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Forest restoration benefits common and rare wood-decomposing fungi with a delay

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ABSTRACT

Decline in the amount of dead wood deteriorates habitats for saproxylic organisms globally. This could be compensated by restoration, but it is poorly understood how created dead wood corresponds to the habitat requirements of saproxylic species. Using a large-scale field experiment of 30 restoration sites across Finland, we studied the long-term (5–15 years) effects of dead wood creation on wood-decomposing fungi (polypores) in Norway spruce and Scots pine dominated forests. All studied conservation areas had been used for timber production prior to conservation. The average amount and diversity of woody debris was higher on the restoration treatments than on the non-restored controls. Altogether, 56 polypore species were recorded. Restoration treatments had 1.4 and 8 times more species and observations than controls. Eight red-listed polypore species were observed, six on the restored plots (four only from the created dead wood) and two on the controls. Species composition of polypore assemblages differed between the restoration and control treatments, as well as between the spruce- and pine-dominated forests. Following restoration, temporal changes in the polypore assemblages were clear but only partly related to dead wood creation. Unlike previous short-term studies, our results show that dead wood creation by felling and ring-barking trees benefits not only common but also indicator and red-listed polypore species; indeed, 15 years after restoration all red-listed species occurred on created dead wood. As some red-listed species occurred solely on naturally fallen trees five to ten years after restoration, created dead wood alone cannot substitute for natural dead wood.

1. Introduction

Globally, forests have been extensively altered by anthropogenic influences. This has decreased the amount and types of natural forest structures, which in turn has negatively affected biological diversity (Grove, 2002; Gauthier et al., 2015; Seibold et al., 2015). Even many conservation areas lack natural forest structures, because the forests were managed for timber before protection. Thus, restoration is needed to improve their ecological quality (Elo et al., 2019; Sandström et al., 2019). The short-term goal of forest restoration is to re-introduce structural diversity (Kuuluvainen et al., 2002), which in the long term is expected to aid the recovery of natural biota (Similä and Junninen, 2012). Yet, long-term effects of forest restoration on biota are still poorly known.

One of the most important differences in the structure of managed and natural forests is in the quality and quantity of dead wood (Siitonen, 2001). In natural forests, small- and large-scale disturbances, such as pathogens, wind and fire, create diverse types of dead wood, supplying energy and nutrients for many organisms (Harmon et al., 1986; Esseen et al., 1997; Jonsson et al., 2005). Indeed, it has been estimated that saproxylic (dead-wood dependent) species comprise 20–25 % of all forest-dwelling species in Fennoscandia (Siitonen, 2001). One saproxylic group that has declined widely due to degradation of forest ecosystems is the wood-decomposing fungi, of which the declines have been best documented for polypores (Lonsdale et al., 2007; Junninen and Komonen, 2011). Polypores play a key role as wood decomposers (Stokland et al., 2012), thus contributing to essential ecological processes in forest ecosystems. In Finland, nearly 20 % of the 240 species of polypores are classified as threatened (Kotiranta et al., 2019). Hence, polypores is a suitable model group for evaluating the ecological effects of forest restoration on the broader saproxylic community.

In managed forests, enhancing structural complexity and creating

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dead wood in management practices has proven beneficial for biodiversity, including polypores (Brazee et al., 2014; Dove and Keeton, 2015; Vogel et al., 2020; Uhl et al., 2022). Yet, forest restoration in conservation areas is urgently needed in regions where the landscape is dominated by managed forests, as many conservation areas have formerly been managed for timber production (Sandström et al., 2019). In southern Finland, for example, conservation areas cover only 2 % of the forest land, and only a quarter of the forests in these conservation areas can be considered natural or seminatural (Similä and Junninen, 2012). Indeed, the average amount of coarse dead wood in the conservation areas of southern Finland is an order of magnitude lower than in old-growth forests (7.6 m^3ha^{-1} vs. 60–120 m^3ha^{-1}; Siitonen, 2001; Ihalainen and Mäkelä, 2009). Because of the small amount of dead wood, the conservation area network cannot safeguard the populations of all red-listed saproxylic species. Yet, even small set-asides can sustain some demanding polypore species, if suitable dead wood is adequately available (Junninen and Kouki, 2006; Dawson et al., 2020; Moor et al., 2021; Komonen et al., 2021). To improve conditions for saproxylic species, controlled burning and dead wood creation have been carried out in conservation areas, especially in the northern hemisphere (Halme et al., 2013; Sandström et al., 2019). Controlled burning has proven beneficial for red-listed polypores (Berglund et al., 2011; Penttilä et al., 2013; Suominen et al., 2015), but little is known about the long-term effects of dead wood creation (for short-term effects, see Berglund et al., 2011; Brazee et al., 2014; Komonen et al., 2014a; Pasanen et al., 2014; Dove and Keeton, 2015; Elo et al., 2019). If species responses have long delays, short-term studies may lead in false management recommendations.

This study is based on a large-scale field experiment of 30 restoration sites across Finland investigating the long-term (5–15 years) effects of dead wood creation on polyporous fungi. Previous study (Pasanen et al., 2014) five years after restoration showed that the amount of dead wood and the number of common polypore species increased, but no threatened species were present, and the few near-threatened species all occurred on natural dead wood. As threatened polypore species prefer wood in the middle and advanced decay stages, long-term studies are needed to evaluate the ecological benefits of dead wood creation as a restoration method. We asked: (1) how has the quantity and quality of dead wood, and (2) the species richness, abundance and composition in polypore communities changed 5, 10 and 15 years after restoration. We hypothesize that the quantity of dead wood increases and the quality changes, as natural dead wood are formed and decomposition of created dead wood proceeds. For polypores this is likely to increase the overall richness and abundance of species, and change species composition.

2. Material and methods

2.1. Study sites

We studied 30 restoration sites, located in 23 Natura 2000 conservation areas, spanning a maximum distance of 700 km south to north (Fig. S1; see Pasanen et al. 2014 for the results five years after restoration). Thirteen sites were dominated by Norway spruce (*Picea abies* [L.] Karsten) and seventeen by Scots pine (*Pinus sylvestris* L.). All forests were mature (average diameter of trees at breast height (dbh) > 16 cm) and situated on moderately moist and semi-dry heathland. All forests had been used for timber production before protection. They had traces of silvicultural operations, as well as low amounts of natural coniferous dead wood (mean ± SD = 11.62 ± 11.2 m^3ha^{-1} five years after restoration).

On each study site, we established three pairs of circular study plots (radius = 10 m). Each pair had a restored plot and an untreated control plot (Fig. 1). Control plots were located at least 60 m from the restored plots, either in the same forest stand or in a similar forest stand nearby. In the restored plots, dead wood was created by felling or ring-barking living trees in clusters using a chainsaw (mean ± SD = 9.2 ± 5.1 trees or 3.5 ± 1.6 m^3 per plot, which totals 10.5 m^3ha^{-1}). Restoration measures were carried out between 2002 and 2007.

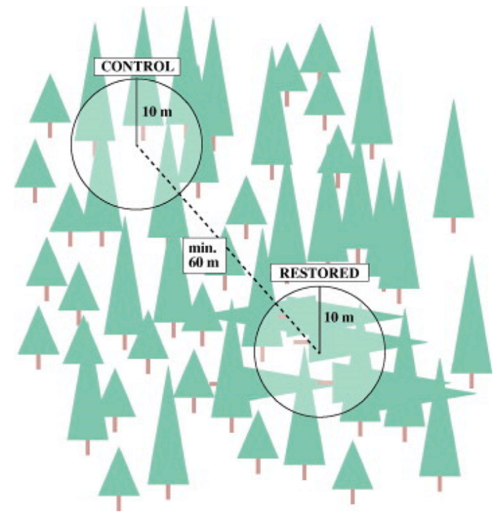

Fig. 1. Study design. Each of the 30 sites had three restored-control plot pairs; restoration was dead wood creation by felling and ring barking trees. Originally published in Pasanen et al. (2014).

2.2. Data collection

Dead conifer trees and polypores were inventoried 5, 10 and 15 years after restoration (with a deviation of 1–2 years on three sites in the 15-year-data). Altogether, we sampled 90 restoration and 89 control plots (we could not locate one control plot 15 years after restoration).

All felled and ring-barked trees (hereafter created dead wood, even if alive) and naturally died trees (hereafter natural dead wood), with a minimum dbh of 10 cm, were measured if the tree base was inside the plot. Tree measurements included species, dbh, decay stage (Table S1) and dead wood type. Dead wood types were natural fallen, natural standing, created felled, created standing and created standing dead wood that had fallen. For trunk parts, average diameter, and total length (with 1 m accuracy; only in the 5-year inventory) were measured.

All living and dead conifer trees (incl. stumps and tree parts), with a minimum diameter of 10 cm, were inspected for polypore fruiting bodies, if the tree base was inside the plot. Standing trees were inventoried as high as possible. For perennial polypores only living fruiting bodies, and for annual polypores both living and recently died (presumably at the inventory year) fruiting bodies were recorded. If a polypore species could not be identified in the field, a sample was taken for microscopic identification. All fruiting bodies of the same species on one dead wood piece (or several pieces belonging to the same tree) were considered as one observation. The fieldwork was carried out during the best polypore fruiting season in September–October (Halme and Kotiaho, 2012). Polypore nomenclature and status as indicators of forest conservation value (hereafter indicator species) are based on Niemelä (2016); the Red List statuses in Finland are according to Kotiranta et al. (2019). Red-listed and indicator species are not mutually exclusive.

2.3. Statistical analyses

For all analyses and data visualizations, we pooled the three plots for each treatment and site. Because one plot could not be relocated on the 15th year inventory, we removed the other two plots for this time, treatment and site. We measured dead wood quantity as the number of dead wood pieces (because of missing height or length on the 10th and 15th year inventories needed for volume calculations).

First, we modeled dead wood characteristics (see 2.2.) with general and generalized linear mixed models (GLMM), having study site (1−30) as a random factor. With GLMM (R package glmmTMB; Brooks et al., 2017), we modeled the number of natural dead wood pieces, using linear parametrization of negative binomial distribution. As explanatory factors, we included the dominant tree species (pine or spruce), treatment (control or restored), time (5, 10 or 15 years after restoration) and the interaction of treatment and time. Similarly, we modeled the number of created dead wood pieces, but used Poisson distribution and included only the dominant tree species and time. Time was included to control for the possible effect of inventory occasion.

We modeled the diameter of dead wood pieces with a linear mixed model (R package nlme; Pinheiro and Bates, 2000; Pinheiro et al., 2023), including dominant tree species (pine or spruce), treatment (control or restored), time (5, 10 or 15 years after restoration) and the interaction of treatment and time as explanatory factors.

Second, to analyse the number of polypore observations and species, we used the same GLMM as for the number of dead wood pieces. In addition to the dominant tree species (pine or spruce), treatment (control or restored), time (5, 10 or 15 years after restoration) and the interaction of treatment and time, we also included dead wood quantity (sum of created and natural) as an explanatory variable. Separately for the restoration treatment, we modeled the effect of dead wood type on the number of polypore observations and species with GLMM (using linear parametrization of negative binomial distribution). The explanatory variables were the dominant tree species (pine or spruce), time (5, 10 or 15 years after restoration), dead wood type (natural, standing; natural fallen; created, standing; created felled; created; fallen) and the interaction of dead wood type and time. We also modeled the effect of dead wood type on the number of species observed in a dead wood piece with GLMM. Here, we used only the data 15 years after restoration, and separately modeled standing dead wood with Poisson distribution, and fallen (or felled) dead wood with linear parametrization of negative binomial distribution. We set the number of species observed in each dead wood piece as a response variable and dead wood type (factor with two levels for standing dead wood: natural or created; factor with three levels for fallen dead wood: natural, created felled or created standing that has fallen), tree species (spruce/pine) and their interactions as explanatory variables. All models included study site (1−30) as a random factor.

Third, we analysed differences in polypore species composition with Non-Metric Multidimensional Scaling using Bray-Curtis dissimilarity index (function metaMDS in R package vegan (Oksanen et al., 2020). We excluded singletons (i.e. species with only one observation in the study), as their occurrence is mostly dictated by chance and yet they can significantly influence the results. Also, we excluded study sites without polypores at a given time. Because the formal analysis (see below) requires an equal number of observations for each group (in our case, treatment × time -group), we only included the plots from those sites for which all three inventories resulted in polypore observations both in the restored and control plots. This left us with 96 plot × time combinations from the maximum of 180.

We tested for the differences in species composition with permutational multivariate analysis of variance using distance matrices (function adonis2 in R package vegan). We modeled species dissimilarity matrix (measured as Bray-Curtis) with dominant tree species (pine or spruce), treatment (control or restored), time (5, 10 or 15 years after restoration) and the interaction of treatment and time. We added site (1−30) as groups ('strata') within which to constrain permutations (number of permutations = 1000). As the permutational multivariate analysis can be sensitive not only to location of the median of groups but also to the dispersion within groups, we tested whether the spread of the groups for each time x treatment combination differed (function betadisper in R package vegan), which is practically a multivariate analogue of Levene's test for homogeneity of variances.

To analyse differences in the total number of species among dead wood types 15 years after restoration, we calculated species accumulation curves (function specaccum in R package vegan) for each dead wood type with 100 permutations (data from restoration and control treatments were pooled).

3. Results

3.1. Dead wood

The average number of all (natural and created) dead wood pieces per site across the years was larger in the restoration (pine: 34.1 ± 13.3; spruce: 42.0 ± 27.4; mean ± SD) than in the control treatments (pine: 8.5 ± 6.7; spruce: 9.8 ± 9.5; Table 1; Fig. S2). Spruce- and pine-dominated forests had similar amounts of dead wood. The average number of natural dead wood pieces per site increased in time both in the restoration and control treatments (Table 1; Fig. S3) but there was no difference between the restoration and control treatments. Created standing dead trees started to fall 5 years after restoration (Fig. S4). The average diameter of dead wood per site was larger in the restoration than in the control treatments across all years (Table S2), largely due to the larger diameter of created (pine: 21.1 ± 5.6; spruce: 21.2 ± 6.3; mean ± SD) than natural dead wood (pine: 15.9 ± 4.7; spruce: 16.8 ± 6.8; Table S3).

Five years after restoration, the decay stage distribution of downed trees was more even (all decay stages present) in the control than in the restoration treatments (dominated by fresh dead wood; Fig. S5), whereas that of standing trees was dominated by middle decay stages in both treatments (Fig. S6). For both the standing and downed trees, decay stage distribution changed more over time in the restoration than in the control treatments. This increase was mainly manifested in the higher proportion of trees at advanced decay stages in the restoration treatments, and partly due to the falling of ring-barked trees.

3.2. Polypores: differences between treatments

Over the three inventories, we observed 3551 polypores belonging to 56 species, of which 3156 observations and 52 species in the restoration treatments, and 395 and 37 in the controls, respectively (Table S4). The five most common species accounted for 60 % of the observations, whereas 12 species were recorded only once. Species composition was different in the restoration and control treatments, as well as in the spruce- and pine-dominated forests (Fig. 2; Table S5). Polypore communities changed differently in time in the restoration and control treatments. Dispersion of the groups (treatment x time) did not differ ($F_{2,93} = 0.01$, $p = 0.990$).

Eight red-listed and 12 indicator species were observed (Table 2). Overall, restoration treatments had about 1.5 times more red-listed and indicator species and over 3 times more observations than controls. The number of red-listed and indicator species almost doubled from five to fifteen years after restoration both in the restoration and control treatments, and the number of observations in the restoration treatments increased 6 times vs. 2 times in the controls.

The average number of polypore observations and species per site was higher in the restoration treatments than in the controls (Fig. 3; Table S6). There was no difference in species richness between the spruce- and pine-dominated forests, although spruce forests had more observations. The higher the number of dead wood pieces, the higher the number of polypore observations and species; yet, restoration treatment had an independent positive effect on the number of polypore observations and species (Table S6). While the average number of polypore observations per site tended to attenuate with time in restoration treatments, it increased in controls (Fig. 3; Table S6). The average number of species per site tended to increase also in the restoration treatments in spruce forests but not in pine forests.

Table 1
Number of created, natural and all dead wood (DW) pieces per site in the restoration and control treatments (GLMM, baselines: Dominant tree = pine, Time = time5 and Treatment = control).

	Created DW				**Natural DW**				**All DW**			
Predictor	**Estimate**	**SE**	**z**	**P**	**Estimate**	**SE**	**z**	**P**	**Estimate**	**SE**	**z**	**P**
(Intercept)	3.26	0.12	26.54	<0.001	1.66	0.18	9.16	<0.001	1.73	0.15	11.31	<0.001
Spruce	0.05	0.19	0.25	0.803	0.17	0.23	0.77	0.441	0.09	0.16	0.56	0.577
Time10	−0.09	0.05	−1.76	0.079	0.32	0.14	2.27	0.023	0.33	0.15	2.24	0.025
Time15	−0.04	0.05	−0.85	0.398	0.51	0.13	3.78	<0.001	0.53	0.14	3.78	<0.001
Restored					−0.03	0.15	−0.17	0.862	1.73	0.12	14.02	<0.001
Restored:Time10					0.00	0.20	0.00	0.998	−0.32	0.16	−1.98	0.048
Restored:Time15					−0.14	0.19	−0.73	0.468	−0.48	0.16	−3.09	0.002

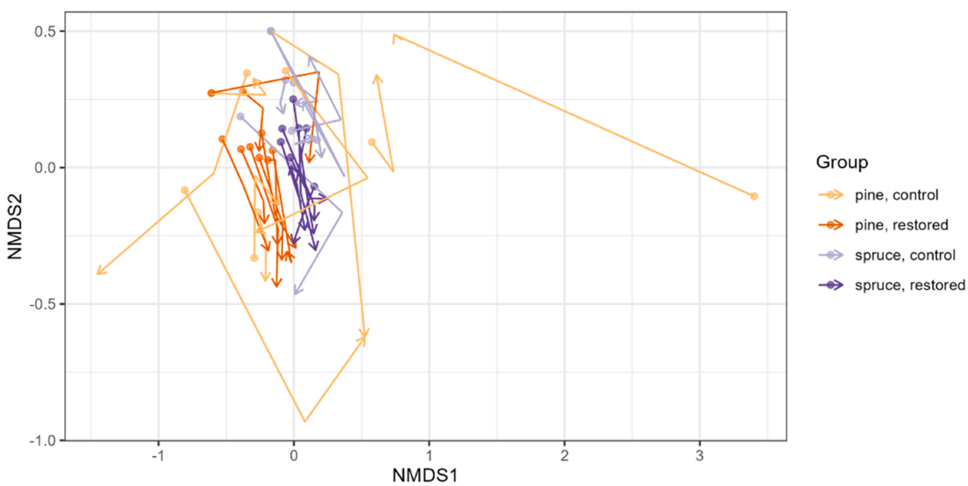

Fig. 2. Polypore community composition in the restoration and control treatments in spruce- and pine-dominated forests 5 (dot), 10 and 15 years (the head of the arrow) after restoration. Stress of the NMDS was 0.178. Removing the outlier (NMDS1 > 3) had no qualitative effect on the results.

Table 2
Number of polypore observations and species that are indicators of forest conservation value or red-listed in Finland on the created (Cre) and natural (Nat) dead wood in the restoration (Res) and control (Con) treatments; red-list categories NT = near-threatened and VU = vulnerable.

	Restored						Control			Total		
	5		10		15		5	10	15			
Species	Cre	Nat	Cre	Nat	Cre	Nat	Nat	Nat	Nat	Res.	Con.	Overall
Anomoporia kamtschatica									1		1	1
Antrodia albobrunnea NT							2	1			3	3
Antrodiella citrinella NT					4					4		4
Dichomitus squalens NT								1			1	1
Fomitopsis rosea NT					4					4		4
Leptoporus mollis	2		9	2	1	7		1	2	21	3	24
Meruliopsis taxicola		1	2			2	1			5	1	6
Oligoporus sericeomollis	1	1		3	1	2	2	6	3	8	11	19
Pelloporus leporinus					1					1		1
Phellinus ferrugineofuscus		2	3	4	19	2			3	30	3	33
Phellinus nigrolimitatus			1	1		1				3		3
Phellinus pini		1	1	1		1	2	1	1	4	4	8
Phellinus viticola		2		2	3	2		1	2	9	3	12
Postia leucomallella		2	4	4	23		2	3	4	33	9	42
Pycnoporellus fulgens			8		3			2	1	11	3	14
Rhodonia placenta			1		3				1	4	1	5
Sidera lenis NT		1								1		1
Skeletocutis brevispora NT		1								1		1
Skeletocutis odora NT					1					1		1
Skeletocutis stellae VU					2					2		2
Number of observations	3	11	29	17	65	17	9	16	18	142	43	185
Number of species	2	8	8	7	12	7	5	8	9	17	12	20
Number of red-listed observations		2			11		2	2		13	4	17
Number of red-listed species		2			4		1	2		6	2	8

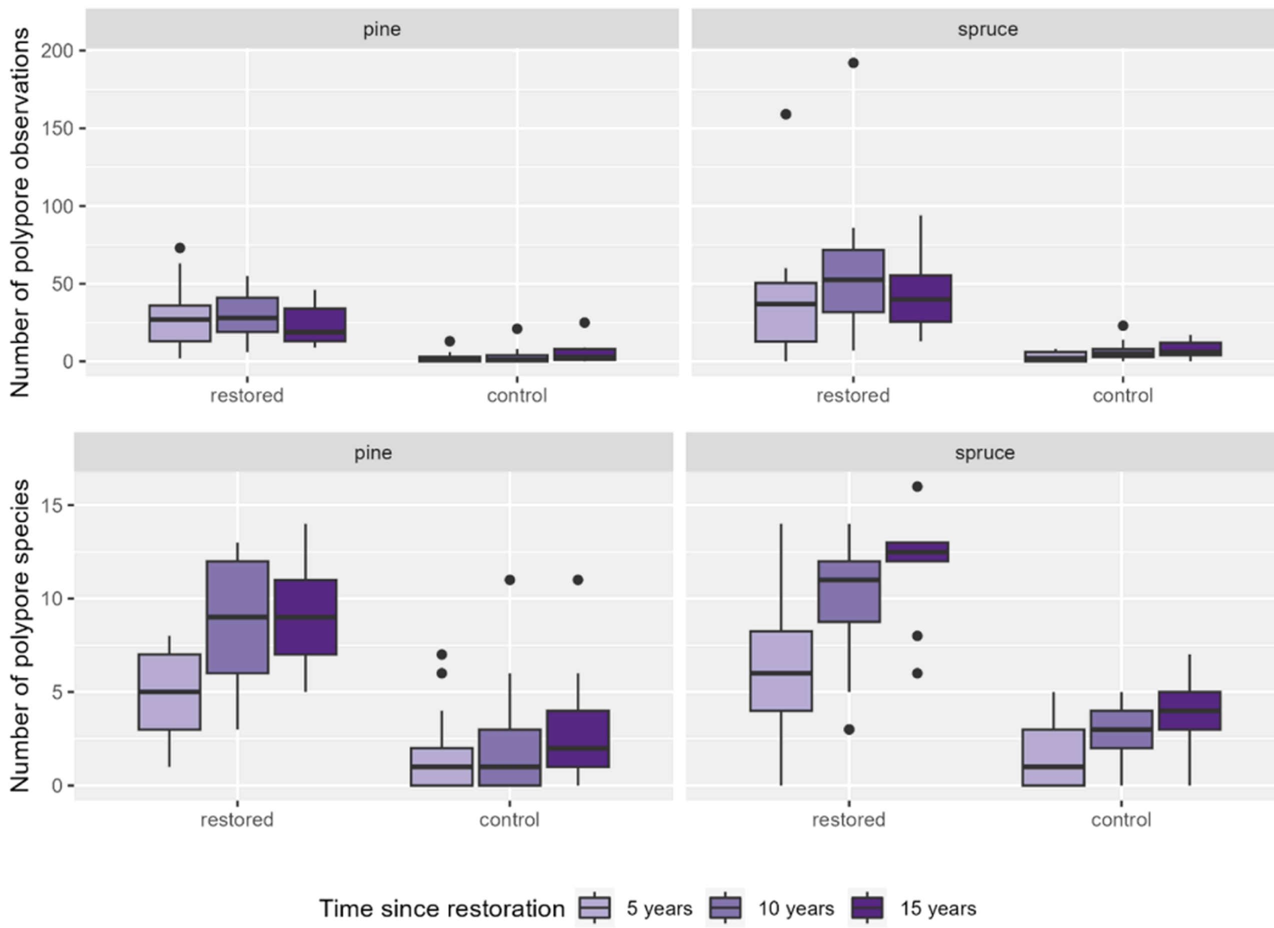

Fig. 3. Number of polypore observations and species per site in the restoration and control treatments dominated by pine or spruce. The box shows the 25th and 75th percentiles, and the horizontal line the median. Whiskers extend to the largest and smallest value no further than 1.5 × distance between 25th and 75th percentiles; dots are outliers.

3.3. Polypores: differences between dead wood types

During the whole study, 48 species were observed from created and 46 from natural dead wood. Ten species (*Antrodiella citrinella, Canopora subfuscoflavida, Fomitopsis rosea, Heterobasidion annosum, Pelloporus leporinus, Porpomyces mucidus, Postia stiptica, Skeletocutis odora, S. stellae* and *S. papyracea)*, four of which are red-listed, were only found from created dead wood. Eight species (*Anomoporia kamtschatica, Antrodia albobrunnea, Byssoporia mollicula, Dichomitus squalens, Fibroporia gossypium, Postia floriformis, Sidera lenis* and *Skeletocutis brevispora*), four of which are red-listed, were only found from natural dead wood. Fifteen years after restoration, the created and natural standing dead wood hosted on average similar number but fewer species than the other dead wood types (Table S7; Fig. S7). For fallen dead wood, by contrast, the average number of species was higher on the created than on the natural dead wood. The average number of species on both standing and fallen (and felled) dead wood was higher in spruce than in pine forests.

In the restoration treatments, the number of species increased not only on the created felled but also on the natural fallen dead wood both in the pine and spruce forests (Fig. 4; Table S8). Despite the higher average number of species on created, felled or fallen dead wood piece, the total number of species was highest on the natural fallen dead wood in pine forests and created felled in spruce forests; however, the difference largely vanishes when comparing samples of equal numbers of dead wood pieces (Fig. 5). In the restoration treatments, the proportion of red-listed and indicator species in the created vs. natural dead wood increased over time: 20, 60 and 80 % of observations and 20, 50 and 60 % of species five, ten and fifteen years after restoration (Table 2). Of the created dead wood, felled trees (11 spp, 45 obs.) and ring-barked trees that had fallen (7 spp., 52 obs.) hosted more species than ring-barked standing trees (3 spp., 6 obs.).

4. Discussion

Our long-term restoration experiment of boreal forest shows that polypore species benefit from dead wood creation. Restoration initially increased the amount and diversity of dead wood in the restored plots, by increasing the number of fresh, large-diameter dead wood. Because also natural dead wood increased over time both in the restoration and control treatments, the dead wood increase was not only related to restoration (see also Pasanen et al., 2014). Likely reasons for natural increase of dead wood are natural aging of trees, self-thinning and natural disturbances. Restoration increased dead wood diversity with a delay, as the created, standing dead wood started to fall 5 years after restoration. As a result of the above-mentioned processes, the decay stage distribution changed more over time in the restoration than in the control treatments.

Polypore diversity increased more in the restored than in the control treatments (see also Brazee et al., 2014; Pasanen et al., 2014; Dove and Keeton, 2015; Elo et al., 2019). This increase could be explained by larger amount, diameter and heterogeneity of dead wood, as well as favorable microclimate in the restoration treatments. The increases in abundance and species richness, however, took mainly place between five to ten years after restoration and then ceased. Early increase in species richness was expected as the number of polypore species on coniferous trees tend to increase from early to middle decay stages

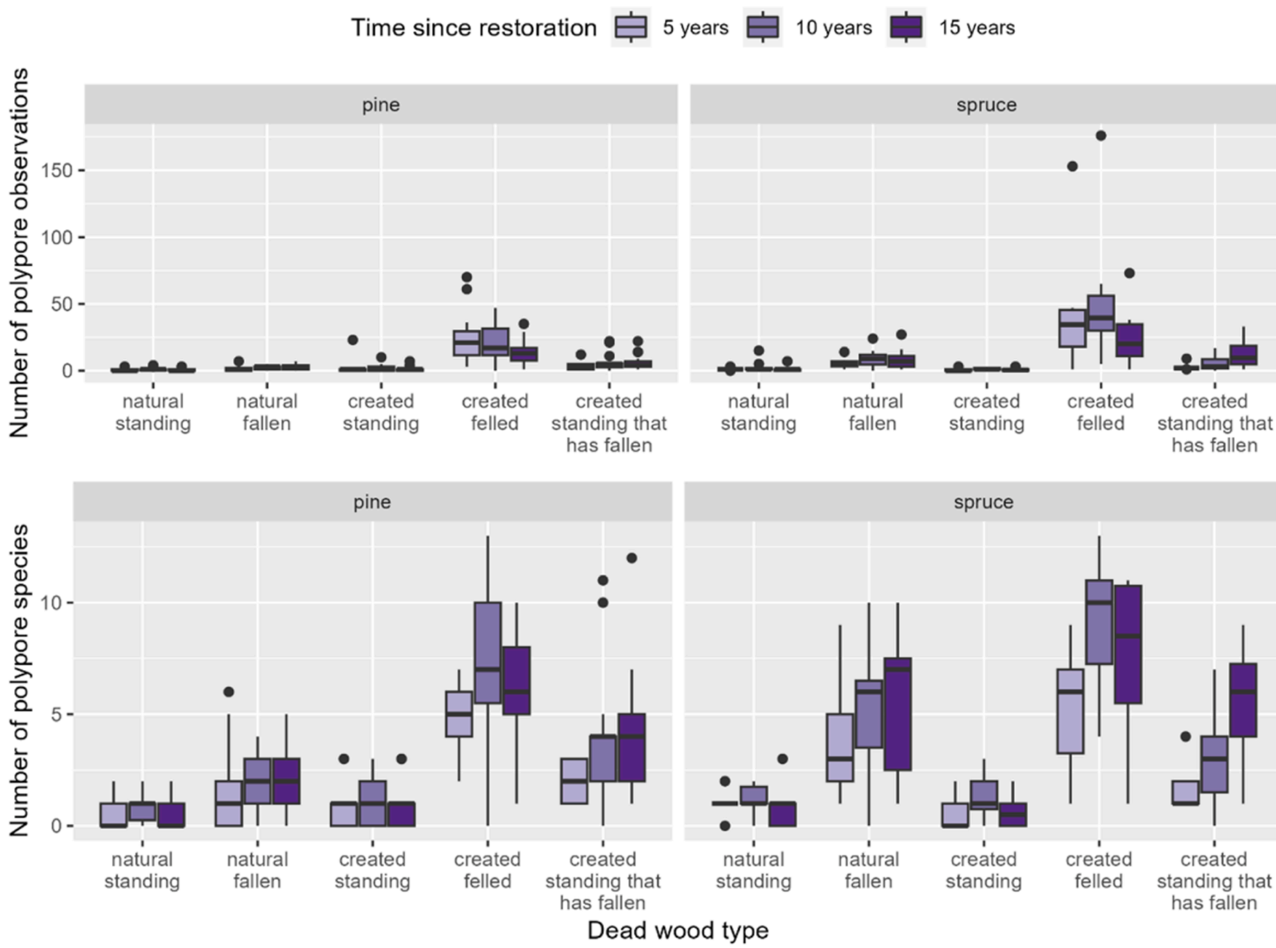

Fig. 4. Number of polypore observations and species on different types of dead wood in the restoration treatments. The box shows the 25th and 75th percentiles, and the horizontal line the median. Whiskers extend to the largest and smallest value no further than 1.5 × distance between 25th and 75th percentiles; dots are outliers.

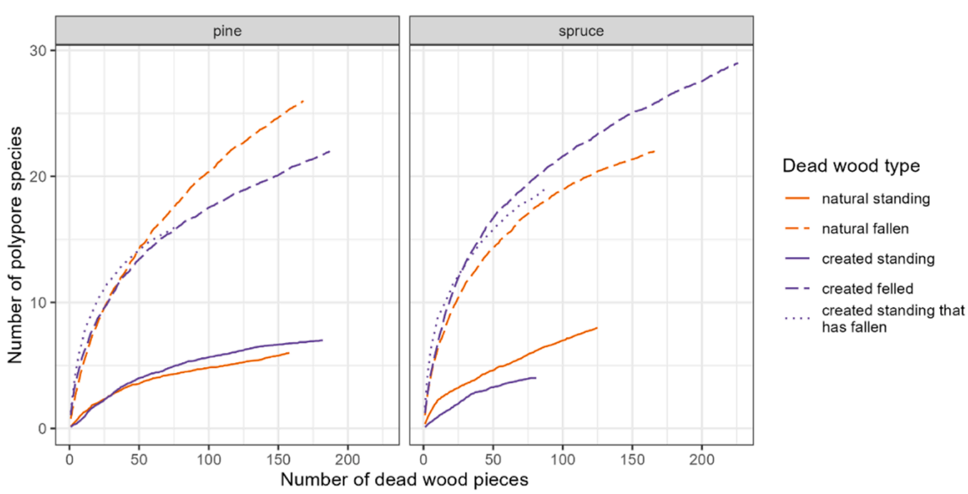

Fig. 5. Species accumulation in different types of dead wood 15 years after restoration (restoration and control treatments pooled). Standard deviations are not shown for clarity.

(Renvall, 1995; Lindblad, 1998; Junninen and Komonen, 2011). The increase in abundance and species richness was similar in the restored spruce- and pine-dominated forests, although in the pine forests the increase in species richness seemed to cease 10 years after restoration. Potential explanations for the cessation of species accumulation in pine forests are that pine hosts generally fewer species than spruce and decays slower (Junninen and Komonen, 2011). Also, the studied forests were not monocultures, which likely evened out the inherent differences in polypore species richness between the tree species. Finally, independent of dead wood amount, restoration had a positive effect on the average number of polypore observations and species, probably due to the large diameter of the created dead wood and opening of the canopy, which altered microclimate (Brazee et al., 2014; Dove and Keeton, 2015; Uhl et al., 2022; Vogel et al., 2020). Our study demonstrates that restoration does create suitable substrates for polypores preferring early and middle decay stages. Because many polypore species favor wood in the advanced decay stages, and there might be longer delays in colonization than the studied 15 years, restoration experiments should be continued over several decades (see also Komonen et al., 2014b).

Created and natural dead wood offered different substrates for polypores. Overall, similar numbers of polypore species were observed from the created vs. natural dead wood. Also, similar numbers of species occupied solely the created or natural dead wood. Yet, fifteen years after restoration, polypore species richness differed between the dead wood types. A created, felled or fallen dead wood piece had on average more polypore species than naturally fallen dead wood, whereas created standing dead wood had a similar number of species to natural standing dead wood; similar patterns were observed five years after restoration (Pasanen et al., 2014). Despite the higher average number of species in created, felled or fallen dead wood pieces, the total number of species was higher in the naturally fallen dead wood. The only exception was the created felled dead wood in spruce-dominated forests, which hosted more polypore species than naturally fallen trees. This indicates somewhat higher variability in species composition, i.e. higher beta diversity, among naturally fallen dead wood pieces (see also Komonen et al., 2014a). This may be related to different decomposition dynamics of created vs. natural dead wood (Renvall, 1995; Berglund et al., 2011; Ottosson, 2013), and/or larger microclimatic variation experienced by natural dead wood, which occurred both in the gap openings and closed-canopy controls (see also Brazee et al., 2014; Dove and Keeton, 2015; Vogel et al., 2020; Uhl et al., 2022). Our study shows that created dead wood enhances polypore diversity but cannot substitute for natural dead wood.

Polypore species composition differed between the restoration and control treatments, as well as between spruce- and pine-dominated forests. This was somewhat expected as different types of dead wood, tree species and forests host different polypore species and in different numbers (Berglund et al., 2011; Junninen and Komonen, 2011; Pasanen et al., 2014; Uhl et al., 2022; Vogel et al., 2020). Over time, species composition changed differently in the restored and control treatments. The probable explanation for the different successional trajectories is that, initially, restoration causes a pulse of resources of similar quality and free of competition. These are then colonized by partly different pioneer species than natural dead wood (Komonen et al., 2014a). Also, increase in the abundance of any pioneer species in created dead wood, whether the same or different from those in natural dead wood, changes successional trajectories between restoration and control treatments. Different successional trajectories can be also partly related to the dynamics of different dead wood types, as well as tree- and site-level variation in wood decomposition. Also, environmental factors (e.g. microclimate), which are not linked with dead wood, could explain some of the changes in community composition (Brazee et al., 2014; Elo et al., 2019; Komonen et al., 2021; Moor et al., 2021; Uhl et al., 2022; Vogel et al., 2020). Our study demonstrates that clear changes in community composition take place just over a decade from restoration.

Red-listed and indicator species colonized created dead wood. Altogether, we observed eight red-listed polypore species, half of which solely from the restoration treatments. Five years after restoration all red-listed species were from natural dead wood (Pasanen et al., 2014), whereas 15 years after all were from created dead wood. Furthermore, the abundance of old-growth forest indicator species increased 530 % in the restoration treatments and 100 % on the controls from five to fifteen years after restoration. This indicates that created dead wood that was too fresh for red-listed or indicator polypores five years after restoration had become suitable. For example, *A. citrinella* and *P. fulgens* – species that requires wood pre-decomposed by *F. pinicola* – were absent from the created dead wood five years after restoration, but occupied felled trees 15 years after restoration. Similarly, red-listed *F. rosea* and indicator *P. ferrugineofuscus* occupied ring-barked trees only after they had fallen. Considering red-listed polypores, it was important that the created dead wood was large enough (see Junninen and Komonen, 2011). Yet, the shortage of trees at advanced decay stages (incl. *kelo* trees; Venugopal et al., 2016) probably limited the occurrence of some red-listed species (see Tikkanen et al., 2006; Junninen and Komonen, 2011). Such specific substrate is difficult or impossible to create artificially, and species dependent on it do not seem to benefit from restoration. Our study shows that species responses, especially of indicator and red-listed species, can be slow and wrong conclusions may be reached in short-term studies (see also Elo et al., 2019).

Considering structural features of natural forests, dead wood quantity is technically easier to restore than dead wood quality (Brazee et al., 2014; Dove and Keeton, 2015). Although some qualitative features of dead wood can be easily created (e.g. dead wood of different diameters), manipulating decay stage or dead wood type is more difficult. In the present study, dead wood was created by ring-barking and felling trunks with a chainsaw. Yet, mortality factors of trees in natural forests are diverse, such as fire, fungi, insects, wind and snow (Kuuluvainen and Aakala, 2011). Different mortality factors cause differences in the chemical and physical wood properties (Stokland et al., 2012), which in turn affect wood decomposition and polypore succession (Renvall, 1995; Ottosson, 2013; Komonen et al., 2014a; Edman and Eriksson, 2016). To enhance substrate diversity, dead wood should be created with variable methods.

Although the present study focused on the substrate- and stand-level characteristics, the landscape context is also important in restoration, especially for rare and red-listed species (Kouki et al., 2012). The proximity of suitable source populations can influence the success of restoration. Although polypores in general are good dispersers (Komonen and Müller, 2018), the poor dispersal ability and/or low propagule pressure of the rarest species preferring advanced decay stages may become visible in some sites in the future (Penttilä et al., 2006; Nordén et al., 2013). Finally, different saproxylic groups have different habitat preferences and dispersal abilities (Jonsson et al., 2005; Norros et al., 2012; Tikkanen et al., 2006; Uhl et al., 2022; Vogel et al., 2020), so generalizations over taxa can be difficult (Hyvärinen et al., 2006; Junninen et al., 2008; but see Vogel et al., 2020; Uhl et al., 2022).

5. Conclusions

Forest restoration, such as dead wood creation, enhances polypore diversity in Fennoscandian boreal forests. Although dead wood creation is not a quick solution for facilitating the populations of rare and red-listed species, it does provide suitable substrate for some species over long periods of time, as we have shown here. Although the dead wood created at one instant is assumed to decay at a similar rate, our study indicates that decay rates vary and, at the same time, natural tree mortality produces new dead wood. Both processes enhance resource continuity and variability for polypores and other taxa, but it is not known whether they can halt local extinctions.

Considering wood-decomposing fungi the main recommendations of our study are applicable both in conservation area management, as well as in biodiversity-oriented forest management. Natural dead wood should be retained in forests as it can harbor different species and higher overall species richness than created dead wood over a decade after restoration. Yet, dead wood creation is a beneficial restoration measure for common, indicator and red-listed species, as exemplified by our study in which all the red-listed species 15 years after restoration were observed from created dead wood. Furthermore, created dead wood should include both standing (ring-barked) and felled trees. Although felled trees can harbor more red-listed species, the standing dead trees that gradually fall maintain dead wood continuity and are suitable substrates for some red-listed polypore species.

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CRediT authorship contribution statement

Kaisa Junninen: Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Atte Komonen:** Writing – review & editing, Writing – original draft, Conceptualization. **Merja Elo:** Writing – review & editing, Formal analysis, Conceptualization. **Janne S. Kotiaho:** Writing – review & editing, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

JSK designed the monitoring network; KJ supervised data collection and managed data; ME analysed the data; AK wrote the initial draft; All authors participated in conceptualizing the research and writing the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122342.

Data Availability

Data will be made available on request.

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