduction

Substantial quantities of logging residues (LR) are produced every year through forest management. These LR may serve as a substrate for the development of certain forest bark- and wood-boring pests (especially bark beetles), and in certain circumstances, they can facilitate pest multiplication and outbreaks (Schroeder 2008). Various strategies for the removal of LR (e.g., hauling, burning, chipping) are often recommended to prevent the multiplication of pests (DeGomez *et al.* 2008). Extensive removal of LR might arise from the current tendency to harvest biomass as a renewable energy source. However, LR form a substantial portion of the dead wood present in managed forests, and their removal can lead to the extinction of scarce saproxylic species and a loss of overall diversity (Siitonen 2001, Jonsell *et al.* 2007, Maňák 2007, Jonsell 2008, Victorsson & Jonsell 2013). Hence, many studies (Kaila *et al.* 1997, Jonsell *et al.* 2004, Lindhe & Lindelöw 2004) have encouraged the deliberate retention of certain parts of trees (e.g., high stumps, snags, tops or branches) in managed forests to increase the diversity of saproxylic insects.

There are a number of studies focusing on LR as a substrate for pest development (Six *et al.*

2002, Hedgren *et al.* 2003, Johansson *et al.* 2006, Kula & Kajfosz 2006, 2007, Zabecki & Kacprzyk 2007, Foit 2012b, Kacprzyk 2012), in addition to many studies addressing the conservational value of LR (e.g., Schiegg 2001, Lindhe & Lindelöw 2004, Jonsell *et al.* 2007, Maňák 2007, Jonsell 2008, Brin *et al.* 2011, Lassauce *et al.* 2012). The occurrence of saproxylic beetles on LR or dead wood is affected by an array of substrate characteristics, including stand conditions and the position of dead wood within the stand (Peltonen & Heliövaara 1999, Sverdrup-Thygeson & Ims 2002, Jonsell & Weslien 2003, McGeoch *et al.* 2007); the total volume, connectivity and continuity of dead wood (Schiegg 2000, Similä *et al.* 2003, Vanderwel *et al.* 2006); bark thickness (Zhang *et al.* 1993, Foit 2010); substrate diameter (Schiegg 2001, Lindhe & Lindelöw 2004, Lindhe *et al.* 2005, Jonsell *et al.* 2007, Maňák 2007, Jonsell 2008, Foit 2010); sun exposure (Jonsell *et al.* 2004, Lindhe & Lindelöw 2004, Lindhe *et al.* 2005, Jonsell 2008); moisture (Wallace 1953, Larkin & Elbourn 1964); the stage of decomposition (Wallace 1953, Vanderwel *et al.* 2006, Jonsell 2008); and the presence of various other organisms (Jonsell *et al.* 2005, Abrahamsson *et al.* 2008, Weslien *et al.* 2011).

Given these associations, it is not surprising that saproxylic beetles colonising LR are influenced by the date of LR production (felling date) (Kula & Kajfosz 2006, 2007, Foit 2012a, b) and deposition (Six *et al.* 2002, Foit 2011, Kacprzyk 2012). The effects of other management strategies, such as the post-felling cutting of LR into shorter sections, might also be substantial but have not yet been documented. Most of the studies addressing LR have been conducted on LR generated from the final felling or thinning in older stands, where only tree tops, branches and stumps remain. However, only few studies (Kula & Kajfosz, 2006, 2007) have specifically examined LR arising from pre-commercial thinning, where whole trees remain in the stand. The fauna of LR generated by pre-commercial thinning might be very specific, comprising species associated with thick bark and the basal part of the trunk that do not find suitable habitats in other types of LR.

The goal of this study was to investigate which bark- and wood-boring beetle (BWBB) species develop and multiply on Scots pine (*Pinus sylvestris* L.) LR generated through pre-commercial thinning and to assess the effects of various habitat variables, including the diameter and bark thickness of the LR fragment, the felling date, and the post-felling cutting of the trees into sections, on the occurrence of the recorded species.

2. Material and methods

2.1. Study site

The study was conducted in the southern part of the Drahanská Highlands in the Czech Republic. The climate of the study area is characterised by mean annual temperatures of 8.4–8.5°C and an average annual rainfall of approximately 580–590 mm. The forests in the study area have traditionally been managed under a clear-cutting system with prevalent artificial regeneration.

The study stand (49°15’38”N/16°36’52”E) had an area of 1.4 ha and was situated between 350 and 385 m elevation on an east- to southeast-facing slope with a gradient of approximately 10–15%. This even-aged stand was approximately 17 years old, and its main canopy was composed primarily of Scots pines (70%), though sessile oak (*Quercus petraea* (Matt.) Liebl.) (8%), European larch (*Larix decidua* Mill.) (8%), silver birch (*Betula pendula* Roth) (6%), small-leaved lime (*Tilia cordata*) Mill. (4%) and European hornbeam (*Carpinus betulus* L.) (2%) were also present.

2.2. Sampling

The studied stand was divided into four parts, each with the same area (0.35 ha), and experimental felling was conducted on a different date in each part. The dates on which felling occurred were 11.IX.2006, 10.II.2007, 10.V.2007 and 12.VIII.2007. During each felling event, 170 (or slightly more) pines were felled (stand density was decreased from 2,200 trees/ha to 1,700/ha). Half of the felled trees were subsequently cut into 1 m-long sections, and the remaining trees were left whole (uncut). The total height of the felled

Table 1. Metric variables (diameter and bark thickness) of the distinguished tree parts represented by the mean ± standard deviation (range).

Tree part	No. of trees with presence of tree part	Diameter (cm)	Bark thickness (mm)
1. trunk section	480	12.2 ± 2.6 (7.0–18.0)	10.4 ± 2.7 (4.0–20.0)
2. trunk section	480	11.2 ± 2.6 (6.0–17.0)	6.0 ± 2.2 (2.0–15.0)
3. trunk section	480	9.2 ± 2.4 (4.0–14.5)	3.7 ± 1.8 (1.0–13.0)
4. trunk section	480	8.2 ± 2.3 (3.0–13.0)	2.4 ± 1.3 (1.0–9.0)
5. trunk section	480	7.2 ± 2.1 (3.0–12.0)	1.6 ± 0.8 (1.0–6.0)
6. trunk section	480	6.2 ± 2.0 (2.0–10.0)	1.3 ± 0.5 (1.0–4.0)
7. trunk section	480	5.2 ± 1.9 (1.5–9.0)	1.1 ± 0.3 (1.0–3.0)
8. trunk section	472	4.3 ± 1.7 (1.0–8.0)	1.0 ± 0.2 (1.0–2.0)
9. trunk section	463	3.5 ± 1.5 (1.5–7.5)	1.0 ± 0.2 (1.0–2.0)
10. trunk section	438	3.5 ± 1.4 (1.0–7.0)	1.0 ± 0.2 (1.0–2.0)
11. trunk section	357	3.0 ± 1.1 (1.0–6.0)	1.0 ± 0.1 (1.0–2.0)
12. trunk section	279	1.9 ± 0.6 (1.0–3.0)	1.0 ± 0.0 (1.0–1.0)
13. trunk section	141	1.8 ± 0.4 (1.0–2.0)	1.0 ± 0.0 (1.0–1.0)
14. trunk section	42	1.8 ± 0.8 (1.0–2.0)	1.0 ± 0.0 (1.0–1.0)
Branches thicker than 1 cm	480	2.0*	1.0*
Branches thinner than 1 cm	480	0.8*	1.0*

* Because all of the branches were not measured, the standard deviation and range could not be calculated (see Methods).

trees was 7–14 m, and their diameter at breast height was 6–17 cm.

Sampling began 14 days after felling and was repeated every 14 days during the vegetative period (23rd April through 10th October) until 12 repetitions had been performed in each part of the stand with a different felling date. During each sampling event, five whole and five cut trees were sampled from each part of the stand felled on the different dates. Thus, 480 trees (60 whole and 60 cut trees in each of 4 parts of the stand) were sampled in total. The trunks of the uncut trees were divided into 1-m-long sections, and 7 to 14 trunk sections (according to the tree height) were distinguished on each sampled tree (cut and uncut); all of these trunk sections were analysed. The upper (upward-facing) and lower (ground-facing) halves (sides) of the trunk section surfaces were sampled separately. Additionally, one upward-facing branch was sampled from each trunk section that had living branches at the time of felling, and sections of the branches that were thicker or thinner than 1 cm were sampled separately. Thus, 9 to 16 tree parts (7 to 14 trunk sections and 2 categories of sampled branches) were distinguished on specific sampled trees (Table 1). The diameter and bark thickness were recorded in the middle of each trunk section, although constant average values of these variables were obtained by measuring two branches on each 10th analysed tree and used for the branch categories (Table 1). Furthermore, contact between the trunk and ground was recorded for each trunk section, and the section was classified as "air" or "ground" if less or more than 1/3 of its length was touching the ground, respectively. Each analysed tree part was entirely debarked, and all of the BWBB (phloemo-, xylo- and xylomycetophagous) species present were identified based on the gallery characteristics or the morphological traits of imagos or larvae (Švácha & Danilevsky 1986, 1987, 1988, Bílý 1989, Bense 1995, Pfeffer 1995). Finally, the gallery coverage of each species was evaluated on a semi-logarithmic, six-degree scale according to the visually estimated percentage of the area exploited by the species within the sample mantle (< 1%, 1–5%, 6–25%, 26–50%, 51–75% and > 75%, see Braun-Blanquet 1964).

2.3. Statistical analyses

The frequency of the occurrence of each species was expressed as the proportion of samples occu-

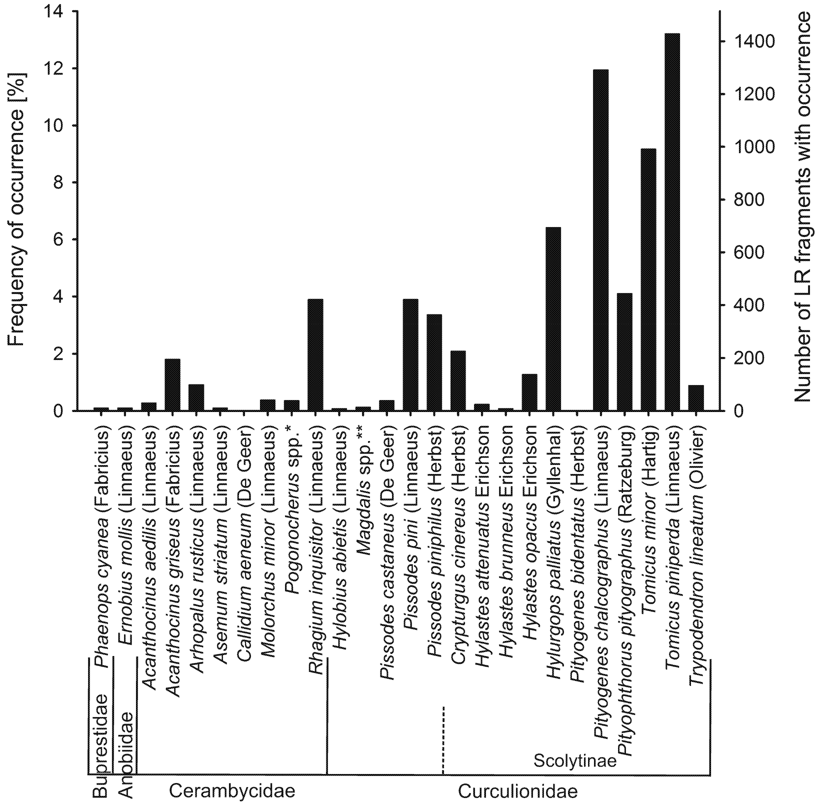

Fig. 1. Frequencies of occurrence of the recorded species. *Includes two species: *Pogonocherus fasciculatus* (De Geer) and *Pogonocherus decoratus* Fairmaire; **Includes two species: *Magdalis frontalis* (Gyllenhal) and *Magdalis rufa* Germar.

pied. In the statistical analysis, the abovementioned six-point scale of gallery coverage was represented by the mean values of the percentage intervals: 0.5%, 3%, 15.5%, 38%, 63% and 88%. A canonical correspondence analysis (CCA) was used to assess the effects of the studied habitat variables on the species composition of the beetle assemblages. A CCA does not require normally distributed data, is not affected by the correlation of habitat factors and assumes unimodal models for the relationships between the responses of each species to the habitat variables. This approach is appropriate for this data set because a preliminarily detrended correspondence analysis showed long gradient lengths (> 3 SD) (ter Braak 1986, 1987). In the CCA, the Monte Carlo permutation test (Manly 2001), with 999 permutations, was used to compute the significance of the relationships between the species responses and habitat factors. When appropriate (i.e., to test for the significance of the tree parts, diameter and bark thickness), Monte Carlo permutation tests were restricted to permutations within blocks referring to particular trees. All of these analyses were performed in CANOCO for Windows (ter Braak 1987). All of the recorded species were included in the analyses; however, to avoid an undesirably high influence of species with low frequency caused by the standardisation by species, which is implicit in unimodal methods, rare species were down-weighted as a separate step of the analyses in CANOCO.

Because of the non-normal distribution of the data in the gallery coverage of particular species (tested by Shapiro-Wilk tests) that could not be corrected by data transformation, nonparametric statistics were used for further analyses (Hollander & Wolfe 1999). To illustrate the strength of association among particular species with the tree parts and their metric variables, Spearman's correlation indices were calculated with the tree identity treated as a covariable, and its effect was removed from the dataset. This calculation was performed by fitting a Poisson generalised linear models (GLM) with a logarithmic link function (Dobson & Barnett 2008) for each tested species

Table 2. Canonical correspondence analysis – results of the Monte Carlo permutation tests for the significance of the studied habitat variables for species composition of bark- and wood-boring beetle assemblages. The percentage of the variance in the species gallery coverage explained by the studied factors is included. Values in parentheses show the results that considered additional covariables.

Variable	F P (%)	Covariables	Additional covariables
Tree identity	4.8 0.001 24.3	–	–
Tree part	11.0 (8.4) 0.001 (0.001) 7.1 (5.5)	Tree identity, sampling date	Felling date, post-felling cutting, contact of LR with ground
Diameter	90.3 (49.5) 0.001 (0.001) 4.0 (2.6)	Tree identity, sampling date	Felling date, post-felling cutting, contact of LR with ground
Bark thickness	67.5 (31.9) 0.001 (0.001) 3.1 (1.4)	Tree identity, sampling date	Felling date, post-felling cutting, contact of LR with ground
Diameter and bark thickness	52.9 (34.5) 0.002 (0.002) 4.7 (3.1)	Tree identity, sampling date	Felling date, post-felling cutting, contact of LR with ground
Felling date	21.9 (17.0) 0.001 (0.001) 3.7 (2.6)	Sampling date	Tree part, diameter, bark thickness, post-fell. cutting, contact of LR with ground
Post-felling cutting (whole/cut)	20.2 (22.6) 0.003 (0.001) 1.2 (1.1)	Sampling date	Felling date, tree part, diameter, bark thickness, contact of LR with ground
Orientation of LR surface towards ground (upper/lower side)	6.3 (5.9) 0.003 (0.001) 0.3 (0.3)	Tree identity, tree part, sampling date	Felling date, diameter, bark thickness, post-fell. cutting, contact of LR with ground
Contact of LR with ground (air/ground)	3.7 (3.4) 0.001 (0.001) 0.3 (0.3)	Tree identity, tree part, sampling date	Felling date, diameter, bark thickness, post-felling cutting
Sampling date	16.9 0.001 0.1	–	–
All variables (except tree identity)	12.9 0.001 16.6	–	–

using tree identity as a predictor. The residuals associated with these models were then extracted, and the correlation indices were calculated using the residuals. The statistical significance of the differences in the gallery coverage of particular species on the LR with different (categorical) characteristics was tested using Kruskal-Wallis tests or Mann-Whitney U tests according to the number of groups to be compared. If significant differences were found by the Kruskal-Wallis tests, then the Mann-Whitney U tests with critical p-values that were decreased by Bonferroni adjustment (i.e., critical $P = 0.008$ for the comparison of four different felling dates) were used to identify the pairs of datasets with significant differences. To test the effect of contact of LR with the ground, only the data for three basal trunk sections were considered because these tree parts without branches exhibited contact with the ground at a greater frequency. All of these calculations were performed in Statistica 10.0 (StatSoft 2013).

3. Results

Among the 28 collected species of BWBB (Fig. 1), the family Curculionidae (17 species) was the most abundant. Most of the identified curculionids (11 species) were bark beetles (Scolytinae), and *Tomicus piniperda* (Linnaeus) and *Pityogenes chalcographus* (Linnaeus) were encountered most frequently (Fig. 1).

All of the studied habitat variables were significantly associated with the species composition of the BWBB assemblages and were able to explain 16.6% of the observed variability in the species' gallery coverage (Table 2, Fig. 2). The tree parts and metric variables were the most significant variables affecting the species composition of the BWBB assemblages. The felling date also had a comparably strong impact. The post-felling cutting of the trees affected the composition of the BWBB assemblages to a much lesser degree, although it was still considerable. In contrast, the effects of the orientation of the LR surface with respect to the ground and contact of the LR fragments with the ground were negligible although still statistically significant.

Particular species were associated with certain tree parts and their metric variables (Table 3, Fig. 2), and many of these associations were statistically significant. Among the species found on at least 100 LR fragments, *Arhopalus rusticus* (Linnaeus), *Rhagium inquisitor* (Linnaeus), *Tomicus minor* (Hartig) and *Trypodendron lineatum* (Olivier) exhibited the strongest associations with the tree parts (Table 3). The remaining species were more closely associated with the metric variables of the tree parts, and the following six species exhibited stronger associations with diameter: *Acanthocinus griseus* (Fabricius), *Pissodes pini* (Linnaeus), *Crypturgus cinereus* (Herbst), *Hylastes opacus* Erichson, *Hylurgops palliatus* (Gyllenhal) and *Pityophthorus pityographus* (Ratzeburg); however, the following six species exhibited stronger associations with bark thickness: *A. rusticus*, *R. inquisitor*, *P. chalcographus*, *T. minor*, *T. piniperda* and *T. lineatum*.

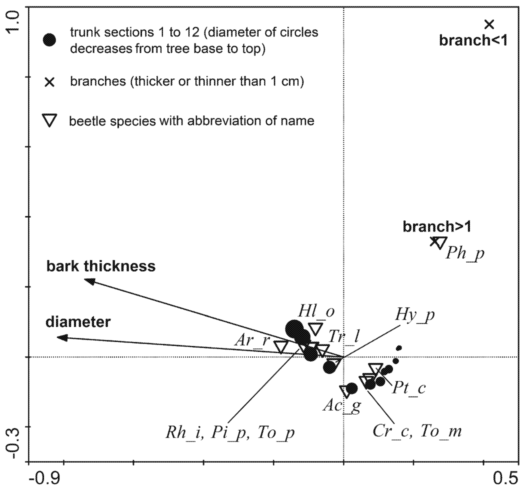

Fig. 2. Canonical correspondence analysis – associations of the tree parts and their basic variables with the species composition of bark- and wood-boring beetle assemblages (covariables: tree identity and sampling date; sum of eigenvalues of first and second axes = 1.653, sum of all eigenvalues = 11.543, $F = 90.3$, $P = 0.001$). Species are denoted with the following abbreviations: *Ac_g* (*Acanthocinus griseus*), *Ar_r* (*Arhopalus rusticus*), *Cr_c* (*Crypturgus cinereus*), *Hl_o* (*Hylastes opacus*), *Hy_p* (*Hylurgops palliatus*), *Pi_p* (*Pissodes pini*), *Ph_p* (*Pityophthorus pityographus*), *Pt_c* (*Pityogenes chalcographus*), *Rh_i* (*Rhagium inquisitor*), *To_m* (*Tomicus minor*), *To_p* (*Tomicus piniperda*) and *Tr_l* (*Trypodendron lineatum*). Only the species recorded on at least 100 LR fragments are shown.

The felling date significantly affected the overall species composition of the BWBB assemblages developing on the studied trees (Table 2). The gallery coverage of all species that were present on at least 100 LR fragments differed significantly between different felling dates (Table 4, Fig. 3a). Trees felled in November and February were regularly colonised by a majority of the species, with *R. inquisitor*, *H. palliatus*, *T. piniperda* and *T. lineatum* showing the highest frequency of occurrence on the trees from November and *C. cinereus*, *P. chalcographus* and *T. minor* being the most frequent on trees from February. Two species that avoided the colonisation of LR from November and/or February were *A. rusticus* and *T. lineatum* (avoided LR from February). While a few species (*A. griseus*, *A. rusticus* and *P. pini*) displayed the highest frequency of occurrence on trees felled in May, more species avoided these

Table 3. Spearman correlation indices among the tree parts and their metric variables and among the tree parts, their metric variables and gallery coverage of each species. The effect of tree identity was removed from the data (n = 10,810) for the gallery coverage prior to calculating the indices by extracting the residuals from the fitted generalised linear model for each species using the tree identity as the predictor (see Methods). Only the species recorded for at least 100 logging residue fragments were tested, and the highest absolute value in each row is highlighted in bold; the higher absolute value for the diameter and bark thickness is underlined.

	Tree part	Diameter	Bark thickness
Tree part	1.000	–0.921*	–0.772*
Diameter	–0.921*	1.000	0.752*
Bark thickness	0.772*	–0.752*	1.000
Acanthocinus griseus	0.011	**0.088***	0.005
Arhopalus rusticus	**–0.133***	–0.008	0.100*
Rhagium inquisitor	**–0.230***	0.088*	0.199*
Pissodes pini	–0.087*	**0.166***	0.138*
Crypturgus cinereus	0.022	**0.059***	–0.041*
Hylastes opacus	0.022	**0.082***	0.003
Hylurgops palliatus	–0.171*	**0.214***	0.180*
Pityogenes chalcographus	–0.032*	0.040	**–0.101**
Pityophthorus pityographus	0.025	**–0.145***	–0.057
Tomicus minor	**–0.147**	0.031	0.076*
Tomicus piniperda	–0.396*	0.330*	**0.448***
Trypodendron lineatum	**0.131***	–0.023	0.083*

* Significant correlations ($P < 0.05$).

trees (*R. inquisitor*, *C. cinereus*, *H. opacus*, *H. palliatus*, *T. minor* and *T. lineatum*). The trees felled in August were regularly colonised only by *R. inquisitor*, *P. pini*, *H. opacus*, *H. palliatus* and *T. lineatum* and occasionally by *T. piniperda*, whereas other species obviously avoided these trees. *Hylastes opacus* was the only species to exhibit the highest frequency of occurrence on the LR from August.

The gallery coverage of all species present on at least 100 LR fragments (excluding *P. pini* and *T. piniperda*) were significantly affected by the post-felling cutting of the trees, with most species showing a significantly higher gallery coverage on the cut trees (Table 4, Fig. 3b). Furthermore, several species (*A. griseus*, *H. opacus*, *H. palliatus*, *P. chalcographus* and *T. minor*) exhibited significant differences in their gallery coverage between the upper and lower sides of the LR fragments (Table 4, Fig. 3c), with most of these species (excluding *P. chalcographus*) exhibiting a higher gallery coverage on the lower side. Species such as *R. inquisitor*, *H. opacus* and *H. palliatus* were significantly more abundant on LR fragments that were in substantial contact with the ground. In contrast, *A. griseus* and *T. minor* occurred in greater numbers on LR without or with negligible direct contact with the ground (Table 4, Fig. 3d).

4. Discussion

Logging residues from pre-commercial thinning offer more diverse habitats for the development of BWBB than LR from fellings in older stands, i.e. where trunks are removed. Accordingly, the number of species found in the present study (28) was considerably higher than that reported in studies performed on other types of Scots pine LR, such as pine stumps (8 species, England, Wallace (1953); 17 species, Czech Republic, Foit (2012a)) or pine branches and tops generated through thinning or main felling (16 and 25 species respectively, Czech Republic, Foit (2011)). Moreover, the number of recorded species was comparable to that found on whole standing mature Scots pine trees (17 species, Finland, Väisänen *et al.* (1993)); 23 species, Poland, Zabecki (1999); 34 species, Czech Republic, Foit (2007, 2010)). Although no red-listed BWBB species were observed, the high total number of species

Table 4. Statistical significances of differences in the gallery coverage of particular species on logging residue (LR) fragments with various characteristics (felling date, post-felling cutting, orientation of the LR surface towards the ground and contact of the LR with the ground). The differences were tested using the Kruskal-Wallis test (felling date) or Mann-Whitney U test (other variables). Only the species recorded on at least 100 LR fragments were tested.

	Felling date	Post-felling cutting (whole/cut)	Orientation of LR surface towards ground (upper/lower side)	Contact of LR with ground (air/ground)*
	KW-H(3; 10,810) *P*	*U*(n1=n2=5,405) *P*	*U*(n1=n2=3,365) *P*	*U*(n1=n2=1,440) *P*
Acanthocinus griseus	41.0	1885078	736733	50832
	< 0.001	< 0.001	0.025	< 0.001
Arhopalus rusticus	68.7	1902946	745347	52126
	< 0.001	< 0.001	0.490	0.677
Rhagium inquisitor	55.4	1834488	736717	48076
	< 0.001	< 0.001	0.660	0.004
Pissodes pini	69.3	1920676	736717	51137
	< 0.001	0.556	0.121	0.351
Crypturgus cinereus	86.3	1888563	745368	51969
	< 0.001	< 0.001	0.621	0.164
Hylastes opacus	15.1	1900966	738650	48124
	0.002	< 0.001	0.023	< 0.001
Hylurgops palliatus	105.4	1726878	721289	46178
	< 0.001	< 0.001	0.003	< 0.001
Pityogenes chalcographus	263.0	1841358	725769	51973
	< 0.001	< 0.001	0.044	0.167
Pityophthorus pityographus	90.6	1882568	745395	–
	< 0.001	< 0.001	0.509	–
Tomicus minor	321.1	1813523	692109	46042
	< 0.001	< 0.001	< 0.001	< 0.001
Tomicus piniperda	89.1	1926001	746744	50252
	< 0.001	0.936	0.928	0.316
Trypodendron lineatum	37.0	1894509	743618	51335
	< 0.001	< 0.001	0.237	0.113

* For LR in contact with the ground, only the data for the three basal sections of trunk were used (see Methods).

identified within the studied insect group suggests that the overall saproxylic insect assemblages associated with these LR might be notably species rich and conservationally valuable. Additionally, the recorded species comprised several pests (Gregoire & Evans 2004), chiefly *P. chalcographus*, *T. minor* and *T. piniperda*. Because these species were the most frequent species recorded in the present study, it is clear that they can multiply on LR generated through precommercial thinning. The importance of LR for the multiplication of certain BWBB pests, including *P. chalcographus* and *T. minor*, has been previously documented in several studies (Six *et al.* 2002, Kula & Kajfosz 2007, Kula *et al.* 2011, Foit 2012b, Kacprzyk 2012). In contrast, the observation of such extensive multiplication of *T. piniperda*, which requires thick bark for development (Schwenke 1972), on the relatively thin LR generated from the pre-commercial thinning of these young stands was unexpected. However, Långström and Hellqvist (1993) also recorded a heavy attack of baited 30-year old Scots pine trees by this species in central Sweden.

All of the studied habitat factors (tree part, diameter, bark thickness, felling date, post-felling cutting of the LR, orientation of the LR surface towards the ground, and contact of the LR with the ground) significantly affected the composition of the BWBB assemblages and were able to

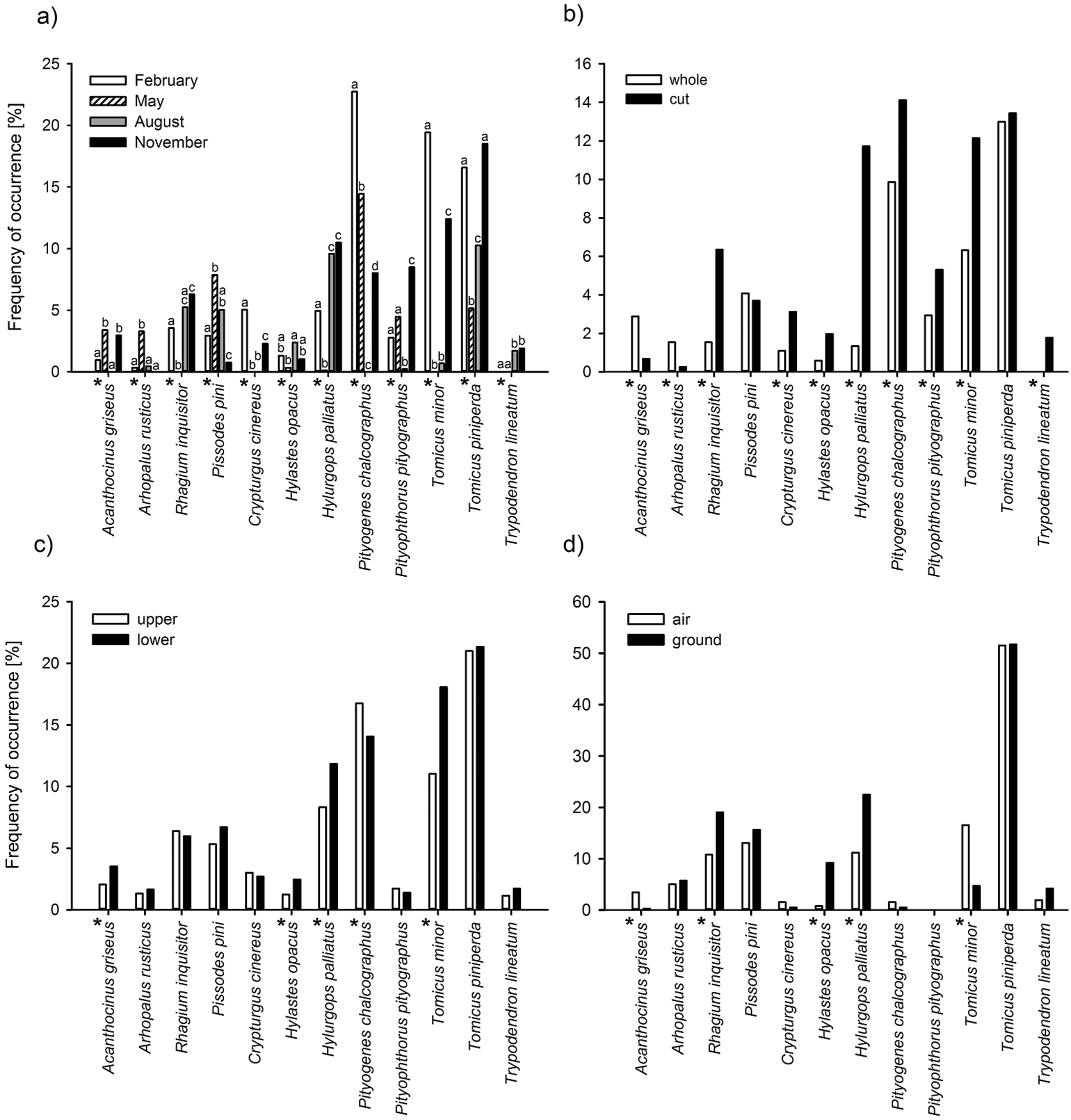

Fig. 3. Frequencies of occurrence of the recorded species with respect to: – a. Felling date. – b. Post-felling cutting. – c. Orientation of the logging residue (LR) surface towards the ground. – d. Contact of the LR with the ground (only data on the three basal sections of trunk were included – see Methods). Different letters within species show significant differences, see Methods. An asterisk (*) indicates species showing significant differences in the gallery coverage (Table 4). Only the species recorded on at least 100 LR fragments were included in the analyses.

explain a substantial portion (16.6%) of the variability in the species' gallery coverage (Table 2), with tree part, diameter, bark thickness and felling date the most important factors. Some of these associations have been previously noted. For example, the part of the tree was found to be the most important factor affecting the species occurrence of BWBB on standing Scots pine trees (Foit 2010), and the effect of the substrate diameter and bark thickness on the occurrence of saproxylic beetles has been illustrated in several other studies (Zhang *et al.* 1993, Schiegg 2001, Lindhe & Lindelöw 2004, Lindhe *et al.* 2005, Jonsell *et al.* 2007, Maňák 2007, Jonsell 2008, Foit 2010, Brin *et al.* 2011). Furthermore, the impact of the felling date was previously documented in studies on different types of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine LR (Kula & Kajfosz 2006, 2007, Foit 2012a, b).

The tree parts exhibited stronger explanatory power than did the metric variables (diameter and bark thickness) together (Table 2), which most likely reflected the strong correlations between bark thickness and diameter with the tree parts (Table 1, 3). Indeed, the majority of the variance in these factors can be explained by the tree parts alone, and the tree parts may be more strongly correlated with certain unstudied variables (e.g., substrate humidity and anatomical and chemical constitution). Some species were significantly associated with certain tree parts (Fig. 2), and these associations more or less fit known substrate preferences (Schwenke 1972). Among the four species found to be more closely associated with the tree parts than with their metric variables (Table 3), a clear explanation was only found for *A. rusticus* because this species was mostly bound to the first basal trunk section (Fig. 2). However, the diameter explained a higher proportion of the variability in the species composition of assemblages (Table 2) and was the most important metric varible of tree parts for the gallery coverage of the six assessed species (Table 3), whereas bark thickness, which was only different on the basal part of the tree trunks (Table 1), exhibited similar explanatory power and was a more important variable than diameter in determining the gallery coverage of six species (Table 3). Accordingly, Foit (2010) documented bark thickness as the most important metric variable affecting the occurrence of BWBB on standing Scots pines. Not surprisingly, mostly species associated with the lower part of the trunk, with thick bark (*A. rusticus*, *R. inquisitor*, *T. piniperda* and *T. lineatum*), showed stronger association with bark thickness than with diameter in the present study (Table 3, Fig. 2). In contrast, *P. chalcographus*, which exhibited the strongest association with bark thickness, could colonise almost every part of the felled trees covered by thin bark regardless of diameter (in most cases). The diameter of the tree parts was the most important variable for several species associated primarily with the middle (*A. griseus* and *C. cinereus*) to lower (*P. pini*, *H. opacus* and *H. palliatus*) part of the trunk. These species most likely avoided substrates that were too thin and had a tolerance for various bark thicknesses (Escherich 1923, Schwenke 1972, Bense 1995, Sauvard 2004). In contrast, *P. pityographus* (also associated mostly with diameter) evidently preferred thin substrates on branches and extreme tree tops (Fig. 2), where the thickness of the almost uniformly thin bark (Table 1) may not have played a significant role.

The substantial impact of the month of felling (Table 2, 4, Fig. 3a) was most likely associated with the timing of the species' mating/egg laying, and with requirements of particular species for the stage of substrate dieback/decay. As the majority of the recorded species exhibit spring-to-early summer mating/egg-laying periods (Schwenke 1972), the trees felled in August were not colonised in the year of felling and remained attractive only to secondary species (*R. inquisitor*, *P. pini*, *H. opacus*, *H. palliatus, T. lineatum* and occasionally *T. piniperda*) (Escherich 1923, Schwenke 1972, Gregoire & Evans 2004, Wermelinger *et al.* 2008, Foit 2014) in the following year. In contrast, the LR produced in the winter were densely colonised by the most aggressive recorded species (*P. chalcographus* and *T. minor*) (Escherich 1923, Schwenke 1972, Gregoire & Evans 2004, Wermelinger *et al.* 2008, Foit 2014) early after felling. Trees felled in May were frequently used as a breeding substrate, predominately by species with later mating/egg-laying periods (*A. griseus*, *A. rusticus*, *P. pini*) (Schwenke 1972), whereas species exhibiting earlier egg laying notably avoided such trees (*T. minor*, *T. piniperda* and *T. lineatum*). Logging residues produced in November did not show distinct patterns of colonisation by any particular species, as these residues entered the vegetative period in an overly degraded state to be attractive to typical secondary species (*R. inquisitor*, *H. palliatus* and *T. lineatum*), but were still sufficiently fresh to attract some of the more aggressive species (*P. chalcographus*, *T. minor* and *T. piniperda*). These findings correspond to results of other studies in which *P. chalcographus* was documented to avoid LR from summer fellings and to be most frequently found on LR from the winter and spring (Kula & Kajfosz 2007, Foit 2012b). Despite the slightly later egg-laying period of *C. cinereus* (Schwenke 1972), this species showed almost the same pattern of occurrence on

LR from particular months as *T. minor*, which might have been caused by the association of *C. cinereus* with the latter species as determined by the Spearman correlation index after removing the effects of the tree identity, tree part, diameter and bark thickness by fitting the GLM and extracting the residuals: s = 0.191, $P < 0.05$. *Crypturgus cinereu*s is known to use the entrance holes of other scolytids for access to areas under the bark of trees (Pfeffer 1955, Schwenke 1972) and was found to mainly exploit *T. minor* entrance holes for this purpose in the present study.

The post-felling cutting of the trees showed only a weak effect on the overall species composition of the BWBB assemblages (Table 2). This effect was not decreased by the addition of other habitat covariables in the calculation, and remarkable effects on the occurrence of particular species were found (Table 4, Fig. 3b). Species associated with the basal part of the trunk (i.e., *R. inquisitor*, *H. opacus*, *H. palliatus* and *T. lineatum*) that prefer a substrate with sufficient humidity (Pfeffer 1955, Schwenke 1972) and are attracted to ethanol (a product of ongoing substrate degradation/fermentation, Schroeder & Lindelöw 1989, Byers 1992, Sweeney *et al.* 2007) preferred cut trees in the present study. This suggests that the loss of water from the basal parts of trunks with no living branches was slowed by the disruption of water-conducting tissues (in the case of cut trees), thereby enabling the subsequent fermentation of tissues. In contrast, several of the first-colonising species associated with the upper parts of trees were also significantly more abundant on cut trees (*C. cinereus*, *T. minor*, *P. chalcographus* and *P. pityographus*), which could have been due to the higher levels of attractive volatiles emitted from cut trees. Only *A. griseus* and *A. rusticus* (both late mating/egg-laying species (VI–VIII)) (Schwenke 1972) were found to be more abundant on uncut trees, which could simply be the result of stronger competition with earlier egg-laying species on cut trees.

However, the effects of the LR surface orientation towards the ground and contact of the LR with the ground on the overall species composition of the BWBB assemblages were almost negligible (Table 2), although several species were significantly affected by these variables (Table 4, Fig. 3c, d). *Pityogenes chalcographus* was significantly more abundant on the upper side of LR, most likely due to its requirements for higher temperatures, as this species has been shown to prefer sunny clear-cut areas (Peltonen & Heliövaara 1999, Johansson *et al.* 2006) and to be most abundant in the top layer of LR piles (Kacprzyk 2012). In contrast, the higher gallery coverage of *T. minor* on the lower side of LR might be related to its strong association with mutualistic fungi (*Ophiostoma canum* (Münch) Syd. & P. Syd. and *Ambrosiella tingens* (Lagerb. & Melin) L.R. Batra) (Kirisits 2004, Jankowiak 2008) requiring a certain level of humidity. The documented preference of *R. inquisitor*, *H. opacus* and *H. palliatus* for fragments of LR showing substantial contact with the ground and higher gallery coverage of *H. opacus* and *H. palliatus* on the lower sides of the LR most likely reflected the species' requirements for higher humidity (Pfeffer 1955, Peltonen & Heliövaara 1999). In contrast, the association of *A. griseus* and *T. minor* with LR that did not have significant contact with the ground was not easily explained, although it might have been related to the species avoiding high humidity.

5. Conclusions and implications for forest management

Leaving trees in a stand that have been felled during pre-commercial thinning provides substrates for the development of a substantial number of BWBB species and most likely supports a number of other saproxylic species. The occurrence of different species and, thus, the overall composition of the assemblages differs significantly among various tree parts and is strongly affected by substrate diameter, bark thickness and the date of felling and, to a lesser extent, by the post-felling cutting of trees into 1 m sections, the contact of the LR with the ground and the orientation of the LR surface towards the ground (upper/lower side).

In contrast, it has been documented that LR generated from pre-commercial thinning can enable the multiplication of a number of pests, such as *P. chalcographus*, *T. minor* and *T. piniperda*. The occurrence of all these species is significantly affected by the felling date, and based on the results of the present study, we can infer that the risk of their multiplication can be minimised if fellings are conducted between July and September. Furthermore, leaving whole trees in a stand, without cutting them into smaller parts, should reduce the multiplication of certain pests (*P. chalcographus*, *T. minor* and *P. pityographus*).

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