Received: 12 January 2023 | Revised: 24 April 2023 | Accepted: 11 May 2023

DOI: 10.1002/eap.2892

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Prescribed fire is an effective restoration measure for increasing boreal fungal diversity

Ellinor Ramberg[1] | **Håkan Berglund**[2] | **Reijo Penttilä**[3] | **Joachim Strengbom**[1] | **Mari Jönsson**[2]

[1]Department of Ecology, Swedish University of Agricultural Science, Uppsala, Sweden

[2]Swedish Species Information Centre, Swedish University of Agricultural Science, Uppsala, Sweden

[3]Natural Resources Institute Finland (LUKE), Helsinki, Finland

Correspondence
Ellinor Ramberg
Email: ellinor.karin.ramberg@slu.se

Funding information
Skogssällskapet, Grant/Award Number: 2019-655-Steg 2 2018

Handling Editor: Carolyn Hull Sieg

Abstract

Intensive forestry practices have had a negative impact on boreal forest biodiversity; as a consequence, the need for restoration is pressing. Polypores (wood-inhabiting fungi) are key decomposers of dead wood, but, due to a lack of coarse woody debris (CWD) in forest ecosystems, many species are under threat. Here, we study the long-term effects on polypore diversity of two restoration treatments: creating CWD by felling whole trees and prescribed burning. This large-scale experiment is located in spruce-dominated boreal forests in southern Finland. The experiment has a factorial design ($n = 3$) including three levels of created CWD (5, 30, and 60 m^3 ha^{-1}) crossed with burning or no burning. In 2018, 16 years after launching the experiment, we inventoried polypores on 10 experimentally cut logs and 10 naturally fallen logs per stand. We found that overall polypore community composition differed between burned and unburned stands. However, only red-listed species abundances and richness were positively affected by prescribed burning. We found no effects of CWD levels created mechanically by felling of trees. We show, for the first time, that prescribed burning is an effective measure for restoring polypore diversity in a late-successional Norway spruce forest. Burning creates CWD with certain characteristics that differ from what is created by CWD restoration by felling trees. Prescribed burning promotes primarily red-listed species, demonstrating its effectiveness as a restoration measure to promote diversity of threatened polypore species in boreal forests. However, because the CWD that the burning creates will decrease over time, to be functional, prescribed burns need to be applied regularly on the landscape scale. Large-scale and long-term experimental studies, such as this one, are invaluable for establishing evidence-based restoration strategies.

KEYWORDS
boreal forest, coarse woody debris, long-term experiment, polypore, prescribed fire, restoration

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INTRODUCTION

Globally, the degradation of ecosystems due to human activities has led to a decline in biodiversity, and consequently, the need to restore natural habitats is recognized globally (European Commission, 2022; IPBES, 2018). However, to be successful, restorations need to be tailored to fit the specific habitat type, and for this, in-depth knowledge of species ecology is necessary (Halme et al., 2013).

In boreal forests of northwestern Europe, there is a great need to restore values lost due to the long history of large-scale forestry (Halme et al., 2013; Kuuluvainen & Gauthier, 2018; Östlund & Zackrisson, 1997). Practices such as clear-cutting and planting of monocultures have degraded boreal forest landscapes such that there is a lack of key structural components (e.g., dead wood) and functions (e.g., natural processes such as disturbances) (Jonsson et al., 2016; Lindberg et al., 2020; Ramberg et al., 2018; Siitonen, 2001). Consequently, many species associated with these structures and functions are threatened, including many saproxylic (wood-inhabiting) species (Hyvärinen et al., 2019; SLU Artdatabanken, 2020; Tomao et al., 2020).

Polypores (saproxylic fungi with poroid hymenophore) play a key role in the decomposition of dead wood in boreal forest ecosystems (Siitonen, 2001). Due to the aforementioned lack of dead wood, several polypore species are red-listed in Fennoscandia. Many have specific habitat quality requirements and are confined to dead wood of particular size, decay stage, and tree species (Berglund, Hottola, et al., 2011; Junninen & Komonen, 2011; Penttilä et al., 2004). The diversity and abundance of polypores also increase with increasing local abundance of coarse woody debris (CWD) (Junninen & Komonen, 2011; Penttilä et al., 2004; Tomao et al., 2020). Therefore, restoration of polypore communities needs to target both the quality and quantity of CWD.

In forests with natural dynamics, disturbances such as wind throws and fire create large amounts of CWD. Restoration of CWD volumes in degraded forests commonly aims to emulate these natural disturbances by, for example, mechanical felling of living trees (Sandström et al., 2019; Similä & Junninen, 2012). Although CWD created by felling trees promotes overall species richness of saproxylic species (Koivula & Vanha-Majamaa, 2020; Sandström et al., 2019), such measures tend to deliver a rather uniform type of CWD that lacks much of the variation in quality that is characteristic of naturally generated CWD. Hence, the benefit of this type of measure for red-listed polypores seems limited (Pasanen et al., 2014, 2019; Sandström et al., 2019). Prescribed burning (hereafter burning) is another way of emulating a natural disturbance that creates CWD. Besides generating a pulse of CWD by instantly killing many trees, fire also injures trees, which successively die and fall down, creating CWD several years after the initial disturbance. Although many polypores seem to die from the fire, and so burning in general has an immediate negative effect, polypore communities usually recover quickly and commonly diversify within a few years after a burn (Berglund, Jonsson, et al., 2011; Koivula & Vanha-Majamaa, 2020; Penttilä et al., 2013). Additionally, burning modifies the characteristics of the dead wood itself (e.g., hemicellulose structure), which has shown to influence polypore community composition (Alen et al., 2002; Carlsson et al., 2012; Edman & Eriksson, 2016; Kamdem et al., 2002).

Although adding CWD and burning are commonly used restoration measures in boreal forests that appear to promote polypore diversity, their effectiveness in promoting threatened species, especially in the long term, is surprisingly poorly understood (however, for pine forests see Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015). In managed spruce forests, long-term and large-scale experimental studies that compare different restoration measures are particularly lacking, especially considering the importance of spruce forests for highly specialized species (such as red-listed polypore species) (Hyvärinen et al., 2019; SLU Artdatabanken, 2020). Nevertheless, identifying the long-term responses of biological communities to restoration under field experimental conditions is fundamental to inform and refine evidence-based conservation strategies (Halme et al., 2013; Seibold et al., 2015).

In this study we analyzed the long-term effects on polypore community composition (abundance and species richness) by restoration of CWD by felling of whole trees and by prescribed burning in spruce-dominated boreal forests. For this we utilized a unique large-scale and long-term forest restoration experiment (the Evo experiment; Lilja et al., 2005; Vanha-Majamaa et al., 2007) located in a managed landscape in southern Finland. In particular, we examined whether the effects on diversity of red-listed and specialized polypore species differed depending on CWD levels (from cut logs) and if effects depended on whether or not CWD levels were crossed with burning. Finally, we addressed the extent to which log origin (i.e., cut logs compared to naturally fallen logs) influenced the polypore community.

MATERIALS AND METHODS

Study area

The study was located in the Evo-Vesijako region of Finland (61° N, 25° E). The region is within the southern boreal vegetation zone (Ahti et al., 1968) and has an annual average precipitation of ~670 mm, a mean annual temperature of +3.1°C, and a growing period of 160 days. The region is dominated by forests, mostly publicly owned, and has a long tradition of ecological research (Vanha-Majamaa et al., 2007). The Evo-Vesijako region has a long history of the use of prescribed fire in the landscape, and burns have been executed on both standing forest and clear-cuts in the area for at least 70 years (Hyväluoma et al., 2022).

For this study, we included the same 18 experimental stands studied by Berglund, Jonsson, et al. (2011). The forest stands are located within an area of 25 × 15 km, and each stand has an area of 1–3 ha. Prior to treatment in 2001, all stands had been influenced by forest management, and their average stand age was 80 years (60–100 years). The stands were predominantly of the mesic type, dominated by mature Norway spruce (*Picea abies*), with no significant pretreatment differences in volume of living trees or dead wood among stands (Lilja et al., 2005).

Experimental design and polypore inventory

The 18 stands are part of a field experiment set up in 2001 (Lilja et al., 2005; Vanha-Majamaa et al., 2007). The stands were subjected to different treatments following a standard factorial design with three replicates of each treatment. All treatments were randomized among the stands. First, in the winter of 2002, all stands were subjected to partial cutting, maintaining a constant volume of standing retention trees of 50 $m^3\ ha^{-1}$. A portion of the felled trees was then used to create three CWD levels (5, 30, and 60 $m^3\ ha^{-1}$, six stands per level) by retaining the cut trees on the forest floor. The remaining timber was removed from the stands. Second, in the summer of 2002, half of the stands (three of each CWD level, nine in total), were burned, while the other half remained unburned.

In 2018, 16 years after the treatments, we inventoried polypores on 10 experimentally cut logs and 10 naturally fallen logs per stand. However, in three stands we were unable to find 20 logs, so there we inventoried all available logs (14, 16, and 19 logs, respectively). Broken logs (with stem breakage at ≥2.5 m height) or logs lying on top of each other were excluded. All logs were randomly selected based on the nearest distance to the center point of each stand. The dbh (cm) and decay class according to Karjalainen and Kuuluvainen (2002), modified from Renvall (1995), was measured for each log.

In total, we surveyed 349 Norway spruce logs in 2018. The polypore species were recorded by the presence of fruiting bodies per log, an efficient method of surveying dominant species (Allmer et al., 2006). Besides polypore species, we also followed and recorded a few red-listed or indicator corticoid fungi (Corticiaceae) if they were found. Dead identifiable fruiting bodies were also included, as we focused on the general temporal effect rather than records for a specific year. The nomenclature of polypores follows Niemelä (2016), while that of corticoid fungi follows Kotiranta et al. (2009). Red-listed species were classified according to Finnish red lists for 2019, 2010, and 2000 (Hyvärinen et al., 2019).

Statistical analyses

Data collected from a total of 20 logs of different origin (10 cut, 10 natural) were compiled and analyzed for each stand. In this way, all results per stand were based on the 20 logs, except for the aforementioned three stands with fewer logs. All analyses were done in RStudio in the statistical programming environment R (version 4.1.2; R Core Team, 2021). We analyzed different measures of polypore species diversity. First, we analyzed the abundance and species richness when considering all species, but also when considering red-listed species only. The abundance of species was measured as the total number of species records made in each stand, and one record corresponded to a finding of an individual species on a single log. The species richness was measured as the total number of species recorded across all the logs sampled in each stand. Second, we analyzed the species composition of stands considering all species and red-listed species.

We tested how the variation in polypore species diversity between stands was explained by the two main experimental treatment factors: (1) CWD level (5, 30, and 60 $m^3\ ha^{-1}$) and (2) burning (burned vs. unburned). The effects of the main factors were thus tested using independent measures of species diversity from each stand. The effects of the main treatment factors and their interaction on abundance and species richness were analyzed with generalized linear models ("glm" function, MASS package; Venables & Ripley, 2002). Poisson models with a log-link function are appropriate for count data and were therefore first used. However, to account for overdispersion and underdispersion (a dispersion parameter 0.5 above or below 1, respectively) quasi-Poisson models were often more appropriate and therefore used for analyzing the abundance and species richness of all species and the abundance of red-listed species. To assess model validity, Fisher-Pitman permutation tests based on 10,000 Monte Carlo resamplings were run ("oneway_test" function, coin package; Hothorn et al., 2006).

To test whether species composition differed between main treatments, we used nonmetric multidimensional scaling (NMDS) ordination ("metanmds" function, vegan package; Oksanen et al., 2020) with Euclidean distances on Hellinger transformed data. Assumptions of homogeneity of spread were tested ("betadisper" functions, vegan package; Oksanen et al., 2020). Dissimilarities detected between main treatments were tested with permutational multivariate analyses of variance (PERMANOVA; "Adonis" function, vegan package; Oksanen et al., 2020). As significant dissimilarities were found only between burned and unburned stands, and not across stands of different CWD levels, only the ordination for burning was included in the results. Finally, the relative contribution of each species (%) to the dissimilarity between ordination groups was analyzed ("simper" function, vegan package; Oksanen et al., 2020).

To further explore the effects of burning, the effects of the subfactor log origin (cut vs. naturally fallen) were tested on species abundance and richness. This was done in a separate set of analyses, including two measures from each stand, one for species found on cut logs and one for species found on naturally fallen logs. Thus, this test included two correlated measures from each stand. Again, generalized linear models were fitted using Poisson or quasi-Poisson with a log-link function. Models were compared with and without the random effect of stand identity to assess the impact of the correlation. As there was no significant difference between the models, the simpler model without the random effect (stand identity) was used. To assess model validity, Fisher-Pitman permutation tests were run ("oneway_test" function, coin package; Hothorn et al., 2006). Additionally, the polychoric correlation between log origin and decay class was tested ("polychor" function, polycor package; Fox, 2022).

RESULTS

Effects of CWD and burning on all species

In total, we recorded 1153 fruiting bodies of 39 species (Appendix S1: Tables S1 and S2). There were no significant differences between CWD levels, though there was a tendency toward increasing abundance at higher levels of CWD (Figure 1, Table 1). Likewise, we found no difference between burned and unburned stands, either for abundance or richness (Figure 1, Table 1). Altogether 576 records of 32 species were made in the burned stands and 577 records of 33 species in the unburned stands (Appendix S1: Table S1). We found no interaction between burning and CWD levels (Table 1).

Effects of CWD and burning on red-listed species

In total we recorded 70 fruiting bodies of nine red-listed species (Appendix S1: Tables S1 and S2). No significant differences were found between the three CWD levels, that is, varying levels of downed logs by felling alive trees, had no significant effect on either the abundance or richness of red-listed species (Figure 2, Table 2). By contrast, the burned stands had generally both higher species abundance and richness in comparison to unburned stands (Figure 2, Table 2). In total, 54 records of nine red-listed species were made in burned stands and 16 records of five red-listed species in unburned stands (Appendix S1: Table S1). Additionally, we found no significant interaction between the main treatment factors burning and CWD level (Table 2).

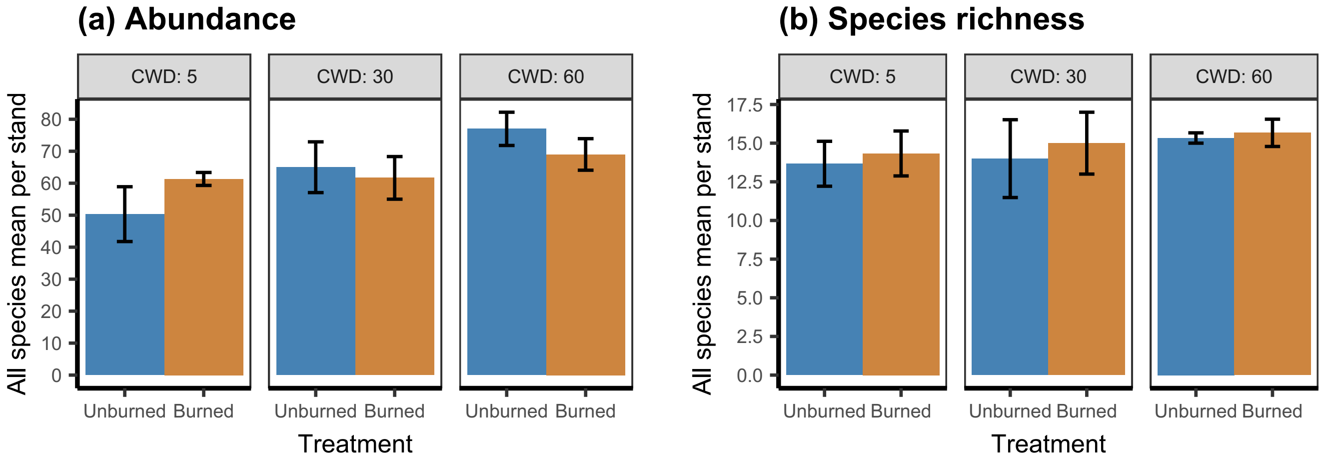

FIGURE 1 Response of polypores to main treatment factor creation of coarse woody debris (CWD) at levels 5, 30, and 60 $m^3 ha^{-1}$ and prescribed burning (burned vs. unburned) showing mean and ± SE ($N = 1153$) of abundance (a) and species richness (b) per stand (20 logs).

TABLE 1 Results of generalized linear model (Quasi Poisson with log link function, *F* test) ANOVAs for effects of the main treatment factors coarse woody debris (CWD) levels (5, 30 vs. 60 m^3 ha^{-1}) and burning (burned vs. unburned) on the abundance and species richness of all polypore species.

Diversity measure	Treatment	df	Deviance	Residual df	Residual deviance	*F* value	*p* value	Resampling *p*-value
Abundance	CWD level	2	13.84	14	28.57	3.53	0.062	**0.042**
Abundance	Burning	1	9 e-04	16	42.41	4 e-04	0.98	1
Abundance	CWD-level × burning	2	4.93	12	23.73	1.23	0.33	…
Species richness	CWD-level	2	0.47	14	6.33	0.44	0.65	0.59
Species richness	Burning	1	0.14	16	6.81	0.25	0.62	0.64
Species richness	CWD-level × burning	2	0.025	12	6.31	0.024	0.98	…

Note: Dispersion parameter for abundance is 1.96 and species richness is 0.54. The last column shows results of Fisher-Pitman permutation tests with 10,000 Monte Carlo resamplings. Statistically significant results are written in bold. Model coefficients can be found in Appendix S1: Table S3.

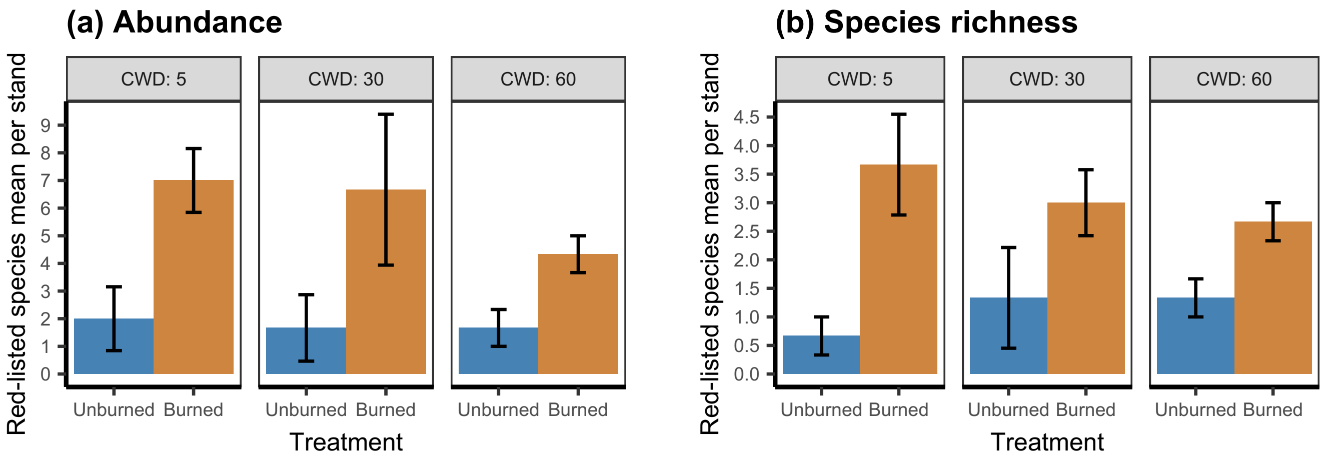

FIGURE 2 Response of red-listed polypores to main treatment factor creation of coarse woody debris (CWD) at levels 5, 30, and 60 m^3 ha^{-1} and prescribed burning (burned vs. unburned) showing mean and ± SE ($N = 70$) of abundance (a) and species richness (b) per stand (20 logs).

TABLE 2 Results of generalized linear model ANOVAs for effects of the main factors coarse woody debris (CWD) levels (5, 30 vs. 60 m^3 ha^{-1}) and burning (burned vs. unburned) on the abundance (Quasi Poisson with log link function, *F* test) and species richness (Poisson with log link function, χ^2 test) of red-listed polypore species.

Diversity measure	Treatment	df	Deviance	Residual df	Residual deviance	*F* value	*p* value	Resampling *p* value
Abundance	CWD level	2	1.99	14	21.63	0.62	0.55	0.73
Abundance	Burning	1	21.78	16	23.62	13.57	**0.003**	**0.001**
Abundance	CWD level × burning	2	0.36	12	21.26	0.11	0.89	…
Species richness	CWD level	2	0.05	14	10.01	…	0.97	1
Species richness	Burning	1	8.88	16	10.07	…	**0.003**	**0.002**
Species richness	CWD level × burning	2	1.31	12	8.70	…	0.52	…

Note: Dispersion parameter for abundance is 1.6 and species richness is 0.6. The last column shows results of Fisher-Pitman permutation tests with 10,000 Monte Carlo resamplings. Statistically significant results are written in bold. Model coefficients can be found in Appendix S1: Table S4.

Community composition

The main factor burning had a strong effect on the polypore community, resulting in a difference in community composition between burned stands and unburned stands (Figure 3; PERMANOVA $R^2 = 0.41$, $F_{1,16} = 11.13$, $p = 0.001$). The five most influential species contributing to the dissimilarity were *Trichaptum abietinum*, *Fomitopsis pinicola*, *Gloeophyllum sepiarium*, *Antrodia serialis*, and *Antrodia sinuosa* (SIMPER analysis; Table 3).

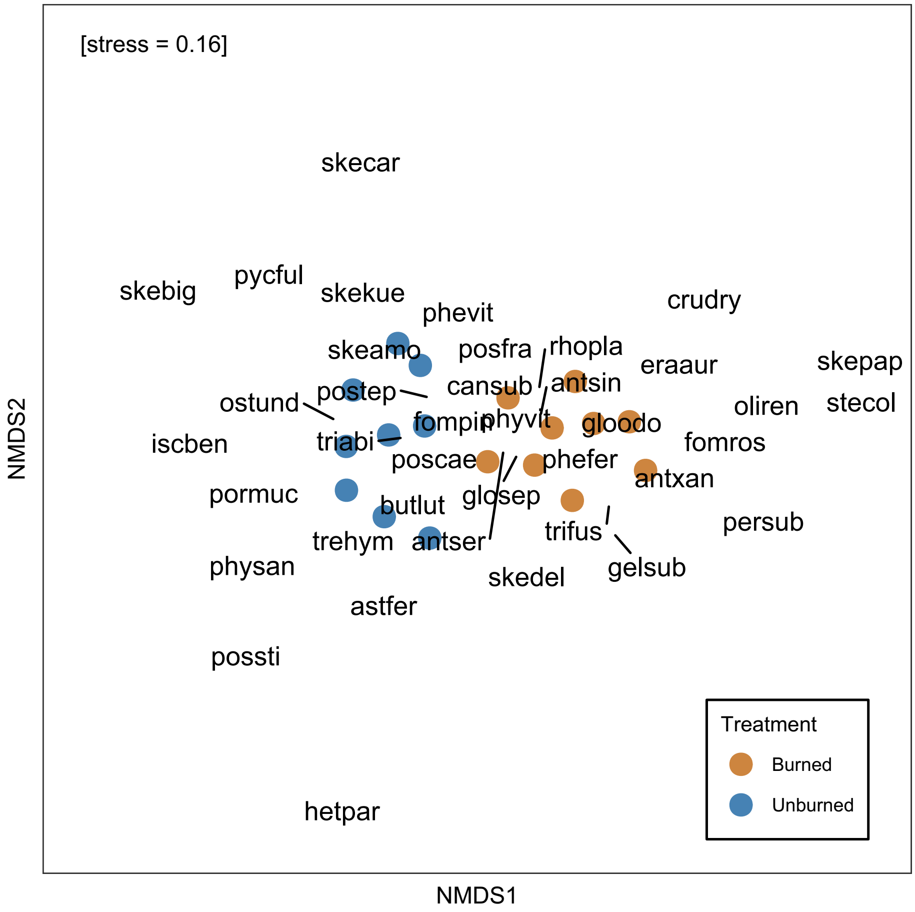

FIGURE 3 Nonmetric multidimensional scaling ordination plot showing polypore communities in burned (orange) and unburned (blue) stands. The two-dimensional stress ratio was 0.16. Species abbreviation explanations can be found in Appendix S1: Table S2.

TABLE 3 Results of SIMPER analysis for the five most influential species, showing the species contribution to average between-treatment dissimilarity, the cumulative contribution, and the average abundances in the burned and unburned stands.

Species	Abbreviations used in Figure 3	Average	Cumulative	Average abundance: Burned stands	Average abundance: Unburned stands
Trichaptum abietinum	triabi	0.07	0.15	4	12.89
Fomitopsis pinicola	fompin	0.06	0.27	5.78	12.78
Gloeophyllum sepiarium	glosep	0.05	0.39	13.44	7.00
Antrodia serialis	antser	0.05	0.50	15.78	10.22
Antrodia sinuosa	antsin	0.03	0.57	6.11	2.33

Log origin and decay class

Though we found no effect of burning alone on the whole community (Figure 1), we detected effects of burning when we accounted for log origin (cut vs. naturally fallen) (Appendix S1: Figure S1). For abundance, we found a significant interaction between burning and origin, which was that the effect of burning depended on log origin (Appendix S1: Figure S1 and Table S5). Burning was negative for species abundance on cut logs, and there was a tendency toward the same pattern for species richness (Appendix S1: Figure S1 and Table S5). The opposite was true of natural logs, with burning increasing mean responses.

For red-listed species, we detected positive treatment effects of burning even when controlling for origin, with no significant interaction between burning and log origin (Figure 4, Table 4). Burning and natural log origin had independent significant positive effects on abundance and species richness of red-listed species (Figure 4, Table 4).

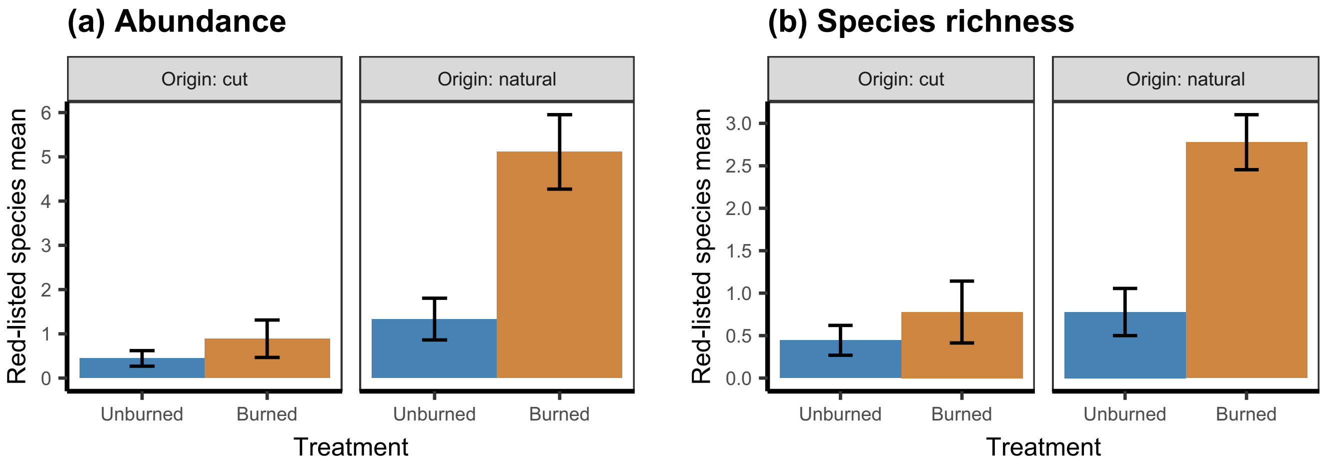

FIGURE 4 Response of red-listed polypores to main treatment factor prescribed burning (burned vs. unburned) and the subfactor log origin (cut vs. natural) showing mean and ± SE ($N = 70$) of abundance (a) and species richness (b).

TABLE 4 Results of generalized linear model (Poisson with log link function, χ^2 test) ANOVAs for effects of main treatment factor burning (burned vs. unburned) and subfactor log origin (cut vs. natural) on abundance and species richness of red-listed polypore species.

Diversity measure	Treatment	df	Deviance	Residual df	Residual deviance	*p*-value	Resampling *p*-value
Abundance	CWD level	1	21.78	34	80.69	**3.05 e-06**	**0.007**
Abundance	Burning	1	32.90	33	47.79	**9.70 e-09**	**4 e-04**
Abundance	CWD level × burning	1	0.84	32	46.94	0.36	…
Species richness	CWD level	1	10.71	34	32.65	**0.001**	**0.006**
Species richness	Burning	1	10.71	33	31.94	**0.001**	**0.005**
Species richness	CWD level × burning	1	0.86	32	31.08	0.35	…

Note: Dispersion parameter for abundance is 1.3 and species richness is 0.8. The last column shows results of Fisher-Pitman permutation tests with 10,000 Monte Carlo resamplings. Statistically significant results are written in bold. Model coefficients can be found in Appendix S1: Table S7.

With regard to log origin alone, natural logs in general had higher species richness and abundance with regard to both the entire community (Appendix S1: Figure S1 and Table S5) and red-listed species (Figure 4, Table 4), though not always significantly so. Log origin was negatively correlated with log decay class (−0.85), with cut logs being more decayed (median decay Stage 3 to 5) than natural logs (median decay stage 2 to 3.5) in unburned and burned stands at time of inventory (Appendix S1: Table S1).

DISCUSSION

Our study reveals that the mechanical creation of CWD (by felling whole trees) and CWD generated by prescribed burning results in different effects on polypore communities. Prescribed burning promoted higher species diversity of wood-inhabiting fungi, especially red-listed species, which had both higher abundance and higher species richness in burned stands compared to unburned stands. Our results highlight that fire can also be important for restoring high species diversity in habitats traditionally perceived as less fire adapted and underlines the long time scales needed for understanding polypore community-level responses to restoration.

Responses to CWD levels

In our experiment, the creation of different CWD levels by felling whole trees and leaving them as cut logs did not affect the diversity of polypores over time, which is in accordance with the findings of Berglund, Jonsson, et al. (2011), who reported the same effects 5 years after the treatments. The lack of effect from CWD levels was consistent irrespective of burn treatment, and for both the entire community and red-listed species. Thus, restoration in terms of increasing local CWD levels (5–60 m^3 ha^{-1}) in ecologically degraded forests by just felling live trees appears to have limited long-term conservation benefits with regard to the restoration of polypore diversity.

These findings are surprising since others have demonstrated positive responses; species diversity among polypores increases with local CWD availability in both descriptive (Junninen & Komonen, 2011; Penttilä et al., 2004) and experimental studies (Koivula & Vanha-Majamaa, 2020; Sandström et al., 2019; Seibold et al., 2015; Suominen et al., 2015). Essentially, a positive relationship is expected from general theory. The species–energy hypothesis (Stokland et al., 2012; Wright, 1983) states that increasing volume results in more available energy, which can sustain a higher abundance and richness of species. In addition, according to the species–area relationship (MacArthur & Wilson, 1967), an increase in volume entails more area and resources for colonization and growth of species.

What might explain our contradictory findings? The CWD in this study was created by felling trees and leaving them as cut logs at one time point, resulting in a homogeneous addition of CWD with similar characteristics. The trees' great qualitative similarity may in turn limit differentiation of polypore communities among cut logs and explain why increasing CWD levels alone has no clear effect on overall species diversity. Previous studies showed that CWD heterogeneity was an important predictor of polypore diversity, especially for rare species, which generally have more specific habitat requirements (Berglund, Hottola, et al., 2011; Junninen & Komonen, 2011). This is also supported by theory, with the habitat–heterogeneity hypothesis stipulating that species diversity will increase with habitat diversity (MacArthur & MacArthur, 1961; Seibold et al., 2016). In addition, earlier experimental studies revealed short-term positive biodiversity effects of CWD enrichment (e.g., Sandström et al., 2019; Seibold et al., 2015), but those studies did not examine long-term persistence. Polypores are known to experience succession and colonization on a decadal time scale (Penttilä et al., 2013; Suominen et al., 2015). As a result, long-term studies, such as this one, are essential to fully understand the ecology of polypores.

Effects of prescribed burning

Our study is the first large-scale experimental study to show that CWD restoration by prescribed burning has strong, unique, and long-lasting (up to 16 years) effects on polypore diversity in Norway spruce-dominated forests. The great majority of earlier studies focused on the importance of prescribed burning in fire-prone Scots pine-dominated forests (Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015), where species are considered to be adapted to reoccurring wildfires (Zackrisson, 1977). In pine-dominated forests, fire has been shown to have positive effects on polypore community diversity, especially on longer time scales (Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015). Our results show that prescribed burning also promotes diversity of red-listed polypores in less fire-prone spruce-dominated forest. We found, as in a few previous studies (Penttilä et al., 2013; Ylisirniö et al., 2012), that species (e.g., *Fomitopsis rosea*) earlier thought to be mainly confined to old-growth forests seemed to also thrive well on CWD in burned and open forest habitats.

There are several potential explanations of the positive effects of burning on both abundance and species richness of red-listed polypores. First, the community assembly may be a legacy of the heating effect fire generates, with species that have more heat-resistant mycelia gaining an advantage (Carlsson et al., 2012). In addition, heat can affect wood characteristics, such as moisture content, hemicellulose structure, and organic compounds (Alen et al., 2002; Kamdem et al., 2002), and create a habitat type that favors certain polypores over others (Edman & Eriksson, 2016).

Second, it is likely that the community assemblages that we observed are shaped by priority effects, that is, that pioneer wood-inhabiting fungal communities determine the assemblages of secondary communities (Fukami et al., 2010; Weslien et al., 2011). It is well known that wood-inhabiting fungal communities are influenced by such priority effects (Ottosson et al., 2014; Rajala et al., 2015). Community assembly trajectories have not been specifically tested for burned CWD. However, in controlled laboratory conditions, both temperature and assembly history jointly appear to determine dead-wood decomposition rate and polypore community assembly trajectories (Edman et al., 2021). In addition, Komonen et al. (2014) found differences in polypore communities between natural and created spruce logs after 8 years, suggesting that the manner in which dead wood is created (i.e., tree mortality mode) affects community trajectories. Thus, the initial differences in community composition found by Berglund, Jonsson, et al. (2011) may have been instrumental in determining the community composition observed in the present study.

Finally, burning not only creates a pulse of CWD but also injures trees, killing them gradually. The burn treatment results in a more continuous addition of CWD over a longer period than adding cut logs, creating a diversity of CWD, allowing for more specialized substrates that red-listed species often need (Berglund, Hottola, et al., 2011; Junninen & Komonen, 2011). A longer continuity of CWD also means that suitable habitat is available for a longer time (on the stand and landscape scales). Ylisirniö et al. (2012), for example, concluded in their study that CWD created by fire provided habitat for wood-inhabiting fungi for up to 70 years. In our study, the experimentally cut logs were often decayed to such a degree that the habitat quality of the logs was diminished for most polypores. However on naturally generated CWD, the positive effects we found for red-listed species remained significant decades after burning, indicating that burning has long-term conservation benefits with regard to restoration of polypore diversity. The continuity of CWD that fire creates seems to be necessary for promoting the diversity of red-listed polypore species, which is in accordance with previous studies in which red-listed species have often started to occur first 10 years or so after a fire (Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015). The significance of the continuous addition of CWD for diversity also underlines the importance of reoccurring fires in the landscape. This might be especially important for spruce-dominated forest, where fires are more likely to be stand-replacing, which implies that, although the addition of CWD may occur over decades, it will eventually end, and the wood-inhabiting species will need to relocate to more recently disturbed areas. In the Evo-Vesijako region, fire has occurred in the landscape at fairly regular intervals (Hyväluoma et al., 2022). In an intensively managed landscape without fire continuity, the occurrence and dispersal of rare species is likely to be lower (see e.g., for beetles; Kouki et al., 2012) as appropriate habitats are lacking.

Our findings regarding the effects of burning may to some extent be confounded by the fact that the local CWD volumes in burned stands increased due to the high mortality of the retained trees. The higher abundance and species richness of red-listed species in burned compared to unburned stands may therefore be related to the higher stand-level resource (energy) availability (Stokland et al., 2012; Wright, 1983), in combination with the trait-dependent colonization rates of different species (Moor et al., 2021). However, we compared fungal communities in standardized samples, that is, 10 cut and 10 natural logs, and found no effect of increasing stand-level volumes in either unburned or burned stand treatments. It is therefore more likely that the CWD qualities created by burning (discussed earlier) account for the positive relationships found between burning and red-listed polypore diversity.

Conclusions and implications

This study shows that prescribed burning is an effective restoration measure that can promote species diversity of polypore communities. Restoration by burning in boreal forests previously primarily targeted pine-dominated forest, but our results demonstrate that it is also an effective measure to promote red-listed species in forests less adapted to recurring fires, such as spruce-dominated forests. Burning results in the continuous addition of CWD and creates CWD of different characteristics, compared to CWD that is generated by felling trees. Thus, restoring CWD by burning is more beneficial for conserving polypore biodiversity. Our results underscore how managed Norway spruce forests should also be included in forest fire restoration programs. However, because the resource pulse that burning generates will be fairly short-lived, prescribed burning needs to be applied with regular intervals on a landscape scale. It is common practice to combine forest restoration treatments with partial cuttings, where the harvested wood covers the costs of restoration actions without compromising the restoration goals (Vanha-Majamaa et al., 2007). Future studies need to investigate whether CWD restoration treatments affect fungal communities similarly in uncut, closed forest stands. Lastly, this study confirms that red-listed polypore species recruitment works on a decadal time scale, and therefore it is not possible to understand the effectiveness of prescribed burning as a restoration measure over shorter periods. Our study highlights that long-term experimental studies, such as this one, are invaluable for establishing evidence-based restoration strategies necessary for the successful conservation of biodiversity in boreal forests.

AUTHOR CONTRIBUTIONS

Ellinor Ramberg, Håkan Berglund, Reijo Penttilä, Joachim Strengbom, and Mari Jönsson conceived the ideas of the study. Håkan Berglund, Reijo Penttilä, and Mari Jönsson designed the methodology. Håkan Berglund, Mari Jönsson, and Reijo Penttilä collected the data. Ellinor Ramberg and Mari Jönsson analyzed the data. Ellinor Ramberg, Joachim Strengbom, and Mari Jönsson interpreted the initial results. Ellinor Ramberg led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for the article's publication.

ACKNOWLEDGMENTS

HAMK, University of Applied Sciences, Metsähallitus, UPM-Kymmene Ltd., the City of Hämeenlinna, and the Finnish Forest Research Institute (Metla) provided the stands for the study and implemented the treatments. Burning activities were organized by Timo Heikkilä. We thank Ilkka Vanha-Majamaa, Saara Lilja, and Timo Kuuluvainen who planned and initiated the Evo experiment. We also thank Henrik Lindberg for his help with practical issues and Elisabet Ottosson for her field assistance. The study was financially supported by

Skogssällskapet (Grant 2019-655-Steg 2 2018) to Joachim Strengbom.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ramberg et al., 2023) are available in Dryad at https://doi.org/10.5061/dryad.g1jwstqw9.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ramberg, Ellinor, Håkan Berglund, Reijo Penttilä, Joachim Strengbom, and Mari Jönsson. 2023. “Prescribed Fire is an Effective Restoration Measure for Increasing Boreal Fungal Diversity.” *Ecological Applications* 33(6): e2892. https://doi.org/10.1002/eap.2892