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Reinventory of permanent plots show that kelo lichens face an extinction debt

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ABSTRACT

Intensive forestry has led to landscape level deficits of important substrates such as deadwood and its associated biodiversity. Several taxa face extinction debts due to continuous declines and lack of regeneration of important habitats. Deadwood-dependent lichens are of great conservation concern due to a general lack of deadwood and due to their slow establishment, especially of rare species. In a field restoration experiment in central Sweden, we studied deadwood-dependent lichens for eight years, their association to different types of deadwood and their response to environmental change caused by variable retention forestry, deadwood enrichment and prescribed burning. Prescribed burning and site preparation caused depauperate lichen species assemblages throughout the study period but retention felling did not majorly affect lichen species assemblages. We found that lichen species were nested along deadwood qualities and deadwood created in the experiment only hosted a subset of lichen species found on kelo wood. Despite large reductions of kelo wood with lichen occurrences over the study period, overall species richness did not decrease. The fact that a large part of the lichen community occur only on kelo wood and that kelo wood is not regenerated implies that lichens associated with kelo wood face an extinction debt. In order to avoid local extinctions of deadwood-dependent lichens, site preparation and prescribed burning should be avoided in areas rich in high quality deadwood. There is urgent need to start creating new kelo wood through reoccurring fires in order to halt the impending extinction debt.

1. Introduction

Human land use and subsequent loss of habitat are considered important drivers of biodiversity loss globally (Sánchez-Bayo and Wyckhuys, 2019; Almond et al., 2020; Jaureguiberry et al., 2022). The majority of global, terrestrial biodiversity is found in forests (Thompson et al., 2009), yet forests are continually being degraded and fragmented (Haddad et al., 2015; Venter et al., 2016; Potapov et al., 2017). This is also true for the boreal forest ecosystems of northern Europe and America where forest management has transformed natural habitats into monocultures lacking in natural dynamics and structures (Esseen et al., 1992; Cyr et al., 2009; Shorohova et al., 2011). In Fennoscandia, natural and semi-natural forests now only remain in small and fragmented patches with larger areas being confined to the mountain region (Svensson et al., 2020). Despite a more conservation-oriented management (Kruys et al., 2013; Kyaschenko et al., 2022), many forest and deadwood-dependent species are on the national and European Red List (Hyvärinen et al., 2019; Swedish Species Information Centre, 2020; IUCN, 2022). Late seral Scots pine (*Pinus sylvestris*) forests in particular have become rare both due to direct harvesting of living and dead trees but also due to fire suppression resulting in lack of regeneration of structures such as fire scars and burned wood. Consequently, unique properties found in such forests are lost from the forest landscape. Kelo wood is the unique deadwood legacy of several centuries' old pine trees characterized by tar-impregnated wood and a silvery-coloured surface. Kelo wood is resistant to decay and can endure for many centuries (Sirén, 1961; Niemelä et al., 2002). The unique properties of kelo wood are formed when slow-growing trees are injured by disturbances such as fire. As a response, the trees impregnate the wood with decay-resistant chemicals (Venugopal et al., 2016a, 2016b). Kelo wood is known to occur across the Palearctic boreal forests throughout Europe and Russia but due to a long period of intensive logging, it has disappeared from

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large parts of Europe and is increasingly rare in Fennoscandia (Niemelä et al., 2002; Kuuluvainen et al., 2017). A few studies have examined the importance of kelo wood for biodiversity, and the findings indicate that kelo trees support specialised lichen and fungal species. Moreover, kelo wood may act as sources of species dispersal during succession in disturbed forests (Niemelä et al., 2002; Santaniello et al., 2017).

Several studies on short-lived and mobile organisms suggest that different deadwood substrates complement each other and that a diversity of substrates is needed to support intact species assemblages (Thorn et al., 2020; Löfroth et al., 2023). For sessile organisms, assemblages are often nested, i.e., species-rich substrates or sites contain the complete assemblage while more species poor sites contain only a subset of the species from the richer sites (Wright et al., 1997; Zhao et al., 2015). If deadwood derived from restoration displays species assemblages that are distinct from natural deadwood, the complementary effect of restoration is greater than if species assemblages are nested, with created deadwood only supporting a subset of species found on natural deadwood.

Lichens are an important part of forest biodiversity and can be found on a range of substrates (Boch et al., 2013), although some species such as deadwood-dependent lichens are often overlooked (Spribille et al., 2008). Substrate type and quality has proven to be important to deadwood-dependent lichens and therefore retaining deadwood legacies in felling operations is instrumental in maintaining lichen diversity (Svensson et al., 2016; Santaniello et al., 2017). Disturbances including fire generally have a direct negative effect on lichens. Furthermore, species that are rare in managed forests recolonize at a slow rate (Johansson, 2008; Hämäläinen et al., 2014; Lõhmus et al., 2018). Lichen response to disturbance might however be trait-specific, with for example, pine associated species responding positively to increased sun-exposure (Johansson et al., 2006; Benítez et al., 2018; Ranlund et al., 2018). Due to lack of deadwood, specialised lichen species face a forestry-induced extinction debt (Berglund and Jonsson, 2005; Öckinger and Nilsson, 2010), one that can take a long time to realise due to slow extinction rates (Johansson et al., 2013, 2018). In order to halt species loss, the colonisation credit, through restoration, needs to be greater than the extinction debt (Watts et al., 2020), occur at a faster rate and needs to include rare and threatened species. Kelo-associated lichen species especially risk extinction debt due to the scarcity and isolation of kelo wood, making them highly sensitive to anthropogenic and stochastic extinction.

We investigated the effects of forest management and the importance of substrate type and quality for deadwood-dependent lichens. We revisited a large-scale experiment with permanent plots in pine forests subjected to felling, mechanical site preparation and restoration treatments to follow up on a study conducted by Santaniello et al. (2017). We also included untreated and burned stands in order to address forest management in a broader sense. Although large-scale experimental monitoring of biodiversity responses to forestry and restoration has been studied in other parts of the world (Wiersma, 2022), in Fennoscandia, studies usually spans a few years and long-term studies are rare (Koivula and Vanha-Majamaa, 2020). Our experiment provides a unique opportunity to follow the response of lichen diversity to forest management and restoration in the initial phases of lichen regeneration and recolonization while simultaneously providing opportunity to follow the future development in more long term.

More specifically we:

I) Examine changes in diversity patterns of lichens over time for different deadwood qualities.
II) Investigate how site preparation, prescribed burning and tree retention affect lichen species richness, abundance and composition over time.
III) Analyse the lichen diversity patterns in relation to substrate quality and type.

We expected both site preparation and prescribed burning to result in lower species richness and abundance of lichens due to substrate destruction while tree retention will maintain lichen species richness and abundance due to a maintained microclimate and deadwood legacies. Moreover, we expected that harvested areas outside of the retention would be affected by increased sun exposure that may have mixed or intermediate effects on lichen diversity. We expected lichen species richness to benefit from deadwood enrichment. We also expected kelo wood to host more red-listed species than old wood without kelo-qualities and deadwood generated during restoration, but that different deadwood qualities would host distinct, non-overlapping species assemblages.

2. Methods

2.1. Study design and field survey

The study was conducted in Effaråsen (60°58′29″N, 14°01′55″E), Dalarna county, in the southern boreal vegetation zone of Sweden (Ahti et al., 1968). The study area comprises 24 stands with a mean size of ~5 ha and the entire study area comprise around 140 ha. Scots pine (*Pinus sylvestris* L.) dominated the stands with an age of around 120–140 years. Norway spruce (*Picea abies* (L.) H. Karst) and birches (*Betula pendula* Roth. & *Betula pubescens* Ehrh.) occurred in sparse populations. The area has a history of forest management but has not previously been clear-felled. In 1888, there was a wildfire in the area, remnants of which is seen in form of living trees and kelo wood with fire scars.

In 2012–2013, the 24 stands were randomly allotted and subjected to harvest treatments with varying levels of tree retention (3–100 %), deadwood enrichment and prescribed burning. Mechanical site preparation was performed in felled areas in 2014, after the first lichen inventory. Retained trees were further divided in all stands, except the burned and unharvested, into: 1) Green tree retention of single trees or groups of trees, 2) high-stump creation at ~3 m height, 3) log creation by felling trees and 4) damaging of trees by bark-peeling by the harvester head. For further details, see Santaniello et al. (2016).

In 2014, ten circular permanent sampling plots (5.64 m radius) along transects were laid out in each stand covering the longest possible distance within the stand. In cases where ten plots did not fit within the transect, a second transect was laid out covering the second longest distance. In 2014, 15 stands were surveyed (i.e., deadwood and lichen inventory), excluding the prescribed burned and the control stands. In 2021, prescribed burned and control stands were surveyed additionally, and the plots from 2014 were resampled (due to an error, only nine plots were established in one of the stands in 2014), resulting in 239 plots. Based on the stand-level treatments, we categorized five plot types: 1) Closed; plots within retention patches with a closed canopy, varying in size depending on the felling intensity, 2) Open with no site preparation; plots in felling areas without retained canopy/open canopy, 3) Open with site preparation; plots in felling areas that were subjected to site preparation, 4) Untreated; plots within control stands with no treatment, and 5) Burned; plots within stands subjected to prescribed burning. Due to large variation among and within stands, these plot types occur across several stand and treatment types.

2.1.1. Deadwood inventory

Within each plot, we registered and measured all deadwood objects with an overall area of exposed wood ≥25 cm^2, excluding parts outside of the plots. Deadwood was classified into different types: low-stump (stump <50 cm height), snag (dead, standing tree >50 cm height) and log (downed deadwood). Deadwood quality was classified according to a combination of age and characteristics being: Kelo (since before or during the wildfire of 1888, 130+ years, with kelo-quality), Old (after the wildfire but before treatment, usually around 70–80 years, lacking kelo-quality), Young (created during or after treatments, <10 years), and Burned (created in the prescribed burning, <10 years). For standing deadwood, diameter was measured at breast height (DBH) and height was measured up to a maximum of two meters, as this was the limit for surveying lichens without using a ladder. For downed deadwood, top and bottom diameter and length was measured. We calculated deadwood surface area based on the formula of a cylinder and high-cut stumps were given a height of two meters since lichens were only inventoried to this height. The estimated bark and bryophyte cover was subtracted from all substrates and for logs by subtracting 20 % of the area as we estimated this area to be in contact with the ground and thus not surveyed. For low-stumps and snags, we also subtracted the bottom diameter since the bottom part is below ground. Deadwood types were analysed separately per deadwood quality: Young, Old and Kelo. Burned deadwood was left out of this part of the analysis due to too few replicates when separated into different types.

2.1.2. Lichen inventory

Deadwood-dependent lichens according to Spribille et al. (2008) were surveyed in 2013–2014 (here referred to as before treatment, as the response to the treatment one to two years prior likely had little effect in that time) and again in 2021 (post treatment) in order to examine the development over time. Both inventories were performed by the same person (G. Thor) using the same methodology (see Santaniello et al. (2017)). All deadwood-dependent lichens were surveyed on objects with an area available for colonisation of at least 25 cm^2 (decorticated wood), up to two meters on standing objects.

The facultatively lignicolous species *Cladonia botrytes* was searched for on the ground along all transects but was only found lignicolous in this area and was thus treated as lignicolous.

Trapeliopsis sp. is a distinct species that has not yet been described. Classification of the genus *Xylographa* follow Spribille et al. (2014).

We recorded all species of lichens and calculated species richness as the number of unique species divided by the sampled decorticated deadwood (m^2) per plot or per deadwood category per plot to account for differences in deadwood amount. Species abundance was calculated as the number of discrete species records on each substrate, divided by the sampled decorticated deadwood (m^2), then summarised per plot or by deadwood category per plot. The total number of plots used for each analysis can be found in Table A.2.

2.1.3. Canopy cover

We photographed the canopy using a phone camera with a fisheye lens, at the centre of each plot, from approximately 1 m above ground. The photos where then analysed in ImageJ (Schneider et al., 2012) using the Hemispherical 2.0 plugin (Beckschäfer, 2015) in order to achieve data on the canopy gap fraction. Gap fraction data was then divided into 2 classes, open or closed canopy ranging from 0.45 to 0.8 for closed canopy and 0.8–1 for open canopy.

2.2. Data analysis

All statistical analyses were performed using the open source programme R (R Core Team, 2020).

Due to non-normality in the data, we used Kruskal-Wallis tests followed by Wilcoxon pairwise tests to analyse relationships between lichen richness and abundance with deadwood type and quality, year and treatment effects on plot level. When testing for deadwood types and qualities, analysis were performed on deadwood type per plot and only for plots containing species abundance on that specific type of deadwood. Fine woody debris (<10 cm) was included in analysis of treatment but excluded from comparisons between deadwood types. Rarefaction curves were produced using the package iNEXT (Hsieh et al., 2016) to relate species richness to the accumulated sample effort. We rescaled the x-axis of the rarefaction curves to represent the cumulative wood surface area.

We produced a Jaccard distance matrix, followed by BETADISPER and subsequent ANOVA to test for differences in mean distance to the community centroid, which we treat as beta diversity. With non-significant results in BETADISPER, we performed a PERMANOVA to test for differences in species composition, with Jaccard distance, 999 permutations. We visualised species assemblages with NMDS, with 999 permutations and Jaccard distance except for young deadwood where Bray-Curtis distance was used. We used the vegan package to perform the BETADISPER, PERMANOVA and NMDS functions which were all done on stand level (Oksanen et al., 2017).

To identify indicator species, we used package indicspecies, with 999 permutations (Cáceres and Legendre, 2009). To test whether or not lichen species assemblages were nested within deadwood types, we followed Leibold and Mikkelson (2002), summarising species abundances by deadwood type and quality, using a binary matrix and the metacom package (Dallas, 2014).

3. Results

In total, we surveyed 787.7 m^2 decorticated deadwood with potential lichen occurrences; 451.3 in 2014 and 336.4 in 2021, resulting in a total of 27 deadwood-dependent lichen species. The species with the highest abundances were *Mycocalicium subtile* (21 % total abundance), *Micarea denigrata/nowakii* (14 %) and *Xylographa parallella/pallens* (13 %). Six of the species found were categorized as NT in the 2020 Red List of Sweden (Swedish Species Information Centre, 2020); *Calicium denigratum*, *Carbonicola anthracophila*, *C. myrmecina*, *Cladonia parasitica*, *Elixia flexella* and *Hertelidea botryosa* that together make up 11 % of the total abundance (Table A.1).

3.1. Deadwood quality — time and treatment effects

Our results show that lichen species richness increased slightly on kelo wood in the permanent plots between 2014 and 2021 but remained the same for red-listed species, when correcting for the sampled deadwood amount (Table A.2). Rarefaction curves revealed similar total species richness on kelo wood, despite an 80 % reduction in sampled wood surface area (from 26 m^2 to 4.9 m^2) with lichen occurrences between 2014 and 2021 (Fig. 1). The total species richness increased slightly on old deadwood between 2014 and 2021 (Fig. 1c). Assemblage composition on kelo- and old deadwood differed between years but not among treatments (PERMANOVA, $p = 0.001$, $R^2 = 0.03$).

3.2. Treatment effect on lichens

Untreated control plots, closed canopy and open canopy plots displayed similar total species richness while site prepared and burned plots, displayed lower species richness (Fig. 2). Species richness did not decrease between 2014 and 2021 on plot level (Table A.2). Rarefaction curves were overlapping between year and treatment but with a significant decrease of species richness in site prepared plots between 2014 and 2021 (Fig. 1b). Species assemblages differed between plot types (PERMANOVA, $p = 0.02$, $R^2 = 0.16$) with partial overlaps between closed canopy, open canopy and site prepared plots while control plots displayed assemblages not overlapping with any plot type. Assemblages in burned areas overlapped with open canopy and areas affected by site preparation (Fig. 2). PERMANOVA results of year * treatment were non-significant ($p = 0.185$), although visual interpretation of NMDS plots suggest that site preparation caused a shift in species assemblage between 2014 and 2021 while the assemblages in the other plot types did not change (Fig. 2).

3.3. Deadwood quality and type

Kelo wood had similar species richness as young and burned deadwood on plot level while rarefaction curves revealed a greater total species richness on old and kelo wood compared with young and burned deadwood (Fig. 1c, Table A.2). All red-listed species in 2021 were found

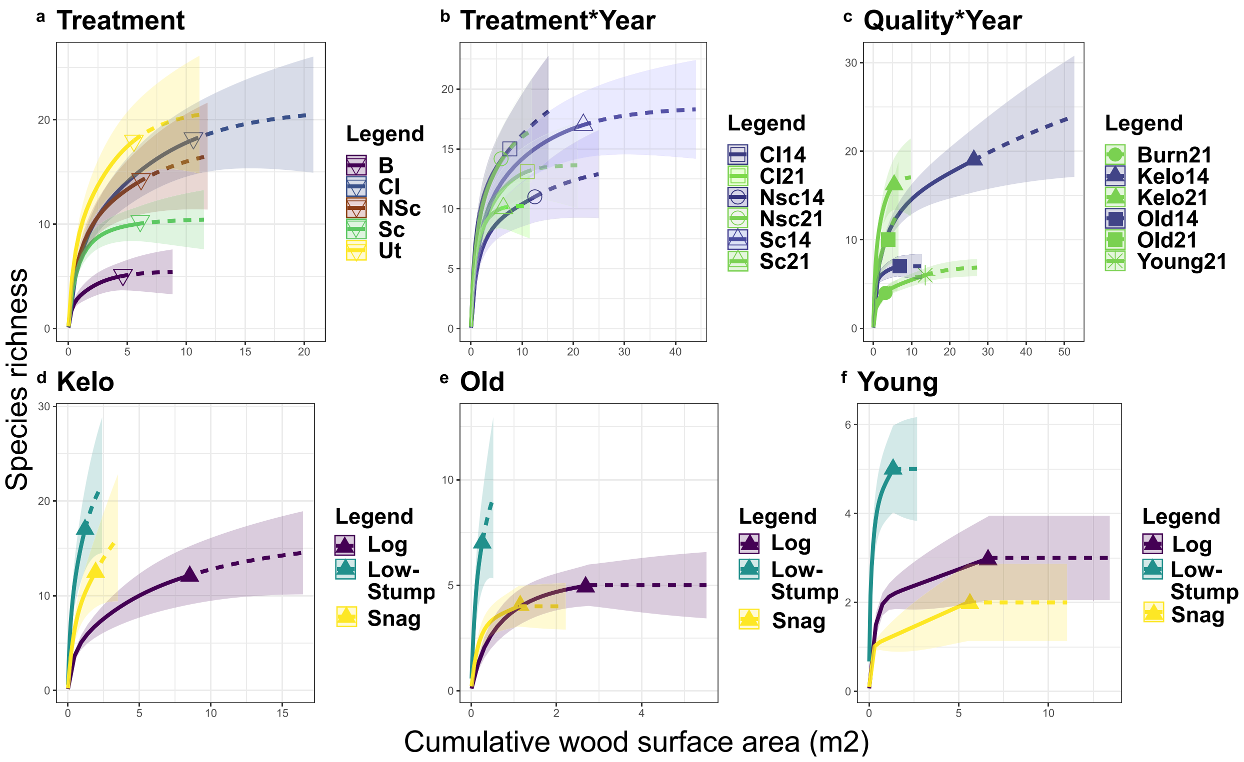

Fig. 1. Rarefaction curves displaying species richness of different treatments and deadwood types and qualities. Y-axis represents observed (full lines) and extrapolated (dashed) species richness. X-axis may differ between panels and represents the sample effort in cumulative wood surface area (m^2). Error bars show 95 % S.E. a) Treatment types sampled in 2021. b) Treatment types sampled both 2014 and 2021, untouched and burned not included since they were only sampled in 2021, legend indicates treatment * year of sampling. c) Deadwood qualities and sampling year. d) Kelo deadwood by type, snags, logs and low-stumps. e) Old deadwood by type, snags, logs and low-stumps. f) Young deadwood by type, snags, logs and low-stumps.

Abbreviations: B = burned plots. Cl = retention plots. Nsc = harvested plots with no site preparation. Sc = harvested plots with site preparation. Ut = untreated control.

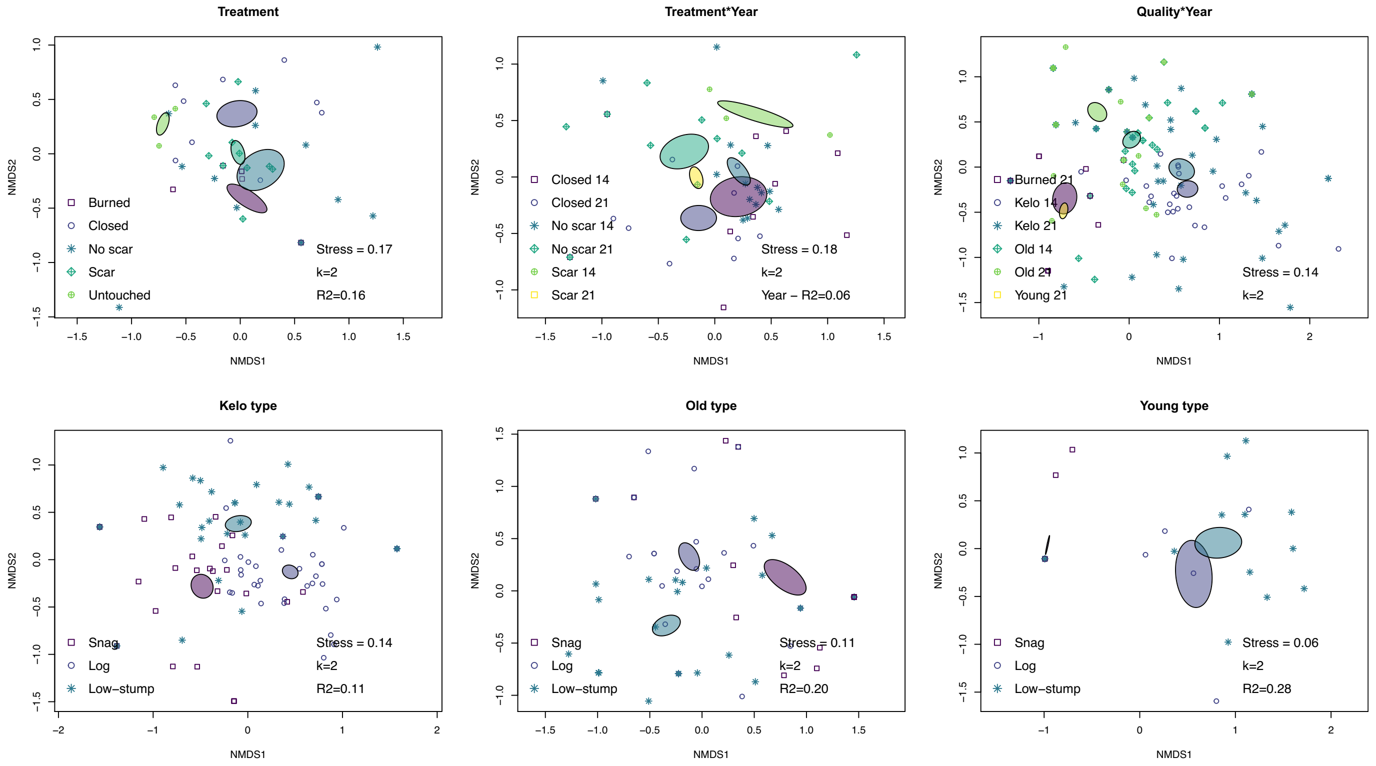

Fig. 2. NMDS plot visualising species assemblages between deadwood quality, type and treatments. Ellipsoids visualize the centroids with standard error, conf = 0.95.

on kelo wood substrates. Beta diversity was similar between kelo and old deadwood types within stands but lower on young and burned deadwood types (BETADISPER, $p \leq 0.001$), which would explain the low species richness on plot level and the high total richness of those qualities (Figs. 2 & A.1, Table A.2). Lichen assemblages were nested with clumped species loss among deadwood qualities (metacommunity analysis with positive coherence ($p \leq 0.001$), negative turnover ($p \leq 0.001$) and positive species clumping ($p \leq 0.001$)) (Fig. A.1). Indicator species analysis revealed the following species as indicators of kelo wood: *Hertelidea botryosa* (NT), *Cladonia parasitica* (NT), *Carbonicola anthracophila* (NT) and *Xylopsora friesii*. Notably *Elixia flexella* (NT), *Carbonicola myrmecina* (NT) and *Calicium denigratum* (NT) were only found on kelo wood but in such low numbers that they had no indicator value (Fig. A.1).

On plot level, there were only small differences in lichen species richness and abundance between snags and logs while low-stumps displayed a higher richness when controlled for the sampled deadwood amount (Table A.2) which was also seen rarefaction curves, revealing a higher potential total richness on low-stumps although low-stumps comprised a smaller sample (Fig. 1d, e, f). Eight years after treatment, low-stumps, snags, and logs displayed distinct species assemblages in all quality classes. Deadwood type explained 28 %, 20 % and 12 % of the differences in young, old- and kelo wood qualities, respectively ($p = 0.001$) (Fig. 2).

4. Discussion

Our data show that kelo wood is a key feature for deadwood-dependent lichen conservation in boreal pine forests and retained kelo wood after felling hosts unique lichen assemblages. However, the kelo-associated lichen assemblages face an extinction debt. The amount of kelo wood with lichen occurrence decreased by >80 % between 2014 and 2021 (Fig. 1). This is in large part caused by substrate destruction. However, this did not affect overall species richness (Fig. 1c) and composition (Fig. 2c) on kelo wood, which we, together with the greater beta diversity, interpret as a potential extinction debt. Our results also show that deadwood-dependent lichen species assemblages are seemingly resilient to low severity disturbance through changes in light exposure by retention felling, with similar diversity patterns in closed and open canopy plots. High severity disturbance, such as site preparation and high severity burning caused depauperate deadwood-dependent lichen species assemblages, as a direct effect of substrate destruction. Our results also clearly suggest that species assemblages of deadwood-dependent lichens confined to both old deadwood and newly generated deadwood are a subset of those occurring on kelo wood. This limits the potential of restoration and suggest that for lichens species specialised on kelo wood, conservation of existing substrate is of major importance. Thus, deadwood enrichment benefits common deadwood-dependent lichen species, but rare species risk extinction without future recruitment of kelo wood.

4.1. Disturbance emulation, forest management and lichen diversity

Our results are consistent with previous studies showing that lichen response to disturbances is highly dependent on severity and whether or not substrate legacies remain in disturbed forests (Johansson, 2008; Hämäläinen et al., 2014; Rudolphi et al., 2014). We found that increased sun-exposure from retention felling had no effect on the deadwood-dependent lichen diversity. However, our results clearly show that direct and highly destructive measures such as prescribed burning and site preparation diminished the lichen diversity through reductions in species richness and abundance. Disturbance and sun-exposure are natural elements in pine forests resulting in open forests rich in deadwood (Nilsson et al., 2002). Organisms associated with pine deadwood are therefore adapted to such conditions, explaining why a more open canopy due to felling does not influence lichens in our study. Eight years may also be a relatively short time to study indirect effects on persistence of deadwood-dependent lichens, meaning that the effect of such factors as indirect sun-exposure may be lagging behind. Thus, to reveal long-term responses to restoration monitoring over several decades is needed.

Heavy disturbance such as fire typically alters the species composition, favouring certain lichen species and disfavouring others (Lõhmus et al., 2018). That fire does not always have a positive effect on species has also been shown for other taxonomic groups such as bryophytes (Espinosa del Alba et al., 2021; Rudolphi et al., 2011). The significance of stand replacing fires has lately been questioned with studies showing that non-stand-replacing disturbance play a much larger role in pine dominated boreal forest than previously thought (Kuuluvainen and Aakala, 2011; Berglund and Kuuluvainen, 2021). Repeated low severity fires are also what creates kelo wood along with other important structures (Niemelä et al., 2002). Furthermore, without heavy landscape alteration, natural borders such as lakes, wetlands or other topographical factors would release certain areas from the most severe fires (Zackrisson, 1977; Hellberg et al., 2004). In our study, the changed species assemblage is mainly a result of species loss, with limited recolonization during the time span of 8 years. This is in contrast with, e.g., (Lõhmus et al., 2018) who showed partial recolonization after 9 years in pine dominated stands. However, they studied a wider range of lichens, while we only studied deadwood-dependent species. Species such as *Carbonicola anthracophila* and *C. myrmecina* grow exclusively on charred wood, indicating a fire dependency (Bendiksby and Timdal, 2013), although their colonisation could potentially take centuries (Esseen et al., 1992; Hämäläinen et al., 2014). Wildfires or prescribed burning is most likely a prerequisite for the establishment of such species. The destructive effect of fire shown in this study suggest that our burned stands are in the initial stages of recovery. During the coming decade we expect partial recolonizations of generated deadwood structures, as shown in Motiejūnaitė et al. (2014), Lõhmus et al. (2018) and Salo et al. (2019). Burned stands could therefore be subject to a colonisation credit, that may be fulfilled if studied over a longer timespan (Cristofoli et al., 2010; Jackson and Sax, 2010; Gjerde et al., 2012) and under the condition that source populations are available in the surrounding landscape (Hämäläinen et al., 2023). Lichens on intact kelo trees could potentially survive fires better than the kelo remnants in our study. Our results suggest that the extinction rate is greater than the colonisation rates, that kelo wood is not generated and that dispersal sources are disappearing. Repeated prescribed burning and conservation of existing deadwood is needed to reverse this trajectory, a slow process that may be possible due to the apparent longevity of lichens.

4.2. Deadwood type

Our results show that kelo wood supports a large proportion of the total lichen diversity and a number of red-listed, deadwood-dependent lichens are exclusively found on kelo wood which was also seen in Santaniello et al. (2017). In addition, we show that lichens on this substrate show a high beta diversity and that there is a nested pattern among deadwood qualities. This means that individual kelo wood substrates host unique species making them sensitive to anthropogenic and stochastic extinction (Hanski and Ovaskainen, 2002) and that deadwood lacking kelo-qualities only supports a subset of the deadwood-dependent lichen diversity found on kelo wood. Because we did not include natural forest in this study, we cannot evaluate if the higher beta diversity of kelo wood also occur in old-growth forests rich in natural structural elements or if this is a result of a continuous decrease of kelo wood in the landscape. Kelo qualities are formed during the trees' life and cannot be formed after tree death. Therefore, we do not expect lichen diversity on young deadwood to reach up to the levels of kelo wood as it is lacking the unique qualities found on kelo wood. Our findings show that for conservation of lichen diversity, it is of outmost importance to retain existing kelo wood, and that restoration through deadwood enrichment is not sufficient for conservation of deadwood-dependent lichens. It is possible that the remaining trees that survived the prescribed burning, as well as the partially bark-peeled trees will develop suitable kelo-characteristics in the future. However, this is a slow process that probably demands repeated restoration measures, such as repeated prescribed burnings and bark peelings. As the already rare kelo wood is not recreated in the managed forest landscape (nor in old-growth reserves), a bottleneck situation is evident for kelo-associated species. If kelo wood volumes continue to decrease in the landscape, kelo wood may symbolise an extinction debt yet to be paid.

In addition to deadwood quality, a variety of substrate types is needed to support lichen diversity, though some previous studies have investigated epiphytic lichens on deadwood while we investigated obligate lignicolous lichen species (Caruso and Rudolphi, 2009; Svensson et al., 2016). We show that different species assemblages on deadwood types (logs, snags and low-stumps) are maintained over time and that this pattern is evident across different deadwood qualities. This means that deadwood types complement each other and contribute to the full assemblage. On kelo wood, snags and low-stumps supported more red-listed species than logs. Snags may provide a favourable microclimate for lichens due to their sun-exposure and lack of ground contact, as is shown in Lõhmus and Lõhmus (2001) and Svensson et al. (2016). In addition, low-stumps have shown to support high number of species, probably because they provide both vertical and horizontal surfaces and support terricolous species (Caruso and Rudolphi, 2009). We observe that low-stumps support high species numbers also for lignicolous lichen species. Young snags supported the least species and seems to be of relatively low importance for lichens in the short-term, something that may change with increasing deadwood age (Hämäläinen et al., 2021). We only inventoried lichens up to 2 m in this study, which means that we might have missed species occurring higher up and on vertical surfaces higher up. This could possibly explain observed differences between low-stumps and snags, although previous studies have shown that 2 m is enough to capture a significant part of the overall species assemblage (Caruso and Thor, 2007; Svensson et al., 2014).

4.3. Conclusions

This study provides novel information on deadwood-dependent lichen ecology related to deadwood types and response to varying disturbances. We show that deadwood quality and type are important to explain diversity patterns of deadwood-dependent lichens. We also show that the creation of new deadwood has limited effect, in the short-term regardless of volume created.

In order to conserve a rich lichen diversity, a variety of substrates is needed although we can likely not substitute naturally developed deadwood with deadwood generated at restoration operations. Thus, the conservation of kelo wood is a prerequisite for deadwood-dependent lichen conservation. As many lichens are poor at dispersal (Hilmo and Såstad, 2001), and rich source populations are scarce and fragmented (Berglund and Jonsson, 2005), assisted colonisation through transplantation may be needed. Site preparation and high-severity prescribed burning is detrimental for deadwood-dependent lichens. Such actions should therefore be planned carefully to avoid the destruction of high-quality deadwood. We suggest that prescribed burning should be performed in close affinity to, but not within, hotspot areas for lichen diversity to avoid local extinctions. This could potentially also promote colonisation at the same time as it would improve conditions for future recruitment of kelo wood. Felling-induced light exposure seems to have small effects on deadwood-dependent lichens as long as deadwood legacies are maintained and continuously added. We can therefore conclude that direct (site preparation & burning) but not indirect effects (retention logging) of forest management result in a decrease in deadwood-dependent lichen diversity. Although studies show that landscape connectivity increase lichen species richness (see, e.g., Kärvemo et al. (2021)), studies that directly investigate dispersal and colonisation of deadwood-dependent lichens are scarce (but see Caruso et al. (2010)). Studies on both natural and assisted dispersal and colonisation are thus urgently needed (Mallen-Cooper and Cornwell, 2020). By all accounts, lichens on kelo wood face an extinction debt that is continuously realised through substrate destruction. There is no indication that current measures like tree retention and creation of high stumps constitute a colonisation credit, as these measures will not contribute to the generation of kelo wood. To halt this extinction debt there is urgent need to start creating new kelo wood by reoccurring prescribed fires or other methods such as bark-peeling to induce tar production.

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CRediT authorship contribution statement

All authors contributed to the conceptualization of the study. TL initiated the project and obtained funding, GT collected field data on lichens and ALE on deadwood. ALE performed the formal analysis and wrote the original draft. All authors contributed to reviewing and editing of the manuscript.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

Data will be made available on request.

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