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Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides

Ruaridh Hägglund[1], Joakim Hjältén*

Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

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ABSTRACT

In many parts of the boreal biome intensive forest management has resulted in profound changes in forest structure, tree species composition and dead wood availability, and by so negatively effecting forest biodiversity. Restoration of degraded forest habitats is therefore of high priority, both internationally and nationally. Consequently, it is of uttermost importance to develop cost-efficient restoration methods. We have therefore initiated a cost neutral ecological restoration experiment aimed at increasing the variety and volume of dead wood in voluntary set-asides (as part of the FSC certification requirements) by mimicking the two natural disturbances, forest fire and small scale gap dynamics. We studied how tree species and substrate type, i.e. the way in which a tree was killed (cut, girdled, tipped over or cut to produce a high stump), affect species composition, abundance and species richness of saproxylic beetles. We found that species composition differed between tree species in burned as well as gap-cut stands, and that tree posture, i.e. standing or downed trees, also affected species composition in gap-cut stands. In addition, abundance and species richness differed between tree species in gap-cut stands, generally being higher in spruce than in pine and birch. Based on our results we recommend a wider practice of dead wood creation involving a multitude of tree species and tree postures, through mimicking natural disturbances in the management of boreal forests. Furthermore, we suggest that voluntary set-asides provide an excellent opportunity for restoration as they are wide spread and already available in the forest landscape. Restoration cost can therefore be kept at a minimum or totally avoided as in this study.

1. Introduction

Habitat loss and degradation are recognized as two main causes of declining biodiversity on a global scale (Heinrichs et al., 2016). In many parts of the boreal biomes the introduction and practise of rotation forestry has replaced natural disturbance regimes formerly present (Esseen et al., 1997; Lindenmayer et al., 2006; Kuuluvainen, 2009). Disturbances such as forest fires and death of single or groups of trees, which create gaps in the canopy, were once the main drivers behind the structure and composition of these forests (Esseen et al., 1997; Angelstam and Kuuluvainen, 2004; Kuuluvainen and Aakala, 2011). Formerly complex forest ecosystems with considerable variations in habitat type, including vertical structure, tree species composition, age distribution, and dead wood dynamics, have often been transformed into simplified forest habitat (Esseen et al., 1997; Kuuluvainen, 2009). These are often even aged, single species cohorts of planted trees supporting low levels of dead wood (Kuuluvainen, 2009; Brumelis et al., 2011). Consequently the volume of dead wood has decreased due to biomass extraction and at the same time dead wood diversity has decreased (Siitonen, 2001; Jonsson et al., 2005; Stokland et al., 2012).

Saproxylic species, i.e. dead wood dependent species (Stokland et al., 2012); have evolved under conditions with a great variety of dead wood present in the forest landscape. Hence, different species have adapted to utilize differing qualities of dead wood; manifested through dependencies on certain tree species, diameter intervals, substrate types, e.g., standing or downed wood (Ulyshen and Hanula, 2009; Toivanen and Kotiaho, 2010; Stokland et al., 2012), and different stages of decomposition (Lee et al., 2014), as well as in which environment the dead wood substrates are located, e.g. in shade or sun exposed positions (Lindhe et al., 2005). Considering that saproxylic organisms constitute a large proportion of the species present in boreal forest (Grove, 2002; Gibb et al., 2006; Boucher et al., 2012), reductions in dead wood availability have had profound negative effects on boreal biodiversity (Siitonen, 2001; Grove, 2002; Jonsson et al., 2005; Rassi et al., 2010; Stokland et al., 2012; Gärdenfors, 2015). Ultimately expressed by the high proportion of saproxylic species included in many national redlists of threatened species (Rassi et al., 2010; Gärdenfors, 2015).

Through legal demands and conservation schemes such as the Forest

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* Corresponding author.
E-mail address: joakim.hjalten@slu.se (J. Hjältén).

[1] Present address: Sweco Environment AB, Sweden.

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Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC), today’s forest industry is encouraged to practise a variety of conservation measures improving conditions for biodiversity (Johansson et al., 2013). In boreal regions these measures include: setting forest stands aside from ordinary forestry, leaving buffer zones of trees alongside wetlands and water bodies, leaving snags and logs on clear cuts, and also actively creating dead wood in connection to final harvesting (Gustafsson et al., 2012; Johansson et al., 2013); often high stumps of spruce (*Picea abies*). Prescribed burning of clear-cuts and to some extent standing forests are also included in the FSC-standards for boreal Fennoscandia (Johansson et al., 2013).

However, these efforts do not seem to suffice in restoring biodiversity and we are still witnessing biodiversity losses in boreal ecosystems (Rassi et al., 2010; Johansson et al., 2013; Gärdenfors, 2015). It has therefore been suggested that a more proactive dead wood management is needed to reverse the present negative trend (Shorohova et al., 2011). Lindenmayer et al (2006) propose that ecological restoration is best practiced by mimicking natural disturbances. In boreal settings, Kuuluvainen (2002) and Shorohova et al. (2011) suggest that such practice should include restoration burning of standing forests and mimicking gap scale dynamics. By planning such restoration actions carefully and taking into account the need for a great diversity of different dead wood substrates, both concerning tree species and mortality factor, it should be possible to cater for as many dead wood associated species as possible (Ulyshen and Hanula, 2009; Toivanen and Kotiaho, 2010; Hjältén et al., 2012; Stokland et al., 2012).

The aim of this study was therefore to evaluate if the different dead wood substrates, including three tree species and four substrate types, results in differing saproxylic beetle communities reproducing within the dead wood substrates created during restoration burning as well as artificial gap creation. We therefore address the following questions:

- Does tree species, i.e. spruce (*Picea abies*), pine (*Pinus sylvestris*) or birch (*Betula pubescens* and *B. pendula*) affect the abundance, species richness and composition of saproxylic beetle communities emerging from trees killed during restoration burning?
- Does tree species and substrate type, i.e. if the trees are i) cut at the base and left as logs, ii) tipped over and left as logs, iii) girdled and left standing or iv) cut 3–5 m above ground and left as a high stumps; affect the abundance, species richness and composition of saproxylic beetle communities emerging from dead wood substrates created in gap cut stands?

2. Materials and methods

The study was conducted in the middle and northern boreal zones (Ahti et al., 1968) of northern Sweden (Fig. 1; 63° 23’ N to 64° 30’ N and 17° 37’ E to 21° 20’ E). Sixteen voluntary set asides that have never been clear cut, were similar in tree species composition, tree age, field layer vegetation and standing tree volume were included in the study (for details see Hjältén et al. (2017)). Selection was based on a combination of stand data provided by the land host (Holmen AB) and field visits. Stand size varied between 4.3 and 21.6 ha. All stands were dominated by Norway spruce (*Picea abies*) and/or Scots pine (*Pinus sylvestris*). Deciduous trees such as downy birch (*Betula pubescens*), silver birch (*B. pendula*), aspen (*Populus tremula*) and goat willow (*Salix caprea*) were scattered throughout the stands.

Restoration treatments were applied during the early spring and summer of 2011. Six of the stands were subjected to restoration burning and ten stands were subjected to artificial gap creation. In the six stands assigned for restoration burning 5–35% of the trees were cut during the early spring of 2011. This increased solar radiation, and thereby allowed the forest floor to dry up quicker after snow melt. Except for approximately 5 m^3/ha of the cut trees that were left at site as fuel, the remaining trees were removed to cover costs for restoration. In stands selected for artificial gap creation standard harvesters were used to create six canopy gaps 20 m in diameter per hectare. In every second gap, dead wood substrates were created by killing trees with a standard harvester in four different ways; namely (i) cutting the tree at the base and leaving the log, (ii) simulated windfall by pushing the tree over (with the harvester), thus exposing the root the tree, (iii) girdling trees by removing bark at a height of 4–6 m above ground and (iv) creating 3–5 m tall high-stumps by cutting the trees at this height. Due to the scarcity of deciduous trees in the stands the only way of creating dead wood of birch was by cutting them at the base and leaving the remaining tree as a log. For the two coniferous species all four methods were used. In the remaining gaps all trees were removed to cover costs for restoration.

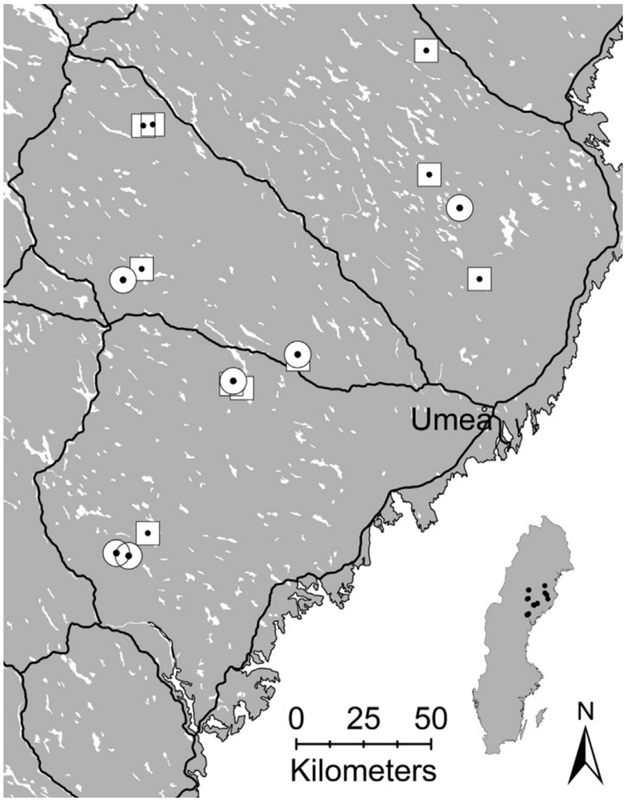

Fig. 1. Map of study area. Circles = burned stands; squares = gap-cut stands.

2.1. Beetle sampling

Beetles were sampled using eclector traps which give a representative sample of the beetles hatching from a certain piece of wood (Okland, 1996; Schiegg, 2001; Alinvi et al., 2006). Each eclector trap consisted of a black plastic mesh wrapped around the trunk of each sampled tree. Traps were attached to the trunk of the sampled trees with plastic straps at the bottom and top end of each trap, approximately 40 cm apart. The enclosed volume of each trap was calculated as a cylinder based on the diameter of the tree trunk and the length of the trap. Foam rubber was used to insure that there were no gaps between the mesh and tree trunk at the two ends of the trap. Three to four metal wires separated the mesh from the trunk of the tree allowing insects emerging from the bark to make their way to the only light source available: a semi-transparent plastic bottle filled to 1/3 with a 50–50 mixture of propylene glycol and water. A small amount of detergent was added to the glycol-water solution breaking surface tension (see Andersson et al. (2015) for illustration). The traps were set up during the first week of June, and collected during the last week of September in 2013.

Sampling was conducted on a total of 12 different substrate types

Table 1
Total number of traps per tree species and substrate type, i.e. the way the tree was killed, included in the analyses of abundance and species richness, and within parenthesis are the numbers of traps used in the species composition analyses.

Tree species	Substrate type				
	Cut at the base	Tipped over	High stump	Girdled	Burned
Spruce	45 (30)	42 (27)	45 (27)	39 (30)	24 (15)
Pine	24 (21)	24 (18)	36 (24)	24 (15)	26 (18)
Birch	28 (18)	–	–	–	26 (18)

(Table 1). In each stand the aim was to sample five trees of each substrate type, but in stands containing less than five trees of a certain substrate type we sampled as many as possible. Traps were attached to killed spruce-, pine, and birch trees in gap cut stands as well as in burned stands. In the burned stands traps were attached to standing trees killed by restoration fire. In the gap cut stands traps were attached to all four different substrate types on spruce and pine. Due to the scarcity of birch; traps were only attached to birch trees that had been cut at the base and left as logs.

2.2. Transmitted solar radiation and volume of sampled dead wood

To evaluate the influence of solar radiation on specific dead wood substrates total transmitted solar radiation was calculated by analysing fish-eye photos taken of the canopy from the forest floor at the exact position of each trap. Care was taken to make sure that each picture was oriented such that the northern point of the picture was known; a tripod with a spirit level attached, was used to insure that the camera was in an entirely level position at the moment of photography. This procedure assured that the analysis of total transmitted solar radiation was as accurate as possible. Solar radiation calculations, measured in MJ/m2/d and averaged over the entire year, were calculated using the software Gap Light Analyser version 2.0 (Frazer et al 1999). The volume of dead wood enclosed by each trap can also influence trapping efficiency. To correct for sampling effort, we calculated the volume of deadwood enclosed as a cylinder, using the diameter and length of each trap.

2.3. Statistical analyses

We fitted generalized linear mixed-effects models with Poisson distributed errors to investigate if there were any differences in abundance and species richness of saproxylic beetles emerging from the different substrate types created. Therefore, abundance and species richness were set as the dependent variables. In order to minimize the risk of different geographical locations of burned and gap cut sites to interfere with the results the burned stands and gap cut stands were analysed separately. In the analyses concerning burned stands, tree species was set as predictive variable, and in the analyses concerning gap cut stands, tree species and substrate type were set as predictive variables; we also studied the interaction term between these two variables. The randomized block design and the fact that the number of usable traps per substrate type differed required us to set the stand identity as a random effect. If tree species, substrate type or the interaction between the two variables significantly affected the abundance or species richness (Type II Wald Chi2) of emerging beetles; pairwise post hoc testing was applied, p-values were adjusted for by applying the Holm-method. Model fit was evaluated by checking residuals for homoscedasticity and normality. In addition overdispersion was estimated; if the quota between residual deviance and degrees of freedom exceeded 2 we made use of observation level random effects (OLRE) to control for overdispersion. All analyses of abundance, species richness and overdispersion were conducted in the statistical software R (R Core Team, 2014) by making use of functions included in the lme4 (Bates et al., 2015), emmeans (Lenth et al., 2018), MuMIn (Barton 2016) and RVAideMemoire (Hervé, 2016) packages.

Permutational multivariate analysis of variance (PERMANOVA) was used to investigate if there were any differences in species composition between substrate types. Prior to analyses we pooled data from three traps per substrate type and stand. Substrate types that were sampled with less than three traps per stand were omitted from that particular stand. Similar to the analysis of abundance and species richness the analysis of species composition was divided into two parts. In burned stands differences in species composition between tree species was analysed by setting tree species as a fixed factor and stand identity as a random factor. In the gap cut stands differences in species composition between tree species and substrate type were analysed by setting these two variables as fixed effects and stand identity as a random effect. In order to reduce the impact of the most abundant species, but at the same time preserving relative abundances, data were fourth-root transformed (Clarke, 1993). We used Bray-Curtis distances as similarity measure (Field et al., 1982); we performed 9999 permutations of residuals for all tests. In the case where we only had one explanatory variable, i.e. the comparison between tree species within the burned stands, we used the permutational method of unrestricted raw data. In the cases where we had two explanatory variables, i.e. the analyses of species compositions in the gap cut stands including both tree species and substrate type; we conducted the analyses under the reduced model. Species contributions to the observed dissimilarity between tree species or substrate types were calculated with SIMPER analyses. SIMPER is not a test of statistical probabilities per se, but a way of conceptualizing what differs between two sets of data. SIMPER calculates the overall percentage contribution that each species makes to the average dissimilarity between two groups and lists the species in decreasing order of their importance in discriminating the two sets of samples. The analyses of species composition (PERMANOVA and SIMPER) were carried out in the statistical software Primer 7 (Clarke and Gorley, 2015) with the add-on package PERMANOVA + (Anderson et al., 2008). The vegan package in R and Microsoft Excel was used to create non-metric Multi-Dimensional scaling (nMDS) visualisations of the distances between species communities. Each symbol in the figure represents the species community of beetles trapped in one forest stand and the closer the symbols are to each other the more similar are the communities.

Due to few replicated study stands potential total amount of transmitted solar radiation at each trapping position and the sampled dead wood volume could not be included in the analyses of abundance, species richness and species composition. Instead, we fitted linear mixed-effect models to investigate if there were any differences in the potential total amount of transmitted solar radiation at each trapping position and the sampled volume of dead wood between substrate types. We set transmitted solar radiation and the volume of sampled dead wood as the dependant variables, respectively. In burned stands tree species was set as a fixed effect. In gap cut stands tree species and substrate type were set as fixed effects, we also studied the interaction term between these two variables. In both cases stand identity was set as a random factor. Model checking was carried out by studying homoscedasticity and normality of residuals. When needed, normally distributed residuals were obtained by log-transformation of the response variables. All analysis on differences in total amount of transmitted solar radiation and the sampled volume of dead wood were carried out in the statistical software R by utilizing the lme4 and multcomp packages.

3. Results

3.1. Restoration burning

2211 individuals and 92 species were collected in the burned area. The dominating species were *Polygraphus* sp. and *Trypodendron lineatum*

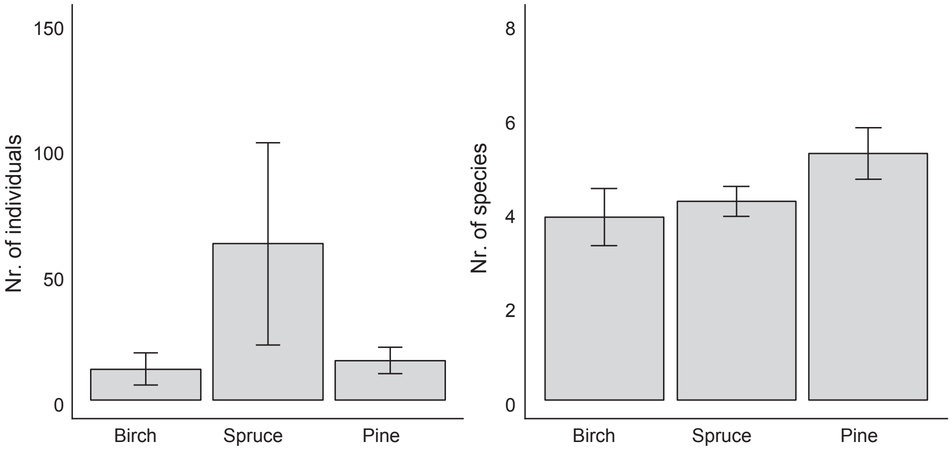

Fig. 2. Average abundance and average species richness of beetles collected per trap in the burned stands.

making up 53% and 11% of the catch in burns. There were no differences in the abundance or species richness of beetles emerging from the three sampled tree species in the burned stands ($Chisq_{ab} = 4.4231$, $df_{ab} = 2$, $p_{ab} = 0.1095$, and, $Chisq_{sp} = 2.8971$, $df_{sp} = 2$, $p_{sp} = 0.2349$ respectively; Fig. 2).

However, the overall species composition differed between tree species (Table 2). Pairwise comparisons revealed that the species composition of beetles emerging from birches differed from those emerging from both spruce and pine trees (Table 2).

The visualisation of the nMDS plots (Fig. 3) together with the almost significant result from the PERMANOVA analyses (Table 2) suggests that there is a trend indicating differences in species composition of the beetles emerging from pine trees compared to that of spruce trees in burned stands. All tree species harboured unique beetle species; pine the most with eight species, birch next with seven species and spruce the least with two unique species (Appendix A). The five beetle species contributing most to the differences in species composition between tree species are presented in Appendix B.

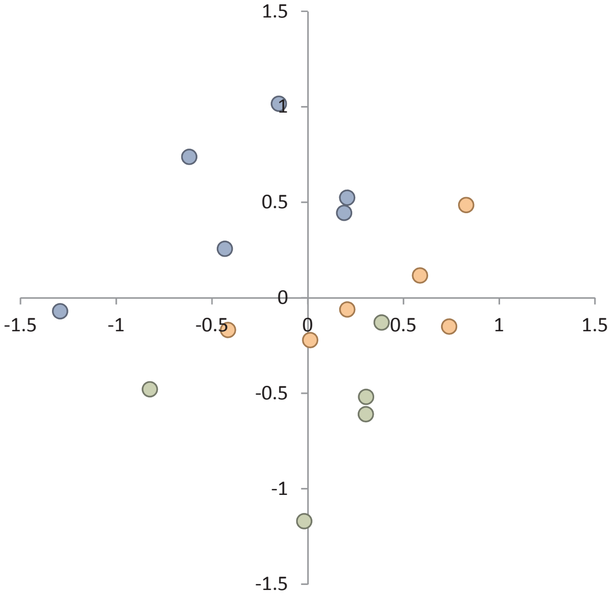

Fig. 3. NMDS visualisation of species composition in the burned stands. Each symbol represents the beetles trapped in one forest stand. Stress = 0.16. Blue = birch, Green = spruce, Orange = pine. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. *Artificial gap creation*

10,287 individuals and 166 species were collected in gap-cuttings with *Crypturgus subcribrosus*, *Trypodendron lineatum* and *Hylurgops palliates* dominating, constituting 39, 13 and 12%, respectively, of the catch. Tree species, and the interaction term between tree species and substrate type significantly affected the abundance of emerging saproxylic beetles in the gap cut stands (Table 3; Fig. 4). Tree species significantly affected the species richness of emerging saproxylic beetles in the gap cut stands (Table 3; Fig. 4). Pairwise post hoc comparisons within the substrate type cut at base revealed that the abundance of emerging beetles was higher for spruce than for both pine and birch, and higher in pine than in birch. In addition, abundance was higher in spruce than pine for all substrate types (Table 3; Fig. 4). In contrast to the results between tree species there were few differences in abundance between substrate types within tree species. The only observed differences lay between spruce trees that were left as high stumps on the one side and logs cut at the base together with tipped over trees on the other side (Table 3; Fig. 4).

Table 2
Results from the PERMANOVA analyses of species composition in the burned stands.

Main test	ss	ms	Pseudo F	p
Tree species	13,956	6977.8	3.23	< 0.01
Stand ID	17,340	3467.9	1.61	0.03
Pairwise tests (post hoc)			t	p
Birch vs Pine			1.69	0.04
Birch vs spruce			2.04	0.02
Pine vs spruce			1.70	0.06

Regarding species richness, post hoc testing revealed that both cut spruce and pine trees harboured higher species richness than cut birch trees, whilst there is no difference between spruce and pine trees cut at the base and left as logs. Spruce trees left as high stumps harbour more species than pine trees left as high stumps. The only significant difference between substrate types within tree species lay between pines that were left as high stumps and those that were cut at the base and left as logs (Table 3; Fig. 4).

The main test of differences in species composition revealed that there were differences in species composition between tree species, substrate types and the interaction term between the two explanatory variables (Table 4, Fig. 5). Pairwise post hoc tests further revealed that the differences in species composition occurred between spruce and the other two tree species investigated, i.e. pine and birch, regardless of substrate type. No significant difference was found between pine and birch for trees cut at the base. In addition, pairwise post hoc testing also

Table 3
Analyses of abundance and species richness of saproxylic beetles in the gap cut stands. Non corrected p-values.

Abundance				
Main test		Chi.sq	Df	p
Tree species		79.61	2	< 0.01
Substrate type		0.91	3	0.82
Tree species:Substrate type		9.72	3	0.02
Pairwise post hoc tests within substrate type	Estimate	Std.error	z-value	p
Cut at the base				
Birch vs pine	−0.84	0.40	−2.08	0.04
Birch vs spruce	−1.70	0.35	−4.92	< 0.01
Spruce vs pine	0.86	0.35	245	0.01
Tipped over				
Spruce vs pine	1.08	0.35	3.01	< 0.01
High stump				
Spruce vs pine	2.16	0.32	6.83	< 0.01
Girdled				
Spruce vs pine	1.07	0.36	2.95	< 0.01
Pairwise post hoc tests within tree species				
Spruce				
High stump vs cut	0.66	0.28	2.33	0.02
High stump vs girdled	0.55	0.30	1.85	0.65
High stump vs tipped	0.62	0.29	2.12	0.03
Cut vs girdled	−0.12	0.30	−0.39	0.70
Cut vs tipped	−0.05	0.29	−0.16	0.88
Girdled vs tipped	−0.07	0.30	0.23	0.82
Pine				
High stump vs cut	−0.64	0.38	−1.69	0.09
High stump vs girdled	−0.55	0.38	−1.44	0.15
High stump vs tipped	−0.47	0.38	−1.24	0.22
Cut vs girdled	0.09	0.41	0.22	0.83
Cut vs tipped	0.17	0.41	0.41	0.68
Girdled vs tipped	0.08	0.41	.019	0.85
Species richness				
Main test		Chi.sq	Df	p
Tree species		27.56	2	< 0.01
Substrate type		5.01	3	0,17
Tree species:Substrate type		6.20	3	0.10
Pairwise post hoc tests within substrate type	Estimate	Std.error	z-value	p
Cut at the base				
Birch vs pine	−0.79	0.20	−4.30	< 0.01
Birch vs spruce	−0.77	0.18	−3.91	< 0.01
Spruce vs pine	−0.02	0.16	−0.12	0.91
Tipped over				
Spruce vs pine	0.23	0.17	1.34	0.18
High stump				
Spruce vs pine	0.51	0.16	3.26	< 0.01
Girdled				
Spruce vs pine	0.09	0.17	0.54	0.59
Pairwise post hoc tests within tree species				
Spruce				
High stump vs cut	−0.04	0.13	−0.30	0.76
High stump vs girdled	0.09	0.14	0.66	0.51
High stump vs tipped	−0.03	0.14	−0.19	0.85
Cut vs girdled	0.13	0.14	0.95	0.34
Cut vs tipped	0.01	0.14	0.11	0.91
Girdled vs tipped	−0.12	0.14	−0.83	0.41
Pine				
High stump vs cut	−0.57	0.18	−3.17	< 0.01
High stump vs girdled	−0.33	0.19	−1.75	0.08
High stump vs tipped	−0.31	0.19	−1.67	0.10
Cut vs girdled	0.25	0.19	−1.29	0.20
Cut vs tipped	0.26	0.19	1.36	0.17
Girdled vs tipped	0.01	0.20	0.07	0.94

revealed that substrate type was of greatest importance amongst spruce trees, with significant differences between all substrate types except for cut and tipped trees (Table 4). There were no significant differences between substrate types for pine but most of the comparisons between standing (high stump and girdled) and downed substrates (cut and tipped) were marginally significant. Thus, the results for both spruce and pine suggest that the strongest differences between substrates was found between standing and downed substrates. The five beetle species contributing most to the differences in species composition between tree species and between substrate types are presented in Appendix B.

3.3. *Transmitted solar radiation and sampled volume of dead wood*

There was a difference in the total amount of transmitted solar radiation reaching traps attached to different tree species in the burned stands (Table 5).

Pairwise post hoc testing revealed that traps attached to pine trees were exposed to more solar radiation than spruce trees, no other differences between tree species were present (Table 6). In gap cut stands model selection revealed that the null model fit the data the best. The model including tree species as the sole predictive variable had a AICc close to that of the null model (Δ AICc = 0.51), we therefore chose to evaluate this model as well. The later model did however not show any significant effects of tree species or substrate type either (Table 5), suggesting that there was no difference in the amount of total transmitted solar radiation reaching the traps; irrespective of tree species or substrate type.

In burned stands the volume of sampled dead wood differed between tree species (Table 5). The sampled volume was higher for pine trees compared to both spruce and birch trees (Table 6). There was no difference in the volume of sampled dead wood between spruce and birch trees (Table 6). In gap cut stands the sampled volume of dead wood differed between tree species as well as between in which way the trees were killed (Table 5).

In gap cut stands the sampled volume was greater for pine than for spruce, which in turn was sampled at higher volumes than birch (Table 6). Tipped over trees were sampled at higher volumes than high stumps and girdled trees. No other differences in the sampled volume between substrate types occurred (Table 6).

4. Discussion

4.1. *Restoration burning*

We found that there were differences in species composition of saproxylic beetles between tree species in stands subjected to restoration burning. The main differences in species composition lay between the two conifer species and birch trees. However, by considering the almost significant difference between spruce and pine trees together with the visualisation in the nMDS-plot, this suggests that there is a trend towards differences in species composition between spruce and pine as well. The five species contributing most to the differences in species composition between birch and pine were *Hylurgops palliates, Phloeonomus pusillus* and *Sphaeriestes stockmanni*, all being more common on pine, and *Epuraea angustula* and *Trypodendron lineatum* being more common on birch. Similarly, the species contributing to the differences between birch and spruce were *H. palliates*, *S. stockmanni* and *T. lineatum* but also *Polygraphus sp*. and *Corticaria rubripes* The bark beetles *H. palliates, Polygraphus* sp. and predator P. *pusillus* are all associated with conifers and *S. stockmanni* and *C. rubripes* are fire associated predator and fungivore, respectively, often collected on conifers (Wikars, 2002; Boulanger and Sirois, 2007; Johansson et al., 2007; Hjältén et al., 2012; Borkowski and Skrzecz, 2016) . However, the higher abundance of *T. lineatum* and *E. angustula* on birch is difficult to explain as both species normally are associated with spruce forest (Johansson et al., 2007; Park and Reid, 2007). One possible explanation is that burning homogenize the tree species in nutrients and structures making them more equal to saproxylic beetles (Wikars, 2002; Toivanen and Kotiaho, 2010) but that this only applies to some specific beetle species. Because overall our results do not provide strong support for this. Even if the differences in assemblage composition between spruce and pine were slightly more apparent in gap-cut than in burned stands

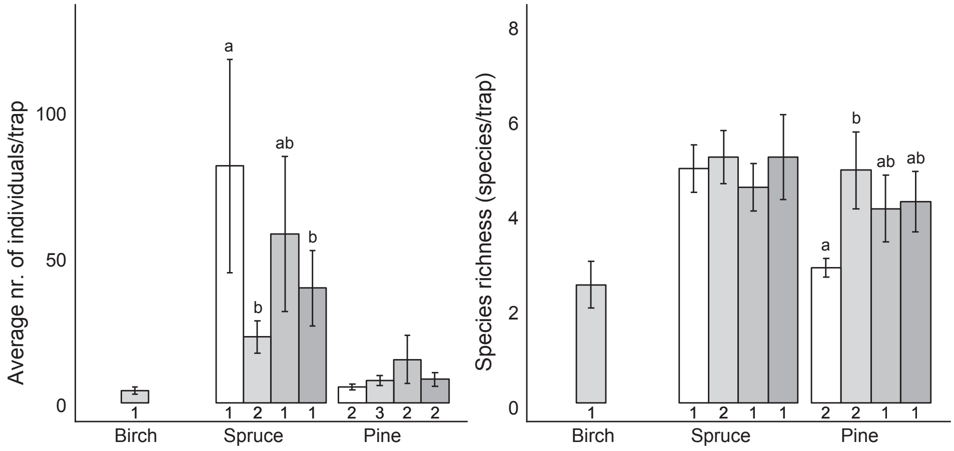

Fig. 4. Abundance and species richness of beetles collected in the gap cut stands. Differing letters above bars indicate significant differences between substrates within tree species, absence of letters indicates no differences within tree species. Differing numbers below bars indicate significant differences between tree species within substrate type. From left to right; white = high stumps, light grey = cut at the base, grey = girdled and dark grey = tipped over.

Table 4
Analyses of species composition in the gap cut stands.

Main test	ss	ms	Pseudo F	p
Tree species	23,533	11,766	4.48	< 0.01
Substrate type	21,346	3013.6	3.26	< 0.01
Interaction term	14,722	4907.3	1.75	0.02
Pairwise post hoc tests within substrate type			t	p
Cut at the base				
Birch vs pine			1.36	0.20
Birch vs spruce			1.83	0.02
Pine vs spruce			1.47	0.04
Tipped over				
Pine vs spruce			1.40	0.08
High stumps				
Pine vs spruce			1.89	0.01
Girdled trees				
Pine vs spruce			2.21	0.02
Pairwise post hoc tests within tree species				
Spruce				
Cut vs high stump			2.79	< 0.01
Cut vs girdled			2.33	< 0.01
Cut vs tipped			1.22	0.19
High stump vs girdled			1.50	0.03
High stump vs tipped			2.76	< 0.01
Girdled vs tipped			2.58	< 0.01
Pine				
Cut vs high stump			1.44	0.06
Cut vs girdled			1.59	0.06
Cut vs tipped			0.80	0.70
High stump vs girdled			1.21	0.24
High stump vs tipped			1.24	0.21
Girdled vs tipped			1.51	0.07

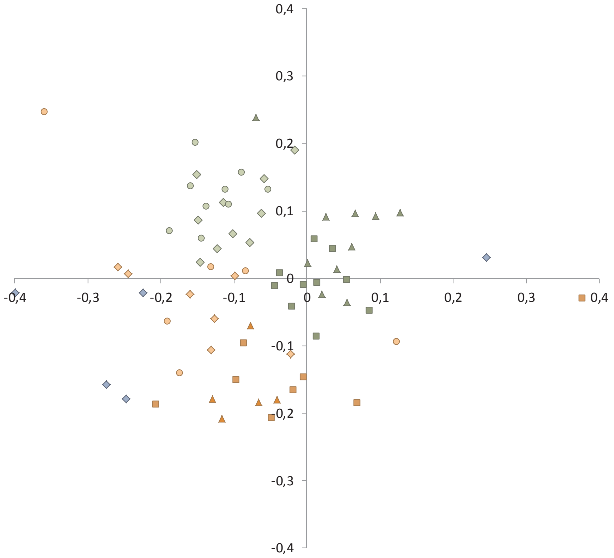

Fig. 5. NMDS visualization of species compositions in the gap cut stands. Each symbol represents the species community of beetles trapped in one forest stand. One data point, representing the species community collected from birch trees in one stand, was removed from the figure in order to increase the clarity of the results. The coordinates of the removed point were x = 4.82, y = 0.01. Stress = 0.16. Blue = birch, Green = spruce, Orange = pine; Diamonds = cut trees, Circles = tipped over trees, Triangles = girdled trees, Squares = high stumps. For clarity, standing substrate types have a slightly darker color than substrate types that are lying down on the forest floor. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

we still see strong indication of a differentiation in burned stands also. As the burnings were of rather low intensity it is likely that the trees were still intact enough to differentiate in resources present, and by so attracting different species of saproxylic beetles (Wikars, 2002; Saint-Germain et al., 2004; Ulyshen et al., 2010). Our results are especially interesting as there were no differences between tree species in abundance or species richness of the beetles collected at burned sites, suggesting that differences in assemblage composition per se explain the observed differences in species composition. Nevertheless, the lack of difference in abundance and species richness between tree species is interesting in itself. This because, a greater volume of sampled dead wood, i.e. the pine trees, would be expected to result in higher abundances of saproxylic beetles than a lower volume of dead wood; simply because there is more resource available in a larger piece of dead wood (McGeoch et al., 2007). Furthermore, increased solar radiation has been shown to increase both species richness and abundance of saproxylic

Table 5
Results from the linear mixed effects models investigating differences in potential transmitted solar radiation and the volume of sampled dead wood.

Transmitted solar radiation	Chi.sq	Df	P
Burned stands			
Tree species	6.94	2	0.03
Gap cut stands			
Tree species	5.51	2	0.06
Volume of sampled dead wood			
Burned stands			
Tree species	42.96	2	< 0.01
Gap cut stands			
Tree species	71.63	2	< 0.01
Substrate type	18.18	3	< 0.01

Table 6
Pairwise post hoc testing investigating differences potential transmitted solar radiation and the volume of sampled dead wood. The species or substrate with higher solar radiation or larger volumes of dead wood are indicated in parenthesis after the significant p-value.

Transmitted solar radiation	Estimate	Std.error	z-value	p
Burned stands				
Spruce vs birch	−0.98	0.54	−1.81	0.14
Spruce vs pine	−1.39	0.54	2.58	0.03 (pine > spruce)
Pine vs birch	0.41	0.52	0.79	0.43
Volume of sampled dead wood				
Burned stands				
Spruce vs birch	0.0007	0.0015	0.465	0.64
Spruce vs pine	−0.0083	0.0016	5.334	< 0.01 (pine > spruce)
Pine vs birch	0.0090	0.0015	5.928	< 0.01 (pine > birch)
Gap cut stands				
Spruce vs birch	0.49	0.11	4.38	< 0.01 (spruce > birch)
Spruce vs pine	−0.39	0.06	6.38	< 0.01 (pine > spruce)
Pine vs birch	0.88	0.12	7.47	< 0.01 (pine > birch)
Cut vs high stump	−0.15	0.08	−1.87	0.19
Girdled vs high stump	0.05	0.08	0.58	0.56
Tipped vs high stump	−0.27	0.08	−3.38	< 0.01 (tipped > high)
Girdled vs cut	0.20	0.09	2.31	0.08
Tipped vs cut	−0.12	0.08	−1.49	0.27
Tipped vs girdled	−0.32	0.09	−3.75	< 0.01 (tipped > girdled)

beetles (Lindhe et al., 2005; Vodka and Cizek, 2013). Increased solar radiation could increase the temperature of dead wood and thereby increase the metabolic rate and the growth rate of beetles developing within a given piece of dead wood (Allen et al., 2002), allowing for more individuals to hatch during the sampling period. However, we found no indications that either of these factors influenced beetle abundance in our data. At the same time we should be aware that this study not was designed to primarily evaluate the effect solar radiation and dead wood volume and consequently the variation in these factors could have been low in our data. Consequently, no clear conclusion can be made from this study regarding the effect of these variables in abundance and species of saproxylic beetles.

4.2. Artificial gap creation

Contrary to that of the restoration burnings, we did find differences in abundance and species richness between the three tree species sampled in the gap cut stands. For both abundance and species richness, spruce was generally the species with the highest counts; in addition pine trees displayed higher species richness and abundance than birch trees. These differences cannot entirely be explained by the volume sampled or the potential solar radiation reaching the position of each trap. There were differences between trees species in the volume of dead wood sampled in the insect traps. Pine trees had higher sample volume than both spruce and birch and spruce had higher sample volume than birch. This could possibly explain why more beetles were caught in the traps attached to spruce trees compared to those on birches, but not explain why the abundance of beetles was higher in the traps attached to spruce trees compared to those attached to pine. As the only significant difference in potential solar radiation was between spruce and pine but in the direction that pine trees received more light than the spruce trees our results support those by Wu et al. (2015), i.e. that the differences in abundance and species richness of saproxylic beetles cannot be explained entirely by the potential amount of solar radiation reaching each trap either. A more likely explanation to the differences in abundance and species richness between spruce and pine is that more beetle species are known to be associated with spruce trees compared to pine trees in Fennoscandia (Jonsson et al., 2005; Stokland et al., 2012). This is, however, not true for birch trees compared to the other studied tree species, in contrary more beetle species are known to be associated with birch trees compared to both spruce and pine (Stokland et al., 2012), suggesting that we would expect to find more species collected from birch than spruce and pine. Wikars et al. (2002) also reported a lower species richness of birch compared to spruce logs in unburned forests, suggesting this to be a result of birch being disturbance favoured and thus attracting more species in disturbed sites, e.g., after fire. Thus, more species could be found in birch simply because it occurs in more habitats than spruce and has a higher beta diversity. In addition, birch were rarer in the stands than spruce and pine, which potentially means that species pool of potential colonizing beetles species are smaller for birch than for spruce and this could potentially lead to lower species richness in birch (Seibold et al., 2017). Furthermore it is possible that the lower number of beetles emerging from birch trees is an effect of sampling effort as birch trees were sampled at significantly lower volumes for individual logs than both spruce and pine in the gap cut stands (Table 6).

Similar to the case in the burned stands, there were differences in the composition of saproxylic beetles communities between all three tree species sampled. For trees cut a base, *Pityogenes chalcographus, Dryocoetes autographus* and *Crypturgus hispidulus* contributed most to these differences being more common in spruce than in the other tree species (Appendix B). All these species are regarded as mainly spruce associated even if they occur on other conifers as well (Johansson et al., 2006; Bertheau et al., 2009; Komonen et al., 2014). In addition, spruce, birch and pine trees all harboured a large number of unique species, including red-listed species like *Bius thoracicus* listed as vulnerable in the Swedish red-list and only found in spruce in our study, *Epuraea oblonga* only found in pine in our study and the rare *Euryusa castanoptera* only found in birch. This further suggests that the tree species per se is an important factor when it comes to which beetle species are attracted to and manage to reproduce in the different tree species. However, it should be noted that different species explained differences in assemblages between tree species in burned and gap-cut stands suggesting that fire influences both substrate and habitat quality.

We also found that substrate type played a significant role in the compositions of beetles emerging from different substrates, especially for spruce trees. The general pattern was that dead wood substrates lying down on the forest floor had separate beetle communities than from those that were standing up. Higher densities of cambivorous bark beetles *Crypturgus subcribrosus and H. palliatus* and the predator *Plegaderus vulneratus* in standing dead wood and lower densities of cambivores *P. chalcographus* and *D. autographus* contributed strongly to this pattern. *Plegaderus vulneratus* is a known predator on bark beetles, probably tracking increased density of bark beetles in standing dead wood (Schroeder and Weslien, 1994; Hilszczanski et al., 2007). However, we also found differences in saproxylic communities between high stumps and girdled trees, both being standing substrates. One possible explanation for this is that girdling leads to a slower process of die-off than cutting a tree four meter above ground. This could potentially results in differences in beetle colonization of high stumps and girdled trees. Although the patterns concerning pine trees were not as pronounced as for spruce trees, near significant PERMANOVA results together with the nMDS-visualisation suggests that there is a trend towards the same pattern as for spruce trees. Differences in species composition between standing and lying dead wood have been reported earlier (McGeoch et al., 2007; Ulyshen and Hanula, 2009; Hjältén et al., 2012). A possible explanation behind this pattern is that the moisture levels in dead wood substrates that are lying down differ from those standing up, and thereby attract different species (Boulanger and Sirois, 2007). However, since we did not measure moisture levels within the dead wood substrates sampled we cannot confirm this. Neither can we find a valid explanation as to why the species composition of sampled beetles differed between spruce high stumps and girdled spruce trees. However, a possible explanation is that girdled trees will keep their canopy for a couple of years, reducing sun exposure and affecting humidity, thereby influencing species composition.

5. Conclusions and implications for forest management

Experimental studies similar to ours have been conducted in the boreal regions surrounding the Baltic Sea (Laarmann et al., 2013; Hekkala et al., 2014; Heikkala et al., 2016). However, since our trapping method allowed us to study beetles actually reproducing within the dead wood substrates created, with little risk of catching so called "tourists", our experimental setup has allowed us to, in more detail than other studies, investigate which effect artificial creation of different dead wood substrates has on saproxylic beetle communities in boreal forests.

In accordance with other studies (Boulanger and Sirois, 2007; McGeoch et al., 2007; Ulyshen and Hanula, 2009; Toivanen and Kotiaho, 2010; Hjältén et al., 2012) we found that, regardless of restoration method, tree species and substrate type matters for the composition of saproxylic beetle communities, to some extent also abundances and species richness. Different tree species hosted different species communities, as well as harboured their own unique species. It is also evident that substrate type, i.e. the way the trees die, makes a difference in the composition of saproxylic communities utilizing dead wood substrates. The most apparent differences occurred between standing and lying dead wood. We therefore conclude that it is of importance to create dead wood substrates of as great variation as possible when aiming at improving conditions for saproxylic biodiversity in boreal forest landscapes. We therefore suggest that great effort is put down during planning and executing of forest management actions, and by so ensuring that as much variety in dead wood substrates, i.e. multiple tree species and substrate types, as possible is created. Even though our study was conducted under experimental conditions aiming at restoring natural disturbances the methods used were cost neutral and could therefore be applicable in forest management on a large scale.

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Appendix A. . Nutritional preference, fire class and the number of collected beetles from each tree species and treatment type

Species	Nutritional preference	Fire class	Restoration burning			Artificial gap creation			Total
			Birch	Spruce	Pine	Birch	Spruce	Pine	
Acanthocinus aedilis	C	ffc	0	0	1	0	0	3	4
Acidota crenata	P		0	0	0	0	0	2	2
Acmaeops septentrionis	C,W	fd	0	0	2	0	0	0	2
Acrotrichis rugulosa	D, F		0	0	0	0	0	1	1
Acrulia inflata	?F		0	0	0	2	0	1	3
Agathidium nigrinum	F		0	0	0	0	1	1	2
Agathidium nigripenne	F		0	0	1	1	0	0	2
Agathidium seminulum	F		0	0	0	1	0	3	4
Ampedus nigrinus	P,W		0	0	0	0	1	0	1
Ampedus tristis	P,W	ff5	0	1	1	0	0	1	3
Anaspis arctica	P		0	0	0	0	0	3	3
Anaspis marginicollis	P		0	0	0	0	0	5	5
Anaspis rufilabris	P		0	0	0	0	1	0	1
Anisotoma axillaris	F		0	0	0	0	0	2	2
Anisotoma castanea	F		0	0	0	0	1	2	3
Anisotoma glabra	F		0	0	12	0	8	13	33
Anthaxia quadripunctata	C		0	2	0	0	0	0	2
Arhopalus rusticus	C,W	ffc	0	0	0	0	0	1	1
Aspidiphorus orbiculatus	F		0	0	0	0	1	4	5
Atheta brunneipennis	?F,?D,P		0	0	0	1	0	1	2
Atheta corvina	?P		0	0	0	0	3	0	3
Atheta crassicornis	?F,?D,P		0	0	0	0	1	0	1
Atheta crassicornis/ A. paracrassicornis			0	0	0	0	1	0	1
Atheta euryptera	?F,?D,P		0	0	0	0	0	1	1
Atheta picipes	?F,?D,P		3	0	1	1	2	1	8
Atheta pilicornis	?F,?D,P		0	0	0	0	2	1	3
Atheta subtilis	?F,?D,P		0	0	0	3	2	1	6
Athous subfuscus	P		0	0	2	0	1	1	4
Atomaria bella	F		0	0	0	1	14	11	26
Atomaria bescidica	F		0	0	0	1	0	0	1
Atrecus longiceps	P		0	0	0	0	4	0	4
Baeocrara variolosa	D		0	0	0	0	2	0	2
Bibloporus bicolor	P		0	0	0	1	3	5	9

Bibloporus minutus	P		2	0	1	0	0	3	6
Bius thoracicus	D		0	1	0	0	3	0	4
Cacotemnus rufipes	W		0	0	0	0	1	0	1
Cerylon ferrugineum	F		6	0	0	2	4	2	14
Cerylon histeroides	F		1	0	0	3	5	13	22
Cis boleti	F		0	0	0	0	1	0	1
Cis comptus	F		0	0	0	0	0	1	1
Cis punctulatus	F		0	1	0	0	0	1	2
Corticaria ferruginea	F	ffc	4	4	8	0	0	0	16
Corticaria interstitialis	F		2	2	2	0	7	10	23
Corticaria lateritia	F		0	0	0	0	12	7	19
Corticaria longicollis	F		0	5	0	0	0	0	5
Corticaria longicornis	F		0	0	0	0	1	0	1
Corticaria obsoleta	F		0	0	0	0	3	0	3
Corticaria orbicollis	F		0	2	2	0	14	4	22
Corticaria rubripes	F	ffc	5	29	13	0	2	4	53
Corticeus linearis	P		0	0	1	0	5	0	6
Cortinicara gifdosa	F	ffc	1	0	0	0	0	0	1
Coryphium angusticolle	D		1	0	1	0	0	0	2
Cryptolestes abietis	P		0	2	0	0	12	0	14
Cryptophagus corticinus	F	fd	1	0	0	0	0	0	1
Cryptophagus lapponicus	F		1	1	0	0	0	0	2
Cryptophagus lysholmi	F		0	0	0	0	1	0	1
Cryptophagus quadrihamatus	F		0	0	0	0	1	0	1
Cryptophagus tuberculosus	F		0	0	0	0	1	0	1
Crypturgus hispidulus	C		1	0	0	2	39	1	43
Crypturgus pusillus	C		0	0	0	0	29	1	30
Crypturgus subcribrosus	C		0	49	0	1	3974	3	4027
Cyphea latiuscula	P		0	1	0	0	0	0	1
Dacne bipustulata	F	ffc	0	0	2	0	0	0	2
Dadobia immersa	?F		2	1	0	2	5	7	17
Dendrophagus crenatus	F		0	0	0	1	0	4	5
Dienerella filum	F		5	0	1	0	1	0	7
Dinaraea arcana	?F		0	0	0	0	0	1	1
Dinaraea linearis	?F		0	0	0	0	0	1	1
Dolichocis laricinus	F		0	0	0	0	2	1	3
Dropephylla clavigera	P	ff5	0	0	0	0	1	0	1
Dropephylla linearis	?F,?P		0	0	0	0	0	2	2
Dryocoetes autographus	C		0	2	0	6	544	30	582
Endomychus coccineus	F		0	0	0	4	0	0	4
Enicmus fungicola	F		0	0	0	0	0	1	1
Enicmus rugosus	F		2	0	8	0	3	36	49
Epuraea angustula	F,P		25	1	6	3	8	7	50
Epuraea boreella	F,P		0	0	0	2	3	0	5
Epuraea laeviuscula	P		1	1	2	0	23	2	29
Epuraea marseuli	D,F		3	0	0	0	8	2	13
Epuraea oblonga	D,F		0	0	0	0	0	3	3
Epuraea pygmaea	D,F		5	0	0	3	24	2	34
Epuraea rufomarginata	F		0	4	3	0	2	1	10
Ernobius explanatus	W		0	1	0	0	0	0	1
Euplectus decipiens	P		0	0	0	0	1	2	3
Euplectus karstenii	P		0	0	0	1	2	2	5
Euplectus mutator	P		0	0	0	0	0	1	1
Euplectus piceus	P		0	0	0	0	1	0	1
Euplectus punctatus	P		2	0	0	2	5	6	15
Euryusa castanoptera	?F		2	0	0	3	0	0	5
Eutheia linearis	P		0	0	1	0	2	0	3
Gabrius expectatus	P		1	0	0	1	7	6	15
Gabrius splendidulus	P		0	1	0	0	0	0	1
Glischrochilus quadripunctatus	F,P	ffc	8	0	0	0	0	2	10
Gnathoncus buyssoni	P		0	0	0	0	0	1	1
Homalota plana	?F	ffc	0	1	0	0	0	0	1
Hylastes brunneus	C		0	0	0	0	4	13	17
Hylastes cunicularius	C		0	0	0	1	4	2	7
Hylobius abietis	C,W	ffc	2	0	9	0	0	11	22
Hylurgops glabratus	C		0	0	0	0	574	2	576

Hylurgops palliatus	C		0	121	54	0	1142	78	1395
Ips duplicatus	C		0	0	0	0	5	3	8
Ips typographus	C		0	1	0	0	27	3	31
Ischnoglossa elegantula	?F		0	0	0	0	5	2	7
Ischnoglossa prolixa	D, P		0	0	0	1	2	2	5
Latridius gemellatus	F		0	0	0	0	2	0	2
Latridius hirtus	F		0	0	1	0	3	6	10
Leptophloeus alternans	P		0	0	0	0	1	0	1
Leptusa norvegica	?F		0	0	0	0	3	2	5
Liogluta microptera	?F		0	0	0	0	0	2	2
Liotrichus affinis	?		0	0	0	0	0	1	1
Litargus connexus	F	ffc	8	6	5	0	0	0	19
Lordithon speciosus	P		0	0	0	0	0	1	1
Magdalis violacea	C		0	0	0	0	1	0	1
Malthodes brevicollis	H,P		0	0	0	0	2	0	2
Malthodes fuscus	P		0	0	2	0	1	0	3
Malthodes guttifer	P		0	0	0	1	13	9	23
Melanotus castanipes	P,W		0	1	2	0	1	2	6
Micrambe abietis	F		0	0	0	0	0	1	1
Microscydmus minimus	P		0	0	0	0	1	0	1
Monochamus sutor	C,W	ffc	0	0	0	0	6	0	6
Neuraphes coronatus	P		0	0	0	1	0	0	1
Nudobius lentus	P		6	2	6	0	14	12	40
Omalium rivulare	?P		0	0	0	0	1	0	1
Orthocis alni	F		0	0	1	0	0	0	1
Orthoperus atomus	F		0	0	0	0	1	0	1
Orthoperus rogeri	F		0	0	0	0	1	0	1
Orthotomicus suturalis	C	ffc	0	10	8	0	6	1	25
Oxypoda soror	?F		0	0	1	0	0	0	1
Pediacus fuscus	F	ffr	0	0	0	0	1	0	1
Pentanota meuseli	?P		0	0	0	0	0	1	1
Philonthus addendus	?P		0	0	0	0	0	1	1
Philonthus marginatus	?P		0	0	0	0	1	0	1
Phloeonomus pusillus	P	ffc	4	4	15	4	57	75	159
Phloeonomus sjobergi	P?	ffc	0	1	1	9	40	2	53
Phloeopora testacea	?P		0	1	0	0	0	0	1
Phloeostiba lapponica	P	ffc	19	6	14	0	16	17	72
Phloeotribus spinulosus	C		0	0	0	0	1	0	1
Pissodes gyllenhalii	C		0	1	1	0	0	0	2
Pissodes harcyniae	C		0	0	0	0	25	19	44
Pissodes pini	C		0	0	1	0	6	33	40
Pissodes piniphilus	C		0	1	1	0	0	0	2
Pityogenes chalcographus	C		0	5	2	0	349	2	358
Pityophagus ferrugineus	P		0	0	0	0	1	3	4
Placusa atrata	?P	ffc	6	2	2	1	1	0	12
Placusa cribrata	?P		0	0	0	0	11	0	11
Placusa depressa	?P		0	4	0	0	5	2	11
Placusa incompleta	?P		0	1	0	1	5	1	8
Placusa tachyporoides	?P		0	0	0	0	6	0	6
Platysoma angustatum	P		0	0	0	0	1	0	1
Platystomos albinus	W	ffc	0	0	1	1	0	0	2
Plegaderus vulneratus	P		0	3	4	0	76	88	171
Podistra schoenherri	P		0	2	7	0	1	4	14
Pogonocherus decoratus	C,W		0	0	1	0	0	0	1
Pogonocherus fasciculatus	C,W		0	0	0	0	4	0	4
Polygraphus sp.	C		0	1172	3	0	365	0	1540
Pterostichus oblongopunctatus	P		0	0	0	0	1	1	2
Pteryx suturalis	F		0	0	0	1	4	7	12
Ptinella johnsoni	F		0	0	0	0	1	0	1
Pytho depressus	C		0	0	0	0	1	0	1
Quedius plagiatus	P		1	0	0	4	19	13	37
Quedius tenellus	?P		0	0	0	1	4	1	6
Quedius xanthopus	?P		0	0	0	0	2	0	2
Rabocerus foveolatus	P		1	0	0	0	0	0	1
Rabocerus gabrieli	P		1	0	0	0	0	0	1
Rhizophagus dispar	P		0	0	1	12	36	14	63

Rhizophagus fenestralis	P		17	0	0	25	1	0	43
Rhizophagus nitidulus	P		0	0	0	1	6	15	22
Rhyncolus ater	W		0	0	0	0	18	9	27
Salpingus ruficollis	P		2	0	0	3	0	1	6
Scaphisoma agaricinum	?F		0	0	3	0	0	1	4
Scydmoraphes helvolus	D		0	0	0	0	0	1	1
Sepedophilus immaculatus	F		0	0	0	1	0	0	1
Sepedophilus littoreus	F		0	0	0	1	7	14	22
Sepedophilus testaceus	F		0	0	0	0	0	1	1
Sericoda quadripunctata	P	fd	1	0	0	0	0	0	1
Silvanoprus fagi	?P		0	0	0	0	1	1	2
Sphaeriestes stockmanni	P	fd	3	38	21	0	0	0	62
Stenichnus bicolor	P		0	0	1	0	5	2	8
Stenotrachelus aeneus	C,W	fd	0	0	1	0	0	0	1
Stephanopachys substriatus	C	fd	0	0	0	0	2	2	4
Synchita humeralis	D,F		1	0	0	0	0	0	1
Tetratoma ancora	F		0	0	0	0	0	1	1
Tetropium castaneum	C		0	5	2	0	21	1	29
Tetropium fuscum	C		0	0	0	0	2	0	2
Thanasimus femoralis	P		0	0	0	0	2	0	2
Thanasimus formicarius	P		2	1	3	0	4	3	13
Tomicus piniperda	C		0	0	19	0	0	201	220
Trypodendron domesticum	F		2	0	0	0	0	0	2
Trypodendron laeve	F		0	0	0	0	156	4	160
Trypodendron lineatum	F		150	0	100	0	1329	1	1580
Wanachia triguttata	F	ff5	0	0	27	0	4	13	44
Xylita laevigata	F		0	1	5	0	0	3	9
Xylostiba monilicornis	P		0	0	4	0	1	1	6
Total number of collected beetles			**310**	**1501**	**400**	**117**	**9224**	**946**	**12,498**

Nutritional preference: C = Cambium consumers, D = Detrivores, F = Fungivores, H = Herbivores, P = Predators, W = Wood borers and ? = uncertain classification. Fire class: ffc = fire favored common, ffr = fire favored rare, fd = fire dependent, ff5 = attracted to burned forests 5 years after fire

Appendix B. . Output from SIMPER analysis of the differences in species composition between tree species and substrate types in the burned and gap cut forest stands that were included in the study. Listed taxa are the five species that contribute the most to the differences between sample groups. Collectively the five species per analysis group explain between 20 and 40% of the dissimilarity between sample groups.

Burned stands

Dissimilarity between tree species

	Average abundance			
Species	Birch	Pine	% contribution to dissimilarity	Cumulative %
Hylurgops palliatus	0	1,07	6,07	6,07
Trypodendron lineatum	0,94	0,72	5,92	11,99
Epuraea angustula	0,77	0,56	4,06	16,05
Phloeonomus pusillus	0,5	0,82	3,91	19,96
Sphaeriestes stockmanni	0,17	0,71	3,79	23,74
	Birch	Spruce		
Polygraphus sp.	0	1,51	8,84	8,84
Corticaria rubripes	0,36	1,36	7,04	15,89
Hylurgops palliatus	0	1,16	6,79	22,67
Trypodendron lineatum	0,94	0	4,86	27,53
Sphaeriestes stockmanni	0,17	0,68	4,84	32,38
	Pine	Spruce		
Polygraphus sp.	0,17	1,51	7,75	7,75
Hylurgops palliatus	1,07	1,16	5,93	13,68
Sphaeriestes stockmanni	0,71	0,68	5,16	18,83
Corticaria rubripes	0,53	1,36	4,95	23,78
Phloeostiba lapponica	1,16	0,44	4,31	28,09

Gap cut stands

Dissimilarity between substrate types within tree species

Spruce	Average abundance			
Species	High stumps	Cut at the base	% contribution to dissimilarity	Cumulative %
Crypturgus subcribrosus	2,66	0,3	11,17	11,17
Pityogenes chalcographus	0,2	1,54	6,4	17,57
Dryocoetes autographus	0,49	1,61	5,51	23,08
Plegaderus vulneratus	1,32	0,2	5,26	28,34
Hylurgops palliatus	1,95	1,23	4,88	33,22
	High stumps	Girdled		
Crypturgus subcribrosus	2,66	2,3	6,87	6,87
Hylurgops palliatus	1,95	0,86	6,87	13,74
Plegaderus vulneratus	1,32	0,55	5,95	19,69
Polygraphus sp.	0,76	0,9	4,71	24,4
Pityogenes chalcographus	0,2	0,68	4,24	28,63
	High stumps	Tipped over		
Crypturgus subcribrosus	2,66	0,11	11,49	11,49
Hylurgops glabratus	0	1,53	5,83	17,32
Hylurgops palliatus	1,95	1,18	5,73	23,05
Plegaderus vulneratus	1,32	0,11	5,47	28,52
Dryocoetes autographus	0,49	1,68	5,43	33,95
	Cut at the base	Girdled		
Crypturgus subcribrosus	0,3	2,3	9,62	9,62
Dryocoetes autographus	1,61	0,4	6,09	15,72
Pityogenes chalcographus	1,54	0,68	5,9	21,62
Polygraphus sp.	0,72	0,9	4,49	26,11
Crypturgus hispidulus	0,78	0	3,98	30,09
	Cut at the base	Tipped over		
Hylurgops glabratus	0,76	1,53	6,68	6,68
Polygraphus sp.	0,72	0,84	5,54	12,22
Hylurgops palliatus	1,23	1,18	5,37	17,59
Pityogenes chalcographus	1,54	1,31	4,59	22,18
Dryocoetes autographus	1,61	1,68	3,84	26,02
	Girdled	Tipped over		
Crypturgus subcribrosus	2,3	0,11	10,1	10,1
Dryocoetes autographus	0,4	1,68	6,33	16,43
Hylurgops glabratus	0,1	1,53	6,27	22,7
Polygraphus sp.	0,9	0,84	5,28	27,98
Pityogenes chalcographus	0,68	1,31	4,63	32,62
Pine				
Species	High stumps	Cut at the base	% contribution to dissimilarity	Cumulative %
Hylurgops palliatus	0,38	1,12	5,34	5,34
Enicmus rugosus	0,9	0,29	4,33	9,66
Phloeonomus pusillus	0,9	1,02	3,72	13,38
Dryocoetes autographus	0	0,73	3,53	16,91
Plegaderus vulneratus	0,83	0,46	3,41	20,32
	High stumps	Girdled		
Enicmus rugosus	0,9	0,64	5,33	5,33
Phloeostiba lapponica	0,15	0,8	5,2	10,53
Hylastes brunneus	0	0,7	4,63	15,16
Plegaderus vulneratus	0,83	1,29	4,1	19,27
Phloeonomus pusillus	0,9	1,26	3,9	23,17
	High stumps	Tipped over		
Enicmus rugosus	0,9	0	5,52	5,52
Hylurgops palliatus	0,38	0,89	4,99	10,51
Plegaderus vulneratus	0,83	0,36	4,46	14,97
Phloeonomus pusillus	0,9	0,72	4,23	19,2
Dadobia immersa	0	0,5	3,7	22,89
	Cut at the base	Girdled		
Hylurgops palliatus	1,12	0,26	5,52	5,52
Plegaderus vulneratus	0,46	1,29	4,71	10,22
Phloeostiba lapponica	0,33	0,8	3,77	13,99
Dryocoetes autographus	0,73	0,2	3,57	17,56
Hylastes brunneus	0,43	0,7	3,38	20,94
	Cut at the base	Tipped over		

Phloeonomus pusillus	1,02	0,72	4,54	4,54
Hylurgops palliatus	1,12	0,89	4,37	8,91
Dryocoetes autographus	0,73	0,43	3,96	12,87
Pissodes pini	0,4	0,58	3,58	16,45
Rhizophagus dispar	0,47	0,53	3,44	19,89
	Girdled	Tipped over		
Plegaderus vulneratus	1,29	0,36	6,69	6,69
Phloeonomus pusillus	1,26	0,72	5,43	12,12
Phloeostiba lapponica	0,8	0,17	4,77	16,89
Hylurgops palliatus	0,26	0,89	4,72	21,61
Hylastes brunneus	0,7	0,17	4,18	25,79
Dissimilarity between tree species within substrate types				
High stumps		Average abundance		
Species	Spruce	Pine	% contribution to dissimilarity	Cumulative %
Crypturgus subcribrosus	2,66	0,13	14,06	14,06
Hylurgops palliatus	1,95	0,38	8,65	22,71
Enicmus rugosus	0,2	0,9	4,33	27,04
Polygraphus sp.	0,76	0	3,69	30,72
Phloeonomus pusillus	0,71	0,9	3,32	34,05
Cut at the base				
Species	Birch	Spruce		
Pityogenes chalcographus	0	1,54	9,06	9,06
Dryocoetes autographus	0,39	1,61	7,75	16,81
Hylurgops palliatus	0	1,23	6,87	23,68
Crypturgus hispidulus	0	0,78	4,88	28,56
Rhizophagus dispar	0,3	0,57	4,19	32,75
	Birch	Pine		
Hylurgops palliatus	0	1,12	7,32	7,32
Phloeonomus pusillus	0,5	1,02	5,37	12,68
Rhizophagus dispar	0,3	0,47	4,31	16,99
Dryocoetes autographus	0,39	0,73	4,25	21,24
Atomaria bella	0,17	0,57	4	25,24
	Spruce	Pine		
Pityogenes chalcographus	1,54	0	7,18	7,18
Dryocoetes autographus	1,61	0,73	5,1	12,29
Crypturgus hispidulus	0,78	0,14	3,47	15,76
Phloeonomus pusillus	0,78	1,02	3,36	19,12
Hylurgops palliatus	1,23	1,12	3,32	22,43
Girdled				
Species	Spruce	Pine		
Crypturgus subcribrosus	2,3	0	11,73	11,73
Plegaderus vulneratus	0,55	1,29	5,37	17,1
Phloeonomus pusillus	0,48	1,26	5,09	22,2
Hylurgops palliatus	0,86	0,26	4,73	26,93
Polygraphus sp.	0,9	0	4,62	31,54
Tipped over				
Species	Spruce	Pine		
Dryocoetes autographus	1,68	0,43	6,94	6,94
Hylurgops glabratus	1,53	0	6,61	13,55
Pityogenes chalcographus	1,31	0,17	6,18	19,73
Hylurgops palliatus	1,18	0,89	4,86	24,59
Phloeonomus sjobergi	0,91	0	4,3	28,89

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