Decadal effects of forest fire on biodiversity and browsing

A comparison between wildfire and prescribed burning

Emelie Fredriksson
Faculty of Forest Sciences
Department of Wildlife, Fish and Environmental Studies
Umeå

SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS

Umeå 2021

Acta Universitatis Agriculturae Sueciae
2021:82

Cover: Acrylic painting of a forest fire
(Painting: M. Fredriksson)

ISSN 1652-6880
ISBN (print version) 978-91-7760-841-7
ISBN (electronic version) 978-91-7760-842-4

Umeå
Print: Orginal Tryckeri, Umeå, 2021

Decadal effects of forest fire on biodiversity and browsing – a comparison between wildfire and prescribed burning

Abstract

The role of fire as a natural disturbance in northern European boreal ecosystems has largely disappeared due to effective fire suppression with large consequences for fire-associated biodiversity. Recently, prescribed burns have been introduced as a conservation action that aims to promote biodiversity. Not only fire regimes but also wildlife densities have been heavily impacted by human activities. Forest fires can result in pervasive changes with early successional forest stages, large amounts of deciduous trees, and newly formed deadwood, habitats which are largely missing in the managed boreal landscape. In this thesis, I evaluate decadal post-burn effects on community composition of wood-inhabiting polypores, beetles, bird and mammal species, vegetation differences, and moose browsing levels. I compare three unusually large wildfires in northernmost Sweden with nearby unburnt forests and five prescribed burns. I found differences in community composition among all taxa a decade after burning and a distinct turnover of beetles the years immediately post-burn. No wildlife species had higher visitation frequency in the wildfire areas, suggesting that burnt areas did not necessarily add much habitat in a landscape already dominated by early successional forest stages. Unburnt forests were also important for red-listed polypores, reindeer, and western capercaillie. However, wildfire, in contrast to prescribed burning, did provide large amounts of deadwood and rich field layer vegetation impacting biodiversity and functional trait composition of beetles and polypores and changing moose forage availability and browsing levels. Thus, for prescribed burning to mimic wildfire and better emulate wildfire impacts of biodiversity, I emphasise the importance of higher tree mortality.

Keywords: Boreal forest, *Coleoptera*, community composition, disturbance regime, functional groups, indicator species, turnover, traits

Author's address: Emelie Fredriksson, SLU, Department of Wildlife, Fish and Environmental studies, SE-901 83 Umeå, Sweden. *E-mail:* emelie.fredriksson@slu.se

Långsiktiga effekter av skogsbrand på biodiversitet och bete – en jämförelse mellan naturlig brand och naturvårdsbränningar

Sammanfattning

Brandens roll som naturlig störning i boreala ekosystem har i stort sett försvunnit på grund av effektivt brandbekämpning vilket har medfört stora konsekvenser för den brandrelaterade biologiska mångfalden. Skogsbränder skapar områden med tidiga successionsstadier med stora mängder lövträd och nybildad död ved. Dessa livsmiljöer saknas till stor del i dagens skogslandskap. Nyligen har naturvårdsbränder införts som en åtgärd för att främja den biologiska mångfalden. I den här avhandlingen utvärderar jag effekterna efter brand på artsammansättning av vedlevande tickor, skalbaggar, fågel- och däggdjursarter, vegetation i fält- och buskskikt samt älgbete. Jag fann skillnader i artsammansättning bland alla taxa ett drygt decennium efter brand och en tydlig förändring hos skalbaggar åren omedelbart efter brand. Inga däggdjur eller fåglar nyttjade skogsbränderna till en högre grad jämfört med den obrända skogen, vilket tyder på att de brända områdena inte tillför så mycket i ett landskap redan präglat av habitat i tidiga successionsstadier. De obrända skogarna var även viktiga livsmiljöer för bland annat rödlistade tickor, ren och tjäder. Skogsbranden skapade unika strukturer i form av stora mängder död ved och rik fältskiktsvegetation men jag upptäckte distinkta skillnader jämfört med naturvårdsbränderna. Naturvårdsbränder påverkade inte den biologiska mångfalden hos tickor, skalbaggar, eller fodertillgången och nyttjande av älg i samma grad som naturliga skogsbränder. Därför betonar jag vikten av högre brandintensitet om naturvårdsbränningar ska efterlikna skogsbränders effekter på biologisk mångfald i större utsträckning.

Nyckelord: Artsammansättning, biologisk mångfald, barrskog, boreal skog, *Coleoptera*, naturliga störningar, funktionella grupper

Författarens adress: Emelie Fredriksson, SLU, Institutionen för Vilt, Fisk och Miljö, Umeå, Sverige

Dedication

Till Pappa -
Om det inte vore för ditt ovärderliga stöd hade jag aldrig vågat sikta så högt

”*Allt stort som skedde i världen*
skedde först i någon människas fantasi”

Astrid Lindgren
(1907-2002)

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Fredriksson, E.*, Pettersson, R.M., Naalisvaara, J., & Löfroth, T. (2020). Wildfire yields a distinct turnover of the beetle community in a semi-natural pine forest in northern Sweden. Ecological Processes, 9:44

II. Fredriksson, E.*, Vahlström, I, Dahlberg, A., Magnusson. M., & Löfroth, T. Deadwood and trait associations of polypores and saproxylic beetle communities a decade post-burn. (manuscript)

III. Fredriksson, E.*, Cromsigt J.P.G.M. & Hofmeester T.R. Wildfire influences the boreal wildlife species composition and feeding type utilisation after more than a decade in northern Sweden. (manuscript)

IV. Fredriksson, E.*, Wallgren, M., & Löfroth, T. Wildfire and prescribed burning impact moose forage availability and utilisation in the northern boreal forest. (in review)

The contribution of Emelie Fredriksson to the papers included in this thesis was as follows:

I. Main author. Received data partly from JN. Conceived idea of follow-up with TL and RMP. Collected data adopting the study design from JN. Species identification performed by external experts. Performed the analysis and wrote the manuscript with contributions from the co-authors.

II. Main author. Designed the study together with TL and IV. Collected the data with IV. Species identification of beetles was performed by external experts and IV identified the polypores. Performed the analysis and wrote the manuscript with contributions from the co-authors.

III. Main author. Study design, data collection, and data integration by TH. Performed the analysis and wrote the manuscript with contributions from the co-authors.

IV. Main author. Study design and data collection with contribution from the co-authors. Performed the analysis and wrote the manuscript with contributions from the co-authors.

1. Introduction

Wildfires have been one of the largest stand-replacing disturbances in the boreal forest, before large-scale anthropogenic impacts, in terms of shaping forest characteristics such as multi-layered canopies, tree species composition, deadwood amount, and diversity (Engelmark, 1999; Esseen *et al.*, 1992). Large areas of the boreal forest have also had long continuity and a high amount of coarse woody debris (Esseen *et al.*, 1992) where natural processes of disturbance and succession create diversity in habitat and niches for boreal biodiversity (Jackson & Sax, 2010). Historically there has been a large variation in fire impact with some areas experiencing high tree mortality, however, most were likely not stand replacing (Berglund & Kuuluvainen, 2021). Fire creates unique substrates and immediate effects such as burnt wood, charred bark, high heat exposure, reduce the ground layer of organic matter, and exposes bare mineral ground (Granström, 2001). Disturbances in general and fire, in particular, create virgin habitat, to differing degrees, which start over successional processes and allow new species to establish. More long-term effects of fire in boreal forests often include an increase in the amount of primary successional tree species in the field layer, such as birch (*Betula* spp.) and Scots pine (*Pinus sylvestris*) (Foster *et al.*, 2016; den Herder *et al.*, 2009). By having these broad effects on the vegetation structure, fires can affect the availability of food and shelter for wildlife in the boreal forest (Engelmark, 1999). The amplitude of these changes is connected to the burn severity but will also be different depending on several factors such as time since disturbance, latitude, and productivity (Fang *et al.*, 2018). Burn severity, in contrast to fire intensity, has to do with organic matter being lost while fire intensity is about energy being released from the fire (Keeley, 2009).

This concept; that spatial and temporal heterogeneous properties of fire will lead to higher diversity, is not a new concept and is closely linked to the intermediate disturbance hypothesis (Connell, 1978). At the landscape scale, the diversity of fire disturbance, i.e. pyrodiversity, would then lead to higher biodiversity, which has been observed in for example birds (Tingley *et al.*, 2016; Fuhlendorf *et al.*, 2006), however, this is not always the case (Taylor *et al.*, 2012). Alternatively proposed by Seibold *et al.* (2017), highly diverse habitats can result in low amounts of specific habitat types and therefore lead to local extinctions through low connectivity. When studying scale among a wide variety of taxa, one needs to carefully consider differences in aspects such as dispersal abilities or home range, since, for smaller species like insects, the same physical area can be considered as habitat scale while for a larger animal it will be considered as patch scale (Johnson, 1980). Not only spatial but also temporal aspects are important to take into account when studying species communities and traits. Several factors drive turnover, i.e. the changes in species occurrence and abundance over time (Chesson & Huntly, 1997). Chesson and Huntly (1997) argued that life history differences among species make it possible for species to inhabit different ecological niches and by doing so utilise different successional stages, which leads to temporal shifts in species composition. These shifts and differences have been observed for vegetation, fungi, and insects (Koivula & Vanha-Majamaa, 2020) as well as for mammals and birds (Fisher & Wilkinson, 2005). Life history and strategies come with trade-offs that make some species more adapted to early successional stages, while other species have a different ecological strategy that is more favoured in the later successional stages with higher competition and sparser resources. Turnover in this sense is driven by colonization and local extinction (White, 2004). Functional traits provide a framework to follow these temporal and spatial changes after a disturbance to expand our knowledge of the drivers behind species distribution and occurrence.

It has been shown that fore affects the biodiversity of a diverse number of taxa in the boreal forests of Fennoscandia, both generally in terms of abundance, richness, and community composition but also specifically how fire creates habitats for species with specific traits. For example, short-term responses of beetle (*Coleoptera*) communities to fire and fire suppression show that their community composition changes immediately after the fire and that fire-associated species can have problems to colonise in landscapes with a long history of fire suppression (Kouki *et al.*, 2012; Johansson *et al.*, 2011; Hekkala & Tolvanen, 2008; Toivanen & Kotiaho, 2007; Vanha-Majamaa *et al.*, 2007; Hyvärinen *et al.*, 2006; Wikars, 1997). Other studies show lower abundances immediately after fire of wood-living fungi, i.e. polypores, however with positive long-term (+20 y) effects, especially for red-listed species (Penttilä *et al.*, 2013). Wood living taxa such as beetles and polypores have a multitude of interactions (Birkemoe *et al.*, 2018) in terms of dispersal, nutrition, and habitat. But both also serve as important decomposers contributing to nutrient cycling (Grove, 2002) and as prey for wildlife species (Young, 2015; Pechacek & Kristin, 2004).

The community composition of boreal wildlife responses to fire is not well studied, especially in the managed forest landscape of Fennoscandia. However, studies from North America indicate a wide variety of responses among taxonomic and trophic levels of wildlife species (Fisher & Wilkinson, 2005). Herbivores, such as moose (*Alces alces*) and hares (*Leporidae*), can often find abundant forage available post-burn when deciduous trees establish (Lord & Kielland, 2015). While others, like reindeer (*Rangifer tarandus*), have been seen to avoid burnt patches due to increased predation risk or lack of forage (lichens) (Joly et al., 2010). Since wildfire is a natural part of the boreal forest in Fennoscandia, having shaped species to unique adaptations, it is not surprising that many species today are threatened by effective fire suppression, while others such as moose have seen in increasing numbers due to higher forage availability due to current forestry practices (Bergqvist *et al.*, 2018; Hörnberg, 2001).

Human activities in boreal forests have during the last 100–150 years, replaced natural disturbance regimes with intense timber and pulp production. This has transformed the landscape from the natural old-growth forest with natural disturbance regimes towards managed conifer plantations (Östlund *et al.*, 1997). Clear-cutting has to a large extent replaced fire as the main stand-replacing disturbance. With its common use in forest management, available habitat for thousands of species has been reduced and ecosystem functions have been altered (Gauthier, 2009; Bergeron *et al.*, 2002). In forested biomes, one structure of high importance for biodiversity is deadwood since it can provide resources for saproxylic species for centuries (Stokland, 2001). During the last decades, environmental consideration and restoration actions have been implemented to benefit biodiversity and to resemble natural disturbances (Angelstam, 1998). These include deadwood creation, green tree retention, and prescribed burning, which have been implemented in Swedish forestry from the early 1990s (Anonymous, 2015; Johansson *et al.*, 2013; Gustafsson *et al.*, 2010; Wikars *et al.*, 2005) to restore structural diversity in managed landscapes. Prescribed burning is also demanded in the FSC certification and is performed on approximately 5% of the clear-cut area every year (Forest Stewardship Council Sweden, 2010). As mentioned previously, positive impacts of prescribed burning have been found on saproxylic species in Fennoscandia. However, to what degree they in practice mimic natural wildfires' impacts on biodiversity in a wider context and especially at longer time scales is still unclear.

1.1 Objectives and outline of this thesis

The main objective of this thesis was to contribute to the knowledge of fire impact on the community composition of beetles, polypore fungi, wildlife, and browsing by moose. This is in the context of intensely managed boreal forests with effective fire suppression and more recent conservation management actions by prescribed burning. The four papers in this thesis rest on two pillars;

- An ecological exploration of successional patterns, species functional traits, and community compositional differences
- Management implications of burning on biodiversity and impacts on moose utilisation

My interest compasses both natural disturbance and prescribed burnings on a decadal scale while also including aspects of the naturalness of forests and values in need of protection rather than burning. In a generally degraded forest landscape, restoration actions are and will become more important. Since prescribed burning is a resource-demanding action, I hope that this thesis can help pinpoint aspects of wildfires that are essential to emulate for prescribed burning to mimic natural occurring fires. I asked the following questions:

- What are the effects of forest fire on the community composition of beetles during the first decade post-burn? (Paper I and II)

- How does burning affect polypore and beetle functional traits and deadwood associations? (Paper II)
- How does wildfire impact the community of mammals and birds and to what degree do different feeding types use the burnt areas? (Paper III)
- What are the decadal effects of fire on forage availability, browsing levels, and utilisation of moose? (Paper III and IV)
- To what degree does prescribed burning mimic the effects of wildfire when it comes to the biodiversity of saproxylic communities and as a tool for creating valuable forage resources for moose? (Paper II and IV)

2. Method

2.1 Study areas

Three uncommonly large wildfires occurred during the summer of 2006, which was unusually dry and warm, in the County of Norrbotten, Sweden. All three wildfires were relatively large (~300 ha), situated in the northern boreal vegetation zone (Ahti *et al.*, 1968), at a latitude of 66.15°N at the most southernmost area (Table 1). This provided me with a unique opportunity to study the effects of wildfires in fire suppressed landscapes with different management histories. I matched the wildfires with ‘unburnt’, i.e. not recently burnt, areas close by as controls (<2km, Figure 1). I specifically looked for areas with similar topography, tree species composition, ground vegetation type, and forest age distribution, based on satellite images combined with field visits and registered stand characteristics from the forest company Sveaskog. All three wildfire areas were included in each of the four papers in this thesis except for the first paper that is based on a time series from one of the wildfire areas.

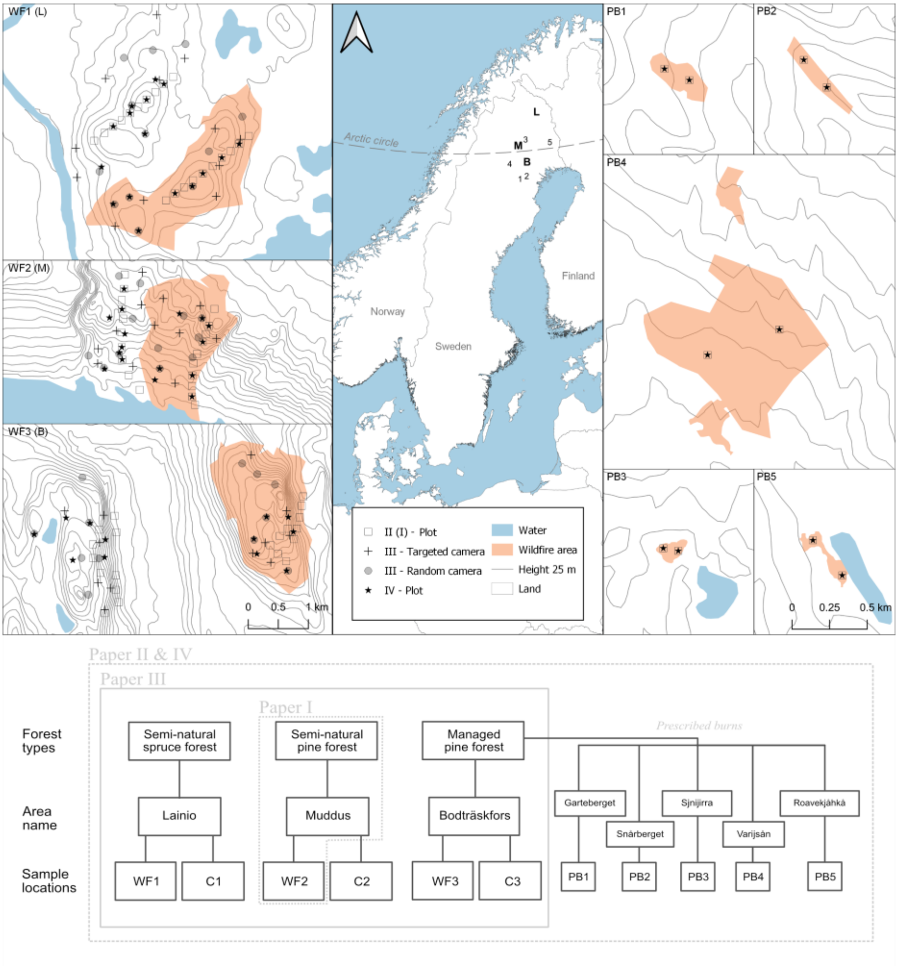


Figure 1. Study area in northern Sweden with the three wildfire areas; WF1 Lainio (L), WF2 Muddus (M), and WF3 Bodträskfors (B), nearby unburnt forested controls C1-3 and the five prescribed burns PB1-5. The contour line interval is 25 m. The roman letters in the map legend correspond to the papers of this thesis. At the bottom of the figure is a schematic overview of the study design of each paper of the thesis.

Table 1. Description of sampled locations including forest type, basal area, forest age, latitude, fire, and management characteristics. Roman letters correspond to the thesis chapters listing sample sizes. WF1-3 refers to the wildfire areas, C1-3 to the unburnt forest, i.e. controls, and PB1-5 to the prescribed burns. Age, height, and basal area are reported as mean ± standard deviation. Latitude is reported in WGS84. *The table continues on the next page.*

Area name	**Lainio**		**Muddus**		**Bodträskfors**	
Study area	WF1	C1	WF2	C2	WF3	C3
Size of burn [ha]	400	-	300	-	300 (1900)[1]	-
Year burnt	2006	-	2006	-	2006	-
Tree mortality, fire type	High, crown fire	-	Medium, ground fire	-	High, mixed fire types	-
Management History	Reindeer herding, clear-cut burning		National Park, selective logging, reindeer herding		Intense management for timber	
Dominant canopy species	Spruce		Pine		Mixed coniferous	
Age of tree layer [y]	110±50	95±20	95±10	105±25	65±50	135±40
Height of tree layer [m]	13±1	11±2	16±1	13±3	10±4	16±2
Coniferous trees [m^2/ha]	2±3	8±3	20±6	18±6	4±4	15±5
Deciduous trees [m^2/ha]	0	4±1	0	0.2±0.5	1±1	6±6
Latitude [WGS84]	67.90°N, 22.16°E		66.76°N, 20.16°E		66.15°N, 20.82°E	
Sample size [n]	II: 10 III: 12 IV: 8	II: 10 III: 12 IV: 8	I: 7(10)[2] II: 10 III: 12 IV: 8	II: 10 III: 12 IV: 8	II: 10 III: 12 IV: 6	II: 10 III: 12 IV: 6

Area name	**Garteberget**	**Snårberget**	**Sjnijirra**	**Roavekjåhkå**	**Haisujärvi**
Study area	PB1	PB2	PB3	PB4	PB5
Size of burn [ha]	6	5	2	83	3
Year burnt	2008	2005	2006	2006	2006
Tree mortality, fire type	Low, ground fire	Low, ground fire	Medium, mostly ground fire	Medium, mostly ground fire	High, mostly crown fire
Management History	Intense management for timber	Intense management for timber	Ecopark[3] Leipipir	Ecopark[3] Varijsån	Intense management for timber
Dominant canopy species	Pine	Pine	Mixed coniferous	Pine	Pine
Age of tree layer [y]	81±10	113±49	61±2	90±8	62±87
Height of tree layer [m]	13±3	15±1	13±1	15±0.4	6±8
Coniferous trees [m^2/ha]	14±0.08	24±1	12±1	11±5	5±5
Deciduous trees [m^2/ha]	>1	0	5±0.1	0	0
Latitude [WGS84]	65.57°N, 20.07°E	65.65°N, 20.67°E	66.95°N, 20.87°E	66.13°N, 19.27°E	66.76°N, 23.03°E
Sample plots [n]	II: 2 IV: 2	II: 2 IV: 2	II: 2 IV: 2	II: 2 IV: 2	II: 2 IV: 2

[1] Total area of the wildfire in parenthesis, however, most was salvage logged so sampling was only done within the remaining 300 ha of forest.

[2] The first 3 years post-burnt 7 traps were used to sample beetles while 10 traps were used and at 12 years follow up.

[3] Ecoparks are large areas where nature conservation actions and timber production management are combined by the state-owned forest company Sveaskog.

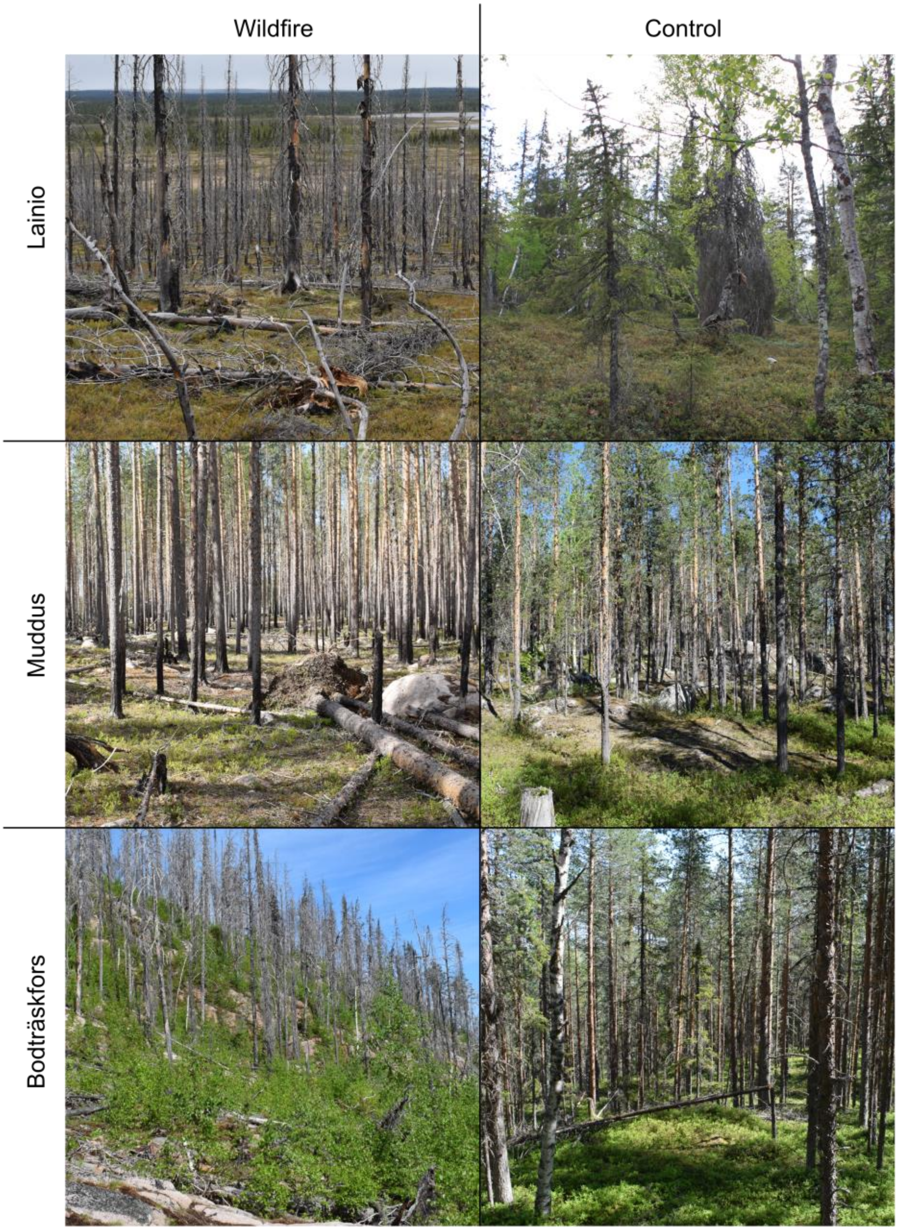


Figure 2. Pictures were taken in June 2018, of the three wildfire areas and their paired unburnt forests (i.e. controls) 12 years post-burn. Lainio = WF1/C1, Muddus = WF2/C2 and Bodträskfors = WF3/C3.

The northernmost area (WF1), close to the village of Lainio (Kiruna municipality) was a 400 ha high severity burn in a semi-natural spruce forest, with a high tree mortality rate. The early season crown fire left most of the field and ground vegetation intact. The dominant tree species was Norway spruce (*Picea abies*, (L.) H. Karst) but Birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth, hereafter referred to as 'birch') also occurred in the entire area. The fire originated from a clear-cut while it was being burnt as soil scarification before planting and spread to the nearby forest. This area has low productivity, i.e. timber growth is estimated to be ~2.5 m^3 per ha and year (Hägglund & Lundmark, 1977) and has a history of reindeer herding.

The second area (WF2) was located in the southern parts of Muddus (Muttos) National Park, close to the Lule river (Figure 1), and covered ~300 ha. The fire started from a lightning strike and burnt for a total of six days before being put out (Ola Engelmark, 2013). The fire never reached the tree crowns and remained a ground fire, reducing the severity to low-moderate and with a relatively low tree mortality rate. Muddus NP is one of the largest forested National Parks in Sweden and is located within the Laponia World Heritage site. The National Park was protected in 1942 and has been relatively unaffected by human activities. However, large trees along the river have been selectively cut during the timber floating era of the late 19th century. Other uses of the park and wildfire area include reindeer grazing and historical haymaking on wetlands. Due to these activities, we have chosen to refer to this area as semi-natural, using the same rationale as for the first area (WF1). Both these areas differ from the managed forest landscape by their tree continuity and old average tree age. This area also has low productivity, similar to Lainio, but is dominated by Scots pine with scattered occurrences of birch and spruce.

The third wildfire area (WF3), the one located furthest to the south, was a 1900 ha burn close to the village of Bodträskfors (Boden municipality). The fire started with a lightning strike and lasted for 29 days before being completely extinguished (Boden municipality, 2006). The majority of the burnt area was salvage logged, however, ~300 ha were left unlogged and it is here I have performed the data collection. The forest landscape at and around the wildfire area was managed pine forests, i.e. a matrix of clear-cuts, young planed stands as well as more mature stands. However, the sample plots were distributed in mature forest, some plots in stands with semi-natural characteristics.

I compared the wildfire WF3 to prescribed burns in two papers (Paper II & Paper IV). These locations were chosen based on available data on prescribed burns that I acquired from the forest company Sveaskog. I choose five that were of similar age to the wildfires in Norrbotten (burnt between 2005 and 2009). All prescribed burns were located within a managed pine forest landscape, hence I only compared them to the wildfire and control areas in Bodträskfors and not to the two less managed and more natural forests of Lainio and Muddus. Due to the small size of the prescribed burns, I only placed two sampling plots in each one, making a total of ten plots, matching the sampling effort of one wildfire or control area.

2.2 Insect sampling, identification, and traits (Paper I & II)

Insect sampling in this thesis was performed using flight intercept traps (model Polish IBL2, Figure 3A), which were applied from June to September each sampling year (2007-2009 & 2018). The traps were made from a triangular semi-transparent plastic of ~0.35 m^2 with a funnel and collection bottle of 600 ml at the bottom of each trap. Each trap had a water module to deter rainwater and avoid bottles to overfill. The bottle was filled with one-third of polypropylene glycol mixed with water (50/50) and a small amount of detergent (Stenbacka *et al.*, 2010). I used ropes to tie each trap between two living trees if available, otherwise, I used standing dead trees. The insect sampling was performed in one of the wildfire areas (Muddus) during the three years following the fire (2007-2009) by the County Administration Board of Norrbotten using 10 flight intercept traps. Since long-term studies on beetle community composition are lacking in Fennoscandia, I combined their data with a follow-up sampling during 2018, i.e. twelve years post-burn where an adjacent control was added (Paper I). Three of the ten traps per year from 2007-2009 were treated with pheromones and excluded. In 2018 I also sampled the two other wildfire areas (Lainio and Bodträskfors, ten traps in each wildfire/control, Paper II). Trap placement followed a transect and was decided upon before going out into the field. However, due to the difficult terrain in Bodträskfors, I had to change some plot locations in the field. Insect traps were never closer than 140 meters from each other (Figure 1). Everything in the bottles that were not beetles was removed from the samples before each individual beetle was counted and identified by expert Stig Lundberg (Muddus samples from 2007-2009) and Sven Lennartsson (all samples from 2018). Taxonomy and nomenclature for all species follow (Swedish Species Information Centre, 2021). All individuals were identified to species level and assigned traits/functional groups. Each species was categoriesed into functional groups. For detailed descriptions of the groups see method sections in Paper I and II.

Figure 3. Picture of the flight intercept traps used to sample beetles (A) and the camera trap used to capture wildlife community visitation frequencies (B).

2.3 Polypore sampling, identification, and traits (Paper II)

I sampled polypores in a 25-meter radius plot at the same locations where the beetle window traps were placed (Figure 1). On each log, which was >15 cm in diameter, with its base within the plot, I noted all occurrences of sporocarps of polypore fungi. Fruiting bodies (sporocarps) were identified to species directly in the field and a few specimens were collected for identification in the lab. The numbers of fruiting bodies were not counted. I defined abundance of polypores as the number of logs per plot with a species present. Similar to the beetle species, I used available data on polypore species traits (details found in the method section of Paper II).

2.4 Deadwood related environmental variables (Paper II)

Since deadwood amount and diversity is arguably the most important factor for saproxylic taxa, such as polypores and beetles, detailed measurements of deadwood at each location were made. Both deadwood (i.e. ‘coarse woody debris’) and forest structure were measured in the same 25-meter plots as the polypore sampling with the centre being at the flight intercepting traps for beetles. Within each plot, I inventoried deadwood; logs as well as standing deadwood (snags), and forest stand characteristics. All logs and snags, which were >10 cm in diameter and >1.3 m long, were included. Each deadwood piece was identified to species (if possible). Decay class was determined as well as burn proportion and depth, and ground contact proportion. Based on these measurements, I calculated the volume of deadwood per hectare (detailed descriptions can be found in paper II and its supplementary material).

2.5 Camera trap placement and data (Paper III)

In each of the wildfire/control areas, twelve cameras traps (Figure 3) were placed to quantify the visitation frequency of wildlife. I implemented two different camera-trap placement strategies, since I was interested in both herbivores and carnivores, by placing half of the cameras in random locations and half targeted to wildlife trails (Figure 1). The latter was done since random placement has been seen to have limited success in capturing predators (Hofmeester, 2021; Bubnicki *et al.*, 2019), and high ruggedness features are often used by both Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) (Rauset *et al.*, 2013). Each camera-trap was placed on a tree, 20-50 cm above the base of the tree. When its passive-infrared sensor was triggered by movement each camera took a series of ten pictures (Figure 3B). The camera-traps were active in the sample areas for approximately three months during the summer of 2018 (example pictures in Figure 4). The images taken by the cameras were classified using the Trapper software (Bubnicki *et al.*, 2016), and species and number of individuals were checked and corrected for. I also corrected for detection differences among species and camera locations (details in the method section of paper III). All species were lastly divided into feeding types (Wilman *et al.*, 2014).

2.6 Forage availability and browsing levels (Paper IV)

In early June 2018, I sampled moose forage availability, browsing levels, and inventoried dung pellet group counts in a total of 54 plots (Figure 1). The plots were divided among wildfire areas, unburnt control forests, and prescribed burns (Table 1). The placement of the plots was preferably random but due to practical reasons also along transects e.g. topography and sampling in other projects taking place at the same time. Sample plots were selected with a minimum of 100 m from each other prior to going out into the field (Figure 1). I used two sizes of circular plots with the same centre point, one larger plot with a radius of 10 m and a smaller plot with a radius of 3.5 m. In the larger plots, I sampled environmental variables, as well as counted dung pellet groups. The pellet groups had to contain >20 pellets and were determined to be from the latest winter by only including fresh pellets above the previous year's fallen litter. The 'environmental' variables (relevant variables that might be altered by fire disturbance) included canopy cover which was visually determined, deadwood amount, and bare ground cover. The measurements related to burn severity in this thesis were canopy cover (related to tree mortality) and basal area of living trees. Cover and height of the field layer (0-0.3 m), which were measured in the large plot, i.e. environmental variables, that also were considered as variables related to forage availability. All other forage and browsing variables were measured in the smaller plot with higher detail, including bilberry cover and height. All tree saplings were counted and their height measured. In total 1651 saplings were measured. I counted the number of shoots on each sapling and noted how many shoots were browsed. General browsing effect/’degree’ was also noted for each sapling. Details can be found in the method section of paper IV. Note that this sampling was done in spring. Therefore, it was browsing and utilisation (pellets) of moose in winter that was captured with this data in comparison to the camera-trap data that measured activity during summer.

Figure 4. Pictures with examples of species captured by the camera traps from the different wildfires and unburnt forests (i.e. controls) as noted on each picture.

2.7 Statistical analysis

In almost all instances the data was not normally distributed, which is not unusual for ecological data of vegetation and species composition. Hence, most statistical methods used in this thesis had to be non-parametric and/or compatible with this type of data. I did not implement transformation of variables in the final analysis, since this did seldom improve the distribution of the data and made interpretations more difficult. For more simple comparisons of environmental variables, abundances, richness, etc. among treatments, I used Kruskal-Wallis non-parametric rank tests and Wilcox pairwise comparisons when adding a third category, i.e. all three wildfire areas or prescribed burns). When the data was normally distributed, I used a parametric equivalent such as the Tukey HSD, t-test, or ANOVA. See individual papers for specific details. All analyses in this thesis were performed using R Studio version 3.6.2 (RStudio & Team, 2020).

Species diversity tells us about the identity and relative abundance of species within the community. Therefore, it describes more than just the abundance of individuals or number of species but also how abundances are distributed among species (evenness). There are many ways to evaluate or compare diversity and I included a wide range of methods in this thesis. One of them being diversity indices where the number and evenness among species are taken into account. So I always included one or several diversity indices in all of the papers. An example is the Shannon-Weaver index, using the function *diversity* from the *vegan* package (Oksanen *et al.*, 2019). I compared the post-burn years in terms of indicator species in Paper I using the function *multipatt* from the *indicspecies* package (De Cáceres & Legendre, 2009), which combines two indices including how exclusive the species appear in one group (‘specificity’) and what proportion of samples it appears in within that group (‘fidelity’).

Linear and generalised linear mixed models were used both in Paper I and IV. I used a negative binomial generalised mixed model (Paper I) to compare the abundance of different functional groups among the post-burn years after a wildfire using plots/traps as a random factor (using the function *glmer.nb* in the *MASS* package (Ripley *et al.*, 2013). Other model distributions such as Poisson were evaluated but due to the over-dispersed count data the negative binomial family fit the data best (lowest model AIC). In paper IV, I compared forage availability and browsing level of moose among treatments using the first axis of the PCAs as response variables. In this paper, I chose this approach since I wanted to capture many facets of forage/browsing and did not just want to compare each variable separately. I did this for two of our three main hypothesis and compared forage availability and browsing level among treatments and environmental variables such as canopy cover.

To visualise community composition change either among years (paper I) or between burnt and unburnt areas (Paper II & III), I used ordinations, specifically non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarities. NMDS is a rank-based and robust method (Shi, 1993) that can handle data with large amounts of zeros. It is not possible to add random effects or constrain NMDS ordination but one can group the plots visually with polygons as I did in Paper I or add supplementary variables on top of the ordination plot to visualise directions of traits as one example. I did the latter in Paper III using the function *envfit* from the *vegan* package (version 2.5-5; Oksanen *et al.*, 2019). To then statistically test differences between and among years and treatments, I used two approaches; one of them was a permutational multivariate analysis of variance (PERMANOVA), performed with the function *adonis* from the *vegan* package (Oksanen *et al.*, 2019), which is a non-parametric test that compares the distances among the group centroids. This method has been shown to be a powerful analysis for analysing changes in communities over time, especially for communities with large numbers of species (Irvine *et al.*, 2011). Therefore, I used this method in the papers evaluating beetle and polypore communities (paper I and II). The other approach was a multivariate generalised linear model (ManyGLM), from the *mvabund* package (version 4.0.1; Wang *et al.*, 2012). I used this second approach when comparing wildlife community composition changes (paper III) as well as its univariate results for individual species differences. ManyGLM is a method, which stacks species distribution models, compared to a PERMANOVA, which resembles an analysis of variance (ANOVA). ManyGLM was developed specifically for multivariate abundance data. Due to the large numbers of zeroes and overdispersion in the data, I ended up fitting a model with a negative binomial distribution (Warton *et al.*, 2012), which showed a better fit than a Poisson distribution. In all community analysis, even if not included in the final paper, a presence-absence (or detection-non-detection) ordination and following test (PERMANOVA or ManyGLM) were always performed to check if potential outliers would impact the overall pattern. I generally found only small differences and nothing that changed the overall patterns or conclusions of the studies.

To take the analysis of community composition further and linking it not only with species traits but also environmental variables, I performed a type of “fourth-corner” analysis (Paper II). The idea of the “fourth-corner problem”; the problem of associating traits and environmental variables to species community abundances, is not new (Legendre *et al.*, 1997). The name comes from the thought that a fourth table (or corner) is what I seek, i.e. the missing direct link from traits to the environment. As I have one table of species abundances, the second of environmental variables from the areas the species were sampled and the third table of traits each individual species has - what is in the fourth-corner? To answer this question I decided to use the “RLQ” analysis (*sensu* Thioulouse *et al.*, 2018) using the 'ade4' package, which is an exploratory ordination approach (Dolédec *et al.*, 1996). Hence, this is not a hypothesis testing approach. The RLQ analysis does this by finding multivariate associations with the highest covariance based on combinations of traits (Table Q) and environment (Table R) that are weighted by the species abundances (Table L) (Dolédec *et al.*, 1996). As the last step, I performed a fourth-corner analysis (Dray & Legendre, 2008; Legendre *et al.*, 1997) using the function *fourthcorner* to reveal bivariate associations (as seen by negative or positive interactions between individual environmental variables and traits). For details on the exact procedure, see the method section of paper II.

3. Results & Discussion

I found distinct differences among unburnt, wildfire, and prescribed burnt areas a decade post-burn in vegetation characteristics, community composition of both saproxylic and wildlife species as well as moose browsing levels. The prescribed burns included in this thesis did were in many regards more similar to the unburnt forests than the wildfires (Table 2).

The three years after the wildfire in Muddus, as well as for the 12 year follow-up, I recorded in total 11,156 individuals of 452 different beetle species (Paper I). The most abundant functional group was fungivores with 5,859 individuals from 157 different species. When including all study areas I recorded 829 individuals of 50 polypore species (and the ascomycete *Daldinia locata*) and 7,721 individuals of 296 saproxylic beetle species (Paper II). Of these species, a total of 5 polypores species were associated with fire and 17 beetles were classified as pyrophilous while 18 polypores species and 23 beetle species were classified as red-listed of at least near-threatened status. When capturing the usage of the wildlife community with camera traps the resulting effort was 6,924 camera trapping days where I in total observed 27 mammal and bird species, 17 of which were found in both wildfire and unburnt areas (Paper III). When studying winter moose utilisation of burnt areas I sampled a total of 1,611 tree sampling of 6 different tree species, counted a total of 14,620 shoots as well as a total number of 63 pellet groups (Paper IV).

Table 2. Overview of general differences between the unburnt forest, the wildfires, and prescribed burns. These effects are relative among treatments (i.e. high/low). Note that prescribed burns were not included in paper III. The difference between the two burns is highlighted as *italic text* when prescribed burns were similar to the unburnt forest and **bold text** when similar to the wildfire.

Paper	Unburnt forest	Wildfire	Prescribed burn
IV	↑ High canopy cover ↓ Low field layer richness and diversity ↑ High bilberry cover	↓ Low canopy cover ↑ High tree field layer richness and diversity ↓ Low bilberry cover	↑ *High canopy cover* → Intermediate field layer richness and diversity ↓ **Low bilberry cover**
II	↓ Low amount of deadwood ↑ High proportion of deadwood with high decay class	↑ High amount of deadwood ↑ High proportion of deadwood with low decay class	↓ *Low amounts of deadwood* ↑ *High proportion of deadwood with high decay class*
III, IV	↓ Low visitation and browsing level by moose ↑ High visitation of reindeer, western capercaillie, and European pine marten	↑ High winter visitation and browsing level by moose — No bird or mammal species-specific visitation frequency differences	↓ *Low winter visitation* and intermediate browsing levels by moose
II	↓ Low richness and abundance of polypores ↑ High richness and abundance of beetles ↑ Positive trait association for red-listed polypores, disturbance favoured beetles	↑ High richness and abundance of polypores ↓ Low richness and abundance of beetles	↓ *Low diversity, richness, and abundance of polypores and beetles* ↓ No red-listed and fire-associated polypores ↓ Few red-listed and pyrophilous beetles ↑ *Positive trait association for disturbance favoured beetles* and larger body size

3.1 Burn severity and deadwood diversity (Paper IV & II)

The burn severity of a fire, i.e. the organic matter loss (Keeley, 2009), depends on a large array of variables that influence the fire intensity, such as topography, humidity, fuel load, wind, and temperature (Fang *et al.*, 2018). I found that canopy cover was lower in the wildfire than in prescribed burns, however, canopy cover was not a significant explanatory variable in either the forage availability or browsing level mixed effect models. Corroborating the results of lower canopy cover I also showed that the basal area of living trees per ha was much lower in the wildfire areas compared with the unburnt control areas (however not to the same degree in the prescribed burns). The considerable differences in deadwood amount and composition between unburnt and burnt forest were mainly related to increased tree mortality due to the wildfires.

A decade after burning the wildfire areas had larger amounts of deadwood as well as a different composition of deadwood substrates compared to the unburnt forests. Specifically, wildfire areas had more coniferous logs and snags as well as deciduous snags. In contrast, the prescribed burns had similar deadwood amounts as the unburnt forest or even lower (Figure 5), and also a similar proportion of decay stages (Figure 6). High severity prescribed burns performed in an experimental setup in Finland generated high deadwood amounts and diversity (Hekkala *et al.*, 2016). Another notable difference is in the distribution of decay stages of deadwood among the treatments, where late decay stages dominated the unburnt areas and early decay stages dominated in the wildfires (Figure 6). Wood of later decay stages are important for red-listed species. This highlights not only large quantities of deadwood created by the wildfires but also the importance of the unburnt forest that can host high-quality substrates (Stokland *et al.*, 2012). These high-quality substrates are otherwise likely removed by burning.

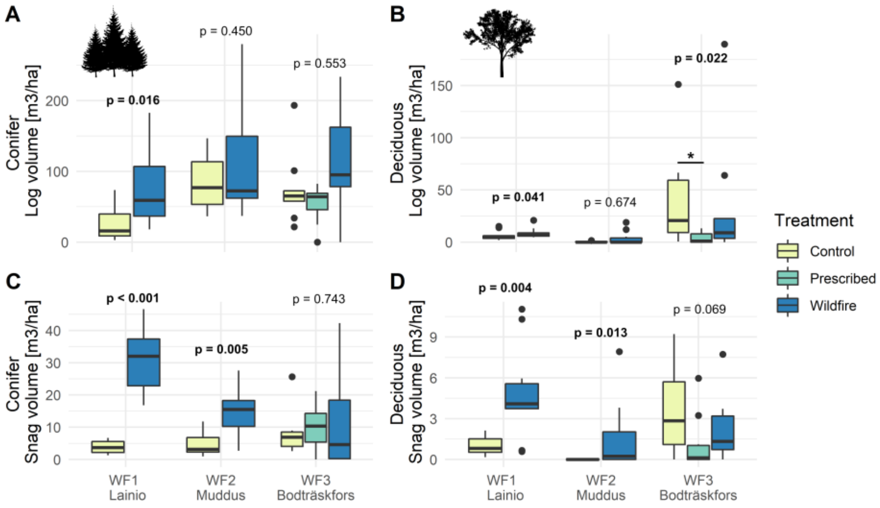


Figure 5. Log and snag volume per area and treatment, divided among coniferous (left column) and deciduous (right column) trees. Note the different scales on the y-axis. Significance (p-values) are depicted above each study area based on a Kruskal Wallis test and within-group p-values < 0.05 denoted by a '*' based on a Wilcox pairwise comparison. Bold letters indicate a p-value of less than 0.05. Each individual boxplot has an n = 10.

3.2 Species community differences (Paper I, II & III)

Communities of polypores, beetles, wildlife as well as the richness of vegetation differed between wildfires and unburnt forests (Figure 7). For beetles, there was a fast turnover the first few years, i.e. temporal changes in abundance and richness of individual species as well as functional groups (Paper I). I found differences in community composition between burnt and unburnt forests among beetles, polypores (Paper II), and wildlife a decade after the fire (Paper III). Even though abundance and/or richness did not always differ, the composition still did. I found a drop in beetle diversity (Shannon index) the third year after the wildfire, corresponding with high abundances, and dominance, of fungivores (Paper I). However, 12 years post-burn the diversity was similar in wildfires and unburnt controls (Paper I and II). It is well established that the beetle community composition is impacted by the fire at least short-term (Johansson *et al.*, 2011; Hyvärinen *et al.*, 2005; Saint-Germain *et al.*, 2004). I found a fast turnover of beetle species the first three years post-burn with the highest abundance and richness the second year but with remaining differences in community composition after 12 years (Paper I). Long-term effects on beetle species communities are not extensively researched. Hekkala *et al.* (2014) suggest introducing fire in neighbouring areas in 5-year intervals so that habitats for pyrophilous species within dispersal distance are continuously created. I found examples of both pyrophilous (and red-listed) beetle species 12 years post-burn, such as *Acmaeops marginatus* (EN), *Dentricollis borealis* (NT), and *Pachyta lamed* (NT), although in small numbers, suggesting that the wildfires can support pyrophilous and rare species even after a decade. There was however a distinct difference between the two types of burns in this regard, with prescribed burning hosting fewer of both red-listed and pyrophilous species. The quick turnover in beetle species (paper I), with a community that a decade later showed indications of recovering to a late-seral community (paper I and II), is not what I found in the polypore community. Polypores, compared to beetles, have not reach as far in their successional turnover after a decade due to their different life history strategies. Due to differences in temporal scale responses within the community which are dominated by early successional species such as *Trichaptum fuscoviolaceum* and *T. abietinum*. Several polypores are negatively affected by fire (Penttilä *et al.*, 2013) as their habitat, decayed wood, often is consumed by the fire. However, long-term studies, +5 years, have found positive effects on abundance of polypores, including red-listed and rare species (Koivula & Vanha-Majamaa, 2020; Suominen *et al.*, 2015; Penttilä *et al.*, 2013). For the wildlife, i.e. mammal and bird communities, I found differences in usage of the wildfire areas compared to unburnt controls (Paper III). Studies from Fennoscandia are mainly lacking but in a review on North American wildlife by Fisher and Wilkinson (2005), they found general utilisation patterns for certain trophic levels and taxonomic groups but did not do a comparison of community composition. Their results are in line with ours as they found that herbivores like moose and hares had high abundances in burnt habitat when vegetation had recovered, while caribou utilise unburnt forest to a higher degree. However, the review by Fisher and Wilkinson (2005) highlights species-specific temporal differences and contrasting responses among wildlife species between burnt and unburnt forests.

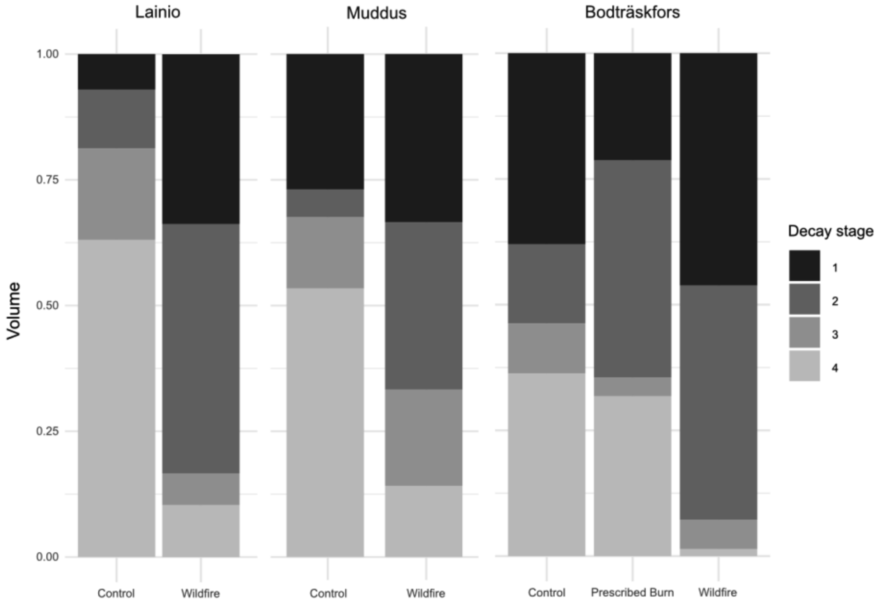


Figure 6. The proportion of decay classes of conifer log volume among treatments and study areas. Decay class was measured using four categories (Gibb *et al.*, 2005); 1) bark intact or starting to loosen, >50 % bark remaining, wood hard; 2) <50 % bark remaining, the surface of wood smooth, but beginning to soften, wood hard; 3) lacking bark, the surface of wood soft, some crevices and some small pieces of wood lost or bigger wood fragments lost with a deformed surface; and 4) lacking bark, wood soft, but still possibly having a heart of hardwood, the surface of object hard to define, the outline of object indefinable.

3.3 Nutritional differences (Paper I & III)

3.3.1 Turnover in beetle nutritional groups (Paper I)

When comparing the temporal changes in the beetle community following wildfire I found different functional groups of beetles (i.e., different niche preferences) to exhibit a turnover among the years from more early successional species towards late-successional groups. Specialists such as pyrophilous species have been found to be immediately attached to burnt areas (Byers, 1992; Eidmann *et al.*, 1990). Generally, the abundance and richness of all groups was high the first years post-burn and decreased after 12 years. Primary successional species, like cambivores, leave as soon as the cambium is consumed within a few years, which would explain the lower abundance and species richness year 3 and year 12. Secondary successional species such as predators, fungivores, and saproxylic species that use other parts of the wood than the cambium such as the tracks left in the bark by other beetles, followed the primary successional species. The time it takes to observe distinct changes in the communities of saproxylic beetles can be as soon as a couple of years (Esseen *et al.*, 1997) or not be measurable after over a decade as was found by Boulanger and Sirois (2007). In this study, I found a post-burn decrease in species richness and the abundance for both pyrophilous and red-listed beetles over time.

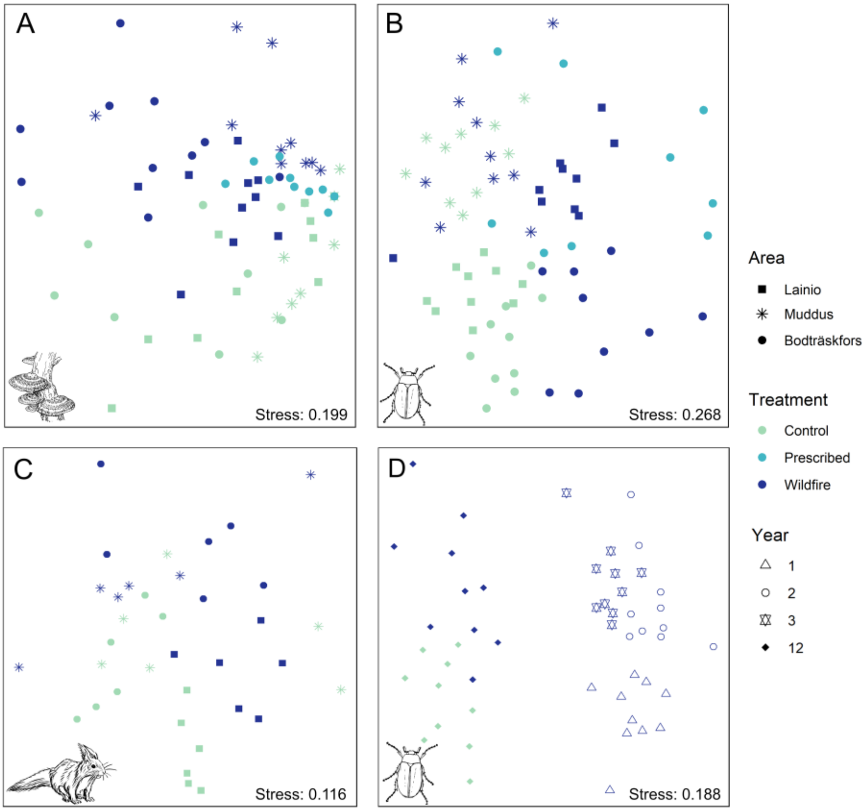


Figure 7. Plotted NMDS ordination to visualize the polypore (A), saproxylic beetle (B), and wildlife (C) community composition and beetle turnover among the years after the fire in Muddus (D). Each symbol represents the species composition in one plot. The symbol shapes denote the different study areas and/or years. Stress of each ordination is written out on each subplot.

3.3.2 Wildlife community feeding type differences (Paper III)

I found that herbivores had higher visitation frequencies in the unburnt areas compared to the burnt, however, there was species-specific variations within the feeding type (Figure 8). This was in contrast to my prediction that herbivores should find abundant forage resources in burnt areas (Paper IV) (Felton *et al.* (2020) & Milligan and Koricheva (2013)) and therefore display high utilisation. Rich forage resources should also provide cover for the smaller species such as hares (Pulliainen & Tunkkari, 1987). Utilisation degrees for different habitats of herbivores depend on a multitude of factors besides forage availability, such as cover (Hernández & Laundré, 2005) and obstacles (de Chantal & Granström, 2007). The herbivores with the highest visitation frequencies (and having the most influence on the results) were Western capercaillie, mountain hare, moose, and reindeer (Paper III). These species responded differently to the wildfires; with higher visitation frequencies of reindeer and western capercaillie in the unburnt forest while moose and hares had a trend towards higher visitation in the wildfires. This is likely why I see no overall difference for this feeding type. The main forage resource used by reindeer are lichens and their cover can be severely negatively affected by fire and take a long time to recover (Lafontaine *et al.*, 2019; Joly *et al.*, 2010). The feeding type associated with the wildfire areas were most prominently insectivores with higher visitation frequency but also birds, omnivores, and carnivores pointing to the burnt areas in the ordination. In a study by Edenius (2011), surveying birds in Muddus and Lainio, they observed that ground-feeding insectivores were common in burnt areas three years post-burn and burnt areas also had higher abundances of birds in general. I found no difference in bird visitation frequency, again having two species within the group with opposite patterns (Western capercaillie and fieldfare). Birds have been found to be dependent on deadwood amounts and large trees with fungi and beetles, which are often are lacking in managed forests (Paillet *et al.*, 2010), however abundant especially in our sampled wildfire areas. Differences in standing dead/live trees accounted for the difference in bird communists post-burning and harvest in a Canadian study (Hobson & Schieck, 1999).

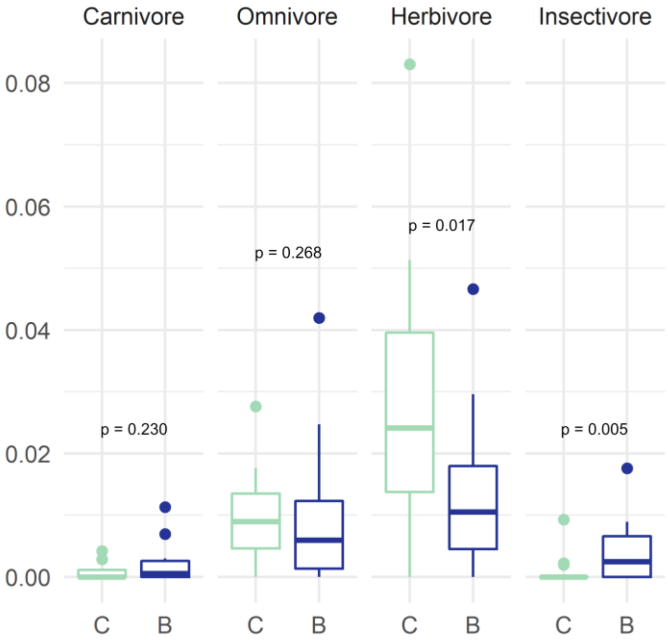


Figure 8. Visitation frequency among the feeding types; Carnivore, Omnivore, Herbivore, Insectivore, between the treatments C = Control and B = Burn. The y-axis represents the individual species number of passages per effectively measured meter per day. All study areas are included. Results from a Kruskal–Wallis rank test among each feeding type between treatments are displayed on the figure.

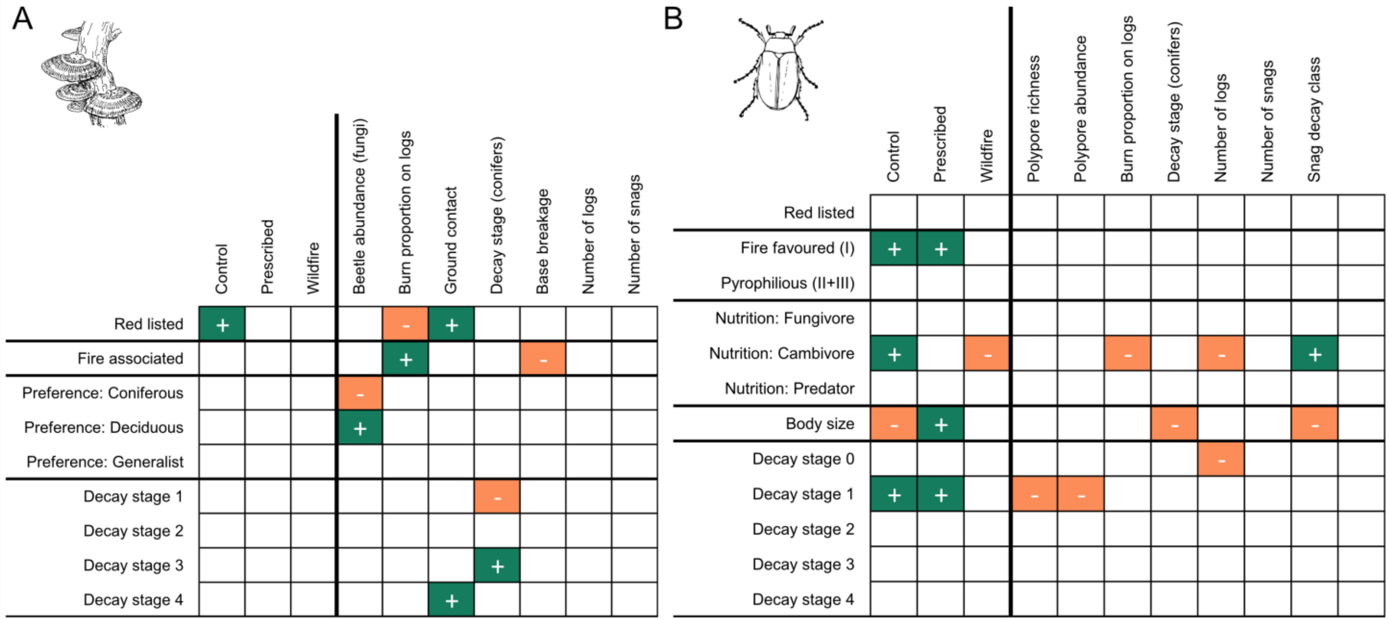
Basal area of live trees was similarly and expectedly lower in the wildfire areas while the amount and volume of snags were higher than in unburnt areas (Paper II). Since I did not aim to make a complete inventory of the bird community, but rather the wildlife community as a whole, I cannot say anything about the bird community as per our results (Paper III). I instead aimed to evaluate the usage of broad feeding types to understand potential trends within the wildlife community. The number of observations for carnivores was very few which makes it difficult to draw general conclusions from them. I expected that carnivores would be associated with the wildfires due to the high prevalence of prey species found in other studies (Nelson *et al.*, 2008; Fisher & Wilkinson, 2005) such as the Western capercaillie and hares. Alternatively, carnivore visitations could instead be influenced by higher total visitations frequencies of all species, not only prey, as I see in the unburnt areas, such as what Cave *et al.* (2021) found when coyotes tracked prey availability regardless of the habitat. Alternatively, predators might hunt for smaller prey that was not captured by the camera traps. My results suggest that feeding types as a wildlife trait is too broad in this context to provide additional information outside of studying specific species regarding utilisation of burnt or unburnt forests in this context.

3.4 Functional traits and deadwood interactions (Paper II)

A functional trait (or group) would consist of species with similar characteristics in morphology, ecology, or life history. Based on data availability and/or relevancy to my hypothesis, I divided the polypores and saproxylic beetles based on nutrition, habitat preferences such as decay stage and species of deadwood, body size, and specialist characteristics such as fire dependency. (Paper II). For both taxa, I found that functional traits linked to deadwood-related environmental variables (Figure 59). This idea builds on the hypothesis that habitat conditions match traits in organisms (but different tactics are also possible within the same habitat, i.e. functional redundancy) (Southwood, 1977). I used an ordination approach to do this, called RLQ analysis, which is a multivariate analysis that weights traits and environmental variables, related to deadwood diversity, with species abundances. Specifically, I found associations in the RLQ analysis between polypore functional traits and links to deadwood-related variables of decay stages, ground contact, charring, and an interaction to fungivore abundance (Figure 9). Polypore species with a preference for late decay stages of wood and ground contact were associated with the unburnt conditions, implying the importance of these habitats for, especially red-listed polypore species. Ylisirniö *et al.* (2012) found similar patterns where one of the most influential factors on community composition of polypores was the deadwood decay stage. In regards to the beetle community, I found that preferences for deadwood variables linked to the wildfire, such as large amounts of deadwood, early decay stages, charring, and high abundance of polypore sporocarps, were negatively associated with several abundant beetle groups such as cambivores (Figure 5). Similarities in responses of the unburnt forest, i.e. control and prescribed burn can be seen for fire favoured and early decay stage preference beetles. Fire favoured species comprise a large number of species, many not directly linked to fire specifically but to early successional habitats in general which are supported by previous studies. Lastly, no interactions with environmental variables were found for pyrophilous beetle species suggesting that the burnt areas at this point in the post-burn succession are no longer the most suitable habitat for them (Wikars, 1997).

3.5 Moose utilisation of burnt areas (Paper III & IV)

Using two different approaches I evaluated moose utilisation of the burnt and unburnt areas both in summer and winter in northern Sweden a decade post-burn. I found that summer visitation frequencies of moose did not differ between wildfires and unburnt forests (Paper III) despite the large differences in forage availability between the two habitats. For example, sapling numbers and diversity were much higher in the wildfire areas while field layer plants were larger and more abundant in the unburnt forest. The change in forage availability is in accordance with previous studies from wildfire locations at similar latitudes and time frames (Ruokolainen & Salo, 2006; Schimmel & Granstrom, 1996). In contrast, I found that utilisation and browsing levels were higher in winter (Paper IV). The difference in utilisation rate between summer and winter could be related to the low canopy cover in the wildfire areas, which might increase the risk of overheating in summer (Street *et al.*, 2015). In addition, the large number of obstacles increase the potential predation risk. Moose alter their movements patterns and habitat use in response to factors such as forage availability (Månsson *et al.*, 2007; Senft *et al.*, 1987), shelter (Dussault *et al.*, 2004), snow cover (Pfeffer *et al.*, 2021), and predation risk (Ditmer *et al.*, 2018; Hernández & Laundré, 2005). In addition, abundant forage resources for moose in terms of bilberry for example, which was high in the unburnt forests, could also be more easily accessible in summer compared to winter, making the unburnt forest more valuable. The usage of the areas is measured in two different ways in the papers which needs to be taken into account as well before drawing strong conclusions from these results based on seasonal usage by moose. However, I can conclude that wildfire in northern Sweden alters the forage availability and utilisation by moose (at least in winter). Fire thus has the potential to be used to benefit forage production for moose.



	Control	Prescribed	Wildfire	Beetle abundance (fungi)	Burn proportion on logs	Ground contact	Decay stage (conifers)	Base breakage	Number of logs	Number of snags
Red listed	+				-	+				
Fire associated					+			-		
Preference: Coniferous				-						
Preference: Deciduous				+						
Preference: Generalist										
Decay stage 1							-			
Decay stage 2										
Decay stage 3							+			
Decay stage 4						+				

	Control	Prescribed	Wildfire	Polypore richness	Polypore abundance	Burn proportion on logs	Decay stage (conifers)	Number of logs	Number of snags	Snag decay class	
Red listed											
Fire favoured (I)	+	+									
Pyrophilious (II+III)											
Nutrition: Fungivore											
Nutrition: Cambivore	+		-			-		-		+	
Nutrition: Predator											
Body size	-	+					-			-	
Decay stage 0								-			
Decay stage 1	+	+		-	-						
Decay stage 2											
Decay stage 3											
Decay stage 4											

Figure 9. Significant positive (green) and negative (orange) trait-environment associations for polypores (A) and beetles (B) from the fourth-corner analysis. ‘Fire favoured’ polypores here refer to level 1 while ‘Pyrophilous’ beetles are level 2 and 3 combined. ‘Snag decay class’ refers to the Thomas class.

3.6 Prescribed burns ability to mimic wildfire (Paper II & IV)

To my knowledge, this is the first boreal study that compares how well prescribed burns mimic wildfires in terms of ecological effects on community compositions of animals, fungi, and vegetation. My results suggest, that in terms of polypore and beetle biodiversity (Paper II) as well as changing the forage availability type for moose and utilisation of the areas (Paper IV), prescribed burning in northern Sweden does not reach similar effects as a wildfire. For many of the measured variables prescribed burns were more similar to the unburnt forests than to the wildfires. The prescribed burns had notably large variation among each other in many measured aspects, however the most notable differences compared to the wildfires were low amounts and diversity of deadwood, lower saproxylic diversity, lack of red-listed and fire-associated saproxylic species, and relatively small forage availability for moose (in terms of saplings of pine and deciduous tree species). Prescribed burns have been shown to have a wide-ranging effect among species, from positive to negative (Koivula & Vanha-Majamaa, 2020; Eales *et al.*, 2018), however, a growing body of evidence supports the positive effects in terms of abundance and richness of beetles short-term and polypores long-term (Koivula & Vanha-Majamaa, 2020; Penttilä *et al.*, 2013; Saint-Germain *et al.*, 2008; Johansson *et al.*, 2007; Hyvärinen *et al.*, 2006; Hyvärinen *et al.*, 2005; Saint-Germain *et al.*, 2004). If the differences I observe between wildfire and prescribed burns are a direct result of differences in burn severity, area burnt or if instead, they result from geographical differences in for example local species pool and/or smaller size of the prescribed burns is not something I can disentangle in this thesis. The aim of prescribed burning in Sweden is to mimic natural fire disturbance and create habitat for saproxylic biodiversity including fire-associated species and rare and red-listed species. However, prescribed burning has the potential to be used also to create habitats for birds and mammals and increase deciduous species abundance. This demands that prescribed burns emulate characteristics of wildfires such as large area burnt and high burn severity to a larger extent.

4. Conclusions

I found differences in species community compositions of beetles, polypores, and wildlife species in northern Sweden a decade after burning. Beetles showed distinct turnover the first three years following wildfire in a semi-natural pine forest. After a decade, the effects levelled out and only small differences in abundance or richness of wood living taxa existed (Paper I & II). A decade post-burn place the beetles in the wildfire areas into a later successional stage, dominated by fungivores and predators. In contrast, the polypore community was still dominated by early successional species, which are abundant and species rich in the wildfire areas (Paper II). This suggests that the polypores have had time to recover from the likely negative short-term effects of burning as observed in other studies (Koivula & Vanha-Majamaa, 2020; Penttilä *et al.*, 2013). The wildlife community of birds and mammals utilised the wildfire areas at different spatial scales than polypores and saproxylic beetles (Paper III). Most wildlife species in this study have a home range larger than the individual study areas. Hence, the areas only make up a part of the resources used by these species. I found lower visitation frequencies, i.e. patch usage, in the wildfires compared to the unburnt forest. This highlights the importance of the unburnt forest matrix (Paper III). Several red-listed species of beetles and polypores also corroborate the value of not only the wildfire but also the unburnt forest (Paper II). Even though the higher amounts of coarse woody debris (Paper II) and forage (Paper IV) in wildfires created large amounts of habitat for saproxylic species where different decay stages and canopy cover in the unburnt forest, provide unique structures diversifying the landscape. Specifically, deciduous forage was higher in the wildfires and correlated with higher winter browsing and pellet counts of moose compared to the nearby unburnt forest (Paper IV), while summer visitation frequencies were not higher in burnt areas (Paper IV).

When comparing one of the wildfires and its pared unburnt forest to five prescribed burnings of similar age, I found that the impact of the wildfire was of higher magnitude. In many aspects the prescribed burns were more similar to the unburnt forest than wildfire, with low fire severity, leading to small reductions in canopy cover, creation of coarse woody debris, and germination of tree saplings (Paper II and IV). The size of the burns differed largely with prescribed burns in this thesis ranging between 5 and 30 ha while the wildfires were around 300 ha. Additionally, the management history differed largely among the prescribed burns. However, this large variation suggests that prescribed burning could be a potential tool for generating forage by promoting the regeneration of deciduous species. Additionally, the prescribed burns did not produce long-term impacts similar to the wildfires on the biodiversity of beetles or polypores (Paper II). Thus, when prescribed burning is performed, I emphasise that it is important to aim for higher tree mortality than was achieved in the prescribed burns in this study.

5. Reflections, limitation & outlook

The future of wildfires and therefore prescribed burning in the boreal forest in the coming decades will to a large degree be impacted by climate change induced changes in temperature and precipitation. I ask myself what role prescribed burning will have if wildfires increase as predicted (de Groot *et al.*, 2013). I hypothesise that either fire suppression will become even more intense, increasing the demand for prescribed burning aimed as restoration actions to preserve unique features produces by fire, in a safe and controlled way. Or that the usage of prescribed burning will be replaced to a certain degree by letting naturally wildfires burn and leaving them without salvage logging, as the restoration action instead. Since prescribed burning is to a large degree performed by forest companies, the future of timber management will influence this as well. I would suggest, based on my research results, that not only area requirements should be included in environmental certifications such as FSC (Anonymous, 2020) but also aspects of fire severity variation, size variations, and landscape connectivity. This would decrease the possible isolation of burnt areas and increase their chances of being within dispersal distances of pyrophilous and red-listed species, as well as increase heterogeneity in terms of structures created by the fire.

To my knowledge, no coordinated database of burning exist on a national scale in Sweden, outside of local databases on county-level (for example in Västerbotten). Coordination on a landscape, preferably national level, of burns, would make evaluation more easily accessible as well as make it possible from a restoration perspective to coordinate burning to create continuity of habitat. The area of the available and measured prescribed burns in this study are at least ten times smaller than the wildfires, the size of burns is an aspect I need to consider when interpreting my results. Since size and severity comprise the most important differences between wildfires and prescribed burns my study design did not allow me to test for their individual effects on biodiversity, forage availability, and browsing. There were large differences among study areas and large distances to the prescribed burns of similar age. Additionally, the unburnt forest in Bodträskfors, could at least partly be categorised as semi-natural, since natural regeneration, deadwood legacies, and mature deciduous trees still remained in the stands.

As I write the summaries and conclusions of my four years of work I feel like a new aspect to test, measure, present, or evaluate jumps into my mind continuously. There are in other words so many possible stepping stones to go forward from the results of this thesis to further not only my own but also our collective knowledge on the effects of wildfire in the boreal forests of northern Fennoscandia. One of the first things I would like to do is evaluate the implications on browsing levels on pine plantations nearby wildfires/prescribed burns. I hypothesise that the browsing levels would either increase due to association/spillover effect or instead be reduced due to the high forage availability on the burnt areas redirecting the browsing pressure there. I'm also interested in including year-round/seasonal sampling with the same method to test the hypothesis that the abundant forage availability for moose in the wildfire areas is most important in winter. I would also implement a model-based approach to be able to hypothesis test specific associations between traits and environmental variables based on the results of the saproxylic communities response to wildfire and prescribed burning. For example by using the alternative Bayesian inference model-based approach called Hierarchical Modelling of Species Communities (HMSC) by Tikhonov *et al.* (2020). I can see the benefit this approach could have in comparison to the more exploitative ordination approach taken in this thesis. However, the limited availability of resources on these methods limited my opportunity to apply them. For the wildlife community I would instead target sampling at specifically interesting species, such as one of the carnivores, where more knowledge is needed on their burnt patch usage. An additional aspect of prescribed burnings that would be valuable is time series (temporal studies) to evaluate the successional turnover of saproxylic species as well as deadwood diversity. This, and including a larger geographical area, would increase the number of available burns to sample as well as provide larger insights into the successional patterns of different functional traits following disturbance.

References

Ahti, T., Hamet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici,* 5(3), pp. 169-211.

Angelstam, P.K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of vegetation science*, 9(4), pp. 593-602.

Anonymous (2015). *Forests and Forestry in Sweden*. The Royal Swedish Academy of Agriculture and Forestry.

Anonymous (2020). The FSC National Forest Stewardship Standard of Sweden(FSC-STD-SWE-03-2019 EN).

Bergeron, Y., Leduc, A., Harvey, B. & Gauthier, S. (2002). Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fennica*, 36(1).

Berglund, H. & Kuuluvainen, T. (2021). Representative boreal forest habitats in northern Europe, and a revised model for ecosystem management and biodiversity conservation. *Ambio*.

Bergqvist, G., Wallgren, M., Jernelid, H. & Bergström, R. (2018). Forage availability and moose winter browsing in forest landscapes. *Forest Ecology and Management*, 419-420, pp. 170-178.

Birkemoe, T., Jacobsen, R.M., Sverdrup-Thygeson, A. & Biedermann, P.H.W. (2018). Insect-Fungus Interactions in Dead Wood Systems. In: Ulyshen, M.D. (ed. *Saproxylic Insects: Diversity, Ecology and Conservation*. Cham: Springer International Publishing, pp. 377-427. Available from: https://doi.org/10.1007/978-3-319-75937-1_12.

Boden municipality (2006). *Modern tids största skogsbrand, Bodträskfors, Norrbotten [In Swedish]*.

Boulanger, Y. & Sirois, L. (2007). Postfire Succession of Saproxylic Arthropods, with Emphasis on Coleoptera, in the North Boreal Forest of Quebec. *Environmental Entomology*, 36(1), pp. 128-141.

Bubnicki, J.W., Churski, M. & Kuijper, D.P.J. (2016). trapper: an open source web-based application to manage camera trapping projects. *Methods in Ecology and Evolution*, 7(10), pp. 1209-1216.

Bubnicki, J.W., Churski, M., Schmidt, K., Diserens, T.A. & Kuijper, D.P.J. (2019). Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *eLife*, 8, p. e44937.

Byers, J.A. (1992). Attraction of bark beetles,Tomicus piniperda,Hylurgops palliatus, andTrypodendron domesticum and other insects to short-chain alcohols and monoterpenes. *Journal of Chemical Ecology*, 18(12), pp. 2385-2402.

Cave, H., Adams, M., Jaeger, T., Peet, T., Staats, L., Garneau, D. & Lesser, M. (2021). Wildlife Response to Wildfire in a Northern New York Jack Pine Barrens. *Forests,* 12(6), p. 676.

Chesson, P. & Huntly, N. (1997). The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities. *The American Naturalist,* 150(5), pp. 519-553.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *science,* 199, pp. 1302-1310.

De Cáceres, M. & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology,* 90(12), pp. 3566-3574.

de Chantal, M. & Granström, A. (2007). Aggregations of dead wood after wildfire act as browsing refugia for seedlings of Populus tremula and Salix caprea. *Forest Ecology and Management,* 250(1), pp. 3-8.

de Groot, W.J., Flannigan, M.D. & Cantin, A.S. (2013). Climate change impacts on future boreal fire regimes. *Forest Ecology and Management,* 294(Supplement C), pp. 35-44.

den Herder, M., Kouki, J. & Ruusila, V. (2009). The effects of timber harvest, forest fire, and herbivores on regeneration of deciduous trees in boreal pine-dominated forests. *Canadian Journal of Forest Research,* 39(4), pp. 712-722.

Ditmer, M.A., Fieberg, J.R., Moen, R.A., Windels, S.K., Stapleton, S.P. & Harris, T.R. (2018). Moose movement rates are altered by wolf presence in two ecosystems. *Ecology and evolution,* 8(17), pp. 9017-9033.

Dolédec, S., Chessel, D., ter Braak, C.J.F. & Champely, S. (1996). Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics,* 3(2), pp. 143-166.

Dray, S. & Legendre, P. (2008). TESTING THE SPECIES TRAITS–ENVIRONMENT RELATIONSHIPS: THE FOURTH-CORNER PROBLEM REVISITED. *Ecology,* 89(12), pp. 3400-3412.

Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L. & Larochelle, J. (2004). Behavioural responses of moose to thermal conditions in the boreal forest. *Écoscience,* 11(3), pp. 321-328.

Eales, J., Haddaway, N.R., Bernes, C., Cooke, S.J., Jonsson, B.G., Kouki, J., Petrokofsky, G. & Taylor, J.J. (2018). What is the effect of prescribed burning in temperate and boreal forest on biodiversity, beyond pyrophilous and saproxylic species? A systematic review. *Environmental Evidence,* 7(1).

Edenius, L. (2011). Short-term effects of wildfire on bird assemblages in old pine- and spruce-dominated forests in northern Sweden. *Ornis Fennica,* 88(2), p. 71.

Eidmann, H.H., Klingström, A. & Axelsson, R. (1990). *Skadegörare i skogen (in Swedish)*. Stockholm, Sweden: LTs förlag.

Engelmark, O. (1999). Boreal forest disturbances. *Ecosystems of the world,* pp. 161-186.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1992). Boreal Forests—The Focal Habitats of Fennoscandia. In: *Ecological Principles of Nature Conservation*, pp. 252-325.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal Forests. *Ecological Bulletins*(46), pp. 16-47.

Fang, L., Yang, J., White, M. & Liu, Z. (2018). Predicting Potential Fire Severity Using Vegetation, Topography and Surface Moisture Availability in a Eurasian Boreal Forest Landscape. *Forests,* 9(3), p. 130.

Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindbladh, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P. & Ranius, T. (2020). Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. *Ambio,* 49(5), pp. 1050-1064.

Fisher, J.T. & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review,* 35(1), pp. 51-81.

Forest Stewardship Council Sweden (2010). Swedish FSC standard for forest certification including SLIMF indicators. *Sweden: Uppsala.*

Foster, C.N., Barton, P.S., Sato, C.F., Wood, J.T., MacGregor, C.I. & Lindenmayer, D.B. (2016). Herbivory and fire interact to affect forest understory habitat, but not its use by small vertebrates. *Animal Conservation,* 19(1), pp. 15-25.

Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A. & Leslie Jr., D.M. (2006). SHOULD HETEROGENEITY BE THE BASIS FOR CONSERVATION? GRASSLAND BIRD RESPONSE TO FIRE AND GRAZING. *Ecological Applications,* 16(5), pp. 1706-1716.

Gauthier, S. (2009). *Ecosystem management in the boreal forest*: PUQ.

Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjältén, J. & Danell, K. (2005). Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scandinavian Journal of Forest Research,* 20(3), pp. 213-222.

Granström, A. (2001). Fire Management for Biodiversity in the European Boreal Forest. *Scandinavian Journal of Forest Research,* 16(sup003), pp. 62-69.

Grove, S.J. (2002). Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annual Review of Ecology and Systematics,* 33(1), pp. 1-23.

Gustafsson, L., Kouki, J. & Sverdrup-Thygeson, A. (2010). Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. *Scandinavian Journal of Forest Research,* 25(4), pp. 295-308.

Hägglund, B. & Lundmark, J.-E. (1977). *Site index estimation by means of site properties*.

Hekkala, A.-M., Ahtikoski, A., Päätalo, M.-L., Tarvainen, O., Siipilehto, J. & Tolvanen, A. (2016). Restoring volume, diversity and continuity of deadwood in boreal forests. *Biodiversity and Conservation*, 25(6), pp. 1107-1132.

Hekkala, A.-M., Päätalo, M.-L., Tarvainen, O. & Tolvanen, A. (2014). Restoration of Young Forests in Eastern Finland: Benefits for Saproxylic Beetles (Coleoptera). *Restoration Ecology,* 22(2), pp. 151-159.

Hekkala, A.-M. & Tolvanen, A. (2008). 16 Effects of Prescribed Burning on Saproxylic Beetles in the Green Belt of Finland. *Fire and Forest*, p. 67.

Hernández, L. & Laundré, J.W. (2005). Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology*, 11(3), pp. 215-220.

Hobson, K.A. & Schieck, J. (1999). Changes in bird communities in boreal mixed forest: Harvest and wildfire effects over 30 year. *Ecological Applications*, 9(3), pp. 849-863.

Hofmeester, T.R.e.a. (2021). Effects of camera trap placement and number on detection of members of a mammalian assemblage. *Ecosphere,* In press.

Hörnberg, S. (2001). Changes in population density of moose (Alces alces) and damage to forests in Sweden. *Forest Ecology and Management,* 149(1), pp. 141-151.

Hyvärinen, E., Kouki, J. & Martikainen, P. (2006). Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation Biology,* 20(6), pp. 1710-1719.

Hyvärinen, E., Kouki, J., Martikainen, P. & Lappalainen, H. (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management*, 212(1), pp. 315-332.

Irvine, K.M., Dinger, E.C. & Sarr, D. (2011). A power analysis for multivariate tests of temporal trend in species composition. *Ecology*, 92(10), pp. 1879-1886.

Jackson, S.T. & Sax, D.F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, 25(3), pp. 153-160.

Johansson, T., Andersson, J., Hjältén, J., Dynesius, M. & Ecke, F. (2011). Short-term responses of beetle assemblages to wildfire in a region with more than 100 years of fire suppression. *Insect Conservation and Diversity*, 4(2), pp. 142-151.

Johansson, T., Gibb, H., Hjältén, J., Pettersson, R.B., Hilszczański, J., Alinvi, O., Ball, J.P. & Danell, K. (2007). The effects of substrate manipulations and forest management on predators of saproxylic beetles. *Forest Ecology and Management*, 242(2), pp. 518-529.

Johansson, T., Hjältén, J., de Jong, J. & von Stedingk, H. (2013). Environmental considerations from legislation and certification in managed forest stands: A review of their importance for biodiversity. *Forest Ecology and Management*, 303, pp. 98-112.

Johnson, D.H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology,* 61(1), pp. 65-71.

Joly, K., Chapin, F.S. & Klein, D.R. (2010). Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska. *Écoscience*, 17(3), pp. 321-333.

Keeley, J.E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire,* 18(1), pp. 116-126.

Koivula, M. & Vanha-Majamaa, I. (2020). Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. *Ecological Processes,* 9(1), p. 11.

Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P. & Similä, M. (2012). Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Diversity and Distributions,* 18(4), pp. 348-355.

Lafontaine, A., Drapeau, P., Fortin, D., Gauthier, S., Boulanger, Y. & St-Laurent, M.-H. (2019). Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. *Ecosphere,* 10(5), p. e02739.

Legendre, P., Galzin, R. & Harmelin-Vivien, M.L. (1997). Relating behavior to habitat: solutions to thefourth-corner problem. *Ecology,* 78(2), pp. 547-562.

Lord, R. & Kielland, K. (2015). Effects of variable fire severity on forage production and foraging behavior of moose in winter. *Alces: A Journal Devoted to the Biology and Management of Moose,* 51, pp. 23-34.

Månsson, J., Andrén, H., Pehrson, Å. & Bergström, R. (2007). Moose browsing and forage availability: a scale-dependent relationship? *Canadian Journal of Zoology,* 85(3), pp. 372-380.

Milligan, H.T. & Koricheva, J. (2013). Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *Journal of Animal Ecology*, 82(4), pp. 739-748.

Nelson, J.L., Zavaleta, E.S. & Chapin, F.S. (2008). Boreal Fire Effects on Subsistence Resources in Alaska and Adjacent Canada. *Ecosystems,* 11(1), pp. 156-171.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, R.P., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2019). Vegan: community ecology. R package version 2.5-5. https://CRAN.R-project.org/package=vegan.

Ola Engelmark (2013). *Skogsbranden i Muddus nationalpark år 2006 - ekologiska ffekter och naturvård.* (Rapportserie nr 12/2013): County Administrative Board of Norrbotten.

Östlund, L., Zackrisson, O. & Axelsson, A.-L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research,* 27(8), pp. 1198-1206.

Paillet, Y., Bergén, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L.U.C., Fuhr, M., Grandin, U.L.F., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastiá, M.T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K.A.I. & Virtanen, R. (2010). Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. *Conservation Biology,* 24(1), pp. 101-112.

Pechacek, P. & Kristin, A. (2004). Comparative diets of adult and young three-toed woodpeckers in a European alpine forest community. *The Journal of wildlife management,* 68(3), pp. 683-693.

Penttilä, R., Junninen, K., Punttila, P. & Siitonen, J. (2013). Effects of forest restoration by fire on polypores depend strongly on time since disturbance– a case study from Finland based on a 23-year monitoring period. *Forest Ecology and Management,* 310, pp. 508-516.

Pfeffer, S.E., Singh, N.J., Cromsigt, J.P.G.M., Kalén, C. & Widemo, F. (2021). Predictors of browsing damage on commercial forests – A study linking nationwide management data. *Forest Ecology and Management,* 479, p. 118597.

Pulliainen, E. & Tunkkari, P.S. (1987). Winter diet, habitat selection and fluctuation of a mountain hare Lepus timidus population in Finnish Forest Lapland. *Ecography,* 10(4), pp. 261-267.

Rauset, G.R., Mattisson, J., Andrén, H., Chapron, G. & Persson, J. (2013). When species’ ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia,* 172(3), pp. 701-711.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D. & Ripley, M.B. (2013). Package ‘mass’. *CRAN Repos. Httpcran R-Proj. OrgwebpackagesMASSMASS Pdf*.

RStudio & Team (2020). RStudio: Integrated Development Environment for R. RStudio, PBC,

Boston, MA URL http://www.rstudio.com/.

Ruokolainen, L. & Salo, K. (2006). The succession of boreal forest vegetation during ten years after slash-burning in Koli National Park, eastern Finland. *Annales Botanici Fennici,* 43(5), pp. 363-378.

Saint-Germain, M., Drapeau, P. & Buddle, C.M. (2008). Persistence of Pyrophilous Insects in Fire-Driven Boreal Forests: Population Dynamics in Burned and Unburned Habitats. *Diversity and Distributions,* 14(4), pp. 713-720.

Saint-Germain, M., Drapeau, P. & Hébert, C. (2004). Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. *Biological Conservation,* 118(5), pp. 583-592.

Schimmel, J. & Granstrom, A. (1996). Fire severity and vegetation response in the boreal Swedish forest. *Ecology,* 77(5), pp. 1436-1450.

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S. & Müller, J. (2017). An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology,* 98(6), pp. 1613-1622.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987). Large Herbivore Foraging and Ecological Hierarchies:

Landscape ecology can enhance traditional foraging theory. *BioScience,* 37(11), pp. 789-799.

Shi, G.R. (1993). Multivariate data analysis in palaeoecology and palaeogeography - a review. *Palaeogeography Palaeoclimatology Palaeoecology,* 105.

Southwood, T.R.E. (1977). Habitat, the Templet for Ecological Strategies? *Journal of Animal Ecology,* 46(2), pp. 337-365.

Stenbacka, F., Hjältén, J., Hilszczański, J. & Dynesius, M. (2010). Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications,* 20(8), pp. 2310-2321.

Stokland, J.N. (2001). The Coarse Woody Debris Profile: An Archive of Recent Forest History and an Important Biodiversity Indicator. *Ecological Bulletins*(49), pp. 71-83.

Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012). Biodiversity in Dead Wood. *Biodiversity in Dead Wood,* pp. 1-509.

Street, G.M., Rodgers, A.R. & Fryxell, J.M. (2015). Mid-day temperature variation influences seasonal habitat selection by moose. *The Journal of wildlife management,* 79(3), pp. 505-512.

Suominen, M., Junninen, K., Heikkala, O. & Kouki, J. (2015). Combined effects of retention forestry and prescribed burning on polypore fungi. *Journal of Applied Ecology,* 52(4), pp. 1001-1008.

Swedish Species Information Centre *Artfakta*. Available at: https://artfakta.se/. Accessed 2021-01-18 [2021-01-18].

Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012). Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity and Distributions,* 18(5), pp. 519-529.

Thioulouse, J., Dray, S., Dufour, A., Siberchicot, A., Jombart, T. & Pavoine, S. (2018). Relating Species Traits to Environment. In: *Multivariate Analysis of Ecological Data with ade4*. Springer, New York.

Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., de Jonge, M.M.J., Oksanen, J. & Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc. *Methods in Ecology and Evolution,* 11(3), pp. 442-447.

Tingley, M.W., Ruiz-Gutiérrez, V., Wilkerson, R.L., Howell, C.A. & Siegel, R.B. (2016). Pyrodiversity promotes avian diversity over the decade following forest fire. *Proceedings of the Royal Society B: Biological Sciences,* 283(1840), p. 20161703.

Toivanen, T. & Kotiaho, J.S. (2007). Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. *Biodiversity and Conservation,* 16(11), pp. 3193-3211.

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T. & Kuuluvainen, T. (2007). Rehabilitating boreal forest structure and species composition in

Finland through logging, dead wood creation and fire: The EVO experiment. *Forest Ecology and Management*, 250(1), pp. 77-88.

Wang, Y., Naumann, U., Wright, S.T. & Warton, D.I. (2012). mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, 3(3), pp. 471-474.

Warton, D.I., Wright, S.T. & Wang, Y. (2012). Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, 3(1), pp. 89-101.

White, E.P. (2004). Two-phase species–time relationships in North American land birds. *Ecology letters*, 7(4), pp. 329-336.

Wikars, L.-O. (1997). *Effects of forest fire and the ecology of fire-adapted insects*: Acta Universitatis Upsaliensis.

Wikars, L.-O., Sahlin, E. & Ranius, T. (2005). A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *The Canadian Entomologist*, 137(3), pp. 304-324.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95(7), pp. 2027-2027.

Ylisirniö, A.L., Penttilä, R., Berglund, H., Hallikainen, V., Isaeva, L., Kauhanen, H., Koivula, M. & Mikkola, K. (2012). Dead wood and polypore diversity in natural post-fire succession forests and managed stands – Lessons for biodiversity management in boreal forests. *Forest Ecology and Management*, 286(Supplement C), pp. 16-27.

Young, O.P. (2015). Predation on dung beetles (Coleoptera: Scarabaeidae): A literature review. *Transactions of the American Entomological Society*, 141(1), pp. 111-155.

Popular science summary

Forest fires have a natural role in our ecosystems and many animals and plants are dependent on fire in different ways. Today, we have reduced these environments by effectively fighting the fire, which has meant that many species, including insects and fungi, are threatened. By deliberately burning forests in a controlled manner, with so-called prescribed burns, we can reintroduce environments that are missing in the forest and thus benefit biodiversity. In this thesis, I have investigated how fire affects wood-living fungi and beetles, mammals, birds, and plants after a decade. But also specifically how moose use the forest. I studied three unusually large natural forest fires, three adjacent unburnt forests, and five prescribed burns in Norrbotten, Sweden. I have come to the conclusion that natural forest fires create distinct differences after more than ten years in both numbers of species as well as their distribution compared to the unburnt forest. The naturally burnt forest has a much larger amount of dead trees which is important for many insects and fungi. I also saw more moose browsing on the young trees in the naturally burnt forest, more dung pellets, and more forage that moose prefer to eat. Prescribed burning does not achieve these effects to the same degree as natural forest fires, probably because they have not burnt as intensively. For mammals and birds, I see that the unburnt forest is used to a greater degree than the naturally burnt areas which may be due to forest plantations contributing to similar environments. I have also come to the conclusion that the unburnt forests are important especially for rare wood-living fungi, and used to a high degree by reindeer and western capercaillie. All in all, natural forest fires create unique environments that positively affect biodiversity in the long term, but unburnt forest, especially older, more untouched forest, is also important.

Populärvetenskaplig sammanfattning

Skogsbränder har en naturlig roll i våra ekosystem och många djur och växter är beroende av brand på olika sätt. Idag har vi genom att effektivt bekämpa brand minskat dessa miljöer vilket har gjort att många djur, bland annat insekter och svampar, är hotade. Genom att medvetet bränna skog på ett kontrollerat sätt, med så kallade naturvårdsbränningar, kan vi återinföra miljöer som saknas i skogen och på så sätt gynna den biologiska mångfalden. I min avhandling har jag undersökt hur brand påverkar vedlevande svampar och skalbaggar, däggdjur, fåglar och växter. Men även specifikt älgens nyttjande av skogen. Jag studerade tre ovanligt stora naturliga skogsbränder, tre intilliggande obrända skogar och fem naturvårdsbränningar i Norrbotten, Sverige. Jag har kommit fram till att naturlig skogsbrand skapar tydliga skillnader efter mer än tio år i både vilka arter som finns där men även deras antal jämfört med hur det ser ut i den obrända skogen. Den naturligt brända skogen har mycket större mängd döda träd som är viktigt för många insekter och svampar. Jag såg också mer bete av älg på träden i den naturligt brända skogen, mer spillning och mer unga träd som älgen föredrar att äta. Naturvårdsbränning uppnår inte dessa effekter i lika stor grad som naturlig skogsbrand, troligen på grund av att de inte brunnit lika intensivt. För däggdjur och fåglar ser jag att den obrända skogen nyttjas till en högre grad än de naturliga skogsbränderna vilket kan bero på att skogsplanteringar bidrar med liknande miljöer som branden skapar. Jag har också kommit fram till att den obrända skogen är viktiga för bland annat ovanliga vedsvampar, ren och tjäder. Sammantaget skapar naturliga skogsbränder unika miljöer som positivt påverkar biologisk mångfald på lång sikt men att även obränd skog, speciellt äldre mer orörd skog, är viktig.

Acknowledgements

It feels somehow ironic and at the same time perfect that my time spent in Umeå, let's call it my academic age, is the same as the age of the burns I've studied in this thesis - twelve years. I never could have guessed the amount of inspiration and joy I found during these years, mainly through meeting so many wonderful people.

Firstly, I would like to thank my main supervisor Therese for allowing me to go through the experience of doing a PhD and for your guidance. Besides the many hours pondering research related things in your office we also have had time to create memories together in the field - hiking up the steep terrain and balancing over logs in Bodträskfors or sliding down ravines in Muddus with insect traps strapped to our backpacks or pulling our car over the Lainio river on that floating bridge. With us on this four-year journey have of course also been my two co-supervisors Märtha and Anders. My thesis and my academic progress would not have been where it is today without your valuable input. Thank you Märtha for introducing me to the fascinating aspects of everything moose and for enduring the 30+ degree heat and thirsty bumblebees in the field together with me. Anders, thank you for pushing my writing to be better, simpler, and to the point, and for reminding me to have fun with it.

I've always felt very welcome within our research group and at the department with the open door policy and tasty Friday fikas. I want to express my gratitude to the whole Restoration Group for these four years of interesting and developing discussions. Specifically, I want to mention Jörgen for your invaluable advice and for making me realise that my doubts in myself and my research were completely normal and okay. And Anne-Maarit for your positive vibes and someone I always could ask for advice.

I’ve made so many great friends during these years and even though the pandemic stopped us from meeting as much we still saw each other on spontaneous video-fikas and went for hikes. To my fellow PhD-students, and recently graduated Doctors, I’ve thoroughly enjoyed sharing this experience with all of you - Olli, Chris, Sabine, Anna, Nannet, Sabrina, Julia, Linda, Robert, Fernanda, Albin, Olle, Lukas & Paulina. I will miss you all!

I cannot end this without sending my biggest thanks and hugs to my family and friends who have believed in me, always. Lastly - To David, my wonderful partner, I don’t know if I would have been able to finish this thesis without your unwavering support and always cheering me on. I love you.

I

Fredriksson *et al. Ecological Processes* (2020) 9:44
https://doi.org/10.1186/s13717-020-00246-5

Ecological Processes

RESEARCH Open Access

Wildfire yields a distinct turnover of the beetle community in a semi-natural pine forest in northern Sweden

Emelie Fredriksson[1*], Roger Mugerwa Pettersson[1], Jörgen Naalisvaara[2] and Therese Löfroth[1]

Abstract

Background: Fires have been an important natural disturbance and pervasive evolutionary force in the boreal biome. Yet, fire suppression has made forest fires rare in the managed landscapes in Fennoscandia, causing significant habitat loss for saproxylic species such as polypores and insects. To better understand how the beetle community changes (species turnover) after a wildfire in a landscape with intense fire suppression, we monitored beetles with flight intercept traps the first 3 years as well as 12 years after a large wildfire in a national park in northern Sweden (a control/unburnt area was set up for the last year of sampling).

Results: Species composition changed significantly among all studied years with a continuous turnover of species following the wildfire. The indicator species analysis showed that year 1 post-fire was mostly associated with cambium consumers and also the pyrophilous species *Batrisodes hubenthali*. Year 2 was the most abundant and species-rich year, with *Tomicus piniperda* as the most important indicator species. The indicator species year 3 were mostly secondary successional species, fungivores, and predators and were characterized by lower species diversity. Year 12 had higher diversity compared with year 3 but lower species richness and abundance. A control area was established during year 12 post-fire, and our analyses showed that the control area and burned area differed in species composition suggesting that the beetle community needs longer than 12 years to recover even after a low-intensive ground fire.

Conclusion: The wildfire area hosted several red-listed and fire-dependent species suggesting that after a century of landscape-level fire suppression in a semi-natural area, the reintroduction of fire benefits rare and pyrophilous species and still impacts species composition after 12 years. This study implies that fire has long-lasting effects on high latitudes and that prescribed burning has the potential to benefit biodiversity over decades in these landscapes while also highlighting the value of considering the whole species community and not only monitoring abundance and richness to assess biodiversity after management actions.

Keywords: Assemblage, Boreal, Coleoptera, Species composition, Conservation, Disturbance, Diversity, Fire suppression, Insects, Protected area, Saproxylic

---

* Correspondence: emelie.fredriksson@slu.se
[1]Wildlife, Fish, and Environmental studies, Swedish University of Agricultural Sciences, Skogsmarksgränd 17, 901 83 Umeå, Sweden
Full list of author information is available at the end of the article

Background

Habitat loss and the subsequent loss of structures and processes are one of the main drivers of biodiversity decline globally (Sánchez-Bayo and Wyckhuys 2019; Grooten and Almond 2018; Angelstam et al. 2013). To reverse this trend, it is crucial to understand the natural processes that maintain biodiversity and how it is affected by current management (Felton et al. 2020; Svensson et al. 2019; Cardinale et al. 2012). In forested biomes, two structures of high importance for biodiversity are dead wood and large mature trees (Paillet et al. 2010; Humphrey et al. 2004; Grove 2002; Nilsson et al. 2002; Stokland 2001; Martikainen et al. 2000; McMinn and Crossley 1996). In Fennoscandia, four to five thousand species are dependent on dead wood and the amount of dead wood has decreased by 90–98% in the last 200 years (Siitonen 2001), with negative effects on many taxa (Penttilä et al. 2004; Grove 2002). With such a large reduction of habitat Siitonen (2001) estimate, a minimum 22–32% decline in saproxylic species in Fennoscandia. For example, a large number of beetle species are directly or indirectly linked with dead wood amount, quality, and/or diversity (Stokland et al. 2012; Grove 2002) and the volume and quality of dead wood vary in time and space depending on the disturbance regime (Bishop et al. 2009) and many species have thus developed adaptations to disturbances such as fire (Wikars 1997).

Before large-scale anthropogenic impact in the boreal forest, the most important stand-replacing disturbances were fire, wind, and insect outbreaks, and small-scale disturbances were common (Engelmark 1999; Esseen et al. 1992). Large areas of the boreal forest had long continuity and high amount of coarse woody debris (Esseen et al. 1992). During the last 100–150 years, there has been an intense use of the boreal forest in Fennoscandia for timber and pulp production, which has transformed the landscape from the natural old-growth forest with natural disturbance regimes towards managed conifer plantations (Östlund et al. 1997) and clear-cutting has to a large extent replaced fire as the main stand-replacing disturbance (Gauthier 2009; Bergeron et al. 2002). From the mid-20th century, the main method for timber harvest and regeneration is clear-cutting and soil scarification followed by conifer plantation. This method partly mimics a natural large-scale disturbance which creates open areas with increased sun exposure that favors some light-demanding species (Jonsell et al. 1998). However, since the trees are removed, the development of dead wood is prevented to a large extent, which removes essential elements for wood dependent species. To reduce the obvious negative effects of clear-felling on biodiversity several measures, including dead wood creation and green tree retention, have been implemented in Swedish forestry from the early 1990s (Anonomous 2015; Johansson et al. 2013; Gustafsson and Perhans 2010; Wikars et al. 2005). Prescribed burning is also demanded in the FSC-certification and performed on approximately 5% of the clear-cut area every year (Forest Stewardship Council Sweden 2010).

The interval between fire events has declined considerably due to modern fire suppression (Wallenius et al. 2007; Zackrisson 1977) with only 0.01% of the productive forest area burn every year in Sweden, compared to approximately 1% with a "natural" fire regime (Granström 2001). Fire suppression is having profound negative effects on numerous species in the boreal forest (Hekkala et al. 2014; Johansson et al. 2007; Toivanen and Kotiaho 2007; Vanha-Majamaa et al. 2007; Hyvärinen et al. 2006; Saint-Germain et al. 2004; Wikars 2001). In addition, the degradation that decreases the quality of the unburnt habitat in the surrounding landscape also contributes to the decline in pyrophilous species (Kouki et al. 2012; Saint-Germain et al. 2008). The remaining semi-natural areas can be central source habitats for biodiversity in the larger ecological landscape (Hansen and DeFries 2007) and also include natural disturbances or have the potential for conservation actions, such as prescribed burning. Prescribed burning can create a high-quality habitat with larger amounts of dead wood and at the same time maintaining elements specific to fire disturbance (Wallenius et al. 2007).

Natural processes such as disturbance and succession are drivers of temporal species turnover (Jackson and Sax 2010). Here we define the term *turnover* as the temporal changes in abundance and occurrences of both individual species and functional groups. There are several factors that drive turnover. Chesson and Huntly (1997) argued that biological differences between species make it possible for them to inhabit different ecological niches and by doing so utilize different successional stages, thus creating a temporal shift in species composition. Life history and strategies come with trade-offs that make some species more adapted to early successional stages, commonly species with long dispersal capabilities that can take advantage of the low competition and high resource availability after a disturbance event such as a fire, while other species (such as predators or secondary saproxylic species) either depend on the early successional species or have a different ecological strategy that is more favored in the later successional stages with higher competition and sparser resources. Turnover in this sense is driven by local extinction and colonization (White 2004). The functional groups provide a framework to follow these temporal changes after a disturbance event to develop our understanding of its importance to species distribution and occurrence.

The aim of this study is to assess the turnover in the beetle community composition after a unique wildfire event in a semi-natural boreal forest in the Muddus

National Park in northern Sweden. Fire generally impacts beetle composition favoring early successional species at the expense of climax species (Hekkala et al. 2014; Johansson et al. 2011), and the effects might last for decades (Heikkala et al. 2016). We predicted that the beetle composition would change among the years and that this turnover shifts from pyrophilous species and early successional species within functional groups such as cambivores, towards later successional species such as fungivores the following years after the wildfire. We also predicted that rare pyrophilous species and red-listed species would occur all the monitored post-fire years but with a declining trend in abundance and richness and that a difference in the beetle composition, richness, and abundance would still be prevalent 12 years after the fire (Koivula and Vanha-Majamaa 2020).

Materials and methods

Study area

The study area is located in northern Sweden, within the northern boreal zone (Ahti et al. 1968), where a wildfire created a 300 ha burnt area during the summer of 2006 (Engelmark 2013). The fire started the 12th of August as a result of a lightning strike. The ground conditions were very dry, and the fire was active during 6 days before it was put out. The year of the wildfire as well as the sampled years' average air temperature between May and September and the total precipitation varied within normal ranges; however, the first year after the wildfire had the most precipitation and the third year had the least amount (Table 1).

The area is dominated by an old-growth pine forest which mostly survived due to the fire's low intensity (Fig. 1) that did not directly kill the trees but reduced the depth of the humus layer (Engelmark 2013). The burnt area forms part of the Muddus (or Muttos) National Park (between 66° 45′ N, 20° 15′ E, and 65° 5′ N, 20° 15′ E), the largest continuous semi-natural forest area below the mountain range in Sweden. The Muddus National Park consists of forested land and mires in about equal parts. The northern parts are mostly covered with mires and Norway spruce (*Picea abies,* (L.) H. Karst) while the southern parts of the park (where the study area is located) are dominated by Scots pine (*Pinus sylvestris* L.) forest (Engelmark 2013). Birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth) occurs over the entire area.

Table 1 Temperature (average of daily temperature ± standard deviation) and total precipitation during the sampling months (including May to September) from a public measurement station in Jokkmokk, about 20 km from the study area (SMHI 2018)

Year	Mean temperature (°C)	Sum precipitation (mm)
2006	12.1 ± 5.3	272
2007	10.4 ± 5.3	425
2008	9.9 ± 4.9	300
2009	12.1 ± 4.3	186
2018	12.0 ± 5.1	257

The fire history in the Muddus is well recorded with the last dated fire before the wildfire in 2006 in 1946 (for more details see Niklasson and Granström (2000)). The area has likely been less impacted by fire suppression than the surrounding landscapes due to its arduous terrain and no roads within the park; however, the frequency of fires has decreased during the last century (Engelmark 1984). A larger extent of the recorded fires has been in the southern parts with a drier pine forest compared with the northern parts with a mosaic of mires (Engelmark 1984). Muddus was protected in 1942 and has been affected relatively little by human activities. The anthropogenic disturbances that have occurred are haymaking at the borders of the park's mires, extensive reindeer grazing, and selective cutting of large trees in the southern parts during the timber-floating period of the late 19th century.

Sampling design and insect collection

Insects were sampled from the burned area for three consecutive years after the fire (2007–2009) by the County Administration Board of Norrbotten. For each of the years, ten flight intercept traps (model Polish IBL2), in the form of a triangular semi-transparent plastic intercept of ~ 0.35 m^2, were placed out along a transect through the burnt area in permanent positions during all 3 years (Fig. 1). The distance between the traps ranged between 140 and 300 m, and the total length of the transect was 1.6 km on the burned area. Twelve years after the fire (2018), a new sampling was done where we also established a control area. We used the same locations for the traps in the burnt area during 2018 as the years 2007–2009. The control area was located adjacent to the burn to the west and had a transect of 1.9 km with ten traps placed 150–300 m apart (Fig. 1). The traps were suspended between two trees using ropes. The traps had a water removing the funnel and a collecting bottle of 600 ml that was filled to a third with propylene glycol mixed with water (50/50) and a small amount of detergent (for more details see Stenbacka et al. (2010)). The traps were in place from late May or the beginning of June until late August or early September with the total sampling time among the years not differing more than a couple of weeks. The differences in sampling start and end are considered to not be an issue since swarming times occur late in the season this far north (see detailed flying times for Scolytinae in Hedqvist (1965), Bakke (1968), and Lekander et al. (1977)). The beetles were counted and identified to species level by experts. *Acrotrichis spp.* was removed from

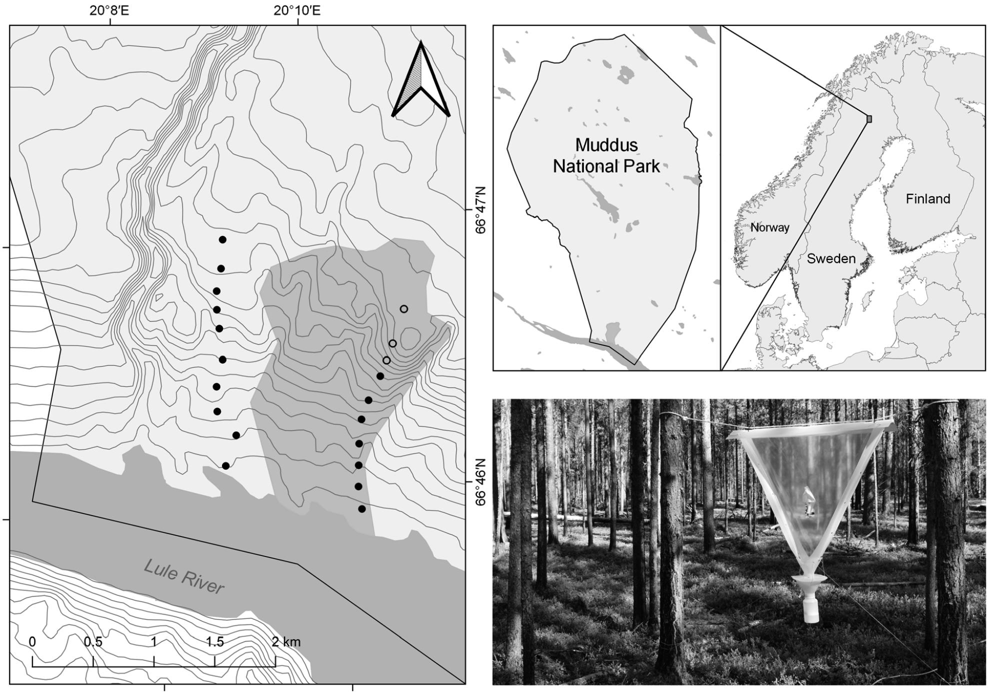


Fig. 1 The wildfire is represented by the orange area. Black circles denote the positions of the insect traps. The not filled circles denote the three traps that were treated with pheromones during 2007. The contour line interval is 25 m. The picture is taken in the burnt area of the Muddus National Park in June of 2018, i.e., 12 years after the wildfire. Charring on the lower parts of the pine trunks can be seen as well as the mostly intact canopy layer. The ground vegetation has recovered to a large extent from the impacts of the fire

the data set because they were not determined and counted all years. The beetles were divided into groups; saproxylic (facultative and obligatory) and non-saproxylic (Stokland et al. 2012; Speight 1989), functional groups based on nutritional preferences (established by Koch (1992); Koch (1989a); Koch (1989b), Lundberg, S pers. comm. and personal experience), red-list status (Westling 2015), and pyrophilous (fire-dependent and strongly fire favored by Wikars (2006), from here referred to as pyrophilous (class III + II)). Taxonomy and nomenclature of the beetles follow Dyntaxa (Liljeblad 2020). Note that some species are classified to more than one functional group and can, therefore, be part of more than one analysis.

Statistical analyses

We used trap-specific differences inside the burned site to compare species composition between the years. All the statistical analyses were performed using the statistical software R (R-Core-Team 2015). During year 1 post-fire, three of the traps had been treated with pheromones and were therefore excluded from all analyses. Differences in abundance and species richness among years were assessed using a negative binomial generalized linear mixed model (overdispersed count data), with the traps as a random factor (function “glmer.nb” in the “MASS” package by Ripley et al. (2013)) and among year comparisons with Tukey’s test (function “glht” in the “multicomp” package by Hothorn et al. (2008)). Diversity indices (Shannon and Simpson) were calculated using the “vegan” package, function “diversity,” and differences among years were tested with Kruskal-Wallis test followed by Wilcox test for pair-wise comparisons. Indicator species analysis was performed using with the function “multipatt” from the “indicspecies” package (De Cáceres and Legendre 2009). The analysis compares the relationship between species occurrence and/or abundance and sites, in this case, “sites” are the years since wildfire (plus control year 12), in total five different sites. As a measure of a species indicator value, the analysis uses an A-index and a B-index. A-index refers to “specificity”, i.e., to the relative exclusivity of the species to that year (1= only found that year), and the B-index refers to "fidelity," i.e. how often the species occurs in the samples within that year (1= found in all samples from that year). The indicator species index combines the A and B indices. To compare species composition among the years after the wildfire, we used two-dimensional non-metric multidimensional scaling (NMDS, function "metaMDS"), based on Bray-Curtis dissimilarities. To test for significant differences among the years, we used PERMANOVA (function "adonis" from the package "vegan" (Oksanen et al. 2015)). PERMANOVA has been shown to be a powerful analysis for analyzing changes in communities over time, especially for communities with large numbers of species (Irvine et al. 2011). To rule out the possibility that the significance from the PERMANOVA analysis stems from differences in dispersion among the samples rather than from an actual difference between years, we ran a permutation test which was non-significant for all groups except the cambivores (Table S1).

Results

In total, we caught 11156 individuals of 452 different species, of which 352 species were saproxylic. The most abundant functional group was fungivores with 5859 individuals from 157 different species (see full species list, Table S3).

Changes in species composition

We found significant changes in the beetle composition among all sampled years after the wildfire and also a difference between the unburnt control and burnt area year 12 (Fig. 2). The pattern is the same and also significant when comparing each nutritional group one by one and when repeating the analysis with only presence data (results not shown).

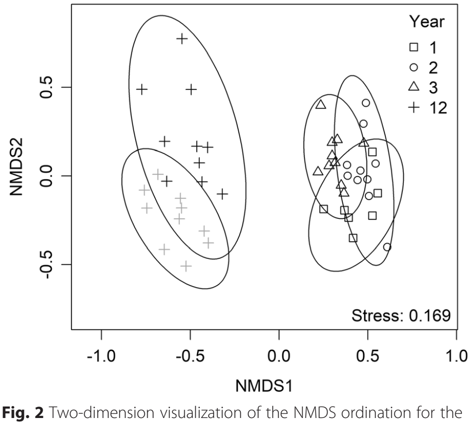


Fig. 2 Two-dimension visualization of the NMDS ordination for the beetle composition of all the species among the years. Each symbol represents the species composition in one trap. The square symbol denotes year 1 post-fire, circle year 2, triangle year 3, and the additions sign year 12. Black points are burned areas while light gray is a non-burnt control. The polygon was drawn based on the standard deviation within each year

Indicator species analysis (see Table S2) showed that year 1 after the fire had 23 significant indicator species, 40 species year 2, 14 species year 3, 10 species year 12, and 9 species at the control area year 12. The indicator species of year 1 was a mix of cambivores, fungivores, and predators while the later years were dominated by fungivores and predators. When excluding the singletons and doubletons, the general proportions of unique species among the years did not change. All indicator species were of red-list category "least concern" (LC), except for *Ips acuminatus* (Gyllenhal, 1827) that is classified as "near threatened" (NT) and *Batrisodes hubenthali* (Reitter, 1913) that is considered "vulnerable" (VU) which were indicators during year 1 while *Enicmus planipennis* (Strand, 1940) (NT) was found year 3. Two pyrophilous species were significant indicators for year 1, *Hylobius abietis* (Linnaeus, 1758) and *Henoticus serratus* (Gyllenhal, 1808). Year 3 had one indicator species that was pyrophilous, *Cryptophagus corticinus* (Thomson, 1863). The majority of the indicator species were saproxylic (80 of 96 species).

Species diversity, abundance, and richness

The overall species diversity index shows a decreased diversity year 3 (Shannon *P* value: 0.0052, Simpson *P* value: 0.0259 between years 2 and 3) and showed a statistically significant increase year 12 when looking at Simpson but not Shannon index (Fig. 3). There was no difference in diversity between the burned and the control area year 12.

Saproxylic beetles constituted the majority of the individuals and species caught and they, as well as most of the other functional groups, display a peak in abundance and species richness years 2 or 3 post-fire (Fig. 4). Pyrophilous species and red-listed abundance indicate a slight decreasing trend from year 1 towards year 12. The abundance and species richness are similar in the burned area and the control year 12 for all functional groups.

Red-listed and pyrophilous species

The total number of red-listed species caught was 33 (18 species year 1, 14 species year 2, 13 species year 3, 8 species year 12, and 4 in the control area year 12 after the fire). The total number of pyrophilous species caught among all years was 18 (12 species year 1, 9 species year 2, 10 species year 3, 7 species year 12, and 4 species year 12 in the control area). The majority of these species were only caught once or twice per year and all were saproxylic. A summary of species that are both red-listed and at least fire favored (I) can be found in Table 2. None of these species were caught all the years after the

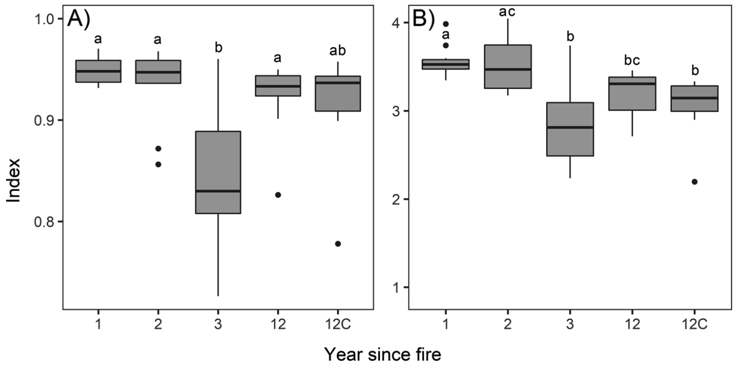


Fig. 3 Diversity index comparing the years since the wildfire of all species (**a** Simpson index, **b** Shannon index). Letters indicate significant differences (*P* value < 0.05, Kruskal-Wallis test and a pairwise Mann-Whitney *U* test, *P* values adjusted). Note the different scales in the plots and the C on the *x*-axis referring to the control area year 12

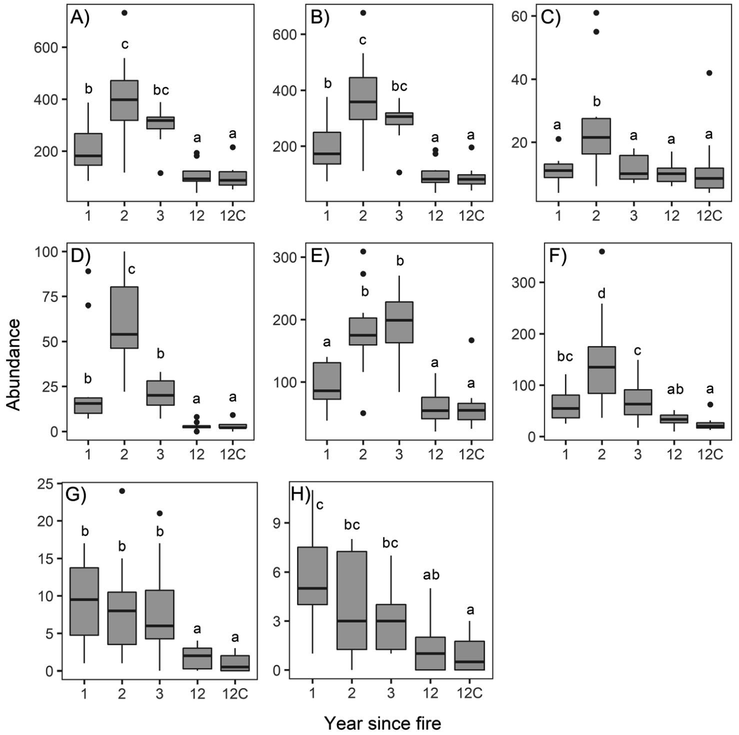


Fig. 4 Boxplot of the abundance of caught beetles' in different functional groups after the wildfire (**a** all individuals, **b** saproxylic, **c** non-saproxylic, **d** cambivore, **e** fungivore, **f** predator, **g** pyrophilous, **h** red-listed). Letters indicate significant differences (*P* value < 0.05, negative binomial GLMM and Tukey's test). Note the different scales in the plots and the C on the *x*-axis referring to the control area year 12

Table 2 Species that are either I = fire favored, II = strongly fire favored, and III = fire-dependent and also has a red-list category of at least NT are presented in the table (NT: near threatened, VU: vulnerable, EN: endangered). The different nutritional preferences of the species are represented with C for cambivore, W for wood-boring, F for fungivore, P for predator, D for detrivore and '?' before the letter indicating the functional group expresses uncertainty in that classification

				Year since fire				
Species	Nutrition	Fire category	Red-list category	1	2	3	12	12C
Acmaeops marginatus	C,D	II	EN	0	0	1	1	0
Acmaeops septentrionis	C,W	II	NT	0	0	2	1	1
Atomaria affinis	?F,?D,P	I	NT	0	0	0	4	5
Batrisodes hubenthali	?P	I	VU	11	1	0	3	2
Carphoborus cholodkovskyi	C	I	NT	3	0	0	0	0
Corticaria polypori	F	I	NT	0	5	3	0	0
Denticollis borealis	P,W	II	NT	2	0	0	0	0
Hadrobregmus confusus	W	I	NT	2	1	0	0	0
Ips acuminatus	C,F	I	NT	13	0	0	0	0
Laemophloeus muticus	F,W,P	III	VU	3	5	2	0	0
Melandrya dubia	?F	I	VU	2	0	0	0	0
Olisthaerus megacephalus	?P	I	NT	2	0	0	0	0
Olisthaerus substriatus	P	I	NT	0	0	1	0	0
Stagetus borealis	F,W	I	NT	0	0	0	1	0
Zilora ferruginea	F	I	NT	1	0	0	0	0
Total abundance				**33**	**12**	**9**	**10**	**7**

fire. The endangered and strongly fire favored species *Acmaeops marginatus* (Fabricius, 1781) was caught year 3 and year 12 post-fire.

The species richness and the abundance decrease with time for both pyrophilous and red-listed beetles but are only significant when comparing year 1 and year 12 (both fire and control, Figs. 4 and 5). Pyrophilous total abundance was highest during the year 1 (year 1 = 95 individuals, year 2 = 87 individuals, year 3 = 81 individuals, year 12 = 18 individuals, control year 12 = 10 individuals). The number of red-listed individuals had the same declining trend following the abundance of year 1 (year 1 = 55 individuals, year 2 = 38 individuals, year 3 = 32 individuals, year 12 = 13 individuals, control year 12 = 9 individuals).

Discussion

Community composition

We found support for our prediction that there was a turnover in beetle community composition after the wildfire (Fig. 1). This change is reflected in differences in species richness, the abundance of the functional groups and continuously shifting species composition. Since the turnover among the years still exists when looking at only presence/absence data, we can be more certain in our conclusion that an actual turnover of species has taken place and that it is not an artifact of very abundant or rare species. We show that the composition after 12 years differs from an unburned control area suggesting that fire has decadal effects on beetle composition at high latitudes. The study area is the largest semi-natural forest below the mountain range in Sweden in a landscape shaped by fire suppression and heavily managed forests, making this uncommonly large wildfire event important to further our understanding of the long-term effects on the beetle community composition. Note that this is a case study with only one area, which means that the non-difference we found in diversity between the control and burned areas year 12 is on the stand scale, however not excluding that fire most likely causes long-term positive effects on landscape-level species diversity. Most studies detecting effects on pyrophilous insects include at most two sampling years after fire (Johansson et al. 2011; Hyvärinen et al. 2006; Wikars 2002) but see Hekkala et al. (2014) and Heikkala et al. (2016) that also suggest decadal effects. Similar to a study by Saint-Germain et al. (2004) that looked at beetle composition 2 years following a large-scale black spruce (*Picea mariana* (Mill.) Britton, Sterns, & Poggen b.) forest fire in North America, our results show that time since fire (year) significantly affects the species composition. Not only wildfire but also restoration fire has been shown to promote changes in beetle composition (Hjältén et al. 2017; Hekkala et al. 2014; Boucher et al. 2012; Hyvärinen et al. 2005). One study showed an increased abundance of red-listed and rare saproxylic beetles following burning (Hyvärinen et al. 2005) while Hjältén et al. (2017) showed

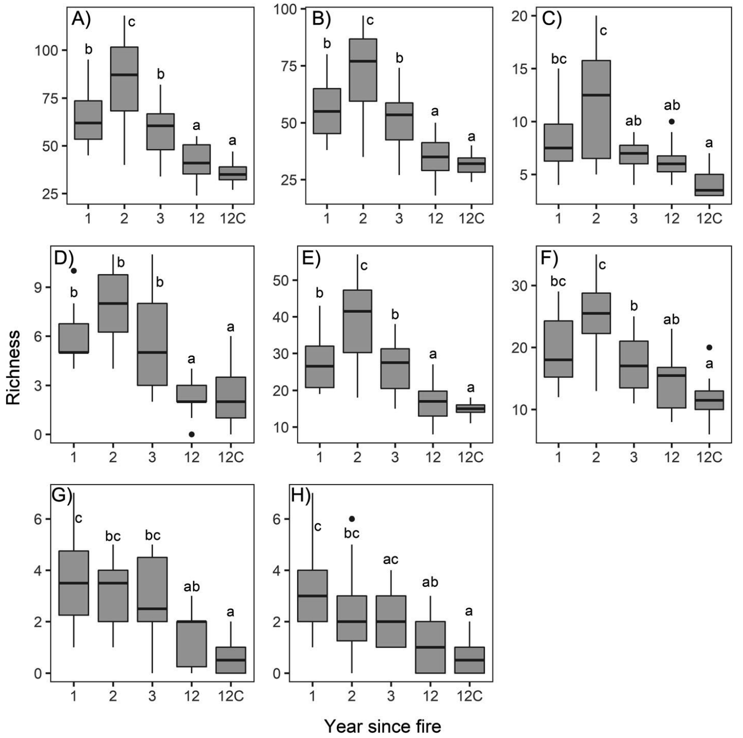


Fig. 5 Boxplot of the species richness of caught beetles' in different functional groups after the wildfire (**a** all individuals, **b** saproxylic, **c** non-saproxylic, **d** cambivore, **e** fungivore, **f** predator, **g** pyrophilous, h red-listed). Letters indicate significant differences (*P* value < 0.05, negative binomial GLMM and Tukey's test). Note the different scales in the plots and the C on the *x*-axis referring to the control area year 12

significant increases in abundance and species richness of beetles the same year of restoration burning. Another study on restoration burning saw a decline of beetles after 5 years following the initial increase after the fire and points out the importance of reoccurrence of fire at the landscape level (Hekkala et al. 2014).

Functional groups

In accordance with our predictions, our results show that the different functional groups of beetles (i.e., different niche preferences) are affected by the changing conditions after the fire and exhibit a turnover among the years from more early successional species towards late-successional groups and more generalist species. The cambivores decline after an initial boost in abundance and species richness, while fungivores have an increase in abundance over the first 3 years but are less abundant again year 12 (Fig. 4). Much of the response year 1 can be attributed to abundant generalist species like *Tomicus piniperda* (Linnaeus, 1758) that are attracted by the dead and dying trees in a burned area (Byers 1992; Eidmann et al. 1990). The decrease in diversity during year 3 is likely due to the dominance of *Rhizophagus fenestralis* (Linnaeus, 1758), *Cryptophagus lapponicus* (Gyllenhal, 1827) and *Trypodendron laeve* (Eggers, 1939) constituting 42% of the catch and a likely result from the increase in available food and hatching during that year. Even though the fire was of low intensity and thus caused low tree mortality, there was still an initial and ongoing addition of new coarse woody debris over the years compared with the control area with lesser amounts of dead wood and with different quality (Vahlström 2019). Most of the functional groups presented an increase in species richness and abundance between year 1 and the year 2 after the fire. Several cambivore species that occurred in large abundances were indicators for the year 2 (such as *T. piniperda, Hylastes brunneus* (Erichson, 1836) and *Hylurgops palliates* (Gyllenhal, 1813)). The low-intensity fire that occurred relatively late in the summer likely delayed the trees from dying and attracted the cambium consumers during year 2 instead of year 1 since they are drawn to fresh dead wood before the cambium is consumed or dries up. However, some species such as *T. piniperda* colonize the wood during year 1 and hatch during year 2, so the large catch year 2 could also be individuals that hatched in spring that year. The cambivores leave as soon as the cambium is consumed which is usually within a few years, this would explain the significantly lower abundance and species richness year 3 and year 12 (Figs. 4 and 5). During year 3 secondary successional species such as predators, fungivores, or saproxylic species that use other parts of the wood than the cambium or the tracks left in the bark by other beetles, followed the primary successional species. These included for example the fungivores *C. lapponicus* and *Atomaria bella* (Reitter, 1875). We saw a general trend of low or lowest species richness and abundance for among all functional groups year 12 (Figs. 4 and 5). In the burnt area year 12, there was still a few indicator species favored by fire (I), like the predator *Lygistopterus sanguineus* (Linnaeus, 1758), but not pyrophilous in the way we define it in this paper, while none of the indicator species in the control area had been fire favored. We found no statistical difference in beetle richness and abundance between control and burned area year 12, which point to the conclusion that the effects from the fire disturbance have ceased.

Pyrophilious and red-listed species

We expected the study area in the Muddus National Park to host a range of rare and pyrophilous species due to its northern geographical location, semi-natural character, and the presence of natural processes like wildfire during centuries. One example being *Quedius lundbergi* (Palm, 1973) that is classified as near threatened (NT) and is not known outside of northern Sweden and Finland. *Q. lundbergi* was caught year 1 and year 3 in this study. Little is known about the ecology of the species, but it is most likely a predator and negatively impacted by clear-cutting since it has only been found in forest retaining old-growth structures (Ljungberg 2005). A more abundant species that also has its distribution in the northern boreal forest is *C. lapponicus*, found in this study a total of 935 individuals all 3 years after the fire (most abundant year 3 with 820 individuals). *C. lapponicus* is classified as of least concern (LC) in Sweden and functionally a fungivore. This species and many other classified as fire favored (I) are often positively linked to large amounts of dead wood created by fire disturbance (among other structures such as sun exposure and reduced competition) (Wikars 2006). A new species for Sweden, *Euplectus lapponicus*, was described in 2010 (Löbl and Mattila 2010), which was after the identification of the specimen from the first 3 years in this study was completed. Most likely some of the individuals identified here during the first three sampled years as *Euplectus punctatus* (Mulsant, 1861) is, in fact, *E. lapponicus*. In a survey by the County Administrative Board of Norrbotten during 2015, *E. lapponicus*, was reported found for the second time globally in an area only about 150 km from the study area (Högdahl et al. 2017). Not much is known about this new species, but the genus is associated with wood (saproxylic) and many are linked to ants. Dead wood amount as well as diversity in successional stages of the wood are important for red-listed invertebrates (Jonsell et al. 1998), and the long continuity of structures and processes found in the study area are very rare in the managed forest landscape in northern Sweden. Muddus is part of a large, natural, and unfragmented area and therefore potentially providing room for natural disturbances and succession to take place, and in combination with its geographic location, it is most interesting with its possibilities for unique northern species. Some studies have observed initial increases of red-listed and rare species after a fire (Kouki et al. 2012; Hyvärinen et al. 2006; Hyvärinen et al. 2005), but the effects of burning on a longer time scale are not well known; however, see Hekkala et al. (2014) who reported a decline in abundance 5 years post-fire while species compositions still were different from unburnt stands. In this study, we only found a statistical difference between year 1 and the control area year 12 for red-listed or pyrophilous species which could be due to the small sample size. However, the fact that we caught 28 different red-listed species during the first 3 years after fire including the fire-dependent *A. marginatus* that has only been recorded in northern Sweden a few times during the last decades, suggests that these species have persisted in the landscape and that they take advantage of the new habitat created by the wildfire, some even 12 years post-fire. The study area is located near the mountain region in Sweden that has large unmanaged areas with high-quality habitat that could be a potential source pool of rare species, as exemplified by the fire in Torneträsk-Soppero mountainous old-growth forest where several pyrophilous species were found after a fire in 2014 (Högdahl et al. 2017). Also fire events in managed landscapes can have positive impacts on strongly fire-favored species, but here, many species were less abundant than could be expected considering the high productivity of the site (Johansson et al. 2011). Thus, this study supports the view that a semi-natural forest can be an important source pool for species adapted to natural disturbances in boreal forest.

Conclusions

This study shows that there is a distinct turnover of species after a wildfire in a protected semi-natural area in northern Sweden. Turnover is fast the first 3 years after fire, but even 12 years after the disturbance, the beetle species composition on the burned area is different from an unburned control area. Since the data collected for this study comes from a single area affected by a wildfire, the conclusions drawn here are at the stand-level; however, our results are in line with previously cited studies that show positive effects on biodiversity of beetles at a landscape level. The slow recovery of the beetle assemblages after a fire and the occurrence of several rare and threatened species imply that burning can be an efficient method with long-lasting effects for biodiversity at high latitudes. This study also points to the importance of long-term monitoring of beetle community composition after disturbance rather than only abundance or richness if one is to efficiently adapt and allocate prescribed burning and similar disturbance mimicking management actions. To generate proper management guidelines, more research is needed in both wildfire areas and prescribed burnings in both managed and natural landscapes.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s13717-020-00246-5.

Additional file 1 Table S1: Output values from the compositional analysis (PERMANOVA) and permutation test (betadisper) when comparing the different functional groups' changes among the years after the wildfire. Note the "*" following the significant value from the permutation test for cambivores. **Table S2**: Significant species among the years reported in order of highest Index-value from the species indicator analysis. Functional group (FG, C – cambivore, D - detrivore, F – fungivore, P – predator, W – wood-boring) and fire category (I = fire favored, II = strongly fire favored, III = fire-dependent) of the significant species with an indicator index of at least 0.6. Red list status indicated in brackets after the Latin name of the species. Star (*) indicate species that, in contrast to the other species, are non-saproxylic. Question mark (?) indicates uncertainty for that species association to the nutritional group. **Table S3**. Complete species list. Abundance per year and total. Functional groups: Saproxylic (SxO = obligate saproxylic, SxF = facultative saproxylic, NS = non-saproxylic), Red-list status (LC = least concern, NT = near threatened, VU = endangered, DD/NA/NE = data deficiency/not evaluated), Fire category (I = fire favoured, II = strongly fire favoured, III = fire dependent), Nutrition = (C = cambium consumer, F = fungivore, W = wood-boring, P = predator, D = detrivore, H = herbivore, '?' = insufficient knowledge)

Abbreviations

LC: Least concern; NT: Near threatened; VU: Vulnerable; EN: Endangered; I: Fire favored; II: Strongly fire favored; III: Fire-dependent; C: Cambivore; W: Wood-boring; F: Fungivore; P: Predator; D: Detrivore; SxO: Saproxylic; NS: Non-saproxylic

Acknowledgements

We would like to thank Stig Lundberg for the identification of the beetles in the first 3 years after the fire. Also, many thanks to Anne-Maarit Hekkala for the comments and discussions about the paper; students Dagmar Bogers, Isak Vahlström, and David Kymmell who helped in the field; and lastly, Sven Lennartsson who did the species identification for year 12.

Authors' contributions

RP and JN designed the original study setup and collected the data 2007, 2008, and 2009. EF and TL set up the control area and collected the data 2018. EF performed all the statistical analyses and was the major contributor in writing the manuscript. The authors read and approved the final manuscript.

Funding

County Administrative Board of Norrbotten funded the data collection. This paper is part of a PhD-project funded by "Stiftelsen Oscar och Lili Lamms Minne" and Skogssällskapet (Grants to TL). Open access funding provided by Swedish University of Agricultural Sciences.

Availability of data and materials

All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1]Wildlife, Fish, and Environmental studies, Swedish University of Agricultural Sciences, Skogsmarksgränd 17, 901 83 Umeå, Sweden. [2]County Administrative Board of Norrbotten, Stationsgatan 5, 972 38 Luleå, Sweden.

Received: 28 February 2020 Accepted: 19 July 2020

References

Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn 5(3):169–211

Angelstam P, Roberge J-M, Axelsson R, Elbakidze M, Bergman K-O, Dahlberg A, Degerman E, Eggers S, Esseen P-A, Hjältén J, Johansson T, Müller J, Paltto H, Snäll T, Soloviy I, Törnblom J (2013) Evidence-based knowledge versus negotiated indicators for assessment of ecological sustainability: the Swedish Forest Stewardship Council standard as a case study. Ambio 42(2):229–240

Anonomous (2015). Forests and Forestry in Sweden. The Royal Swedish Academy of Agriculture and Forestry.

Bakke A (1968) Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. Meddelelser fra det Norske Skogsforsoksvesen 21(6):441–602

Bergeron Y, Leduc A, Harvey B, Gauthier S (2002) Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36(1):81–95

Bishop DJ, Majka CG, Bondrup-Nielsen S, Peck SB (2009) Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. ZooKeys 22:309–340

Boucher J, Azeria ET, Ibarzabal J, Hébert C (2012) Saproxylic beetles in disturbed boreal forests: temporal dynamics, habitat associations, and community structure. Écoscience 19(4):328–343

Byers JA (1992) Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. J Chem Ecol 18(12):2385–2402

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am Nat 150(5):519–553

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90(12):3566–3574

Eidmann HH, Klingström A, Axelsson R (1990) Skadegörare i skogen (in Swedish). LTs förlag, Stockholm, Sweden

Engelmark O (1984) Forest fires in the Muddus National Park (northern Sweden) during the past 600 years. Can J Bot 62(5):893–898

Engelmark O (1999) Boreal forest disturbances. Ecosystems of the world, pp. 161–186

Engelmark O (2013) Skogsbranden i Muddus nationalpark år 2006 - ekologiska effekter och naturvård

Esseen P-A, Ehnström B, Ericson L, Sjöberg K (1992) Boreal forests—the focal habitats of Fennoscandia. In: Ecological principles of nature conservation, pp 252–325

Felton A, Löfroth T, Angelstam P, Gustafsson L, Hjältén J, Felton AM, Simonsson P, Dahlberg A, Lindbladh M, Svensson J, Nilsson U, Lodin I, Hedwall PO, Sténs A, Lämås T, Brunet J, Kalén C, Kriström B, Gemmel P, Ranius T (2020) Keeping pace with forestry: multi-scale conservation in a changing production forest matrix. Ambio 49(5):1050–1064

Forest Stewardship Council Sweden (2010) Swedish FSC standard for forest certification including SLIMF indicators. Uppsala, Sweden

Gauthier S (2009) Ecosystem management in the boreal forest: PUQ

Granström A (2001) Fire management for biodiversity in the European boreal Forest. Scand J For Res 16(sup3):62–69

Grooten M, Almond REA (2018) Living planet report 2018: aiming higher

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33(1):1–23

Gustafsson L, Perhans K (2010) Biodiversity conservation in swedish forests: ways forward for a 30-year-old multi-scaled approach. Ambio 39(8):546–554

Hansen AJ, DeFries R (2007) Ecological mechanisms linking protected areas to surrounding lands. Ecol Appl 17(4):974–988

Hedqvist K-J (1965) Studier över för virkesvårdens viktiga barkborrar längs Umeälv (in Swedish). Department of forest products, Stockholm, Sweden

Heikkala O, Martikainen P, Kouki J (2016) Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biol Conserv 194:39–47

Hekkala A-M, Päätalo M-L, Tarvainen O, Tolvanen A (2014) Restoration of young forests in eastern Finland: benefits for saproxylic beetles (Coleoptera). Restor Ecol 22(2):151–159

Hjältén J, Hägglund R, Löfroth T, Roberge JM, Dynesius M, Olsson J (2017) Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. Biodivers Conserv 26(7):1623–1640

Högdahl A, Wikars L-O, Hellqvist S, Ramqvist T, Hedgren O, Sandström J (2017) Brandeffekter och insekter efter naturlig skogsbrand i TorneträskSoppero fjällurskog 2014

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50(3):346–363

Humphrey JW, Sippola AL, Lempérière G, Dodelin B, Alexander KNA, Butler JE (2004) Deadwood as an indicator of biodiversity in European forests: From theory to operational guidance. EFI Proceedings, Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality. European Forest Institute

Hyvärinen E, Kouki J, Martikainen P, Lappalainen H (2005) Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. For Ecol Manag 212(1):315–332

Hyvärinen E, Kouki J, Martikainen P (2006) Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. Conserv Biol 20(6):1710–1719

Irvine KM, Dinger EC, Sarr D (2011) A power analysis for multivariate tests of temporal trend in species composition. Ecology 92(10):1879–1886

Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends Ecol Evol 25(3):153–160

Johansson T, Gibb H, Hjältén J, Pettersson RB, Hilszczański J, Alinvi O, Ball JP, Danell K (2007) The effects of substrate manipulations and forest management on predators of saproxylic beetles. For Ecol Manag 242(2):518–529

Johansson T, Andersson J, Hjältén J, Dynesius M, Ecke F (2011) Short-term responses of beetle assemblages to wildfire in a region with more than 100 years of fire suppression. Insect Conserv Divers 4(2):142–151

Johansson T, Hjältén J, de Jong J, von Stedingk H (2013) Environmental considerations from legislation and certification in managed forest stands: a review of their importance for biodiversity. For Ecol Manag 303:98–112

Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers Conserv 7(6):749–764

Koch K (1989a) Die Käfer Mitteleuropas. Ökologie, Band 1. Goecke & Evers, Krefeld

Koch K (1989b) Die Käfer Mitteleuropas. Ökologie, Band 2. Goecke & Evers, Krefeld

Koch K (1992) Die Käfer Mitteleuropas. Ökologie, Band 3. Goecke & Evers, Krefeld

Koivula M, Vanha-Majamaa I (2020) Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. Ecol Process 9:11

Kouki J, Hyvärinen E, Lappalainen H, Martikainen P, Similä M (2012) Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. Divers Distrib 18(4):348–355

Lekander B, Bejer-Petersen B, Kangas E, Bakke A (1977) The distribution of bark beetles in the Nordic countries. Acta Entomologica Fennica 32:1–36

Liljeblad J (2020). Dyntaxa. Svensk taxonomisk databas. Version 1.2. SLU Artdatabanken. Checklist dataset https://doi.org/10.15468/j43wfc accessed via GBIF.org on 2020–08-02.

Ljungberg H (2005) Artfakta: *Quedius lundbergi*. Swedish University of Agricultural Sciences, Artdatabanken

Löbl I, Mattila J (2010) *Euplectus lapponicus* (Coleoptera: Staphylinidae: Pselaphinae), a new species from boreal Finnland. Entomologica Fennica 21: 181–186

Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol Conserv 94(2):199–209

McMinn JW, Crossley DA (1996) Biodiversity and coarse woody debris in southern forests: DIANE Publishing

Niklasson M, Granström A (2000) Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology 81(6): 1484–1499

Nilsson S, Niklasson M, Hedin J, Aronsson G, Gutowski J, Linder P, Ljungberg H, Mikusiński G, Ranius T (2002) Densities of large living and dead trees in old-growth temperate and boreal forests. For Ecol Manag 161:189–204

Oksanen J, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens M, Wagner H (2015) Vegan: community ecology. R package version 2:2–1

Östlund L, Zackrisson O, Axelsson A-L (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Can J For Res 27(8):1198–1206

Paillet Y, Bergén L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma R-J, De Bruyn LUC, Fuhr M, Grandin ULF, Kanka R, Lundin L, Luque S, Magura T, Matesanz S, Mészáros I, Sebastiá MT, Schmidt W, Standovár T, Tóthmérész B, Uotila A, Valladares F, Vellak KAI, Virtanen R (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol 24(1):101–112

Penttilä R, Siitonen J, Kuusinen M (2004) Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biol Conserv 117(3): 271–283

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, Ripley MB (2013) Package 'mass'. CRAN Repos. Httpcran R-Proj. OrgwebpackagesMASSMASS Pdf

Saint-Germain M, Drapeau P, Hébert C (2004) Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. Biol Conserv 118(5):583–592

Saint-Germain M, Drapeau P, Buddle CM (2008) Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats. Divers Distrib 14(4):713–720

Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: a review of its drivers. Biol Conserv 232:8–27

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49:11–41

SMHI. Available at: https://www.smhi.se/klimatdata/meteorologi/ladda-ner-meteorologiska-observationer/#param=airtemperatureInstant,stations=all [2018-12-14].

Speight MC (1989) Saproxylic invertebrates and their conservation. Council of Europe

Stenbacka F, Hjältén J, Hilszczański J, Dynesius M (2010) Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. Ecol Appl 20(8):2310–2321

Stokland JN (2001) The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol Bull 49:71–83

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in Dead Wood. (Ecology, Biodiversity and Conservation). Cambridge: Cambridge University Press. Available from: https://www.cambridge.org/core/books/biodiversity-in-dead-wood/32EA8DA79A503B95795384FFA5BC993D

Svensson J, Andersson J, Sandström P, Mikusiński G, Jonsson BG (2019) Landscape trajectory of natural boreal forest loss as an impediment to green infrastructure. Conserv Biol 33(1):152–163

Toivanen T, Kotiaho JS (2007) Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. Biodivers Conserv 16(11):3193–3211
Vahlström I (2019) Community structure of polyporous fungi after wildfire in boreal forest. Diss. Umeå: Swedich University of Agricultural Sciences
Vanha-Majamaa I, Lilja S, Ryömä R, Kotiaho JS, Laaka-Lindberg S, Lindberg H, Puttonen P, Tamminen P, Toivanen T, Kuuluvainen T (2007) Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. For Ecol Manag 250(1):77–88
Wallenius TH, Lilja S, Kuuluvainen T (2007) Fire history and tree species composition in managed *Picea abies* stands in southern Finland: implications for restoration. For Ecol Manag 250(1):89–95
Westling A (2015) Rödlistade arter i Sverige 2015. ArtDatabanken, SLU, Uppsala
White EP (2004) Two-phase species–time relationships in north American land birds. Ecol Lett 7(4):329–336
Wikars L-O (1997) Effects of forest fire and the ecology of fire-adapted insects: Acta Universitatis Upsaliensis
Wikars L-O (2001) The wood-decaying fungus *Daldinia loculata* (Xylariaceae) as an indicator of fire-dependent insects. Ecol Bull 49:263–268
Wikars L-O (2002) Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. J Insect Conserv 6(1):1–12
Wikars L-O (2006) Åtgärdprogram för bevarande av brandinsekter i boreal skog (report number:5610): Swedish Environmental Protection Agency
Wikars L-O, Sahlin E, Ranius T (2005) A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. The Canadian Entomologist 137(3):304–324
Zackrisson O (1977) Influence of forest fires on the north Swedish boreal forest. Oikos 29(1):22–32

Publisher's Note

Supplementary material

Tables

Table S1: *Output values from the compositional analysis (PERMANOVA) and permutation test (betadisper) when comparing the different functional group's changes among the years after the wildfire. Note the "*" following the significant value from the permutation test for cambivores.*

Functional group	R^2	F-value	P-value
Total	0.4319	1.484	0.2229
Saproxylic	0.44077	1.3035	0.2831
Non-saproxylic	0.30394	1.9032	0.1264
Fungivore	0.48495	0.2186	0.9267
Predator	0.35879	2.182	0.08624
Cambivore	0.5125	8.6936	< 0.0001*
Herbivore	0.12045	0.331	0.8538

Table S2: *Significant species among the years reported in order of highest Index-value from the species indicator analysis. Functional group (FG, C – cambivore, D - detrivore, F – fungivore, P – predator, W – wood-boring) and fire category (I = fire favored, II = strongly fire favored, III = fire-dependent) of the significant species with an indicator index of at least 0.6. Red list status indicated in brackets after the Latin name of the species. Star (*) indicate species that, in contrast to the other species, are non-saproxylic. Question mark (?) indicates uncertainty for that species association to the nutritional group next to the question mark.*

Year	Species	Specificity	Fidelity	Index	P-value	FG	Fire category
1	*Hylobius abietis*	0.7647	0.8	0.782	0.001	C,W	II
	Ampedus tristis	0.5755	1	0.759	0.001	P,W	I
	Corticaria rubripes	0.5661	1	0.752	0.001	F	I
	Pityogenes bidentatus	0.6284	0.9	0.752	0.007	C	I
	Rhagium inquisitor	1	0.5	0.707	0.001	C,W	I
	Atomaria pulchra	0.5394	0.9	0.697	0.001	F	I
	Hadrobregmus pertinax	0.5357	0.9	0.694	0.002	W	I
	Cartodere constricta	0.8889	0.5	0.667	0.001	F	-
	*Notiophilus biguttatus**	0.7273	0.6	0.661	0.001	P	-
	Leptusa fumida	0.9661	0.4	0.622	0.009	?F	I
	Henoticus serratus	0.8333	0.4	0.577	0.023	F	II
	Batrisodes hubenthali (VU)	0.6471	0.5	0.569	0.014	?P	I
	Rhyncolus sculpturatus	0.4375	0.7	0.553	0.022	W	I
	Atheta lativentris	0.75	0.4	0.548	0.039	?F,?D,P	-
	Agathidium pisanum	1	0.3	0.548	0.025	F	I
	*Aphodius ater**	1	0.3	0.548	0.037	D	-
	*Cercyon borealis**	1	0.3	0.548	0.037	P	-
	Cis bidentatus	1	0.3	0.548	0.031	F	I
	Epuraea variegata	1	0.3	0.548	0.033	F	I

	Ips acuminatus (NT)	1	0.3	0.548	0.031	C,F	I
	Phloeopora corticalis	0.6	0.5	0.548	0.028	?P	I
	*Amischa analis**	0.7143	0.4	0.535	0.041	P	-
	Wanachia triguttata	0.625	0.4	0.5	0.046	F	-
2	*Tomicus piniperda*	0.9665	1	0.983	0.001	C	I
	Caenoscelis ferruginea	0.8043	0.9	0.851	0.001	F	I
	Rhizophagus fenestralis	0.71	1	0.843	0.001	P	-
	Glischrochilus quadripunctatus	0.6704	1	0.819	0.001	F,P	I
	Hylurgops palliatus	0.9545	0.7	0.817	0.001	C	-
	Epuraea marseuli	0.6623	1	0.814	0.001	D,F	I
	Hylastes brunneus	0.7105	0.9	0.8	0.001	C	I
	Epuraea terminalis	0.6579	0.8	0.725	0.001	F	-
	Triplax aenea	0.5833	0.9	0.725	0.001	F	I
	*Mycetoporus lepidus**	0.5714	0.9	0.717	0.002	P	-
	Scaphisoma assimile	1	0.5	0.707	0.002	F	-
	Bibloporus minutus	0.9545	0.5	0.691	0.002	P	I
	Haploglossa villosula	0.4643	1	0.681	0.001	?F	-
	Trypodendron signatum	0.509	0.9	0.677	0.006	F	I
	Phloeostiba plana	0.5357	0.8	0.655	0.005	?P	-
	Nudobius lentus	0.7	0.6	0.648	0.003	P	I
	Xylita laevigata	0.4128	1	0.642	0.001	F	I
	*Cercyon bifenestratus**	1	0.4	0.632	0.003	P	-
	Cryptophagus dorsalis	0.8	0.5	0.632	0.007	F	I
	*Cyphon variabilis**	1	0.4	0.632	0.009	D,P	-
	Gabrius expectatus	0.4961	0.8	0.63	0.016	P	I
	Trypodendron lineatum	0.4408	0.9	0.63	0.042	F	I
	Epuraea boreella	0.6364	0.6	0.618	0.009	F,P	I
	Epuraea biguttata	0.5417	0.7	0.616	0.007	F	I
	Ampedus balteatus	0.75	0.5	0.612	0.009	P,W	I
	Mycetophagus multipunctatus	0.7273	0.5	0.603	0.008	F	-
	Pityophagus ferrugineus	0.5789	0.6	0.589	0.007	P	I
	Enicmus rugosus	0.3463	1	0.588	0.004	F	I
	Anomognathus cuspidatus	0.3385	1	0.582	0.015	D,P	I
	Caenoscelis sibirica	0.5625	0.6	0.581	0.013	F	I
	Triplax scutellaris	0.4103	0.8	0.573	0.021	F	I
	Phloeostiba lapponica	0.4	0.8	0.566	0.034	P	-
	Corticaria longicollis	1	0.3	0.548	0.044	F	I
	Ptiliola kunzei	1	0.3	0.548	0.036	F	-
	Pytho depressus	1	0.3	0.548	0.033	C	I
	Sphaeriestes bimaculatus	1	0.3	0.548	0.028	P	I
	Phloeonomus sjobergi	0.4815	0.6	0.537	0.046	?P	-
	Rhizophagus bipustulatus	0.7143	0.4	0.535	0.045	P,F	I
	Corticaria orbicollis	0.561	0.5	0.53	0.034	F	I
3	*Cryptophagus lapponicus*	0.877	1	0.936	0.001	F	I
	Atomaria bella	0.7245	1	0.851	0.001	F	I
	Polygraphus punctifrons	1	0.6	0.775	0.001	C	I
	Trypodendron laeve	0.9389	0.5	0.685	0.011	F	-
	*Aphodius rufipes**	0.6923	0.6	0.645	0.004	D	-

	*Bisnius fimetarius**	1	0.4	0.632	0.007	?P	-
	Malthodes fuscus	0.8	0.5	0.632	0.01	P	-
	Cryptophagus tuberculosus	0.9412	0.4	0.614	0.005	F	-
	*Sericus brunneus**	0.4667	0.8	0.611	0.006	?	-
	Enicmus planipennis (NT)	0.7059	0.5	0.594	0.007	F	-
	Thanasimus formicarius	0.4333	0.7	0.551	0.041	P	I
	Atheta gagatina	1	0.3	0.548	0.024	?F,?D,P	-
	Cis comptus	0.4783	0.6	0.536	0.038	F	I
	Cryptophagus corticinus	0.9286	0.3	0.528	0.029	F	II
12	*Lygistopterus sanguineus**	1	0.6	0.775	0.001	?F,?D,P	I
	*Enicmus transversus**	0.7419	0.8	0.77	0.001	P	-
	Dacne bipustulata	0.5895	1	0.768	0.001	F	I
	Epuraea silacea	0.584	0.7	0.639	0.025	F	-
	*Planolinus fasciatus**	0.75	0.5	0.612	0.008	?F,?D,P	-
	Rhizophagus parvulus	0.5	0.7	0.592	0.009	P	I
	Euplectus nanus	0.8	0.4	0.566	0.021	P	I
	Agolinus lapponum	1	0.3	0.548	0.028	F	-
	Euplectus mutator	0.4872	0.6	0.541	0.028	P	-
	Triplax scutellaris	0.7273	0.4	0.539	0.03	F	-
12C	*Ampesus nigrinus*	0.64	0.9	0.759	0.001	P,W	-
	Microambe abietis	0.5014	1	0.708	0.001	F	-
	Absidia schoenherrii	0.7	0.7	0.7	0.002	F	-
	*Anthophagus omalinus**	0.5596	0.8	0.669	0.034	P	-
	*Eanus costalis**	0.4878	0.8	0.625	0.006	?	-
	Hylastes canaliculatus	0.875	0.4	0.592	0.014	C	-
	Anaspis arctica	1	0.3	0.548	0.044	P	-
	Ischnoglossa prolixa	1	0.3	0.548	0.026	D,W	-
	Mycetochara maura	0.625	0.4	0.5	0.046	?	-

Table S3. *Complete species list. Abundance per year and total. Functional groups: Saproxylic (SxO = obligate saproxylic, SxF = facultative saproxylic, NS = non-saproxylic), Red-list status (LC = least concern, NT = near threatened, VU = endangered, DD/NA/NE = data deficiency/not evaluated), Fire category (I = fire favoured, II = strongly fire favoured, III = fire dependent), Nutrition = (C = cambium consumer, F = fungivore, W = wood-boring, P = predator, D = detrivore, H = herbivore, '?' = insufficient knowledge)*

Species	Year 1	Year 2	Year 3	Year 12	Year 12C	Saproxylic	Red-List	Fire category	Nutrition
Abdera affinis	3	0	0	1	1	SxO	LC	I	F
Abdera triguttata	0	0	0	6	7	SxO		I	F
Absidia schoenherrii	0	0	0	6	14	SxO			F
Acmaeops marginatus	0	0	1	1	0	SxO	EN	II	C,D
Acmaeops pratensis	0	0	0	2	2	SxF	LC	II	P
Acmaeops septentrionis	0	0	2	1	1	SxO	NT	II	C,W
Acrossus rufipes	0	0	0	7	6	SxO			C,W
Acrotona fungi	7	5	5	0	0	NS	DD/NA/NE		?F,?D,P
Acrotrichis intermedia	0	0	0	1	5	NS	LC		F
Acrotrichis norvegica	0	0	0	0	1	NS	LC		F
Acrulia inflata	0	1	0	0	1	SxF	LC		?F

Adalia conglomerata	0	0	0	0	2	NS	LC		P
Agathidium badium	0	0	0	2	4	SxF	LC		F
Agathidium mandibulare	0	3	0	0	0	SxF	LC		F
Agathidium pallidum	0	0	1	0	0	SxF	NT		F
Agathidium pisanum	5	0	0	0	0	SxO	LC	I	F
Agathidium rotundatum	1	1	0	0	0	SxF	LC	I	F
Agathidium seminulum	3	9	4	0	0	SxF	LC		F
Agolinus lapponum	0	0	0	3	0	SxF			F
Agolinus nemoralis	0	0	0	1	2	SxF			F
Aleochara fumata	1	0	2	4	0	NS	LC		P
Aleochara moerens	2	0	3	0	0	NS	LC		P
Aleochara sparsa	3	0	0	0	0	SxF	LC		P
Aleochara stichai	0	0	0	2	0	SxF	LC		P
Amara alpina	0	0	0	1	0	NS	LC		H
Amara familiaris	0	1	0	0	0	NS	LC		H,P
Amara lunicollis	0	1	0	0	0	NS	LC	I	H,P
Amara nigricornis	1	3	0	0	0	NS	LC	II	H,P
Amara ovata	0	1	0	0	0	NS	LC		H
Amischa analis	5	2	0	0	0	NS	LC		P
Ampedus balteatus	1	9	1	0	1	SxO	LC	I	P,W
Ampedus karpathicus	1	0	0	0	0	SxO	VU		P,W
Ampedus nigrinus	0	4	4	0	0	SxO	LC	I	P,W
Ampedus tristis	61	16	16	8	5	SxO	LC	I	P,W
Ampesus nigrinus	0	0	0	9	16	SxO			P,W
Anaspis arctica	0	0	0	0	3	SxO	LC		P
Anaspis bohemica	0	1	0	0	0	SxO	LC		P
Anaspis marginicollis	1	3	0	0	0	SxO	LC		P
Anaspis rufilabris	1	1	1	4	5	SxO	LC		P
Anatis ocellata	0	0	0	1	0	NS	LC		P
Anisotoma axillaris	1	4	0	0	0	SxO	LC	I	F
Anisotoma castanea	2	0	0	0	0	SxO	LC	I	F
Anisotoma glabra	8	7	2	1	8	SxO	LC	I	F
Anisotoma humeralis	0	0	0	5	0	SxO	LC	I	F
Anomognathus cuspidatus	16	65	54	45	12	SxO	LC	I	D,P
Anotylus tetracarinatus	0	0	0	1	0	NS	LC		?P
Anthonomus phyllicola	0	0	0	2	0	NS			?P
Anthonomus rubi	0	0	0	3	1	NS	LC		H
Anthophagus omalinus	2	8	22	16	61	NS	LC		P
Anthribus nebulosus	0	0	0	0	1	SxF	LC		D,?P
Aphodius ater	5	0	0	0	0	NS	LC		D
Aphodius borealis	14	20	18	0	0	NS	LC		D
Aphodius depressus	1	1	0	0	0	NS	LC		D
Aphodius fasciatus	0	0	2	0	0	NS	LC		D
Aphodius lapponum	4	3	1	0	0	NS	LC		D
Aphodius rufipes	0	4	9	0	0	NS	LC		D
Aplocneus nigricornis	0	0	0	0	1	SxO			P
Arpedium quadrum	0	0	0	0	1	SxF	LC		?P
Asemum striatum	2	2	0	0	0	SxO	LC	II	C,W

Aspidiphorus orbiculatus	0	0	1	0	0	SxF	LC		F
Atheta corvina	2	0	0	0	0	SxF	LC		?P
Atheta crassicornis	2	0	0	0	0	SxF	LC		?F,?D,P
Atheta cribripennis	0	0	3	0	0	NS	LC		?F,?D,P
Atheta diversa	0	1	0	0	0	NS	LC		?F,?D,P
Atheta divisa	0	2	0	0	0	NS	LC		?F,?D,P
Atheta euryptera	1	0	0	0	0	SxF	LC		?F,?D,P
Atheta fungicola	0	0	0	0	1	SxF	LC		F
Atheta gagatina	0	0	4	0	0	SxF	LC		?F,?D,P
Atheta hypnorum	0	0	0	1	0	SxF	LC		F
Atheta incognita	0	1	0	0	0	SxF	LC		?F,?D,P
Atheta laevicauda	0	1	0	0	0	NS	LC		?F,?D,P
Atheta lativentris	9	2	0	0	1	SxF	LC		?F,?D,P
Atheta palleola	1	0	0	0	0	NS	LC		?F,?D,P
Atheta paracrassicornis	0	0	0	0	0	SxF	LC		F
Atheta picipes	0	0	0	2	1	SxF	LC		F
Atheta pilicornis	1	1	0	0	0	SxF	LC		?F,?D,P
Atheta sodalis	0	1	0	0	0	SxF	LC		F,?D,P
Atheta subtilis	1	3	0	0	0	SxF	LC		?F,?D,P
Atheta vaga	5	7	4	0	0	SxF	LC		?F,?D,P
Athous subfuscus	1	0	0	0	0	SxF	LC		P
Atomaria affinis	0	0	0	4	5	SxF	NT	I	?F,?D,P
Atomaria alpina	1	3	1	0	0	SxO	NT		F
Atomaria apicalis	0	1	0	0	0	SxF	LC		F
Atomaria atrata	0	2	0	0	0	SxF	LC	I	F
Atomaria badia	0	1	0	0	0	SxO	NT		F
Atomaria bella	5	14	71	5	3	SxO	LC	I	F
Atomaria bescidica	0	1	0	1	2	SxF	LC	I	F
Atomaria morio	0	1	0	0	0	SxF	LC	I	F
Atomaria nigrirostris	0	1	0	0	0	SxF	LC		F
Atomaria pulchra	89	39	37	0	0	SxF	LC	I	F
Atomaria subangulata	0	0	0	2	3	SxF	LC	I	?F,?D,P
Atrecus pilicornis	0	0	0	1	1	SxF	LC	I	?F,?D,P
Batrisodes hubenthali	11	1	0	3	2	SxO	VU	I	?P
Bembidion bruxellense	0	1	0	0	0	NS	LC		P
Bembidion grapii	2	1	0	0	1	NS	LC		P
Bembidion hyperboraeorum	0	1	0	0	0	NS	LC		P
Bembidion lampros	0	1	0	0	0	NS	LC		P
Bibloporus bicolor	2	4	0	10	6	SxO	LC	I	P
Bibloporus minutus	0	21	1	0	0	SxO	LC	I	P
Bisnius fimetarius	0	0	4	0	0	NS	LC		?P
Bisnius nigriventris	0	1	0	0	0	NS	LC		P
Bisnius puella	0	2	0	0	0	SxF	LC		?P
Bolitochara pulchra	1	2	0	0	0	SxF	LC		?F,F
Bolitophagus reticulatus	3	3	2	1	0	SxO	LC	I	F
Bryaxis bulbifer	2	1	0	1	1	NS	LC		P
Bryophacis rufus punctipennis	0	1	0	0	0	SxF	DD/NA/NE		?P
Bryoporus cernuus	0	1	0	0	0	SxF	LC		?P

Byrrhus fasciatus	0	1	0	0	0	NS	LC		H
Byrrhus pilula	1	0	0	0	0	NS	LC		H
Caenoscelis ferruginea	2	37	7	0	0	SxF	LC	I	F
Caenoscelis sibirica	0	9	7	0	0	SxF	LC	I	F
Caenoscelis subdeplanata	0	0	0	0	1	SxF	LC		?F,?D,P
Callidium aeneum	0	0	0	1	0	SxF	NT		?F,?D,P
Calopus serraticornis	0	1	0	0	0	SxO	LC		W
Calvia quatordecemguttata	0	0	0	0	1	SxF			?F,?D,P
Cantharis paludosa	1	0	0	0	0	NS	LC		H,P
Carphoborus cholodkovskyi	3	0	0	0	0	SxO	NT	I	C
Cartodere constricta	8	1	0	0	0	SxF	LC		F
Cercyon bifenestratus	0	5	0	0	0	NS	LC		P
Cercyon borealis	3	0	0	0	0	NS	LC		P
Cercyon obsoletus	1	0	0	0	0	NS	LC		P
Cerylon ferrugineum	20	30	23	8	11	SxO	LC	I	F
Cerylon histeroides	45	39	32	11	16	SxO	LC	I	F
Cis bidentatus	5	0	0	0	0	SxO	LC	I	F
Cis boleti	24	5	3	13	5	SxO	LC		F
Cis castaneus	0	1	0	0	0	SxO	LC		F
Cis comptus	1	9	11	2	0	SxO	LC	I	F
Cis dentatus	0	0	0	3	4	SxO	LC	I	F
Cis glabratus	1	0	0	0	0	SxO	LC		F
Cis jacquemartii	0	2	0	0	0	SxO	LC		F
Cis lineatocribratus	0	0	0	0	2	SxO	LC		F
Cis micans	2	3	0	0	4	SxO	LC		F
Cis punctulatus	0	0	2	1	0	SxO	LC	I	F
Cis quadridens	0	0	1	0	1	SxO	LC		F
Corticaria ferruginea	22	20	0	5	10	SxF	LC	I	F
Corticaria interstitialis	1	4	1	0	0	SxF	NT		F
Corticaria lapponica	5	17	4	10	3	SxO	LC	I	F
Corticaria lateritia	7	2	1	0	0	SxO	LC	I	F
Corticaria longicollis	0	3	0	0	0	SxF	LC	I	F
Corticaria longicornis	0	3	2	0	0	SxF	LC		F
Corticaria obsoleta	1	0	2	0	0	SxO	LC	I	F
Corticaria orbicollis	4	23	12	2	0	SxO	LC	I	F
Corticaria polypori	0	5	3	0	0	SxO	NT	I	F
Corticaria rubripes	167	125	3	0	0	SxF	LC	I	F
Corticaria serrata	0	3	0	1	0	SxF	LC	I	F
Corticaria sp1 hona	0	0	0	1	0	SxF			F
Corticaria sp2 hona	0	0	0	1	0	SxF			F
Corticarina minuta	0	1	0	0	0	SxF	LC		F
Corticarina parvula	0	2	0	0	0	SxF	LC		F
Corticeus linearis	0	0	5	3	1	SxO	LC	I	P
Cortinicara gibbosa	2	10	8	0	0	SxF	LC	I	F
Cryptophagus acutangulus	1	0	0	0	0	SxF	LC		F
Cryptophagus confertus	2	0	7	0	0	NS	LC		F
Cryptophagus corticinus	1	0	13	0	0	SxO	LC	II	F
Cryptophagus dentatus	4	8	4	0	0	SxF	LC		F

Cryptophagus denticulatus	0	0	0	0	1	SxF	LC		F
Cryptophagus dorsalis	0	8	1	0	1	SxF	LC	I	F
Cryptophagus lapponicus	43	72	820	0	0	SxF	LC	I	F
Cryptophagus parallelus	1	0	0	0	0	SxO	LC		F,C
Cryptophagus quadrihamatus	0	1	0	0	0	SxO	VU		F
Cryptophagus saginatus	3	0	0	1	1	SxF	LC		F
Cryptophagus tuberculosus	0	1	16	0	0	SxF	LC		F
Crypturgus cinereus	0	0	0	0	1	SxO	LC	I	C
Crypturgus hispidulus	0	3	0	0	0	SxO	LC	I	C
Crypturgus pusillus	2	1	0	0	0	SxO	LC	I	C
Crypturgus subcribrosus	0	2	0	0	0	SxO	LC	I	C
Curtimorda maculosa	0	0	5	0	1	SxO	LC	I	F
Cyphon padi	0	3	1	0	0	NS	LC		D,P
Cyphon pubescens	3	0	1	0	0	NS	LC		D,P
Cyphon punctipennis	0	4	1	0	0	NS	LC		D,P
Cyphon variabilis	0	6	0	0	0	NS	LC		D,P
Dacne bipustulata	2	13	6	56	18	SxO	LC	I	F
Dadobia immersa	2	6	1	0	0	SxO	LC	I	?F
Dalopius marginatus	0	0	1	0	0	NS	LC		?D
Danosoma fasciata	1	4	0	0	0	SxO	DD/NA/NE		P
Dendrophagus crenatus	17	13	13	6	2	SxO	LC	I	F
Denticollis borealis	2	0	0	0	0	SxO	NT	II	P,W
Denticollis linearis	0	2	1	0	0	SxO	LC	I	P,W
Dictyoptera aurora	6	2	4	0	0	SxO	LC	I	P
Dictyopterus aurora	0	0	0	1	0	SxO			?P
Dienerella filum	0	1	0	0	0	SxF	LC		F
Dinaraea aequata	2	2	0	1	0	SxO	LC	I	?F
Dinaraea arcana	0	0	0	1	2	SxO	LC	I	?F
Dinaraea linearis	0	1	0	1	0	SxO	LC	I	?F
Dolichocis laricinus	1	0	2	0	0	SxO	NT		F
Dorcatoma robusta	5	1	0	4	0	SxO	LC	I	F
Dromius agilis	7	1	7	2	3	SxF	LC	I	P
Dromius schneideri	0	1	0	0	0	NS	LC	I	P
Dropephylla clavigera	4	6	2	0	0	SxO	NT		P
Dropephylla linearis	1	3	2	4	2	SxO	LC		?F,?P
Dryocoetes autographus	9	24	18	2	4	SxO	LC		C
Dryocoetes hectographus	2	0	0	0	0	SxO	LC		C
Eanus costalis	6	6	6	3	20	NS	LC		?
Elateroides dermestoides	1	6	0	1	0	SxO	LC		W,F
Enicmus apicalis	1	2	0	0	0	SxO	NT		F
Enicmus fungicola	3	34	33	2	0	SxF	LC	I	F
Enicmus planipennis	0	5	12	0	0	SxO	NT		F
Enicmus rugosus	56	134	79	45	73	SxO	LC	I	F
Enicmus transversus	0	0	0	23	8	NS	LC		P
Ennearthron cornutum	0	2	0	0	0	SxO	LC	I	F
Episernus angulicollis	1	2	0	1	1	SxO	LC	I	W
Epuraea aestiva	1	0	1	0	0	SxF	LC		F
Epuraea angustula	3	26	28	6	3	SxO	LC	I	F,P

Epuraea biguttata	11	13	0	0	0	SxO	LC	I	F
Epuraea binotata	2	2	3	0	0	SxF	LC		F
Epuraea boreella	3	14	0	3	2	SxO	LC	I	F,P
Epuraea contractula	1	0	0	0	0	SxO	LC	I	F
Epuraea laeviuscula	2	5	16	1	1	SxO	LC	I	P
Epuraea marseuli	13	51	10	2	1	SxO	LC	I	D,F
Epuraea melina	0	1	0	0	0	SxF	LC		D,F
Epuraea oblonga	0	1	0	0	0	SxO	NT		D,F
Epuraea opalizans	0	1	0	0	0	SxO	LC		D,F
Epuraea pallescens	1	1	0	0	0	SxO	LC		D,F
Epuraea pygmaea	0	5	4	3	0	SxO	LC	I	D,F
Epuraea rufomarginata	4	17	7	0	0	SxF	LC	I	F
Epuraea silacea	35	5	4	73	8	SxO	LC		F
Epuraea sp	0	0	0	0	3	NS			P
Epuraea terminalis	0	25	13	0	0	SxF	LC		F
Epuraea variegata	4	0	0	0	0	SxO	LC	I	F
Eudectus giraudi	0	2	0	1	2	SxO	LC	I	?F
Euplectus karsteni	0	0	0	9	5	SxF		I	P
Euplectus mutator	0	0	15	19	5	SxO	LC		P
Euplectus nanus	0	0	0	8	2	SxF	LC	I	P
Euplectus piceus	0	1	0	0	0	SxF	LC		P
Euplectus punctatus	67	114	109	26	23	SxO	LC		P
Euryusa castanoptera	6	3	2	0	0	SxO	LC	I	?F
Eusphalerum lapponicum	1	0	0	0	0	NS	LC		H
Eusphalerum luteum	0	0	0	1	6	SxO	LC		?F
Gabrius expectatus	21	64	28	9	7	SxF	LC	I	P
Gabrius splendidulus	0	2	0	0	0	SxF	LC	I	P
Geodromicus plagiatus	0	3	0	0	0	?	LC		?
Glischrochilus hortensis	0	1	0	0	0	SxF	LC	I	D,F
Glischrochilus quadripunctatus	76	181	4	6	3	SxO	LC	I	F,P
Globicornis emarginata	0	3	0	0	0	SxO	LC	I	D
Gonotropis dorsalis	2	0	0	0	0	SxO	NT		C
Gyrohypnus angustatus	0	0	0	2	1	NS	LC		H
Gyrophaena affinis	1	0	3	0	0	SxF	LC		F
Gyrophaena sp hona	0	0	0	1	1	SxF			F
Hadrobregmus confusus	2	1	0	0	0	SxO	NT	I	W
Hadrobregmus pertinax	15	5	3	2	3	SxO	LC	I	W
Hallomenus binotatus	0	1	0	0	3	SxO	LC		F
Haploglossa villosula	26	52	20	11	3	SxF	LC		?F
Harpalus laevipes	0	0	1	0	0	NS	LC		H
Helophorus tuberculatus	0	1	0	0	0	NS	LC	I	H,P
Henoticus serratus	10	2	0	0	0	SxF	LC	II	F
Heterothops quadripunctulus	0	2	1	0	0	?SxF	LC		?P
Holobus flavicornis	1	0	0	0	0	SxF	LC		P
Hydnobius spinipes	0	1	0	0	0	NS	LC		F
Hylastes brunneus	2	216	86	0	0	SxO	LC	I	C
Hylastes canaliculatus	0	0	0	1	7	SxO			C
Hylastes cunicularius	0	6	5	0	0	SxO	LC	I	C

Hylastes opacus	0	1	0	0	0	SxO	LC		C
Hylobius abietis	13	3	0	0	1	SxO	LC	II	C,W
Hylurgops glabratus	0	1	0	1	1	SxO	LC		C
Hylurgops palliatus	0	21	1	0	0	SxO	LC		C
Ips acuminatus	13	0	0	0	0	SxO	NT	I	C,F
Ips typographus	0	6	11	0	0	SxO	LC	I	C
Ischnoglossa elegantula	4	2	0	0	0	SxF	LC		?F
Judolia sexmaculata	0	1	0	0	0	SxO	LC		C,W
Laemophloeus muticus	3	5	2	0	0	SxO	VU	III	F,W,P
Latridius consimilis	1	5	2	0	0	SxF	LC	I	F
Latridius gemellatus	0	2	0	0	0	SxF	LC		F
Latridius hirtus	3	13	7	2	2	SxO	LC	I	F
Leiodes gyllenhalii	0	0	0	1	0	NS	LC		F
Leiodes picea	0	1	0	0	0	NS	LC		F
Leiodes punctulata	0	0	0	0	1	NS	LC		F
Leptusa fumida	57	2	0	0	0	SxO	LC	I	?F
Liotrichus affinis	1	0	2	0	0	SxF	LC		?
Litargus connexus	9	26	5	2	0	SxO	LC	II	F
Lordithon lunulatum	0	0	0	7	0	NS			H
Lordithon lunulatus	0	0	1	0	0	SxF	LC		P
Lordithon speciosus	0	1	3	0	0	SxO	LC		P
Lordithon thoracicus	1	0	0	0	0	SxF	LC		P
Lygistopterus sanguineus	0	0	0	9	0	NS	LC	I	?F,?D,P
Lypoglossa lateralis	2	0	1	0	0	NS	LC		?F,?D,P
Magdalis frontalis	1	0	0	1	0	SxO	LC		W
Magdalis phlegmatica	1	1	0	0	0	SxO	LC		W
Magdalis violacea	0	0	0	1	1	SxO	LC		C
Malthinus biguttatus	0	1	1	0	2	SxO	LC		H,P
Malthinus mysticus	0	0	0	9	0	SxO			H,P
Malthodes brevicollis	0	1	3	0	0	SxO	LC		H,P
Malthodes fuscus	0	2	8	0	0	SxO	LC		P
Malthodes guttifer	0	2	1	11	0	SxO	LC		P
Malthodes marginatus	0	0	0	1	0	SxO	LC		P
Malthodes sp hona	0	0	0	3	4	SxO			P
Megasternum concinnum	0	2	0	0	0	SxF	LC		D,H,P
Melandrya dubia	2	0	0	0	0	SxO	VU	I	?F
Meotica exilis	1	0	0	0	0	NS	LC		?F
Micrambe abietis	0	0	0	174	175	SxF	LC		F
Molorchus minor	0	1	1	0	0	SxO	LC		C,W
Monotoma longicollis	1	0	0	0	0	NS	LC		F
Mycetochara flavipes	2	2	2	1	1	SxO	LC	I	?
Mycetochara maura	0	0	0	3	5	SxO	LC		?
Mycetochara obscura	2	3	6	4	8	SxO	LC	I	?
Mycetophagus decempunctatus	0	0	0	1	0	SxO	NT		?
Mycetophagus multipunctatus	2	8	0	1	0	SxO	LC		F
Mycetophagus populi	1	1	0	0	0	SxO	LC		F
Mycetoporus bimaculatus	0	0	0	4	2	NS	LC		?P

Mycetoporus brunneus	0	0	0	1	5	NS			?F,?D,P
Mycetoporus lepidus	6	12	3	0	0	NS	LC		P
Mycetoporus rufescens	1	0	0	0	0	SxF	LC		P
Myrrha octodecimguttata	0	1	0	0	0	NS	LC		P
Nepachys cardiacae	0	0	0	1	0	SxO	LC	I	P
Nephus bisignatus	0	1	0	0	0	NS	LC		P
Nicrophorus vespilloides	0	1	0	2	1	NS	LC		D,P
Notiophilus aquaticus	2	1	0	0	0	NS	LC		P
Notiophilus biguttatus	8	3	0	0	0	NS	LC		P
Notothecta flavipes	0	1	0	0	0	NS	LC		?F,?D,P
Nudobius lentus	3	7	0	0	0	SxO	LC	I	P
Olisthaerus megacephalus	2	0	0	0	0	SxO	NT	I	?P
Olisthaerus substriatus	0	0	1	0	0	SxO	NT	I	P
Olophrum rotundicolle	0	2	0	0	0	NS	LC		?P
Omalium caesum	2	0	0	0	0	SxF	LC		?P
Omosita depressa	0	1	0	0	0	NS	LC		D,F
Orchesia fasciata	2	1	0	1	0	SxO	NT		F
Orchesia micans	16	5	17	7	5	SxO	LC	I	F
Orithales serraticornis	2	1	0	2	0	NS	LC		?
Orthocis alni	1	3	4	4	0	SxO	LC	I	F
Orthotomicus laricis	0	1	0	0	0	SxO	LC	I	C
Orthotomicus proximus	0	1	0	0	0	SxO	LC	I	C
Orthotomicus suturalis	0	2	1	0	0	SxO	LC	II	C
Oxypoda alternans	0	0	0	1	1	SxF	LC		?F
Oxypoda brevicornis	0	4	1	1	0	NS	LC		?F
Oxypoda haemorrhoa	1	0	0	0	0	NS	LC		?F
Oxypoda skalitzkyi	0	1	2	0	0	SxF	LC		?F
Oxypoda soror	0	1	0	0	0	SxF	LC		?F
Oxytelus laqueatus	1	1	0	0	0	NS	LC		?P
Pachyta lamed	2	0	0	0	0	SxO	LC	II	C
Paraphotistus impressus	1	5	5	4	2	SxF	LC		P
Pediacus fuscus	1	0	0	0	0	SxO	LC	I	F
Peltis ferruginea	0	2	0	0	0	SxO	LC		F
Philonthus corvinus	0	0	0	1	0	SxF	LC		?F
Philonthus discoideus	0	0	0	0	1	SxF	LC		?F
Philonthus lederi	1	1	0	0	0	NS	LC		?P
Philonthus puella	0	0	0	2	1	SxF			?F
Philonthus succicola	1	0	0	0	0	NS	LC		?P
Phloeonomus punctipennis	0	0	0	4	4	SxO	LC	I	?P
Phloeonomus pusillus	47	0	1	4	1	SxO	LC	I	P
Phloeonomus sjobergi	6	13	6	2	0	SxO	LC		?P
Phloeopora concolor	18	10	6	0	0	SxO	LC	I	P
Phloeopora corticalis	6	2	2	0	0	SxO	LC	I	?P
Phloeopora nitidiventris	0	0	0	1	0	SxO	LC	I	?P
Phloeopora testacea	11	6	2	1	4	SxO	LC		?P
Phloeostiba lapponica	60	76	54	0	0	SxO	LC		P
Phloeostiba plana	6	30	8	7	5	SxO	LC		?P
Pityogenes bidentatus	164	58	32	3	4	SxO	LC	I	C

Pityogenes chalcographus	6	22	3	0	0	SxO	LC	I	C
Pityogenes quadridens	2	2	0	0	0	SxO	LC	I	C
Pityophagus ferrugineus	3	11	3	2	0	SxO	LC	I	P
Pityophthorus lichtensteini	0	0	0	1	3	SxO			P
Pityophthorus lichtensteinii	0	7	0	0	0	SxO	LC	I	C
Placusa atrata	47	41	44	7	6	SxO	LC	II	?P
Placusa depressa	6	0	10	5	4	SxO	LC	I	?P
Placusa tachyporoides	2	0	2	0	0	SxO	LC	I	?P
Planolinus fasciatus	0	0	0	6	2	NS			?F,?D,P
Plegaderus vulneratus	4	1	9	1	0	SxO	LC	I	P
Pocadius ferrugineus	5	0	0	0	2	SxF	LC		F
Podabrus alpinus	0	1	0	0	0	NS	LC		?P
Podistra schoenherri	6	2	1	0	0	SxO	LC		P
Pogonocherus decoratus	1	0	0	0	0	SxO	LC		C,W
Pollygraphus subopacus	0	0	0	1	0	SxO			C,W
Polygraphus poligraphus	6	1	4	3	3	SxO	LC	I	C
Polygraphus punctifrons	0	0	8	0	0	SxO	LC	I	C
Polygraphus subopacus	1	0	4	0	0	SxO	LC	I	C
Porrhodites fenestralis	1	0	0	0	0	NS	LC		?P
Prosternon tesselatum	0	0	0	0	1	SxF			D
Prosternon tessellatum	2	2	1	0	0	NS	LC		H
Protaetia metallica	0	0	1	0	0	SxF	LC		D
Proteinus brachypterus	2	0	0	0	0	SxF	LC		?P
Pterostichus adstrictus	0	2	0	0	0	NS	LC		H,P
Pterostichus oblongopunctatus	1	0	0	0	0	SxF	LC	I	P
Pteryngium crenatum	0	1	0	0	0	SxO	LC	I	F
Pteryx suturalis	2	22	0	0	1	SxO	LC	I	F
Ptiliola kunzei	0	3	0	0	0	SxO	LC		F
Ptiliolum caledonicum	0	1	0	0	0	SxO	LC	I	F
Ptinella aptera	0	1	0	0	0	SxO	LC		F
Ptinella limbata	0	1	0	0	0	SxF	LC		F
Ptinus sexpunctatus	0	2	0	0	0	SxO	LC		D
Pytho depressus	0	4	0	0	0	SxO	LC	I	C
Quedius cruentus	0	0	0	0	2	SxF	LC		?P
Quedius laevigatus	0	0	0	2	0	SxF			?P
Quedius lundbergi	3	0	1	0	0	SxO	NT		?P
Quedius mesomelinus	0	0	0	0	1	SxF	LC		?P
Quedius microps	0	0	0	1	1	SxF	LC		?P
Quedius plagiatus	0	1	0	0	0	SxO	LC	I	P
Quedius tenellus	2	2	1	0	0	SxF	LC		?P
Rabocerus foveolatus	0	1	0	1	0	SxO	LC	I	P
Rhagium inquisitor	10	0	0	0	0	SxO	LC	I	C,W
Rhagonycha atra	0	0	0	0	1	NS	LC		P
Rhagonycha elongata	3	2	3	1	2	NS	LC		P
Rhizophagus bipustulatus	0	5	1	1	0	SxO	LC	I	P,F
Rhizophagus dispar	2	1	0	0	0	SxF	LC	I	P
Rhizophagus fenestralis	72	688	209	0	0	SxO	LC		P
Rhizophagus ferrugineus	6	9	2	1	2	SxO	LC	I	P

Rhizophagus nitidulus	0	0	1	1	0	SxO	LC	I	P
Rhizophagus parvulus	0	0	0	21	21	SxO		I	P
Rhopalodontus strandi	2	6	6	0	0	SxO	LC		F
Rhyncolus sculpturatus	14	7	6	1	4	SxO	LC	I	W
Ropalodontus strandi	0	0	0	1	0	SxO			W
Salpingus ruficollis	0	0	3	1	0	SxO	LC	I	P
Scaphisoma agaricinum	38	50	96	35	7	SxF	LC	I	?F
Scaphisoma assimile	0	9	0	0	0	SxO	LC		F
Scaphisoma inopinatum	0	0	0	0	2	SxF	LC		?F
Scaphisoma subalpina	0	0	0	3	0	SxF			?F
Scaphisoma subalpinum	0	2	3	0	0	SxO	NT		?F
Sciodrepoides watsoni	0	1	1	0	0	NS	LC		D
Scolytus ratzeburgi	0	0	0	1	0	SxO		II	C
Scolytus ratzeburgii	14	10	24	0	0	SxO	LC		C
Selatosomus aeneus	0	0	0	5	3	SxF	LC		H
Selatosomus melancholicus	2	1	1	0	1	NS	LC		?
Sepedophilus immaculatus	1	0	0	0	0	SxF	LC		F
Sepedophilus littoreus	1	2	1	1	0	SxF	LC	I	F
Sepedophilus testaceus	0	0	0	0	1	SxF	LC		F
Sericoda quadripunctata	0	0	1	0	0	SxO	LC	III	P
Sericus brunneus	2	7	14	6	1	NS	LC		?
Soronia grisea	0	1	0	0	0	SxO	LC		D
Soronia punctatissima	0	1	0	1	0	SxO	LC		D,F
Sphaeriestes bimaculatus	0	5	0	0	0	SxO	LC	I	P
Sphaeriestes stockmanni	4	3	6	0	0	SxO	LC	III	P
Sphindus dubius	0	0	3	1	0	SxF	LC	I	F
Stagetus borealis	0	0	0	1	0	SxO	NT	I	F,W
Stenichnus bicolor	5	3	0	1	1	SxF	LC	I	P
Stenotrachelus aeneus	1	0	6	4	0	SxO	LC	II	C,W
Stephostethus pandellei	2	2	0	0	1	SxF	LC	I	F
Stephostethus rugicollis	4	3	0	0	0	SxF	LC		F
Stichoglossa prolixa	0	0	0	0	3	SxO			D,W
Strophosoma capitatum	0	4	1	1	0	NS	LC	I	H
Syneta betulae	0	1	0	0	0	NS	LC		H
Tachinus elegans	0	0	0	0	1	NS	NT		?F,?P
Tachinus elongatus	0	5	3	0	0	NS	LC		?F,?P
Tachyta nana	1	4	0	0	0	SxO	LC		P
Tetratoma ancora	13	11	12	19	26	SxO	LC	I	F
Thalycra fervida	0	0	0	2	0	NS	LC		F,?H
Thanasimus femoralis	1	0	0	0	0	SxO	LC	I	P
Thanasimus formicarius	4	12	13	1	0	SxO	LC	I	P
Thiasophila angulata	0	1	0	0	0	NS	LC		?D?P
Thiasophila wockei	0	0	0	2	0	SxF			?D?P
Tomicus piniperda	7	202	0	0	0	SxO	LC	I	C
Trichophya pilicornis	2	0	0	0	0	SxF	LC		?F
Triplax aenea	2	14	3	3	2	SxO	LC	I	F
Triplax russica	16	25	11	20	6	SxO	LC	I	F
Triplax scutellaris	13	16	10	0	0	SxO	LC	I	F

Triplax scutellata	0	0	0	8	3	SxO			F
Trypodendron laeve	6	0	246	0	10	SxO	LC		F
Trypodendron lineatum	24	227	100	37	127	SxO	LC	I	F
Trypodendron signatum	0	85	82	0	0	SxO	LC	I	F
Tyrus mucronatus	0	3	0	0	0	SxF	LC	I	?F
Wanachia triguttata	5	0	3	0	0	SxO	LC		F
Xylita laevigata	52	97	20	24	42	SxO	LC	I	F
Xylostiba monilicornis	0	0	0	2	4	SxO	LC		P
Zilora ferruginea	1	0	0	0	0	SxO	NT	I	F