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Chapter 1

THE POSITIVE EFFECTS OF PRESCRIBED BURNING OF CLEAR-CUTS ON SAPROXYLIC BEETLE DIVERSITY ARE SHORT-LIVED AND DEPEND ON FOREST-FIRE CONTINUITY

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ABSTRACT

Before modern forestry started, forest fire was the dominating large-scale disturbance in boreal forest. Prescribed burning of clear-cuts is increasingly used as a conservation measure but is potentially less beneficial for fire-associated species than burning of intact forest. We investigated the temporal effect of prescribed burning of clear-cuts in two regions in central Sweden: one region with a relatively unbroken forest-fire continuity (Orsa) and one region with a broken fire continuity (Långshyttan) more typical for Fennoscandia. The dead wood associated (saproxylic) beetle fauna was sampled with ten trunk-window traps in each of 16 clear-cuts. We used a paired design with two clear-cuts that had been logged at the same time and where one had been subjected to prescribed burning one or two years after clear-felling. We sampled clear-cuts either the same year as burning (0-year old) or 1-, 2- or 4-years post-burning. In Orsa we sampled five pairs (0-4 years old) and in Långshyttan three pairs (0-2 years old).

We caught 147 species (5908 individuals) of saproxylic beetles and 33 of those species were fire-associated. There was a pronounced temporal effect of prescribed burning on beetle abundance and species richness. The year of the fire there was a higher abundance and species richness in the burnt clear-cuts than in the unburnt clear-cuts. This positive effect disappeared already after one year. This pattern remained when we restricted our analysis to only fire-associated species.

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There were several regional differences consistent with a better fire continuity in Orsa: (1) In four out of five clear-cut pairs in Orsa there was a positive effect of burning on abundance and species richness of fire-associated species. In Långshyttan there was no such effect. (2) In Orsa the species composition of the fire-associated species differed between burnt and unburnt clear-cuts in four out of five pairs. In Långshyttan there was a difference only in one out of three pairs and that difference was smaller than the differences in Orsa. (3) When we restricted our analysis to 0- to 2-year old clear-cuts in order to have identical sample sizes in both regions, we found 725 individuals of 25 species of fire-associated species in Orsa and 218 individuals of 24 species in Långshyttan. (4) The four fire-dependent species that we found were the most specialised species and three of these, *Melanophila acuminata*, *Sphaeriestes stockmanni*, and *Acmaeops septentrionis* were only found in Orsa whereas *Henoticus serratus* was found in both regions.

To conclude, prescribed burning of clear-cuts only had a short-lived positive effect on saproxylic beetle diversity. This result casts doubt on the value of using prescribed burning of clear-cuts as a conservation measure. The better effect of prescribed burning in Orsa than in Långshyttan points to a differential effect of the value of prescribed burning. It also indicates that a long period of restoration burning might be needed in many parts of Sweden in order to increase the populations of fire-associated species.

INTRODUCTION

Before the start of modern forestry, forest fire was the dominating large-scale disturbance in boreal forest ecosystems (Zackrisson 1977; Bonan & Shuggart 1989; Niklasson & Granström 2000) and 0.5-2 % of the forest burned annually (Bonan & Shuggart 1989; Zackrisson & Östlund 1991). Fire intervals varied from 30-50 years for dry sites to an average of 160 years for wet sites (Angelstam 1996). Fire maintains structural complexity within forest stands and this complexity promotes plant and animal diversity (Hansen et al. 1991). Especially among insects there are many species that depend on natural disturbances to create a habitat patch mosaic that ensures species survival (Schowalter 1985; McCullough et al. 1998; Schowalter 2012) and among beetle species that depend on dead wood (saproxylic) there is a positive effect of increased fire frequency on diversity (Moretti et al. 2004). Saproxylic insects make up a large proportion of the boreal forest insect fauna (Stokland et al. 2012). In Sweden, where the beetle fauna is comparatively well known, at least 1257 species are saproxylic (Stokland et al. 2012). This is 28 % of the Swedish total of 4456 beetle species (Gärdenfors et al. 2003).

Among these saproxylic species some are fire dependent and have a distribution restricted to burnt forest. These pyrophilous (fire-loving) species have physiological or behavioural adaptations to fire, such as the infrared sensory organs of *Melanophila acuminata* (Evans 1966; Vondran et al. 1995; Schmitz et al. 1997), attraction to wood smoke (Schutz et al. 1999), or swarming behaviour at burning anthills (Wikars 1992). Other species are fire favoured and have a higher abundance in burnt forest than in other forest types (Wikars 1992; Wikars 2006; Johansson et al. 2011; Victorsson this volume). Again in Sweden, at least 116 beetle species are considered fire associated (Wikars 2006).

Active fire suppression in Fennoscandia generally started in the 19th century (Esseen et al. 1997) and has drastically decreased fire frequencies (Zackrisson 1977)**.** Important factors in fire suppression are an increased density of human habitations, modern forestry, and road construction – all these factors have increased during the 20th century. Forest roads, apart from making forestry possible, also facilitate fire suppression, salvage logging, and snag removal. Snag removal is important since lightning-struck snags are often the start of forest fires (Esseen et al. 1997). Due to this fire suppression many fire-associated species are now threatened or locally extinct (Ehnström & Waldén 1986) and out of 507 threatened forest-living beetle species in Sweden 20 % are favoured by forest fires and/or extensive storm fellings (Berg et al. 1994). Many fire-dependent species have disappeared from southern Sweden and western Finland, the two areas in those countries with the longest history of habitation and forestry (Wikars 2006; Kouki et al. 2012).

Primarily during the 1950s and 60s, burning over of clear-cuts was used in Fennoscandia as a means of soil preparation before regeneration planting (Hörnsten et al. 1995). This method was used primarily in places with a thick humus layer to improve soil quality and prepare the ground for seedlings. Today prescribed burning of clear-cuts is performed more for conservation purposes than for soil preparation. There are no requirements concerning prescribed burning in the Swedish Forestry Act, but current FSC standards require that large forest owners burn 5% of their annual clear-cut area in order to benefit biodiversity (Anonymous 2013). As a result of this, forest companies now burn 2000-3000 ha annually in Sweden, mostly clear-cuts (Wikars 2006).

The conservation value of prescribed burning of clear-cuts is questionable. The effect on ground living (epigeal) beetles range from generally beneficial for the diversity of the group (Gongalsky et al. 2006; Hjältén et al. 2010a) to negative for individual fire-associated species (Wikars 1995). There is a clear conservation value of burning more or less intact forest (Wikars 2002; Toivanen & Kotiaho 2007b; Johansson et al. 2011; Victorsson this volume) but the value of burning logged sites seem to disappear over a period of 1-16 years after burning and depends strongly on the level of pre-fire tree retention (Toivanen & Kotiaho 2007a).

Here we wanted to test the short-term temporal effect of prescribed burning of clear-cuts on saproxylic beetles. Burnt forest and burnt clear-cuts share features, such as heat and smoke at the time of the fire, which could attract fire-associated species. This could lead to a different species composition in a newly burnt clear-cut compared to an unburnt clear-cut that will mainly harbour common species that can utilize stumps and small diameter logging residue (Jonsell 2008; Hjältén et al. 2010b; Victorsson & Jonsell 2013). We also expected a positive effect of burning on total abundance and species richness of saproxylic beetles in general. However, since clear-cuts contain only a small amount of dead wood we expect that this positive effect will fade, and that burnt clear-cuts soon will be indistinguishable from ordinary unburnt clear-cuts, especially regarding fire-favoured species.

Some areas in Sweden have experienced less intense fire suppression and are well suited as reference areas when analysing the effects of broken fire continuity. This study compares one such region with another region with a fire suppression normal for most parts of Fennoscandia. In this regard we expected a larger difference in species composition between burnt and unburnt clear-cuts in the region with an unbroken fire continuity than in the region with the broken continuity, since in the “good” region a more complete fauna of fire-associated species could be expected (Wikars 1997). These species could be attracted to burnt clear-cuts which would lead to an increased difference between burnt and unburnt clear-cuts.

MATERIAL AND METHODS

The Study Sites

The study was performed in two regions in the province of Dalecarlia in south-central Sweden. The regions are separated by only 200 km but differ in their forestry history and fire continuity. The region near the village of Långshyttan (60º 32’N, 16º 06’E) has a broken fire continuity. Intense mining activities, not least from the copper mine in Falun, led to intense forestry between the years 1600 and 1900, after that modern forestry started with forest road construction and efficient fire suppression. In this region, virtually all signs of forest fires such as fire scars in trees are absent (Lundqvist 1994). The other region, Orsa Finnmark (61º 30’N, 14º 50’E) has a good fire continuity. Orsa escaped the intensive logging during the mining period, and the region was indeed considered virgin forest as late as in 1881 (Linder & Östlund 1992). Slash-and-burn agriculture, a practice that would increase the fire frequency, was common in this region during the 18th and 19th century. Road construction and modern forestry started much later here due to local economic conditions. Rather unique for Sweden, the principal forest owner in this region has continued with prescribed burning of clear-cuts to enhance forest regeneration and today they burn 25-100 ha annually (Wikars 1997). Accordingly, signs of fires are very common in the Orsa region and fire scars from up to five consecutive fires can be found in individual trees (Anonymous 1995; Wikars 1997).

Today both regions are dominated by typical Swedish forestry including clear-felling and thinning operations. The two dominating tree species are the conifers Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. Some deciduous tree species, such as birch *Betula* spp. alder *Alnus* spp. and aspen *Populus tremula* occur as admixture.

We used a paired design with two clear-cuts that had been logged at the same time and where one of the clear-cuts had been subjected to prescribed burning one or two years after clear-felling. We collected data on clear-felling and burning date from the principal forest owners in the two regions (Table 1). The intra-pair distance was 600 m or shorter in all but one pair. The proportion of *P. abies* and *P. sylvestris* before clear-felling was similar within the pairs according to the persons responsible for harvesting at the forest companies. We identified five pairs in Orsa and three pairs in Långshyttan. The sampled sites included all burnt clear-cuts in Långshyttan where prescribed burning had just started. In Orsa we used a selection of the clear-cuts available. Age refers to the number of years since the prescribed burning: in a 0-year pair the burnt clear-cut was burnt the year of investigation, in a 1-year pair the year before and so on (Table 1).

Sampling

Each clear-cut was sampled with ten trunk window traps mounted on dead wood substrates along a 90 m transect. The traps were operated during 60 days from the beginning of July to the beginning of September in 1995. The traps consisted of a 15 x 25 cm transparent plastic plate fastened perpendicularly onto dead wood substrates and a small aluminium container fastened underneath to collect the insects (as described in Wikars et al. 2005). The container was filled with 50 % ethylene glycol and a few drops of dish wash detergent and Bitrex added. To avoid subjectively choosing "good" substrates the traps were put up every 10 m along the transect on the first encountered dead wood substrate that fulfilled the following standards: (1) either *P. abies* or *P. sylvestris*; (2) snags, logs, or logging waste; (3) a minimum diameter of 8 cm. On standing substrates the trap was placed 40 cm above ground, on logs at “breast height” and on logging waste at least 50 cm from any of the end parts. The proportion of trap substrates of the two conifer species was similar in all clear-cut pairs except Hirvilampi (Table 1). When possible, the trap was put up facing south on the dead wood substrate, if necessary west or east. Transect routes were chosen such that the ground slope of the route as well as the distance to the nearest forest edge was the same in both clear-cuts in each pair. Since many beetles are more active at higher temperatures, these steps were taken to ensure that the traps would be exposed to the sun in a similar way.

Analysis

All beetles were determined to species or in a few case genus, according to Lundberg and Gustafsson (1995) and Ehnström and Holmer (2007) by JV and Stig Lundberg. Species were classified as saproxylic or ground living (epigeal) according to: Hansen (1964), Koch (1989-1992), and Palm (1951, 1959) from a database made available by Mats Jonsell. Species were classified as associated with fire based on the most recent classification of Swedish insects (Wikars 2006). These fire-associated species can be divided into two groups: (1) *fire-dependent species* have strong behavioural specializations for using burnt forest and almost exclusively occur in burnt forest; and (2) *fire-favoured species* are adapted to fire and/or are more abundant in burnt forest compared to other forest habitats. In all analyses described below we performed separate analyses for (1) all saproxylic beetles and for (2) fire-associated species.

We analysed the temporal effect of prescribed burning on beetle abundance and species richness with two-way ANOVAs with the fixed factors clear-cut type (burnt or unburnt) and clear-cut age (0, 1, 2, or 4 years after buring) and a random factor consisting of individual clear-cuts nested within the interaction clear-cut type x clear-cut age. This means that we had individual traps as observations but eight degrees of freedom in the denominator in the ANOVAs. In the analysis of beetle abundance we used Poisson error and log link as well as quasi-likelihood models to compensate for overdispersion (Quinn & Keough 2002). These analyses were done in procedure GLIMMIX in software SAS ver. 9.3 (SAS, Cary, NC). The temporal effect on species composition was tested with a PERmutational MANOVA (PERMANOVA) (Andersson 2001) using Sørensen similarity which is based on presence/absence data. We used the same fixed and random effects as above and did the analyses in software PRIMER using 9999 randomizations (Clarke & Gorley 2006).

To look for effects of fire continuity on the effectiveness of prescribed burning we analysed the effect of burning on abundance and species richness in each clear-cut pair separately. This was one-way ANOVAs with 18 degrees of freedom in the denominator. These analyses were done in software SAS and abundance data was treated as mentioned above. We performed ANalysis Of SIMilarity (ANOSIM) to get a measure of the magnitude of the difference in species composition (again using Sørensen similarity) between burnt and unburnt clear-cuts in each pair. This analysis gives a test statistic R which goes from 0 to 1 where larger values indicate a greater difference in species composition. This was done in software PRIMER using 9999 randomizations. Furthermore, we performed a group average linkage cluster analysis of Sørensen similarity of all clear-cuts with an attached SIMilarity PROFile test (SIMPROF) analysis in software PRIMER. For this analysis data from the ten traps was pooled for each clear-cut. From this a dendrogram was prepared where solid lines indicate groups with a significant species composition difference at the $P < 0.05$ level and dashed lines indicate non-significant differences (based on 9999 randomizations). Finally, we performed sample-based rarefaction comparing burnt and unburnt clear-cuts in each pair using 9999 randomizations in the software EstimateS (Colwell 2006) to construct 95 % confidence limits. We conclude that there is a significant treatment effect in a rarefaction when the mean of one of the treatments lies outside the 95 % confidence limits of the other treatment.

RESULTS

Overview

We caught 147 species (5908 individuals) of saproxylic beetles. At burnt clear-cuts we recorded 118 species (3648 individuals) and at unburnt clear-cuts 114 species (2260 individuals) (Appendix 1). Of the saproxylic species, 85 species (58 %) were recorded from both clear-cuts types whereas 33 species (22 %) were unique to burnt clear-cuts and 29 species (20 %) were unique to unburnt clear-cuts. We also caught 16 epigeal species (167 individuals) and 11 species (26 individuals) with an unknown habitat association (Appendix 1). We caught five fire-dependent species (four of those were saproxylic), and 30 fire-favoured species (29 saproxylic species) (Appendix 1). Seven species were on the current Swedish red list, from the year 2010 (Appendix 1). Three species, *Tragosoma depsarium*, *Acmaeops septentrionis*, and *Stagetus borealis*, were both saproxylic, red listed and fire-associated. These species were only found the region with a better fire continuity (Orsa).

Temporal Effects of Prescribed Burning

There was a pronounced temporal effect of prescribed burning on saproxylic beetle abundance and species richness (Figure 1). The year the prescribed burning took place (year 0) there was a higher abundance and species richness of all saproxylic species in the burnt clear-cuts than in the unburnt clear-cuts (Figure 1, Table 2). This positive effect of burning disappeared already after one year. The statistical differences were the same for the fire-associated species but for them there was also a (non-significant) tendency toward a positive effect one year after burning (Figure 1, Table 2). The species composition for all saproxylic species differed between burnt and unburnt clear-cuts only in the 2-year old clear-cuts (Table 2). The species composition for the fire-associated species differed between burnt and unburnt clear-cuts only the year of burning (Table 2).

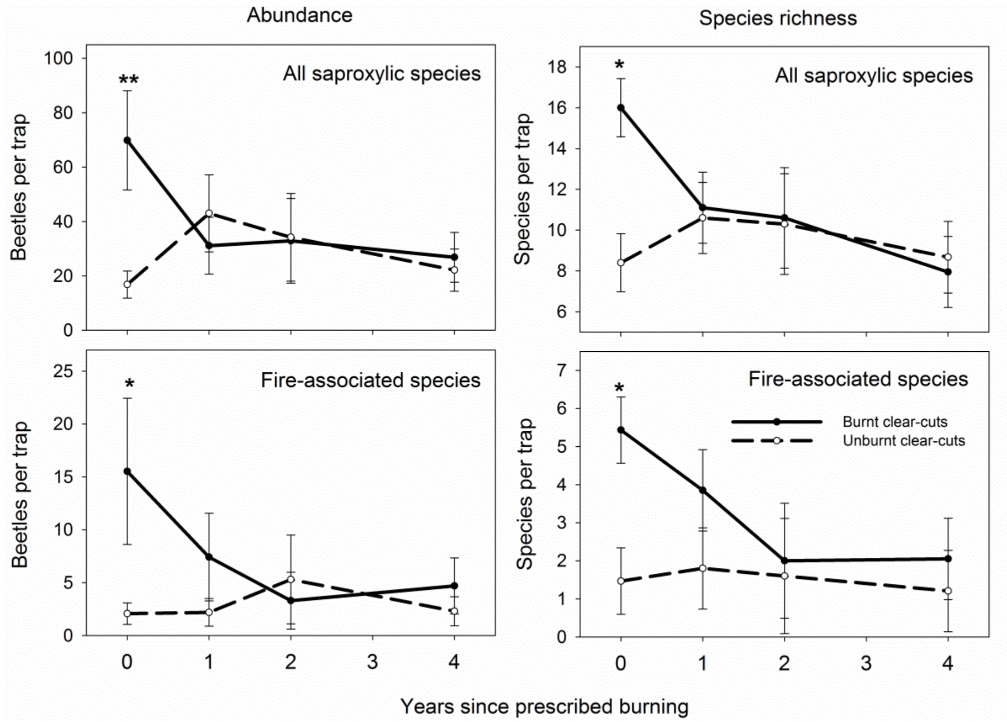

Figure 1. The temporal effect of prescribed burning of clear-cuts on beetle abundance and species richness. The upper panels show results for all 147 saproxylic species. The lower panels show results for 33 species of fire-associated species. Means and SE from ANOVAs. Asterisks denote a significant effect of prescribed burning in that age class (simple effects from the ANOVAs): ** $P < 0.01$, * $P < 0.05$.

Effects of Fire Continuity

There was a positive effect of burning on the abundance of all saproxylic species in the 0-year old clear-cuts both in the region with a better fire continuity (Orsa) and in the region with the broken fire continuity (Långshyttan) (Figure 2). The number of saproxylic species was positively affected by burning in the 0- to 1-year old clear-cuts in Orsa but not in Långshyttan. In four out of five clear-cut pairs in Orsa there was a positive effect of burning on abundance and species richness of fire-associated species (Figure 2). The magnitude of the difference decreased over time and was quite small or non-existent in the 4-year old clear-cuts. In Långshyttan there was no effect of burning on the fire associated species abundance or richness (Figure 2).

The species composition of all saproxylic species differed between burnt and unburnt clear-cuts in all pairs except Lillhamra (Figure 2). The magnitude of the difference was largest in the 0- to 1-year old clear-cuts in Orsa and in the 0-year old pair in Långshyttan. In the 4-year old clear-cuts and in the 1- to 2-year clear-cuts in Långshyttan the difference was smaller. In Orsa the species composition of the fire-associated species differed between burnt and unburnt clear-cuts in all pairs except Lillhamra (Figure 2). In Långshyttan there was a difference only in Dammsjön and that difference was smaller than the differences in Orsa.

Table 1. Clear-cuts sampled in a study of the effects of prescribed burning on saproxylic beetles in central Sweden. The study had a paired design with one burnt and one unburnt clear-cut in each pair. Data on clear-felling and burning date are from forest companies

Region	Clear-cut name	Clear-felling	Burning	Altitude (meters above sea level)	Age	Distance between B and U (meters)	Number of traps with Scots pine as substrate**
Orsa	Avenlam burnt	1992-11-01	1995-06-01	280	0	3200	8
	unburnt	1992-01-01		290			7
	Sälgtjärn burnt	1993	1995	520	0	500	3
	unburnt	1993		550			1
	Pilka burnt	1992	1994	545	1	600	3
	unburnt	1992		550			4
	Hirvilampi burnt	*	1991	280	4	300	6
	unburnt	*		260			10
	Lillhamra burnt	*	1991	350	4	250	9
	unburnt	*		350			7
Långshyttan	Dammsjön burnt	1993-06-01	1995-06-01	200	0	250	5
	unburnt	1993-06-01		205			4
	Nordvik burnt	1993-11-01	1994-05-01	265	1	600	6
	unburnt	1993-11-01		270			6
	Rudtjärn burnt	1993-05-01	1993-05-01	195	2	300	7
	unburnt	1992-12-01		200			6

Notes: * Exact dates could not be obtained from the forestry company. In this region it is normal practise to wait two years after clear-felling before prescribed buring. The probable cutting date is the winter 1988/1989.

** Number of traps with Scots pine *Pinus sylvestris* as substrate out of 10 traps per clear-cut. The other trap substrate was Norway spruce *Picea abies*.

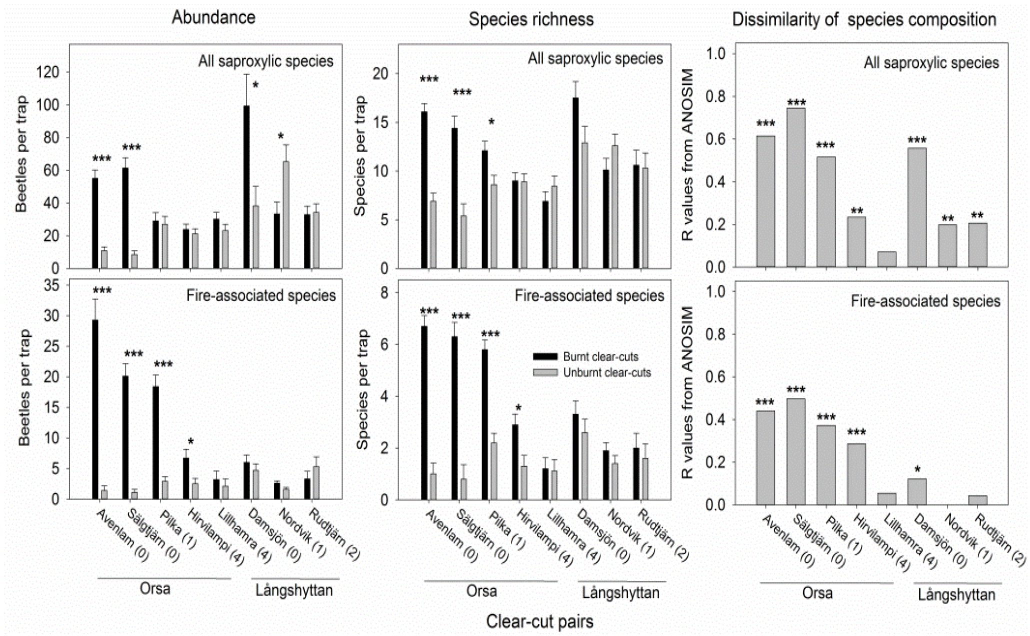

Figure 2. The effect of prescribed burning on beetle abundance, species richness and dissimilarity of species composition in each sampled pair of clear-cuts. The upper panels show results for all 147 saproxylic species. The lower panels show results for 33 species of fire-associated species. The figure in parenthesis after each clear-cut pair name is the number of years since the prescribed burning. The two sampled regions, Orsa with a better fire continuity and Långshyttan with broken fire continuity are indicated on the x-axis. For abundance and species richness the means and SEs are from ANOVAs. For dissimilarity of species composition the values are the test statistic R from an ANOSIM analysis for each pair. R varies between zero and one with larger values indicating an increased dissimilarity. Asterisks denote a significant effect of prescribed burning in that pair: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

The cluster analysis of all saproxylic species identified five groups based on species composition (Figure 3). Five of the six clear-cuts in Långshyttan separated into one group that was different from the Orsa sites. Within that group there was a (non-significant) grouping of the burnt clear-cuts. Within the Orsa region the burnt 0- to 1-year old clear-cuts and one unburnt clear-cut were separated into one group that was different from a group comprising of all the 4-year old clear-cuts and two younger unburnt clear-cuts (Figure 3). In the cluster analysis of fire-associated species a group with all the 4-year old clear-cuts in Orsa separated from the rest (Figure 3). The next group consisted of all four Sälgtjärn and Pilka clear-cuts in Orsa. Within that group there was a (non-significant) grouping of the burnt clear-cuts. The next group consisted of the burnt Avenlam clear-cut in Orsa and all six clear-cuts in Långshyttan. Within that group there were three sub-groups and the two 0-year old burnt sites, Avenlam (Orsa) and Dammsjön (Långshyttan) clustered together.

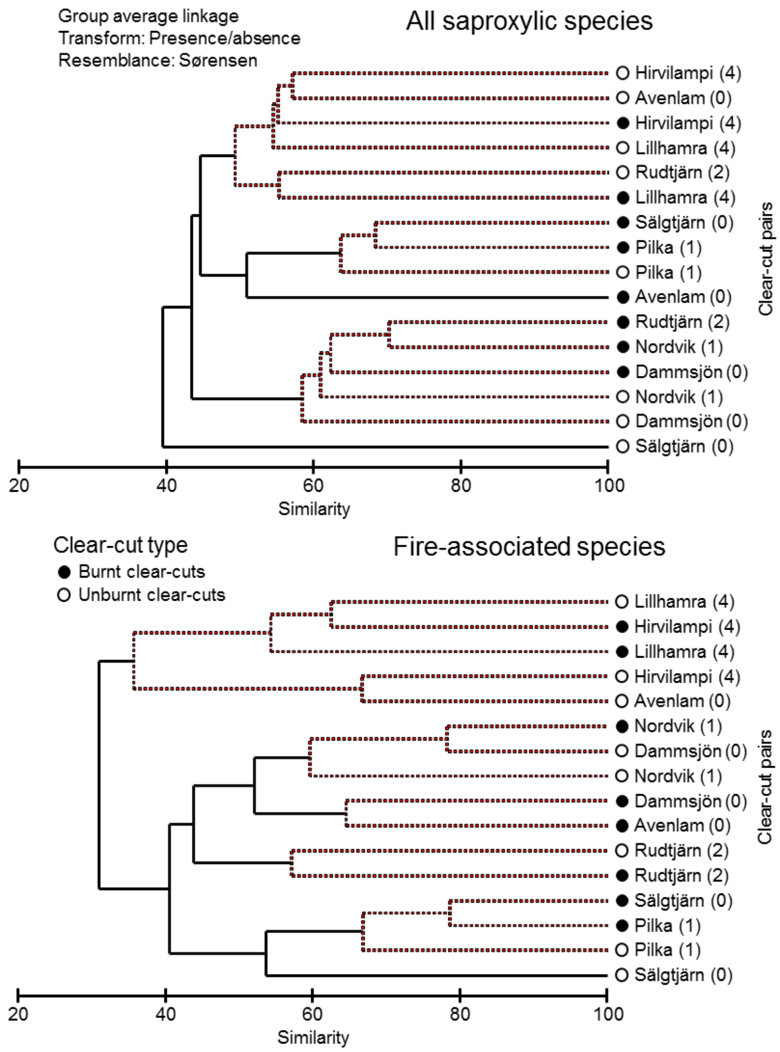

Figure 3. Dendrograms showing similarities in species composition for the 16 clear-cuts. The upper panel shows the result for all 147 saproxylic species. The lower panel shows the result for 33 species of fire-associated species. The tree was produced using group average linkage clustering of Sørensen similarities (presence/absence data). Solid lines indicate groups supported (at $P < 0.05$) by a SIMPROF analysis. The figure in parenthesis after each clear-cut pair name is the number of years since the prescribed burning.

In the rarefaction analysis of all saproxylic species there was higher species richness in the burnt clear-cuts in the two 0-year old clear-cut pairs in Orsa (Figure 4) and there was higher species richness in the unburnt clear-cut in one of the 4-year old clear-cut pairs. In Långshyttan there was no effect of burning on the assemblage of all saproxylic beetles (Figure 4). In the rarefaction analysis of the fire-associated species there was higher species richness in the burnt clear-cuts in four out of five clear-cut pairs in Orsa (Figure 4).

The magnitude of this difference was highest in 0- to 1- year old clear-cuts. In Långshyttan there was a positive effect of burning in one of the three clear-cut pairs (Figure 4).

As an indication of the value of the prescribed burning for fire-associated and threatened species we here compare the species found in the 0- to 2- year old clear-cuts in the two regions since the number of sampled clear-cuts in this age class was the same in both regions. In total we found 725 individuals of 25 species of fire-associated species in Orsa and 218 individuals of 24 species in Långshyttan (Appendix 1). The four fire-dependent species that we found are the most specialised species and they were only found in 0- and 1-year old burnt clear-cuts (Appendix 1). Three of the species, *Melanophila acuminata* (3 individuals in total), *Sphaeriestes stockmanni* (2), and *A. septentrionis* (1) were only found in the Orsa region whereas *Henoticus serratus* (2) was found in both regions. Of the four red-listed saproxylic species we found in these clear-cuts all were found in Orsa and one in Långshyttan (Appendix 1).

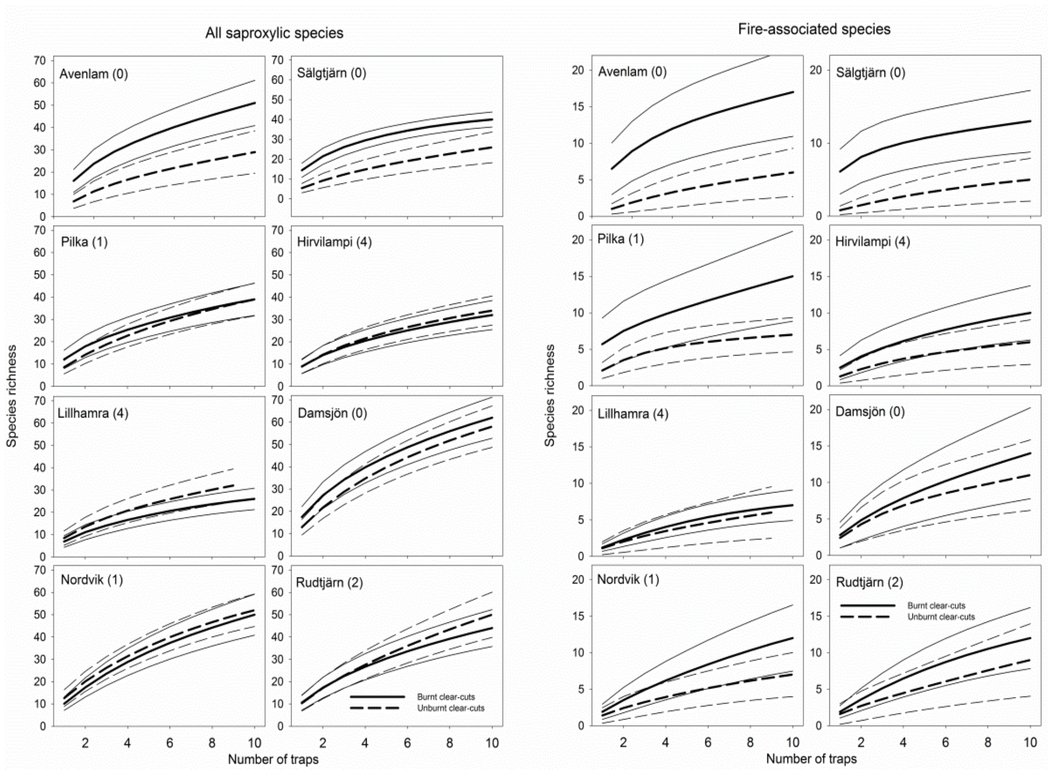

Figure 4. Sample based rarefaction for each inventoried pair of clear-cuts. Thick lines are mean rarefied species richness and thin lines indicate 95 % confidence limits from 9999 randomizations in software EstimateS. Solid lines are burnt clear-cuts and dashed lines are unburnt clear-cuts. The figure in parenthesis after each clear-cut pair name is the number of years since the prescribed burning.

Table 2. Results from tests of the temporal effect of prescribed burning on beetle abundance, species richness, and species composition at 16 clear-cuts in central Sweden

Source of variation	**df**	***F***	***P***	***F***	***P***	***F/t***	***P***
All saproxylic species		***Abundance***		***Species richness***		***Species composition***	
Clear-cut type	1,8	1.48	0.26	2.07	0.19	1.06	0.37
Clear-cut age	3,8	0.57	0.65	1.99	0.19	1.28	0.21
type x age	3,8	3.19	0.08	3.03	0.09	0.69	0.81
Simple effect: burnt clear-cuts	3,8(4)	2.19	0.17	4.62	**0.037**	1.24	0.28
Simple effect: unburnt clear-cuts	3,8(4)	1.68	0.25	0.41	0.75	0.72	0.83
Simple effect: 0-year clear-cuts	1,8	12.98	**0.0069**	14.23	**0.0054**	*1.29*	0.10
Simple effect: 1-year clear-cuts	1,8	0.48	0.51	0.04	0.84	*0.80*	0.67
Simple effect: 2-year clear-cuts	1,8	0	0.96	0.01	0.93	*1.59*	**0.0041**
Simple effect: 4-year clear-cuts	1,8	0.16	0.7	0.09	0.77	*0.88*	0.50
Fire species		*Abundance*		*Species richness*		*Species composition*	
Clear-cut type	1,8	3.92	0.08	4.95	0.06	1.64	0.15
Clear-cut age	3,8	0.38	0.77	1.4	0.31	2.15	**0.014**
type x age	3,8	1.34	0.33	1.19	0.37	0.93	0.53
Simple effect: burnt clear-cuts	3,8(4)	1.44	0.3	2.54	0.13	2.72	**0.013**
Simple effect: unburnt clear-cuts	3,8(4)	0.37	0.78	0.05	0.98	0.84	0.64
Simple effect: 0-year clear-cuts	1,8	9.19	**0.0163**	10.34	**0.012**	*1.55*	**0.022**
Simple effect: 1-year clear-cuts	1,8	2.23	0.17	1.84	0.21	*0.64*	1.00
Simple effect: 2-year clear-cuts	1,8	0.17	0.69	0.04	0.85	*1.10*	0.28
Simple effect: 4-year clear-cuts	1,8	0.75	0.41	0.31	0.59	*1.68*	0.17

The upper part shows results for all 147 saproxylic species and the lower part show results for 33 species of fire-associated species. Abundance and species richness tested with ANOVAs. Species composition tested with PERMANOVAs on Sørensen similarities. The test of simple effects on burnt and unburnt clear-cuts has eight df for abundance and species richness but four df for species composition. Test statistics in italics are t-values and all other are F-values. Statistically significant differences ($P < 0.05$) are shown in bold

DISCUSSION

Temporal Effects of Prescribed Burning

Prescribed burning of clear-cuts had a positive but very short lived effect on the saproxylic beetles in this study. The positive effect on the abundance and species richness disappeared already one year after the fire when we tested both regions together. The reason for the positive effect on abundance and species richness in the year of the burning is probably because a prescribed burning in some ways mimics a natural forest fire. Heat and smoke at the time of fire is perhaps the feature that most closely resembles a natural forest fire.

Both fire-dependent species (Schmitz et al. 1997; Schmitz & Trenner 2003) and other saproxylic beetles (Schutz et al. 1999; Allison et al. 2004) are attracted by smoke which may explain the higher number of individuals and species the year of burning. The scorched and blackened ground after a prescribed burning also mimics the situation in a burnt forest and this creates a warmer microclimate on the burnt clear-cut (Holliday 1991). There is a positive correlation between species richness and sun exposure (and thus temperature) in boreal saproxylic beetles (Kaila et al. 1997; Jonsell et al. 1998; Lindhe et al. 2005). Therefore the increased temperature in burnt clear-cuts could also help explain the higher number of individuals and species the year of burning.

On the other hand, the reason why the positive effect of burning disappeared so quickly is probably because a prescribed burning differs in several ways from a natural forest fire. For example, the blackening of the ground, evident in newly burnt clear-cuts, disappeared rapidly. In all 2- and 4-year old localities the ground was instead to a large degree covered with fireweed *Epilobium angustifolium* that effectively hides the dark ground (personal observation).

This rapid colonization of *E. angustifolium* would result in a lowered ground temperature already two years post fire and could decrease saproxylic beetle abundance at burnt clear-cuts. This is in contrast to a burnt forest where the input of frass from the fire-associated longicorn *Monochamus scutellatus* to the soil decreases germination of *E. angustifolium* in North America (Cobb et al. 2010). This inhibitory effect on *E. angustifolium* would be less important on our clear-cuts because the Swedish congeneric *Monochamus sutor*, that has a similar conspicuous frass production as the North American species, prefers snags over stumps (Ehnström & Axelsson 2002). Due to the low number of snags on our clear-cuts the *Monochamus*-induced inhibition of *E. angustifolium* would not be effective.

The largest difference between prescribed burning and natural forest fires is probably the much larger amount of dead wood in burnt forest. Burning a clear-cut kill trees left after cutting (Toivanen & Kotiaho 2007a) and this increases the local amount of dead wood compared to the situation in an unburnt clear-cut. Some retention trees on the clear-cuts in this investigation had indeed been killed by fire (personal observation). However, burnt clear-cuts contain much less dead wood than burnt forest simply because there are not that many retention trees on a clear-cut that can suffer fire-induced mortality.

Therefore, the burnt clear-cut can only act as a provider of dead wood to small populations of saproxylic species, and as this substrate is consumed the numbers of individuals and species will decline.

The low level of dead wood after a prescribed burning could also lead to high levels of larval resource competition. Primarily because the high level of attraction of beetles the year of the fire that will lead to a high colonization pressure of the limited amount of dead wood available and also because most prescribed burnings tend to be low-intensity fires (Hjältén et al. 2010a) that do not kill that many of the beetles who have already established on the clear-cut during the one to two years that normally elapses between cutting and burning (Wikars 1995).

Saproxylic species arriving at a burnt clear-cut may therefore face intense resource competition. Priority-effects, when the establishment order of individual species affects the species composition of a community, is demonstrated in saproxylic beetles (Weslien et al. 2011; Victorsson 2012) and might exclude fire-associated species under such circumstances.

Our results indicate that prescribed burning of clear-cuts is a conservation measure with only a short-term benefit. Other studies point in the same direction. Hyvärinen and co-authors studied the effects of prescribed burning of logged sites for two years after burning (Hyvärinen et al. 2005; Hyvärinen et al. 2006; Hyvärinen et al. 2009). They find a positive effect of prescribed burning on saproxylic beetle richness the same year as the burning and this positive effect remains also the first year after burning for a subset of rare and threatened species but only if at least 10 retention trees are left per hectare on the clear-cuts. Toivanen and Kotiaho (2007a) studied the effect of prescribed burning from one to 16 years after burning. They also find that species richness and abundance of saproxylic beetles decrease over time.

Our results therefore add to the pattern found in previous studies by documenting a rapid decrease in species richness already one year after buring. The conservation value of prescribed burning increases with increasing tree retention on the clear-cut (Hyvärinen et al. 2005; Hyvärinen et al. 2006; Toivanen & Kotiaho 2007a). This makes sense since studies of fires in intact forest point to a real long-term value for saproxylic beetles (Boulanger & Sirois 2007; Nappi et al. 2010; Boucher et al. 2012). For example, in a retrospective study of burnt sites there was an effect of forest fire up to 28 years post fire (Boulanger & Sirois 2007). The value of burning intact forest can therefore not be overstated.

Effects of Fire Continuity

The species composition of all saproxylic species differed between the two regions and most clear-cuts in Långshyttan separated from the Orsa clear-cuts in the cluster analysis. In the cluster analysis of the fire-associated species the strongest effect was that the 4-year old sites were different from all others. Among the 0- to 2-year old clear-cuts there was then also some regional differentiation. These results point to both regional differences and effects of age on the species composition.

There were several regional differences consistent with a better fire continuity in Orsa. There was a clear benefit of prescribed burning to the saproxylic beetle assemblage in Orsa whereas there was less of a benefit in Långshyttan.

This was seen for example in the rarefaction analysis that showed that in equal-sized samples there were more fire-associated
species in burnt clear-cuts in four out of five clear-cut pairs in Orsa but there was such a pattern in only one out of three pairs in Långshyttan. It was seen also in the larger difference

between burnt and unburnt clear-cuts in species composition of fire-associated species in Orsa than in Långshyttan.

The more positive effect in Orsa could be an effect of a more intact fauna of fire-associated species in that region due to a better fire continuity and this is supported by the fact that we found four fire-dependent saproxylic species in Orsa but only one in Långshyttan. Furthermore, more red-listed saproxylic species were found in Orsa than in Långshyttan. The pattern for these rare species is based on relatively few individuals and should be interpreted with caution. However, the pattern for more common species also indicate a higher quality of Orsa since many common fire-associated species, such as *Acmaeops pratensis*, *Asemum striatum*, *Corticaria rubripes* and *Atomaria pulchra*, showed a pattern with a higher abundance in Orsa than in Långshyttan.

The total number of fire-associated species was similar in both regions but it seems that the populations of these species were larger in Orsa as indicated by the higher abundance of these species. In total we caught three times as many individuals of fire-associated species in Orsa compared to Långshyttan when we compared only the 0- to 2- year old clear-cuts to achieve similar sample sizes in the two regions. Taken together, this indicates that in Orsa there was a saproxylic beetle fauna that could respond positively to prescribed burning, whereas in Långshyttan the fauna in burnt clear-cuts was more similar to that in ordinary clear-cuts.

Furthermore, the positive effect of prescribed burning was possibly more long lived in the north, but the number of replicates in our investigation does not permit a firm conclusion in this respect. We just note that significant differences in rarefied species richness and species composition of fire-associated species was found in the 1-year old clear-cut and in one of the 4-year old clear-cuts in Orsa. A larger sample is needed to clarify this.

Our results are similar to those of a Finish study where restoration burning of young forest is more beneficial in a region where modern forestry started later (Kouki et al. 2012). Other studies also show that regional differences in forestry history can affect the species composition of saproxylic beetles in other habitats than burnt forest (Siitonen & Martikainen 1994; Martikainen et al. 1996; Victorsson 2009) also the geographical proximity to high quality habitat in Southern Sweden affect saproxylic beetles, at least in birch (Lindbladh et al. 2007; Abrahamsson et al. 2009). Our study therefore adds to the emerging picture that the regional species pool is important for local diversity in saproxylic beetles.

The better effect of prescribed burning in Orsa than in Långshyttan points to a differential effect of the value of prescribed burning. It also indicate that a long period of restoration burning might be needed in many parts of Sweden in order to augment the fire-associated fauna. It seems likely that restoration burning of intact forest or of clear-cuts with a high level of tree retention has the best chance of success (Toivanen & Kotiaho 2007b; Kouki et al. 2012). Such attempts at reintroducing forest fire as an important disturbance will probably succeed earlier if they are performed in regions with better fire continuity (Kouki et al. 2012).

The interpretation of the results should be tempered by two facts. Firstly, the southern region is situated at lower latitude *and* altitude and therefore should have more days with a favourable weather for insects. However, it is not evident that this should affect the comparison within pairs of burnt and unburnt clear-cuts that forms the basis for this chapter. Secondly, the difference in fire continuity is linked to forest history. There could be other differences between the regions more directly related to forest history than fire continuity affecting these species. Only further landscape level studies could clarify that.

CONCLUSION

Prescribed burning of clear-cuts mimics natural forest fires in some ways and this was probably the explanation for the strong positive effect on species richness and abundance of saproxylic beetles the same year as the fire. However, clear-cuts also differ from burnt forest in important ways and this probably explains the short-lived response of saproxylic beetles to prescribed burning.

Already one year after burning species richness and abundance was similar in burnt and unburnt clear-cuts. Our study complement Toivanen and Kotiaho (2007a) who find a decreasing species richness of saproxylic beetles over a period of 1-16 years after prescribed burning. Here we demonstrated a pronounced decrease of species richness already the first year after prescribed burning.

However, the positive effect of prescribed burning for fire-associated species was larger in the region with a better fire continuity than in the region with a poor fire continuity more representative for Fennoscandia. This fact points to a differential effect of the value of prescribed burning and to the need for restoration of the fire-associated beetle fauna in many parts of Sweden.

In the "new forestry" in Sweden there is a growing awareness that dead wood must be left or created at clear-felling (Ekbom et al. 2006). In order to maximise the value of conservation measures it is important to understand how they affect forest organisms.

This chapter shows that the beneficial effects of burning of clear-cuts will disappear in a very short period of time. Considering the long-term effect on this fauna after natural fires it seems reasonable to draw the conclusion that natural forest-fire dynamics is not mimicked by this procedure. If the goal is to create conditions similar to those in natural forest, then it is essential to burn more or less intact forest on a regular basis. Nevertheless it should be stressed that burning of clear-cuts can be an important complement, especially in regions with good fire continuity.

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Appendix 1. Species List

Abundance of species caught in trunk window traps in eight pairs of clear-cuts in two regions in central Sweden: Orsa with a better fire continuity and Långshyttan with a broken fire continuity. One clear-cut in each pair was subjected to prescribed burning (B) and the other was unburnt (U). The figure in parenthesis after each clear-cut pair name is the number of years since the prescribed burning. Species relation to fire from Wikars (2006) and its history of red listing is indicated after the species names followed by the publishing year of the Swedish red list (2000, 2005, or 2010).

		Region: Orsa										**Region : Långshyttan**						
family	**Species**	**Avenlam (0)**		**Sälgtjärn (0)**		**Pilka (1)**		**Hirvilampi (4)**		**Lillhamra (4)**		**Dammsjön (0)**		**Nordvik (1)**		**Rudtjärn (2)**		**Total**
	Saproxylic species	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	
Histeridae	*Plegaderus vulneratus*												3					**3**
	Platysoma lineare (NT2010)			2									1					**3**
Leiodidae	*Anisotoma humeralis*															2	4	**6**
	Anisotoma axillaris	8	5		1			43	32	17	11	11	2	3	24	20	41	**218**
	Anisotoma castanea											2	2	2	12	4	4	**26**
	Anisotoma glabra	3	11			3	4	32	19	34	18	11	12	6	13	13	11	**190**
	Agathidium rotundatum									1								**1**
	Agathidium atrum	1																**1**
	Agathidium seminulum														1			**1**
	Agathidium laevigatum										1							**1**
Staphylinidae	*Gabrius splendidulus*											2	2				1	**5**
	Quedius xanthopus					1							1					**2**
	Nudobius lentus														1		1	**2**
	Tyrus mucronatus											1						**1**
	Acrulia inflata								1									**1**
	Hapalarea clavigera (NT2005) FF	4	2					12	5	5	1							**29**
	Phloeonomus planus	2		1		3			1			1		3	2	1		**14**
	Phloeonomus lapponicus FF	6		26	1	11	5					6	3	2	1			**61**
	Phloeonomus pussilus FF	1											2	1	1	2		**7**
	Phloeonomus sjoebergi FF	1		3								1	5	1				**11**
	Coryphium angusticolle	1	1											1				**3**
	Scaphisoma boleti		1			1		7	16		6	8	5	1	1	6		**52**

(Continued)

		Region: Orsa										Region : Långshyttan						
family	**Species**	**Avenlam (0)**		**Sälgtjärn (0)**		**Pilka (1)**		**Hirvilampi (4)**		**Lillhamra (4)**		**Dammsjön (0)**		**Nordvik (1)**		**Rudtjärn (2)**		**Total**
	Lordithon thoracicus								2					1			1	**4**
	Lordithon lunulatus								2									**2**
	Phloeopara corticalis							1										**1**
	Atheta sodalis	2	3		18	1	3		1			6	1	1	6		3	**45**
	Dinaraea aequata										1	2						**3**
	Anomagnathus cuspidatus FF					1		1		4	1						1	**8**
	Homalota plana FF	1										1	1	1	2	2		**8**
	Placusa depressa						1					1	1					**3**
Scarabeidae	*Trichius fasciatus*	74	22	11	10	27		29	12	10	19	18		8	1	14	9	**264**
Lycidae	*Lygistopterus sanguineus*	10	1				5	3		1		33		7		3	11	**74**
Cantharidae	*Malthodes fuscus*		4	6	1	2	2		6		1		4	1	4		1	**32**
	Malthodes marginatus	1	1	1	4	1	2	2	2		4	2	3	1		1	1	**26**
	Malthodes spathifer								1						1			**2**
	Malthodes brevicollis	1		1			1	1										**4**
Elateridae	*Ampedus balteatus* FF									1						1		**2**
	Ampedus tristis FF				1	1		1		1	2	1			1		1	**9**
	Ampedus nigrinus		1		1	3	2			3		1				1	3	**15**
	Melanotus castanipes	9					1	2	1	1	1	1	2	2	2	1	1	**24**
	Cardiophorus ruficollis											1				1		**2**
Buprestidae	*Buprestis rustica* FF	4	1					4	3							1	2	**15**
	Melanophila acuminata (NT2000) FD	3																**3**
	Phaenops cyanea FF		1									1	1	1		3		**7**
	Anthaxia quadripunctata FF												1	1		5	1	**8**
	Chrysobothris chrysostigma FF												1					**1**
	Agrilus viridis												1					**1**
Anobiidae	*Ptinus subpilosus*										1							**1**
	Ernobius nigrinus						2											**2**
	Hadrobregmus pertinax							1	7					1	1	1		**11**
	Stagetus borealis (NT2010) FF							1	1		1							**3**
	Dorcatoma punctulata																1	**1**
Cleridae	*Thanasimus formicarius*											2	8	1	1			**12**
Melyridae	*Dasytes niger*	26	17	3	14	2	1	5	5	160	89	657	46	205	314	145	130	**1819**
Nitidulidae	*Epuraea laeviuscula*											2						**2**

		Region: Orsa										Region : Långshyttan						
family	**Species**	**Avenlam (0)**		**Sälgtjärn (0)**		**Pilka (1)**		**Hirvilampi (4)**		**Lillhamra (4)**		**Dammsjön (0)**		**Nordvik (1)**		**Rudtjärn (2)**		**Total**
	Epuraea angustula												3					**3**
	Epuraea boreella			2			1						1		1			**5**
	Epuraea marseuli						1					1	1		2			**5**
	Epuraea biguttata	1													1			**2**
	Epuraea muehli			3														**3**
	Thalycra fervida								1									**1**
	Glischrochilus quadripunctatus FF			1														**1**
	Pityophagus ferrugineus	1		4		1	1								1			**8**
Aspidiphoridae	*Sphindus dubius*				1	1	1		2	2	1	1	2	1			1	**13**
Monotomidae	*Rhizophagus ferrugineus*	4		10		5	1		1		1	1	3	1	3	3		**33**
	Rhizophagus dispar							1									1	**2**
	Rhizophagus bipustulatus		1															**1**
Cryptophagidae	*Henoticus serratus* FD	1										1						**2**
	Cryptophagus fallax (NT2010)	1																**1**
	Cryptophagus badius	2	1								1							**4**
	Cryptophagus dentatus									1								**1**
	Caenoscellis ferruginea FF	1				1						2						**4**
	Atomaria subangulata (NT2000)				2										1			**3**
	Atomaria bella	1									1	3	1	1	5	23	6	**41**
	Atomaria pulchra FF	28		18		1						1					1	**49**
Erotylidae	*Triplax aena*	1																**1**
	Dacne bipustulata FF									14								**14**
Cerylonidae	*Cerylon histeroides*														1			**1**
Latridiidae	*Latridius consimilis*																1	**1**
	Enicmus rugosus	2	5	3	1	3	4	19	5	11	6	15	22	3	22	7	6	**134**
	Aridius nodifer											2	1		1			**4**
	Corticaria rubripes FF	25	3	9		67	1	2				15	6	11	8			**147**
	Corticaria longicollis																2	**2**
	Corticaria ferruginea FF	90		58		2						8						**158**
Cisidae	*Cis jacquemartii*											1						**1**
	Cis glabratus												1					**1**
	Hadreule elongatula FF															2		**2**
	Sulcacis affinis													1				**1**
Salpingidae	*Sphaeriestes stockmanni* (NT2000) FD			1		1												**2**

(Continued)

		Region: Orsa										Region : Långshyttan						
family	Species	Avenlam (0)		Sälgtjärn (0)		Pilka (1)		Hirvilampi (4)		Lillhamra (4)		Dammsjön (0)		Nordvik (1)		Rudtjärn (2)		Total
Aderidae	*Euglenes pygmaeus*	15	1					2	5			24	14	4	1			**66**
	Anidorus nigrinus											10	4	5	3	12	2	**36**
Tenebrionidae	*Corticeus linearis*			6			2						2		2			**12**
Scraptiidae	*Anaspis bohemica*	1	1	2	4	3	1	1	2		1	2	2	1			1	**22**
	Anaspis marginicollis										1			1	2			**4**
	Anaspis thoracica							1				37		16	1	1	1	**57**
	Anaspis flava											10	1	6	4	1		**22**
Mordelidae	*Curtimorda maculosa*												1		1			**2**
Melandryidae	*Hallomenus axillaris* (NT2005)								4			1	1					**6**
	Orchesia micans	1																**1**
	Abdera triguttata FF							1				4		1				**6**
	Xylita laevigata					2	2			1							1	**6**
Cerambycidae	*Tragosoma depsarium* (VU2010) FF	3																**3**
	Arhopalus rusticus FF									2		1	4	2	1	1	2	**13**
	Asemum striatum FF	1		41		20	7		1									**70**
	Tetropium castaneum			2			2											**4**
	Rhagium mordax			7	1	2	5			3	6						1	**25**
	Rhagium inquisitor FF			3	4	21	3	2								1		**34**
	Oxymirus cursor		1				1				1							**3**
	Pachyta lamed	1																**1**
	Acmaeops septentrionis (NT2010) FD					1												**1**
	Acmaeops pratensis FF	11		7	4	35	2	38		5	1	4		2		1	1	**111**
	Stictoleptura maculicornis							1										**1**
	Stictoleptura rubra											11	1	3	3	1	4	**23**
	Anastrangalia sanguinolenta	5							1	14	3	30	1	1	5	9	2	**71**
	Anastrangalia reyi													1				**1**
	Lepturobosca virens	36	2	2	2	7			4	1	2						1	**57**
	Judolia sexmaculata		1		1	2						2			1			**7**
	Leptura quadrifasciata	1	6				1	1		1	3	3		2			1	**19**
	Stenurella melanura				1			3	1	1		6		5	2	12	1	**32**
	Molorchus minor				1													**1**
	Monochamus sutor FF	3	1	1		1	1	1	1				1		2	2	1	**15**
	Pogonocherus fasciculatus	1		16			2	1			1	2	1	1	2	2	4	**33**

		Region: Orsa										Region : Långshyttan						
family	**Species**	**Avenlam (0)**		**Sälgtjärn (0)**		**Pilka (1)**		**Hirvilampi (4)**		**Lillhamra (4)**		**Dammsjön (0)**		**Nordvik (1)**		**Rudtjärn (2)**		**Total**
Curculionidae	*Rhyncolus sculpturatus*															1		**1**
	Magdalis duplicata	11	4	2		16	35	1	7	5	6	1	4		2		1	**95**
	Hylobius abietis FF	108	6	29	1	18	9		14		13	1	19	2		11	43	**274**
	Pissodes castaneus											1						**1**
	Pissodes harcyinae											1						**1**
	Pissodes piniphilus	1					1		1			1	4			1		**9**
	Hylurgops palliatus												13					**13**
	Hylastes brunneus	3	1	1			3				3	1			4	3	1	**20**
	Hylastes cunicularius			2		1								1		3	2	**9**
	Tomicus piniperda												14	2	3	1		**20**
	Polygraphus poligraphus	2		104														**106**
	Polygraphus punctifrons				1													**1**
	Pityogenes chalcographus			121		1	4					2	1				1	**130**
	Pityogenes quadridens			3	1		1								1			**6**
	Pityogenes bidentatus	30	4	77		14	139	18	45	2		12	12	4	174	1	22	**554**
	Orthotomicus proximus											1			1			**2**
	Orthotomicus suturalis FF			2		1								1				**4**
	Orthotomicus laricis											1	4					**5**
	Dryocoetes autographus			21	5	6	10					1		1	1	2	1	**48**
	Dryocoetes hectographus			1	2								2				1	**6**
	Crypturgus cinereus												1					**1**
	Crypturgus pusillus	1											10	2	2	1	1	**17**
	Trypodendron proximum												6					**6**
	Trypodendron lineatum												110					**110**
	Pityophthorus micrographus				1													**1**
	Saproxylic species total:	**551**	**109**	**613**	**84**	**290**	**270**	**238**	**212**	**301**	**208**	**993**	**382**	**333**	**653**	**329**	**342**	**5908**
	Epigeal species																	
Carabidae	*Dromius schneideri*												1					**1**
	Dromius fenestratus	1																**1**
Staphylinidae	*Quedius tenellus*			1	1								3	1	6		2	**14**
	Proteinus brachypterus														1			**1**
	Acidota crenata	16															1	**17**
	Trichophya pilicornis											1						**1**
	Atheta myrmecobia				1							1		1	2			**5**
Scirtidae	*Cyphon punctipennis*	1																**1**
Cantharidae	*Absidia sp*	11	2	10	26	5	8		1	3	8	12	12	2	5			**105**

(Continued)

		Region: Orsa										Region : Långshyttan						
family	**Species**	**Avenlam (0)**		**Sälgtjärn (0)**		**Pilka (1)**		**Hirvilampi (4)**		**Lillhamra (4)**		**Dammsjön (0)**		**Nordvik (1)**		**Rudtjärn (2)**		**Total**
	Malthodes minimus													1				**1**
Nitidulidae	*Epuraea binotata*											1			1			**2**
Silvanidae	*Silvanoprus fagi*			1														**1**
Cryptophagidae	*Cryptophagus abietis*								1									**1**
Latridiidae	*Cartodere constricta* FF											13	1					**14**
	Corticaria pubescens										1							**1**
	Corticarina similata																1	**1**
	Epigeal species total:	**29**	**2**	**12**	**28**	**5**	**8**	**0**	**2**	**3**	**9**	**28**	**17**	**5**	**15**	**0**	**4**	**167**
	Species with unknown habitat affiliation																	
Scydmaenidae	*Microscydmus minimus*														1			**1**
Staphylinidae	*Oxypoda hansseni*		1															**1**
	Thyasophila wockii	1					1											**2**
	Pentanota meuseli (NT2010)														1			**1**
	Aloconota subgrandis				1													**1**
	Paranopleta inhabilis (NT2010) FD			1									2			1		**4**
Nitidulidae	*Epuraea placida*								1									**1**
Cucujidae	*Pediacus fuscus* FF	2		1		2	1	4										**10**
Cryptophagidae	*Cryptophagus angustus*					1												**1**
	Cryptophagus saginatus					1												**1**
Latridiidae	*Corticaria elongata*			2													1	**3**
	Unknown habitat species total:	**3**	**1**	**4**	**1**	**4**	**2**	**4**	**1**	**0**	**0**	**0**	**2**	**0**	**2**	**1**	**1**	**26**

Abbreviations: B, burnt clear-cut; U, unburnt clear-cut; FD, fire-dependent; FF, fire favoured; NT, near threatened; VU, vulnerable.

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