

Community structure of polyporous fungi after wildfire in boreal forest

Samhällsstrukturen hos tickor efter naturlig brand i boreal skog

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Abstract

Wildfire is a natural disturbance that creates large amounts dead wood and contribute to a landscape of different successional stages, important for biodiversity. The number of wildfires have declined in boreal Fennoscandia due to effective fire suppression. A better understanding of the fire-effects on species communities is necessary to obtain effective conservation. The aim of this study was to compare the community structure of polyporous fungi (polypores) in burned forests with forests with a long history of fire suppression.

I studied three different sites in northern Sweden 12 years post fire; (1) a mixed coniferous forest in a landscape highly affected by forestry, (2) an old growth spruce forest in the proximity to high mountains and (3) a pine forest in a large protected area. In each burned area, I measured the coniferous coarse woody debris and surveyed the wood for polypores. The same was done in control areas next to each of the burned areas.

The amount and quality of dead wood differed between the burned areas and the control areas. The fires created dead wood but also consumed dead wood of later decay stages, resulting in a shift towards early decay stages in burned areas. In all sites, the community structure of polypores differed between burned and unburned areas but various species contributed to the differences. A few generalists were very abundant in the burned areas compared to the control while several red-listed species found in the controls were few or missing in the burned areas. The red-listed *Diplomitoporus crustulinus* was not found in the controls but on charred bark on several logs in the burned areas.

The shift in community structure is likely due to the difference in amount and quality of dead wood and a dryer microclimate in the burned areas, which is more open and have less ground vegetation. Fire does not necessary increase the local diversity but can increase the diversity on a landscape level. This study indicates that the development of the polypore community post fire is influenced by the traits of the pre-fire forest and the fire intensity. Many restoration burns is relatively low-intensity fires in pine forests but I show that also intense fires in spruce-dominated forests can be positive for biodiversity.

Keywords: biodiversity, community composition, natural disturbance, forest fire, polyporous fungi, wood-decaying fungi

Sammanfattning

Brand är en naturlig störning som skapar stora mängder död ved och bidrar till ett landskap med flera olika successtionsstadier, vilket är viktigt för den biologiska mångfalden. Antalet och frekvensen av naturliga skogsbränder har minskat i Fennoskandien på grund av effektiv brandbekämpning. Att förstå skogsbränders effekt på artsamhällena är viktigt för att bedriva en effektiv naturvård. Syftet med studien var att jämföra samhällsstrukturen av tickor mellan brandfält och områden med långvarig brandbekämpning.

Jag har studerat tre olika skogsområden i norra Sverige 12 år efter brand; (1) en barrblandskog i ett hårt brukat landskap, (2) en gammal fjällnära granskog och (3) en tallskog i ett stort skyddat område. I varje bränt område mätte jag grov död ved och inventerade tickor som växte på veden. Samma sak gjordes i kontrollområden utanför brandfälten.

Mängd och kvalitet av den döda veden skiljde sig mellan brandfälten och kontrollerna. Branden skapade ny död ved men konsumerade också död ved i sena nedbrytningsstadier vilket tillsammans ändrade kvalitén på den döda veden mot en större representation av tidiga nedbrytningsstadier. Totalt ökade mängden död ved. I alla tre områden skiljde sig strukturen av tickornas artsamhällen mellan brand- och kontrolltytor men olika arter var orsak till den uppkomna skillnaden. Några generalistarter var mycket vanliga i brandytorna jämfört med kontrolltytorna medan flera rödlistade arter som hittades i kontrolltytorna var ovanliga eller saknades i brandytorna. Den rödlistade arten *Diplomitoporus crustulinus* hittades inte i kontrolltytorna men på bränd bark på flera lågor i brandytorna.

Förändringen av samhällsstrukturen beror sannolikt på en skillnad i mängd och kvalitet av död ved och att ett torrare mikroklimat i öppna, brända ytor med mindre markvegetation. Brand ökar nödvändigtvis inte den lokala diversiteten men kan öka diversiteten på landskapsnivå. Studien indikerar att hur artsamhället av tickor utvecklas efter brand påverkas av skogens egenskaper innan branden och brandens intensitet. Många naturvårdsbränningar är lågintensiva bränder i tallskogar men jag visar att även kraftiga bränder i grandominerade skogar kan gynna biodiversiteten.

Nyckelord: biologisk mångfald, naturlig störning, samhällsstruktur, skogsbrand, tickor

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1 Introduction

Fire is one of the most important natural disturbances in boreal forests. Wildfires create large amounts of dead wood, affect the stand dynamics and structure and create a mosaic landscape consisting of stands at different successional stages (Zackrisson, 1977; Johnson, Miyanishi and Weir, 1998; Niklasson and Granström, 2000; Ryan, 2002; Shorohova *et al.*, 2009). Several species, including groups of insects, fungi and vascular plants, are favored by fire (Granström and Schimmel, 1993; Dahlberg, 2002; Kalamees *et al.*, 2005; Johansson *et al.*, 2010; Olsson and Jonsson, 2010). According to Niklasson and Granström (2000), the average burned area was 0.8 % per year before 1650 when lightning ignition was the main occasion but increased due to expansion of permanent settlements. After a peak in the mid-1800s, when 2.8 % of the area burned per year, the numbers of fires have decreased due to modern forestry and effective fire suppression, and forest fires have almost been totally absent the last century (Linder, Efvig and Zackrisson, 1997; Niklasson and Granström, 2000). Clear-cutting has replaced fires as the main disturbance in Fennoscandia and altered the landscape from post-fire forest of different succession stages with a mix of Scots pine (*Pinus sylvestris* L.), Aspen (*Populus tremula* L.) and Birch (*Betula sp.* L.) to forest dominated by Norway spruce (*Picea abies* (L.) H. Karst) (Zackrisson, 1977; Engelmark, 1987; Bradshaw, 1993; Esseen *et al.*, 1997; Svensson *et al.*, 2019). An important difference between clear-cuts and natural fires is the amount and quality of dead wood, or coarse woody debris (CWD) (Siitonen, 2001; Pedlar *et al.*, 2002; Ylisirniö *et al.*, 2012), a key substrate for biodiversity (Jonsson *et al.*, 2005). Polyporous fungi, or polypores (Basidiomycota), are saproxylic fungi and important decomposers of CWD. Many of them are sensitive to environmental change as they have specialized substrate requirements (Renvall, 1995) and about 40 % of the wood-living polypores in Sweden are currently red-listed, mainly due to forestry that has reduced the amount of dead wood (ArtDatabanken, 2015; Sandström *et al.*, 2015).

As large forest ecosystems characterized by natural disturbance dynamics are missing in Fennoscandia, conservation has started to shift from only forest protection to an increased use of different restoration methods like artificial creation of dead wood and prescribed burnings. The aim of these methods is to mimic natural disturbance to conserve disturbance-dependent species. Creation of dead wood can lead to a short-term increase of abundance and species richness of both saproxylic insects and wood-decaying fungi, even though rare species not necessary are favored (Sandström *et al.*, 2019). Variation in the quality of the created dead wood seems to be beneficial for biodiversity (Sandström *et al.*, 2019). There are several short-term (1-4 years) studies of the effect of prescribed burnings on both saproxylic beetles (Toivanen *et al.*, 2007; Hyvärinen, Kouki and Martikainen, 2009) and wood-decaying fungi (Junninen, Kouki and Renvall, 2008; Olsson and Jonsson, 2010). Those studies showed an increase in species number of saproxylic beetles while the species number of wood-decaying fungi decreased. As the aim of prescribed burnings is to mimic wildfires to conserve biodiversity linked to them we also have to know how the species communities respond to wildfires. There is no studies of the development of the polypore community after wildfires in areas with a long history of fire suppression as the difficulty to make such a study is that wildfires are extremely rare in those areas. Kurth *et al.* (2013) studied the community of wood-decaying fungi in Ponderosa pine (*Pinus ponderosa* (Douglas ex Lawson)) forests of the USA, but they found few polypores. There are relatively few studies of wildfires effects on polypores in Fennoscandia but Ylisirniö *et al.* (2012) compared post-fire forest in different successional stages with clear-cut or selectively logged forests in northern Finland and close-by areas in Russia. These forests were originally spruce dominated and Ylisirniö *et al.* (2012) showed that the increase of coarse woody debris (CWD) due to fire favoured both the overall species richness and the richness of red-listed species many decades after fire. To obtain effective conservation of fire favoured polypore species, knowledge is needed about the development of the polypore community after wildfires in different kind of forests that differ in terms of climate, anthropogenic impact and dominating tree species.

The aim of this study is to compare the polypore community composition in forests with a long history of fire suppression with that in similar forests that burned 12 years ago. I include three types of forests; (1) a spruce forest in the proximity of high mountains with low human impact, (2) an old pine forest and (3) a mixture of pine and spruce in a landscape heavily impacted by forestry. Wildfires create large amounts of CWD in early decay stages but also consume CWD in late decay stages, charcoal the CWD and expose it to wind and sun. Due to these changes of the dead wood amount and quality, I expect the polypore community to be affected by wild-

fires. I hypothesize that (1) the community composition of polypores will differ between burned and unburned forest and (2) that some fire-dependent red-listed species only will be present in the burned areas.

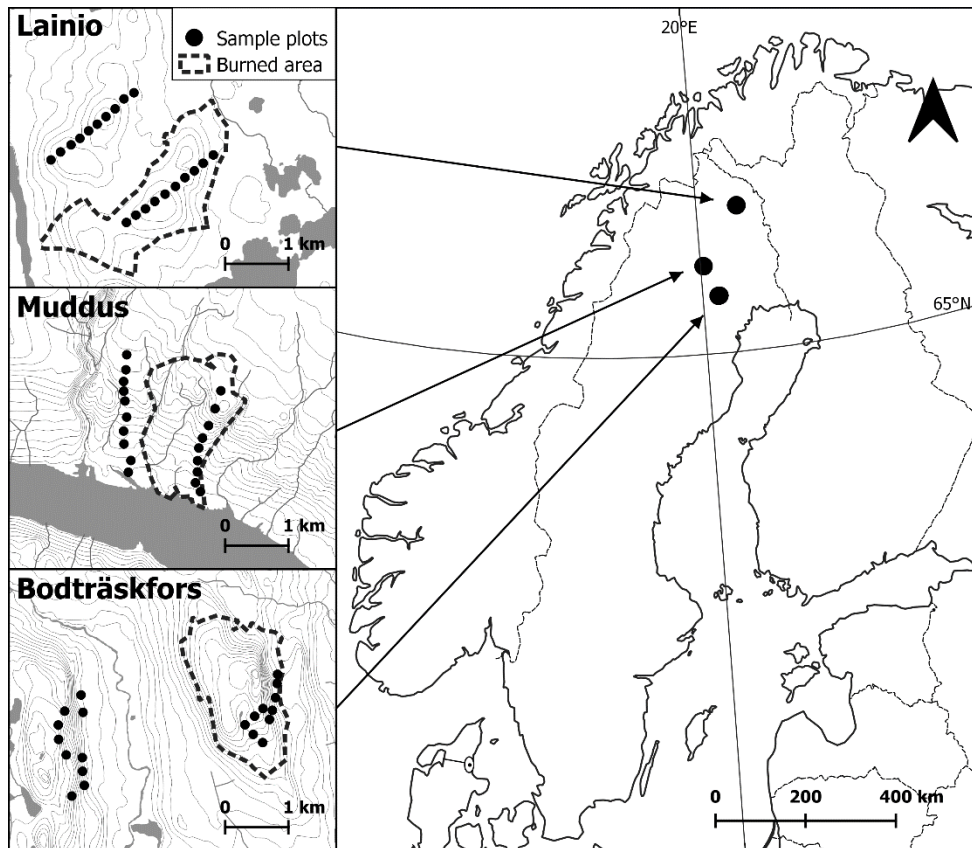


Figure 1. Location of the sites included in the study. Every site includes a burned area and a control, each with 10 sample plots. The plots measure a radius of 25 meters and are at least 140 meters apart.

2 Method

2.1 Study area and design

Three boreal forests in Norrbotten County in northern Sweden were studied (Figure 1). In 2006, these forests were exposed to natural forest fires that covered several hundred hectares and occurred after decades of fire suppression.

The studied sites differed with respect to the composition of tree species, the degree of tree mortality and the size of the burned area (Table 1). The first site is 7 km northwest of Bodträskfors in Boden municipality, a landscape affected of intense

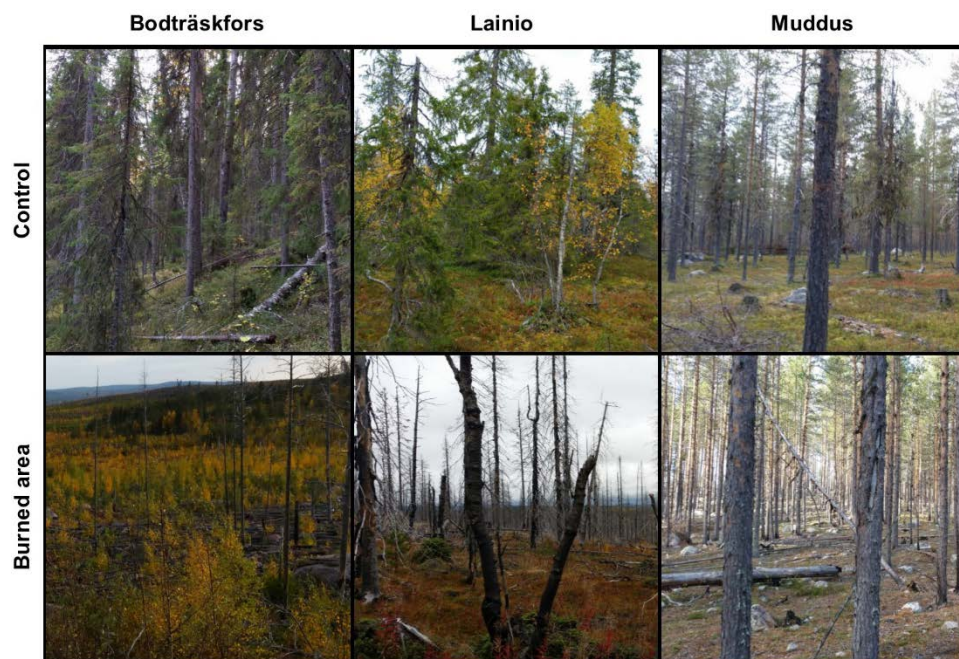


Figure 2. Photos from the study sites. They are not to be seen as before-after photos but examples of what the highly variable sites can look like.

forestry where a mountain covered with clear-cuts, forests of different successional stages and patches with old-growth forest burned (Figure 1). A majority of the trees died and had fallen 12 years after the fire (Figure 2). The relatively flat parts on higher altitudes are dominated by pine, while spruce dominates the steep and more productive parts at lower altitudes. The spruce dominated areas also have clear elements of deciduous trees, mainly birch and aspen. The landscape is highly affected by forestry, but all sampling was done in never clear-cut stands. The regeneration of trees is fast and at places with high productivity, there are dense post-fire birch forests with a height of two meters. At other places the regeneration of post-fire forest is slower but there is tree regeneration over the entire area.

The second site is 17 km north of Lainio in Kiruna municipality. The landscape is relatively flat with a mosaic of wetlands and old-growth forest dominated by spruce with some elements of birch (Figure 2). The amount of dead wood is low compared to Muddus and Bodträskfors, mainly because the forest is very slow growing but also due to sparse dimensional cutting. Prescribed burning is used as regeneration method in the area and the forest fire in Lainio originated from one of those. It developed as an intense fire that killed almost all trees in the area which cover a flat hill (Figure 1). Many of the dead spruces were still standing during this study, 12 years after the fire. It is almost no regeneration of new trees in the area.

The third site is located in the south part of Muddus national park in Jokkmokk municipality. Muddus consist mainly of pine forest located in a south slope towards the Lule river (Figure 1) There have been dimension cutting in the area and the oldest trees are missing. The Muddus area has a long fire history but no natural fires have occurred since 1868 (Engelmark 1984; Granström & Niklasson 2011). In the area, there are lots of tracks of old forest fires on stumps and old logs. The fire in 2006 was a low-intense ground fire. Many of the coarse pine trees survived the fire while many of the thin and small ones died and fell (Figure 2).

Table 1. *Information about the forest fires used in the study.*

Site	Dominating tree species	Burned area (ha)	Mortality of trees	Fire month	Altitude (m a.s.l.)
Bodträskfors (66°9'N, 20°47'E)	Norway spruce Scots pine	1800	High	August	110 - 240
Lainio (67°54'N, 22°10'E)	Norway spruce	440	Very high	June	340 - 400
Muddus (66°46' N, 20°10' E)	Scots pine	300	Low	August	170 - 320

2.2 Inventory of CWD and polypores

The field work was performed in 2018, 12 years after the fire. Close by every burned area, a control area was set up with a similar topography as the burned area. Through each of the burned and the control areas, ten sample plots were placed out on a transect. Every sample plot measured a radius of 25 m and they were at least 140 m apart. In every sample plot, I counted all dead trees laying down (logs) with the base inside the plot and considered only coarse woody debris (CWD) with a diameter > 15 cm and length > 1.3 m. The length was defined as the length of the log with a diameter > 5 cm. For plots with a high density of logs, only 25-50 % of the plot areas were surveyed. In those cases the log number was normalised to represent the total plot area (i.e. x2 if 50 % was surveyed and x4 if 25 % was surveyed). For every log I noted tree species and measured the maximum diameter, the minimum diameter (> 5 cm) and the length. The volume was calculated using the formula of a truncated cone.

$$V = (l\pi/3)(r_{max}^2 + r_{max}r_{min} + r_{min}^2)$$

where l is the length, r_{max} is the maximum radius and r_{min} is the minimum radius. The decay stage of every log was recorded using four categories according to Gibb et al. (2005): 1) bark intact or starting to loosen, > 50 % bark remaining, wood hard; 2) < 50 % bark remaining, surface of wood smooth, but beginning to soften, wood hard; 3) lacking bark, 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 hard wood, surface of object hard to define, outline of object indefinable. If more than one decay stage was present I recorded the dominant decay stage (i.e. dominant in respect to log volume). For every log, I also estimated the percentage of ground contact and percentage charred wood. In every sample plot I also measured the basal area of living trees using a smaller circular sample plot with a radius of 10 meter and measured the diameter in breast height (1.3 m) of every living tree within that circle.

On every CWD unit in the sample plot I recorded fruiting bodies of all polypore species. I also noted if the surface where the fruiting bodies grew was charred or not or if the fruiting bodies were found on both charred and not charred surface. Polypores were inventoried in the full area of the sample plot even if CWD was measured in only 25-50 % due to high density of logs. However, I took the ordinary measurements (except from length and minimum diameter) of logs that had polypores even if they were excluded from the overall CWD volume calculation. All polypores were determined to species level. Specimens that I could not identify in the field were collected for microscope identification. Literature used for identification was mainly Ryvaarden and Melo (2017).

2.3 Statistical analysis

All analyses were performed using R (R Development Core Team, 2019). To compare the difference in the amount of dead wood and dead wood characteristics between the burned areas and the control I used a t-test, except for the comparison of decay stage distribution where I used a chi-square test. I made comparisons between burned and control areas for Bodträskfors, Lainio and Muddus separately. The difference in polypore community between the burned areas and the control areas was analysed with a multivariate generalized linear model (ManyGLM) using the R package mvabund (Wang *et al.*, 2012). I did an overall comparison where I tested the interaction between the sites (Bodträskfors, Lainio or Muddus) and treatment (burned area or control) to see if the effects of fire on the community composition of polypores differed among the different burned areas. I also evaluated which species contributed most to the difference in species community. As there was a significant interaction I performed a ManyGLM analysis for each of the three sites Bodträskfors, Lainio and Muddus to test the effect of forest fire in each of them separately. The sampling plots were used as replicates and I used the number of logs as offset as it was linearly correlated to the number of polypores. As the community of polypores varied due to the proportion of spruce vs. pine, I first controlled for the relative abundance of spruce by putting it as the first explanatory variable. The ManyGLM treats the explanatory variables in the order they are put in so by doing so the other variables are handling the remaining variance. I analysed the data with negative binomial as family and used the log link for the offset.

To visualize the difference in polypore community I used Nonmetric Multidimensional Scaling (NMDS) using the vegan package (Oksanen *et al.*, 2019). Bray-Curtis dissimilarity was used and the data was not transformed. As the NMDS cannot assign random effects it did not take into account the spatial dependence between plots within the same site and treatment. To the data I added a dummy-species which occurred with one individual in each plot. The reason for adding the dummy species is that the NMDS function cannot handle plots without any records of species, which occurred in the data.

Table 2. Characteristics of coarse wood debris (CWD) and basal area at the sites. Differences between fire and control sites were tested with Student's *t*-test except for decay stage where a chi-square test was used.

	Bodträskfors			Lainio			Muddus		
	Burned	Control	P	Burned	Control	P	Burned	Control	P
Number of logs (ha ⁻¹)	138	65.7	0.006	83.0	20.9	0.001	103	95.7	0.734
Log volume (m ³ ha ⁻¹)	73.1	43.9	0.065	48.9	18.7	0.050	64.8	48.1	0.329
Mean log diameter (cm)	20.5	22.4	0.011	22.5	27.6	0.002	22.1	21.7	0.547
Mean decay stage	1.7	2.6	<0.001	2.0	3.1	<0.001	2.5	3.1	<0.001
Mean log volume (m ³)	0.53	0.67	0.015	0.59	0.90	0.034	0.63	0.50	0.008
Mean ground contact (%)	15.9	45.4	<0.001	51.1	66.5	0.011	28.5	61.6	<0.001
Mean charred surface (%)	15.4	1.0	<0.001	25.8	-	-	37.1	3.6	<0.001
Logs with species (%)	60.4	31.9	0.007	60.3	54.3	0.703	30.5	11.0	0.002
Basal area (m ² ha ⁻¹)	4.8	21.7	<0.001	1.8	11.8	<0.001	19.9	18.3	0.585
Deciduous log volume (m ³ ha ⁻¹)	19.3	25.2	0.671	2.8	2.1	0.621	2.0	0.11	0.159

3 Results

3.1 Structure of forests and dead wood

The number of coniferous logs per hectare was higher in the burned area compared to the control in Bodträskfors and Lainio while I could not find any difference in Muddus 12 years after the fire (Table 2). Lainio showed a higher total volume of dead wood in the burned area compared to the control but this difference could not be found in either Bodträskfors or Muddus (Table 2; Figure 3). The mean log volume was lower in the burned area compared to the control in Bodträskfors and Lainio but higher in Muddus (Table 2). In all sites, the decay stage distribution differed between burned area and control (Table 2), where the early decay stages (1 and 2) were more abundant while the late decay stages (3 and 4) were fewer in the burned areas (Figure 3). The mean ground contact was lower and the logs had a higher proportion of charred wood in the burned area compared to the control in all sites (Table 2). I found no difference in the total volume of deciduous dead wood in any of the sites (Table 2). The basal area of living trees was lower in the burned area compared to the control in both Bodträskfors and Lainio but no such difference was found in Muddus (Table 2).

3.2 Species richness and abundances

In total I recorded 610 polypores of 32 species (Appendix 1). The control areas had in total 138 records of 26 species while the burned areas had 472 records of 20 species. All three sites had more records in the burned area compared to the control. In Bodträskfors I recorded 72 polypores of 17 species in the control and 270 polypores of 12 species in the burned area. For Lainio these numbers were 43 records of 16 species in the control and 112 records of 12 species in the burned area. Muddus was the only sites with a higher species number in the burned area, which had 90 records of 13 species compared to the control with 23 records of 10 species. The

most abundant species in this study were *Trichaptum fuscoviolaceum* (Ehrenb.: Fr.) Ryvarden (174 logs), *T. abietinum* (Dicks.:Fr.) Ryvarden (78 logs) and *Gloeophyllum sepiarium* (Wulfen : Fr.) P. Karst. (58 logs). They represented together 51 % of the polypore records. Together with *Antrodia serialis* (Fr.) Donk (42 logs), *A. sinuosa* (Fr.: Fr.) P. Karst. (37 logs), *Phellinus ferrugineofuscus* (P. Karst.) Bourdot. (34 logs) and *Fomitopsis rosea* (Alb. & Schwein.:Fr.) P.Karst. (34 logs), they represented 75 % of the records (Appendix 1). In both Bodträskfors and Muddus the proportion of logs with species was higher in the burned area compared to the control but no difference was found in Lainio (Table 2).

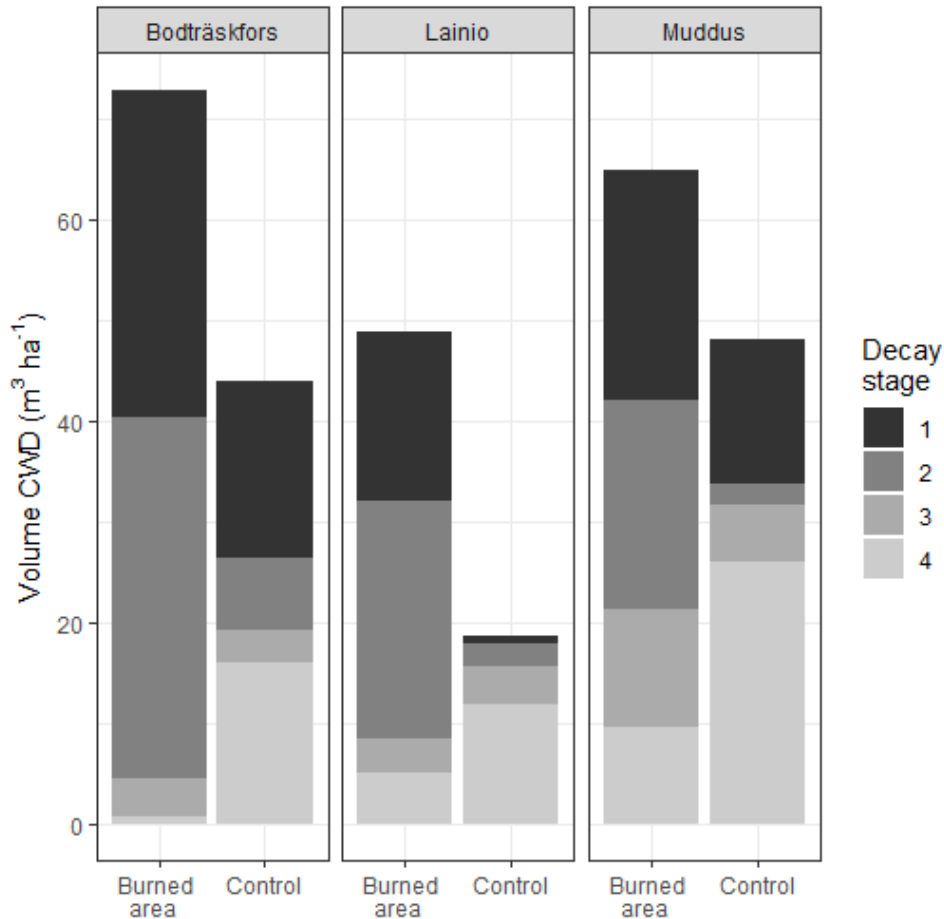


Figure 3. Volume of coniferous CWD (logs with a diameter > 15 cm) in each site. The division of decay stages is according to Gibb et al. (2005): 1) bark intact or starting to loosen, > 50 % bark remaining, wood hard; 2) < 50 % bark remaining, surface of wood smooth, but beginning to soften, wood hard; 3) lacking bark, 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 hard wood, surface of object hard to define, outline of object indefinable.

The total number of red-listed species was lower in the burned area compared to the control at all three sites. In Bodträskfors the number of red-listed species was 4

in the burned area and 11 in the control. However, Bodträskfors was the only site that had more records of red-listed species in the burned area (41 records) compared to the control (33 records). In Lainio I recorded 14 red-listed polypores of 6 species in the burned area and 23 of 10 species in the control. In Muddus the red-listed polypores were 6 records of 3 species in the burned area and 12 records of 4 species in the control.

Table 3. Results from the multivariate test (ManyGLM) for the overall polypore community as a response to site, treatment (burned or control) and the interaction between site and treatment.

Source	df _{res}	Df _{diff}	Dev	P
Proportion spruce	58	1	183.3	0.001
Site	56	2	107.7	0.001
Treatment	55	1	189.6	0.001
Site:Treatment	53	2	74.7	0.001

3.3 Polypore community

The community of polypores differed both among sites and between the controls and burned plots (Table 3). There was also an interaction effect between site and treatment (Table 3), i.e. the difference in community structure between controls and burned areas was different in different sites. The overall community of polypores differed between the burned area and control in all three sites (Table 4). The NMDS ordination indicated a similar difference in community structure in all sites (Figure 4) and some species contributed to the difference in more than one area (Table 5). In Bodträskfors, *T. fuscoviolaceum* and *G. sepiarium* contributed to the difference in the polypore community after controlling for number of logs and proportion of spruce. In Lainio the contributing species were *T. fuscoviolaceum*, *F. rosea*, *A. sinuosa*, *P. viticola* (Schwein. ex Fr.) Donk and *P. ferrugineofuscus* while it was *A. sinuosa*, *A. xantha* (Fr.:Fr.) Ryvardeen, *T. fuscoviolaceum*, *A. albobrunnea* (Romell) Karasiński & Niemelä, *P. viticola* and *Sidera lenis* (P.Karst.) Miettinen in Muddus (Table 5). *T. fuscoviolaceum*, *G. sepiarium*, *A. xantha* and *A. sinuosa* were more abundant in burned areas while *P. ferrugineofuscus*, *P. viticola*, *F. rosea*, *A. albobrunnea* and *S. lenis* were more abundant in the controls where they contributed to the difference in the overall community.

Table 4. Results from the multivariate test (ManyGLM) for the overall polypore community as a response to forest fire. Separate tests are done for each site as the response differed.

Source	df _{res}	Df _{diff}	Bodträskfors		Lainio		Muddus	
			Dev	P	Dev	P	Dev	P
Proportion spruce	18	1	88.71	0.001	35.86	0.062	56.58	0.038
Treatment	17	1	89.64	0.001	84.42	0.001	63.94	0.001

T. fuscoviolaceum was both the most abundant species but also the only species that in all three sites showed a significant contribution to the difference in the overall polypore community. It was recorded once in the controls and 173 times in the burned areas. At 68 % of the logs where it was recorded, at least some fruiting bodies grew on a charred surface, normally bark. 98 % of the records were on logs in decay stage 1 or 2 (the youngest decay stages). These stages represent 60 % of the logs (74 % in the burned areas). Spruce represented 40 % of the total number of logs (41 % of logs in decay stage 1 or 2 located in a burned area) and hosted 52 % of the *T. fuscoviolaceum* records. Also *G. sepiarium* was recorded mainly on logs of decay stage 1 and 2 in the burned areas. It grew almost exclusively on spruce and was recorded on a charred surface on 36 % of its host logs. Both *A. sinuosa* and *A. xantha* showed a positive response to fire. They were recorded on a charred surface in 92 respectively 77 % of the logs where they occurred. They mainly grew on heavily charred wood in older decay stages. The records on decay stage 3 or 4 were 89 % for *A. sinuosa* and 86 % for *A. xantha*. 87 % of the *P. viticola*-records was on logs of decay stage 4 (the rest on decay stage 3) and 53 % was on pine. *F. rosea* was in Lainio more abundant in the burned area than the control and was one of the species contributing to the community difference due to the interaction between treatment and site ($p = 0.024$).

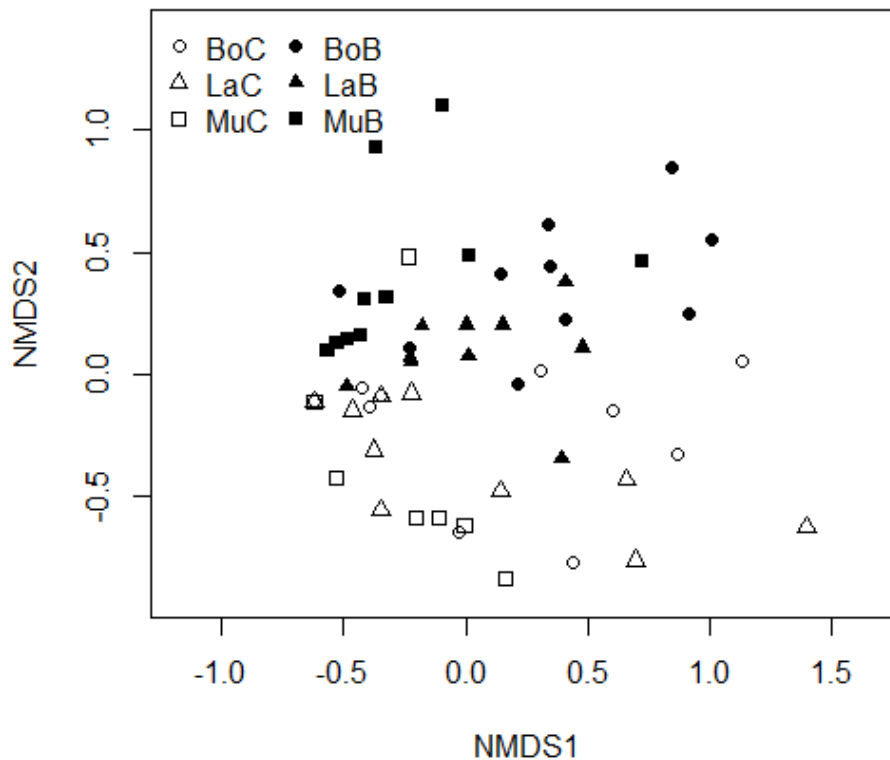


Figure 4. Nonmetric Multidimensional Scaling (NMDS) ordination of polypore community structure. Empty figures denote control in Bodträskfors (BoC), Lainio (LaC) and Muddus (MuC) and filled figures denote burned areas in Bodträskfors (BoB), Lainio (LaB) and Muddus (MuB). Each point represents the polypore community in one sampling plot.

In Bodträskfors, 7 species were found in both the control and the burned area. 10 species were only found in the control and 8 of those were red-listed, including the endangered *A. primaeva* (Renvall & Niemelä) and the vulnerable *Amylocystis lapponica* (Romell) Singer, *A. albobrunnea*, *Antrodiella pallasii* (Renvall, Johannesson & Stenlid), *S. lenis* and *Steccherinum collabens* (Fr.) Vesterholt. 5 species were unique for the burned area and only one, *Diplomitoporus crustulinus* (Bres.) Domański was red-listed. However this vulnerable species was found on 7 logs. All records were on charred bark on spruce logs of decay stage 1 or 2. In Lainio 8 species were found in both the control and the burned area. Eight species, whereof 6 were red-listed in Sweden (ArtDatabanken, 2015) including the vulnerable *A. lapponica*, *A. pallasii*, *Skeletocutis brevispora* (Niemelä), *S. chrysella* (Niemelä) and *S. odora* (Niemelä), were only present in the control. Seven species whereof 2 red-listed, including *D. crustulinus*, were unique for the burned area. In Muddus, I recorded 6 species in both areas, while 4 species (3 red-listed) were unique for the control and 7 species (2 red-listed) for the burned area. The red-listed species unique for the control included 2 vulnerable species (*A. albobrunnea* and *S. lenis*). *A. albobrunnea* was found on 7 logs, all them pine in decay stage 3 or 4.

Table 5. Results from the multivariate test (ManyGLM) that shows the individual response for the five species in each site that contributed to the most difference in polypore communities. Species were I found a significant response to forest fire is marked either with (+) for a positive response and (-) for a negative response.

	Species	Proportion spruce		Treatment		
		Dev	P	Dev	P	Contribution to difference (%)
Bodträskfors	<i>Trichaptum fuscoviolaceum</i>	1.12	1	23.59	0.001 ⁺	26.3
	<i>Gloephyllum sepiarium</i>	3.82	0.689	20.32	0.001 ⁺	22.7
	<i>Phellinus viticola</i>	0.00	1	6.58	0.122	7.3
	<i>Steccherinum collabens</i>	2.85	0.922	5.81	0.154	6.5
	<i>Antrodia sinuosa</i>	0.69	1	5.57	0.190	6.2
Lainio	<i>Trichaptum fuscoviolaceum</i>	1.42	0.968	23.95	0.001 ⁺	28.4
	<i>Fomitopsis rosea</i>	0.33	1	14.98	0.002 ⁻	17.7
	<i>Antrodia sinuosa</i>	1.87	0.951	9.11	0.016 ⁺	10.8
	<i>Phellinus viticola</i>	0.00	1	8.31	0.023 ⁻	9.8
	<i>Phellinus ferrugineofuscus</i>	0.03	1	5.88	0.059	7.0
Muddus	<i>Antrodia sinuosa</i>	3.66	0.46	14.63	0.001 ⁺	22.9
	<i>Antrodia xantha</i>	3.12	0.483	13.60	0.001 ⁺	21.3
	<i>Trichaptum fuscoviolaceum</i>	5.25	0.167	10.09	0.001 ⁺	15.8
	<i>Antrodia albobrunnea</i>	1.19	0.487	6.75	0.016 ⁻	10.6
	<i>Phellinus viticola</i>	1.39	0.483	6.58	0.016 ⁻	10.3

4 Discussion

This is one of the first studies on the polypore communities after wildfires (but see Ylisirniö *et al.* (2012) and Kurth *et al.* (2013)) and the study is unique in the sense that I include three separate fires from the same year. According to my results, the polypore communities 12 years post fire were clearly different from those in unburned control areas. A few very abundant generalist species occurred significantly more frequently in burned areas while the total species number was lower, suggesting that fire results in a short-term reduction in species richness of polypores, agreeing with earlier studies on wood-decaying fungi (Penttilä and Kotiranta, 1996; Junninen, Kouki and Renvall, 2008; Olsson and Jonsson, 2010; Penttilä *et al.*, 2013).

The polypore community composition is dependent on the amount and quality of CWD, which differed between burned areas and controls. The lower amount of CWD of old decay stages in the burned areas is probably explained by the pre-fire CWD being consumed by the fire. The high amount of CWD in young decay stages on the other hand can be explained by that the fire killed many trees which had not reached old decay stages at the time of this study. The fire also changed the microclimate for the logs by reducing the number of living trees which lead to higher exposure to wind and sun. Together with the consumption of ground vegetation and litter it leads to a decrease in log moisture, important for wood-decaying fungi (Boddy, 1983).

To generalize, species that contributed the most to the difference in the polypore community was generalist species (*Trichaptum fuscoviolaceum*, *Gloephyllum sepiarium*, *Antrodia xantha* and *A. sinuosa*) that were more abundant in the burned area and old-growth forest specialists (*Fomitopsis rosea*, *Phellinus viticola* and *A. albobrunnea*), which were more abundant in the controls. An increase of *T. fuscoviolaceum* after a fast increase of dead wood is agreeing with earlier studies both on prescribed burning (Penttilä *et al.*, 2013) but also on felling or girdling of trees (Pasanen, Junninen and Kouki, 2014). Notable is that *T. fuscoviolaceum* is often mentioned as growing mainly on pine (Ryvaarden and Melo, 2017). In this study, I recorded many on spruce too and I argue that the quality of the wood is more important than the species, i.e. it grows preferable on hard and dry wood, which is more common for pine as it usually grow in more exposed sites. That *A. xantha* and *A. sinuosa* were more abundant in burned areas agreeing with earlier studies (Olsson and Jonsson, 2010; Penttilä *et al.*, 2013) and I found both species mainly on heavily charred wood. Even though the total species number and the number of red-listed

species were lower in the burned area than in the control, it is from a conservation perspective important to weight the local diversity against the diversity on a landscape level. Old-growth forests have declined due to forestry (Svensson *et al.*, 2019) but wildfires have almost disappeared from the landscape (Niklasson and Granström, 2000). The control sites in this study had high conservation values, but in the burned area, many values were lost while new were created. A forest with low amounts of dead wood has probably a higher net increase of conservation values due to fire as few conservation values are lost but dead wood is created. As the red-listed species *F. rosea* and *P. ferrugineofuscus* belonged to the most abundant species in the control in Lainio and Bodträskfors while *A. albobrunnea* and *Sidera lenis* belonged to the most abundant species in the Muddus control, it is likely that they are common in the nearby (not clear-cut) areas. The red-listed *Diplomitoporus crustulinus*, on the other hand, was found in the burned area in both Bodträskfors and Lainio but not in any of the controls, which suggests the species is rare in the landscape due to lack of fire. All records were on charred bark but the species is traditionally not described as a fire-favoured species even though single specimens have been found in prescribed burned areas before (Ylisirniö *et al.*, 2012; Penttilä *et al.*, 2013). Perhaps the species prefer highly intense fires with high tree mortality as in Bodträskfors and Lainio, while many of earlier studies are from prescribed burned areas. Some of the red-listed species that were short-time disadvantaged by fire can probably re-establish. Penttilä *et al.* (2013) showed that both *F. rosea* and *P. ferrugineofuscus* had increased 13 years after fire compared to pre-fire numbers. Further, those species were rarer in the burned area in Lainio but more abundant the burned area in Bodträskfors, compared to their respective controls. This indicates that the rate of which they recover is climate dependent. *A. albobrunnea* and *S. lenis* was not found in the burned area but can also be favoured by fire in a long term perspective as they grow on pine trees and pine forests naturally is maintained by wildfires (Engelmark, 1987). Also the control in Muddus can be seen as a succession stage after fire as it burned 150 years ago (Granström and Niklasson, 2011).

Even though 12 years passed since the forest fires, it is likely that the number and abundance of species on dead wood still have not peaked. Penttilä *et al.* (2013) found that both the total number of polypore species and the number of red-listed species reached its peak 13 years after a prescribed burning in eastern Finland. My study sites are on a higher latitude, why it is likely that the species number will reach its peak later, as the decay rate is temperature dependent (Wells and Boddy, 1995). Most pre-fire species that returned after 13 years in the study by Penttilä *et al.* (2013) were absent or very rare at the burned areas in my study even though I observed them in the controls, indicating some of the conservation benefits from forest fire has probably not been obtained yet. That *F. rosea* and *P. ferrugineofuscus* were abundant in the burned area in Bodträskfors indicates that Bodträskfors (in opposite to Lainio) has reached the successional stage when red-listed species start to increase.

To get a better understanding of the ecological response after wildfires it is important to follow burned areas for several decades as forest with a natural fire regime goes through many different succession stages (Bergeron *et al.*, 2002; Ylisirniö *et al.*, 2012). The control area in Muddus can be viewed as a late succession stage as it burned in 1868 (Granström and Niklasson, 2011). Charred stumps and logs were

still clearly visible. In Lainio, forest fires have probably been rare due to the high latitude and short summers. However, after a wildfire in a similar forest 65 kilometers northwest of Lainio, several fire-favoured insects were found (Högdahl *et al.*, 2017), indicating a continuity of fires. Prescribed burning is also used as a method to facilitate regeneration at clear-cuts near Lainio, which might have contributed to the preservation of fire-dependent species in the area. Old growth spruce forest takes a long time to establish after forest fires. First, the pioneer trees (pine and deciduous) establish but they can be outcompeted by spruce over time if there is no new disturbance event (Engelmark, 1987). The wildfire in Bodträskfors will probably have a positive effect on the biodiversity for at least 100 years. First, the dead wood created in the fire will be there for several decades before it is decayed. Second, the post fire forest will have a high proportion of deciduous trees, mainly birch and aspen. Deciduous forest has decreased due to forestry and fire prevention (Esseen *et al.*, 1997; Östlund, Zackrisson and Axelsson, 1997). The deciduous stage after a disturbance is one of the most species-rich forest types in boreal Fennoscandia and many species are associated with deciduous boreal forests including lichens, fungi, bryophytes, insects and birds (Angelstam and Mikusinski, 1994; Kuusinen, 1994; Siitonen and Martikainen, 1994; Crites and Dale, 1998).

The clearly higher number of species per log in the burned area compared to the control in Muddus can be explained by (1) it was a low intensity fire, leaving many trees alive and therefore not having as large of an effect on the microclimate as in the other areas and (2) there were already many polypore species in the area adapted to forest fires. The most effective dispersal of wood-decaying fungi is only within a few hundred meters (Edman, Kruys and Jonsson, 2004; Norros *et al.*, 2012). Pines are adapted to fires and pine forests is often a result of regular fires (Engelmark, 1987) and Muddus National Park has a long fire history (Engelmark, 1984; Granström and Niklasson, 2011). Indicated by the differences in basal area, both Bodträskfors and Lainio had high tree mortality which created lots of CWD but likely also changed the microclimate. In Muddus, on the other hand, I found neither a difference in the basal area nor log density between the burned area and the control.

As natural forest fires have declined due to human activity (Niklasson and Granström, 2000), prescribed burnings can be a way to conserve biodiversity (Olsson and Jonsson, 2010; Penttilä *et al.*, 2013). When prioritizing which area to burn, my study provides important information on the ecological response of the polypore community. I emphasize a few factors that are crucial for how the polypore community develops post fire. Two of these are stand age and composition of tree species. Both these factors are influenced by historical disturbance events such as fire and cutting. Factors like climate and topography will in turn have an impact on the fire-regime. Climate will likely also affect the rate of which the polypore community establish after fire as it influence the re-generation rate of post-fire forest and the decay rate of dead wood (Boddy, 1983).

Most prescribed burnings is relatively low-intense and done in pine-dominated forests. To burn these forests is important for conservation as many species in these forests is adapted to recurring fires. My study indicates that also stand-replacing fires in high-productive spruce forests can have positive effects on threatened polypore species. This indicates a need for a variety of prescribed burns, including stand-

replacing fires in spruce forests. However, more replicated studies are needed to evaluate the effect of fire on the community structure of polypores. Preferably in later successional stages when logs have reached later decay stages and a post-fire forest dominated by deciduous trees has regenerated.

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Appendix 1

Appendix 1. All specimens recorded in the study.

Species and red-list category ¹	Control site				Fire site			
	Bodträskfors	Lainio	Muddus	Total	Bodträskfors	Lainio	Muddus	Total
<i>Amylocystis lapponica</i> VU	1	1	-	2	-	-	-	-
<i>Antrodia albobrunnea</i> VU	1	-	7	8	-	-	-	-
<i>Antrodia primaeva</i> EN	1	-	-	1	-	-	-	-
<i>Antrodia serialis</i>	10	5	-	15	24	1	2	27
<i>Antrodia sinuosa</i>	-	-	2	2	10	1	24	35
<i>Antrodia xantha</i>	1	1	1	3	3	1	15	19
<i>Antrodiella pallasii</i> VU	1	1	-	2	-	-	-	-
<i>Diplomitoporus crustulinus</i> VU	-	-	-	-	7	1	-	8
<i>Fomitopsis pinicola</i>	6	-	1	7	13	1	4	18
<i>Fomitopsis rosea</i> NT	11	7	-	18	15	1	-	16
<i>Gloephyllum sepiarium</i>	-	3	-	3	46	5	4	55
<i>Ischnoderma benzoinum</i>	-	-	-	-	1	-	-	1
<i>Meruliopsis taxicola</i>	3	-	-	3	-	2	-	2
<i>Oligoporus sericeomollis</i>	-	-	-	-	-	-	1	1
<i>Onnia leporina</i> NT	-	2	-	2	-	-	-	-
<i>Phellinus viticola</i>	4	5	5	14	-	1	-	1
<i>Phellinus chrysoloma</i> NT	1	2	-	3	-	4	-	4
<i>Phellinus ferrugineofuscus</i> NT	10	3	-	13	16	1	4	21
<i>Phellinus nigrolimitatus</i> NT	2	3	-	5	-	5	-	5
<i>Phellinus pini</i> NT	-	-	-	-	-	-	1	1
<i>Postia parva</i> NT	-	-	1	1	-	-	-	-
<i>Postia stiptica</i>	-	-	-	-	-	-	1	1
<i>Sidera lenis</i> VU	1	-	3	4	-	-	-	-
<i>Skeletocutis biguttulata</i>	-	-	-	-	-	-	1	1
<i>Skeletocutis brevispora</i> VU	-	1	-	1	-	-	-	-
<i>Skeletocutis carneogrisea</i>	-	1	-	1	-	-	-	-
<i>Skeletocutis chrysella</i> VU	-	1	-	1	-	-	-	-
<i>Skeletocutis odora</i> VU	-	2	-	2	-	-	-	-
<i>Steccherinum collabens</i> VU	3	-	-	3	-	-	-	-
<i>Trichaptum abietinum</i>	15	5	1	21	42	20	15	77
<i>Trichaptum fuscoviolaceum</i>	-	-	1	1	90	66	17	173
<i>Trichaptum laricinum</i> NT	1	-	1	2	3	2	1	6
Number of sampled logs	129	41	188	358	270	163	203	636
Number of species	17	16	10	26	12	15	13	20
Number of records	72	43	23	138	270	112	90	472

¹According to Artdatabanken (2015). Species without red-list category is classified as Least Concern (LC) in Sweden.

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