



Kelo deadwood – an increasingly rare substrate for fungal species

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Abstract

A great threat to forest biodiversity in Sweden is the limited amount of high quality deadwood substrate. The high species diversity associated with deadwood is influenced by a variety of factors, including tree species, microclimate, the stage of decay and the size of the wood. Kelo pine is a unique type of deadwood that is a common element in pristine pine-dominated forests, and a vital substrate for many species of wood-inhabiting fungi. With modern forest practices, pines do not grow old enough for new formation of kelo deadwood to be possible. This makes it more important than ever to study fungal communities associated with this increasingly rare substrate, to determine whether the same fungal species can inhabit other types of deadwood or if they risk extinction alongside the declining number of kelo pines. By collecting sawdust and analysing them through DNA metabarcoding to identify fungal eDNA, I investigated how species composition and species richness differ in pine deadwood of different qualities. The type of pine deadwood had a significant impact on fungal species assemblage composition for all substrate types. Furthermore, no relationship was found between assemblage composition and the microclimatic variables sun exposure and ground contact. Kelo deadwood had a significantly lower species richness compared to all other substrate types, but hosted unique species (including red-listed) not found in other substrate types. In conclusion, these results support earlier findings that highlight the ecological uniqueness of kelo deadwood and the importance of preserving this increasingly rare substrate to support fungal biodiversity in managed forest landscapes.

Keywords: kelo, deadwood, fungal communities, red-listed species

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1. Introduction

Dead trees are not lifeless; they serve as a vital structural component in boreal forests. Rich amounts of deadwood of different qualities is a key factor supporting a high forest biodiversity (Lassauce et al. 2011; Esseen et al. 1997; Skogsstyrelsen 2024). However, a large threat to forest biodiversity is the limited amount of deadwood available in managed forests.

The creation of deadwood is very different in managed forests compared to creation resulted from disturbance regimes in natural forests. Disturbance regimes in natural boreal forests in northern Europe are shaped by multiple drivers that vary in size, spatial configuration, frequency and severity (Kneeshaw et al. 2011). In dry nutrient-poor sites with Scots pine (*Pinus sylvestris* (L.)), cohort dynamics caused by low-severity fires were dominating in shaping forest structure and tree mortality (Berglund & Kuuluvainen 2021). With modern forest practices and implementation of fire suppression, forests with disturbance regimes driven by fire have almost disappeared (Esseen et al. 1997), which in turn change the dynamics in which deadwood is created. Existing deadwood decompose over time, facilitated by various detritivores such as bacteria, fungi and animals (Löfroth et al. 2023). Additionally, deadwood can also be overgrown by ground vegetation or consumed in forest fires (ibid).

The high species diversity associated with deadwood is influenced by a variety of factors, including tree species, microclimate, the stage of decay and the size of the wood (Esseen et al. 1997). The environment for organisms living in an exposed standing tree is very different compared to a fallen tree with ground contact. A unique type of deadwood is kelo pine, which is a common element in pristine pine-dominated forests and contributes to increased structural and substrate diversity (Kuuluvainen et al. 2017). Kelo is a type of pine deadwood that serves as a vital substrate for many wood-inhabiting fungi (Niemelä et al. 2002). Many red-listed species are strongly associated with kelo, including species of lichenised fungi (Nirhamo et al. 2024; Larsson Ekström et al. 2023). The formation of kelo pine is such a slow process that with modern forest practises, pines do not grow old enough for new formation of kelo deadwood to be possible (Niemelä et al. 2002). Rouvinen et al. (2002) estimated that the creation of new kelo pines was one per hectare per decade in the Kalevala National Park in Russian Viena Karelia. Scots pine can in the right circumstances reach an age of 810 years (Siren 1961). However, after 300-500 years, these trees typically begin to exhibit signs of decline, leading to a gradual and prolonged death where the trees after death can remain standing hundreds of years more (Niemelä et al. 2002). The characteristic silver-coloured debarked stem

that kelo has is caused by blue-stain fungi that colonises the sapwood after the death of the pine, making it unattractive for most decay-causing fungi (Niemelä et al. 2002). Given the long lifespan both before and after death of a kelo pine, it is common that they have been exposed to at least one forest fire, leaving fire scars or charred surfaces. Fire is important in the formation process of kelo, because pines exposed to recurrent fires develop wood rich in resins which makes it highly resistant to decay (Niemelä et al. 2002). It is usually not when the kelo pine is still standing that it harbours most species, but it is rather when it later falls down that kelo becomes a suitable substrate for highly specialised fungi (ibid).

Fungal diversity has traditionally been studied by their fruiting bodies through morphological and phylogeny analyses. This can be challenging because fruiting bodies appear sporadically for most fungal species, and can be both small and short-lived (Shirouzu et al. 2020). Another key tool in exploring fungal diversity is environmental DNA metabarcoding (eDNA). Species can be identified by collecting environmental samples such as soil and wood that contain fungal cells, which can reveal species that through fruiting-body inventories could be missed (Shirouzu et al. 2020). This method does not require the same taxonomical knowledge when collecting data but instead rely on sophisticated lab facilities and advanced post sequencing bioinformatics for species identification (Frøslev et al. 2019). EDNA metabarcoding has a wide application range with use for ecosystem and biodiversity monitoring, both in aquatic and terrestrial environments (Ruppert et al. 2019).

Pine deadwood with kelo properties have considerable ecological value and because the creation of new kelo deadwood is very limited, it is of high importance to study fungal communities in this unique and ever-decreasing type of substrate. This knowledge is essential for implementation of effective and functional conservation efforts.

1.1 Purpose and Question statements

My aim with this study is to examine how fungal communities differ between pine deadwood with different quality characteristics. This will be performed by answering these questions:

1. How do the species composition and richness of fungi differ between pine deadwood of different qualities (kelo, old deadwood without kelo qualities and newly created deadwood)?

2. How do microclimatic factors such as sun exposure and ground contact affect species composition and richness of fungi in deadwood?
3. In which substrate type can the highest number of red-listed species be found?

Species diversity will be explored on substrate level (α -diversity), assemblage composition (β -diversity) and the overall diversity in the study area (γ -diversity). I hypothesise that there will be different species of fungi found in kelo pine compared to pine deadwood of other qualities due to its resistance against decay, and that the species richness in kelo will be lower compared to pine deadwood of other qualities. Furthermore, microclimatic factors may have a significant influence on both species richness and composition, where ground contact could increase species richness (Kunttu et al. 2018) due to higher moisture availability.

2. Methods

The study was conducted in Effaråsen, an experimental area located 30 kilometres outside of Mora in Dalarna County (figure 1). The area encompasses 140 hectares with the center point coordinate 60° 58'29"N, 14° 01'55"E. It is subdivided into 24 stands ranging from 3 to 14 hectares with an average size of 5 hectares. The forest is predominantly composed of Scots pine with an age range of 130-150 years, along with Norway spruce (*Picea abies*), Silver birch (*Betula pendula*) and Downy birch (*Betula pubescens*) as well. The area has been managed for wood production, with fertilising and thinning operations performed. More natural structural elements can be found, including old fire-scarred pines and logs which was likely created in the last wildfire year 1888. The 24 stands have undergone eight types of treatment (three stands for each treatment); which are the following:

1. Untreated control
2. Felling with 3% retention and deadwood enrichment
3. Felling with 10% retention and deadwood enrichment
4. Felling with 30% retention and deadwood enrichment
5. Felling with 50% retention and deadwood enrichment
6. 100% retention and deadwood enrichment
7. Prescribed burning following 50% felling
8. Prescribed burning with no felling

The retained trees were in equal proportions either left intact, girdled, felled for creating logs or partly cut for high-stump creation. Intact trees were left both in groups and as individual trees. The partial cuttings were performed during November 2012–January 2013, and the prescribed burning were performed during May–June and August 2013. For more information about the experiment, read Santaniello et al. (2016) and Larsson Ekström et al. (2024).

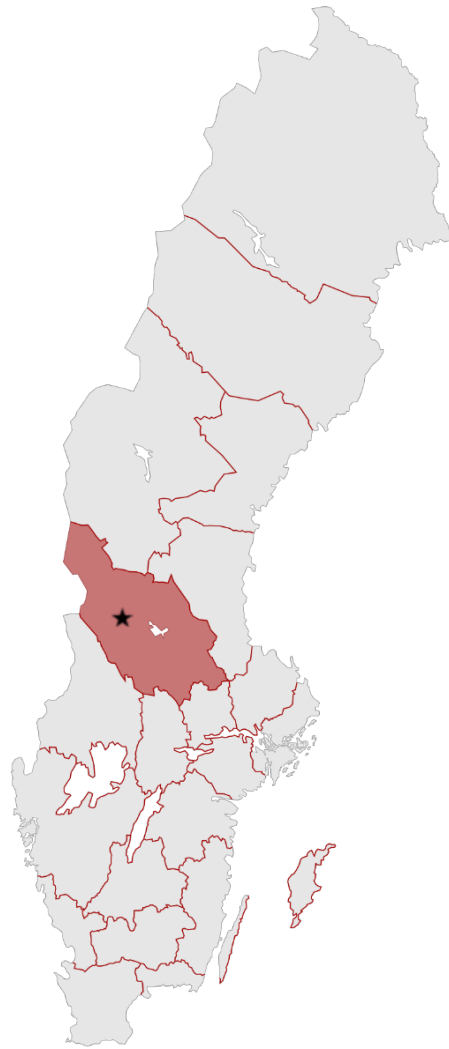


Figure 1: Approximate location of Effaråsen marked with a star. Map of Sweden with Dalarna County highlighted in red. Based on map from Lokal_Profil (2010) (CC BY-SA 2.5).

Sampled deadwood substrates were downed pines (logs), standing pines (snags, figure 2) and standing pines shorter than 50 cm (low-stumps). The substrates were deadwood created with harvester, deadwood created through prescribed burning, deadwood with kelo qualities and old deadwood without kelo qualities. Kelo is characterised by its hard, silver-coloured wood that has lost its bark. Due to the age of the wood, it is common that kelo wood have traces from fire and other previous damages. Old pine wood without kelo properties commonly have a less hard surface and can be cracked. Sampled old deadwood are approximately between 80-100 years old on average. Differences between substrate types are described in Larsson Ekström et al. 2024. Kelo and old deadwood were sampled during May 2024, while deadwood created by harvester and prescribed burning were sampled at an earlier occasion in Larsson Ekström et al. 2024.



Figure 2: Kelo snag with fire scar.

In each stand, samples from up to five substrates of each deadwood quality were collected when possible. If less than five substrates of a given quality were found, the ones found were sampled.

From each object, two samples were collected from opposite sides of the bottom part of the wood (50-150 cm from bottom part). Prior to sampling, the bark and the outermost layer of the wood were peeled away using a disinfected knife. In the peeled area, the samples were collected using a disinfected drill bit and aluminium foil to collect the sawdust. The collected sawdust was then placed into zip lock bags and individually marked by stand name and substrate ID. A new piece of aluminium foil was used for each sample, and the disinfection was done by burning the knife and drill bit between samples. Other measures collected for each object were:

- Sample ID marked with stand and substrate type
- GPS location

- Top and bottom diameter and length for logs
- DBH and height estimation for snags
- Decay stage class (1-5) according to Siitonen & Saaristo 2000
- Presence/absence of fire scar and charred wood
- Sun exposure (exposed, shaded or intermediate)
- Ground contact estimation of logs in %

2.1 DNA Analysis

The sawdust samples were after collection in the field stored in a freezer before the samples were freeze-dried and moved to test-tubes in preparation for further analysis. The DNA analysis was carried out by the company Bioname, where the samples underwent a deep sequencing metabarcoding analysis and turnkey service. The nuclear ribosomal internal transcriber spacer region 2 was targeted using the fITS7-ITS4 primer pair (Ihrmark et al. 2012; White et al. 1989). Negative extraction control samples and PCR blanks were added to test for cross-contamination or contamination of the reagents. The controls resulted in very few reads which indicates no cross-contamination or contamination of the reagents. Low abundance taxa with less than 2 reads were removed from the data.

The bioinformatics pipeline followed Kaunisto et al. (2020), and the ZOTUs (Zero-radius Operational Taxonomic Unit) were assigned to taxa using the UNITE Fungi database 9.0 (Abarenkov et al. 2024). A majority of the ZOTUs were assigned to species, genus or family, with a probability threshold of ≥ 0.90 , 0.70 or 0.50 respectively.

2.2 Data Analysis

All analyses in this study were performed using R statistical Software version 4.4.2 (R Core Team 2024) and iNEXT Online (Chao et al. 2016).

For the purpose of this study, a confidence interval of 0.95 was chosen. To test for differences in species composition between substrate types, I performed a Permutational Multivariate Analysis of Variance (PERMANOVA) with the R package vegan (Oksanen et al. 2025). Community dissimilarity was calculated

using a Jaccard distance matrix with 999 permutations to assess statistical significance. To evaluate pairwise comparisons in species composition between substrate types, I used the function `pairwise.adonis2` in the R package `pairwiseAdonis` (Martinez 2017).

To visualise species assemblages in different substrate types, I created a Non-metric Multi-Dimensional Scaling ordination (NMDS) plot with two dimension ($k=2$) and 20 permutations by using the R package `vegan`. One outlier was excluded from the NMDS in order to create a readable plot. The excluded sample had a total of three ZOTUs, which were all ZOTUs that were not found in any other sample.

I created additional NMDS plots in the same way to visualise species assemblages dependent on the microclimatic variables sun exposure and ground contact. Data for ground contact was not collected for logs of all substrate types, therefore only *kelo* and old logs were included in the NMDS.

Rarefaction curves were created by using `iNEXT` online to see how species richness relate to the accumulated sampling effort. The number of bootstraps was 1000 for the rarefaction curves, with a confidence interval of 0.95.

To test if there are significant differences in species richness between substrate types, the R package `glmmTMB` (Brooks 2017) was used to create a generalised linear mixed model (GLMM) with a negative binomial distribution and stand ID as random factor. Species richness was used as response variable and substrate type (*kelo*, old, burned and harvester created) as predictor variable. For diagnostics of the fitted model, the R package `DHARMa` (Hartig 2024) was used.

Two additional generalised linear mixed models were created to test if sun exposure or ground contact have a significant impact on species richness between substrate types.

An indicator species analysis was performed with the function `multipatt` in the R package `indicspecies` (De Cáceres & Legendre 2009), to identify indicator species for the different substrate types.

3. Results

A total of 491 substrates were sampled and analysed, of which 490 were included in the statistical analyses. A total of 1976 ZOTUs were identified, and 660 of these (33.4%) could be identified to species level. The taxonomic distribution for all identified ZOTUs can be seen in figure 3, where a majority of the identified ZOTUs is categorised as either Ascomycota or Basidiomycota.

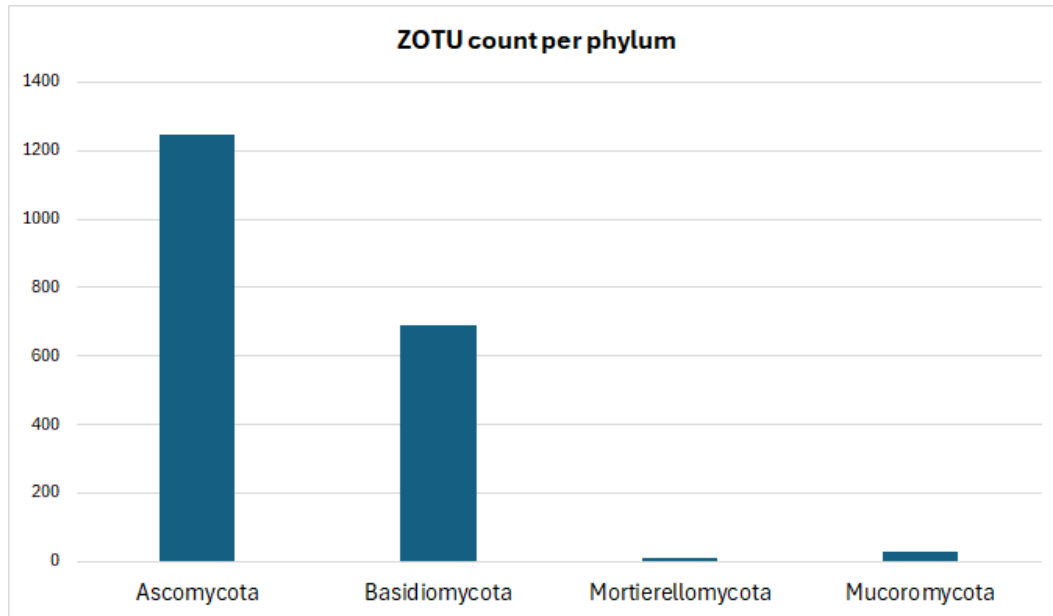


Figure 3: Taxon distribution of found ZOTUs from all collected samples. Ascomycota=1246, Basidiomycota=692, Mortierellomycota=9 and Mucoromycota=29.

3.1 Deadwood quality and assemblage composition

The result of the post-hoc test (pairwise.adonis2) was that there is a significant difference in the assemblage composition (β -diversity) of fungal species between all substrate types ($P < 0.001$). However, substrate type only explains 7.38% of the variation. In figure 4, substrate types form distinct clusters, with assemblage centroids only overlapping between harvester created and burned deadwood.

ZOTUs by Deadwood Type

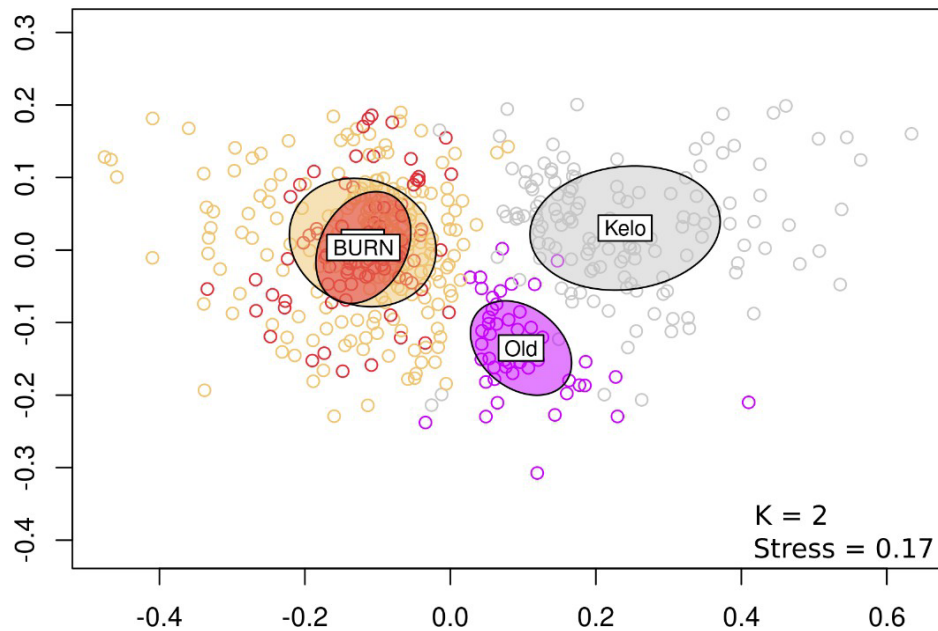


Figure 4: Non-Metric Multidimensional Scaling (NMDS) ordination of fungal communities in collected deadwood samples. Harvester created deadwood in gold.

In the indicator species analysis, indicator species were found for old, kelo and burned deadwood (stat > 0.5, $p=0.005$). Six ZOTUs were identified as indicator species for kelo deadwood, seven ZOTUs for old deadwood and four ZOTUs for burned deadwood. Indicator species that were identified to species level are *Phialocephala melitaea* for kelo deadwood, and *Stereum sanguinolentum* and *Sistotremastrum suecicum* for burned deadwood.

3.2 Deadwood quality and species richness

The average species richness on substrate level (α -diversity) was 20 (SE 0.4), with the highest species richness found in burned deadwood and the lowest number found in kelo deadwood (figure 5). There was a significant difference in species richness for kelo substrates, where they had a lower species richness compared to all other substrate types ($p < 0.0001$).

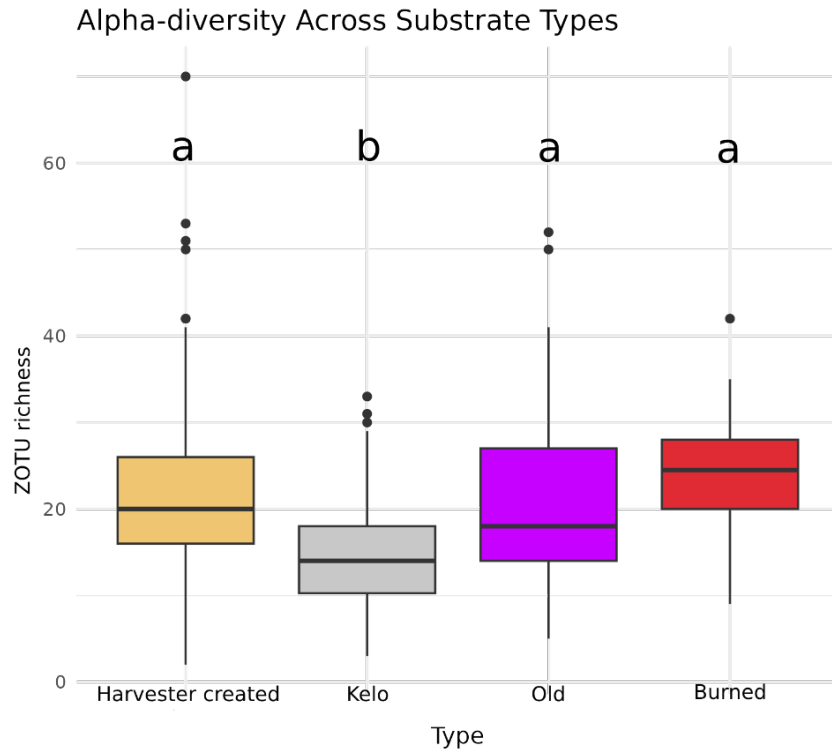


Figure 5: Boxplots of fungal species richness in different substrate types. Letters a and b constitute statistically different groups based on estimated marginal means.

The total species diversity (γ -diversity) for harvest created deadwood showed the highest observed ZOTU richness (figure 6) but was also the substrate type with highest sampling effort. In contrast, kelo had the lowest observed ZOTU richness. The curves are overlapping between harvest created, burned and old deadwood, while the curve for kelo is less steep. Comparison between overlapping trajectories should be interpreted with caution, as neither the observed nor the extrapolated curves reach an asymptote.

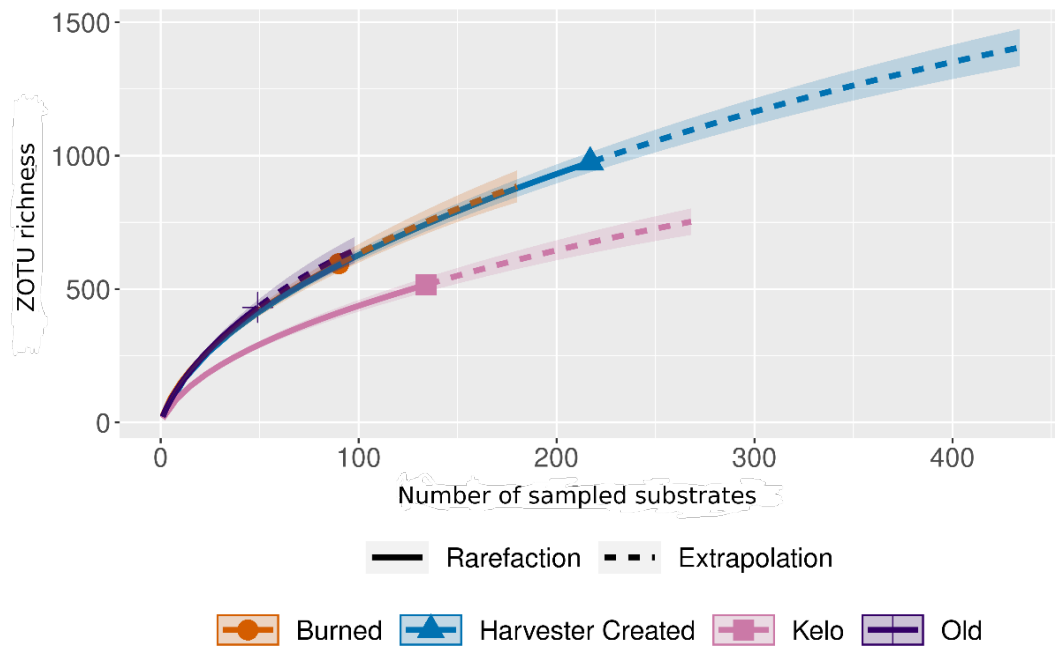


Figure 6: Sample based rarefaction curve for ZOTU richness for each deadwood type. The x-axis represents the number of ZOTUs found and the y-axis stand for the number of sampled substrates (observed values in full line and extrapolated in dotted line). Shaded areas represent 95% confidence intervals.

3.3 Microclimatic Impact

No significant impact was found on species richness and assemblage composition for the microclimatic variables. The results of the GLMM are that while substrate type showed significant effects on species richness, no statistically significant impact was observed for sun exposure alone or for the interactions between sun exposure and substrate type. The p-values for the sun exposure and the interactions with substrate type ranged from 0.10 to 0.89.

The GLMM testing for the effects of ground contact on species richness did not show a statistically significant result. The p-value for ground contact alone was 0.087 and the p-value for the interaction between ground contact and substrate type was 0.218. Thus, neither were significant with the chosen confidence level.

3.4 Red-listed Species

A total of 12 species were identified that are included in the Swedish Red List 2020. The species found can be seen in table 1, where two species are categorised as Data Deficient (DD), seven species as Near Threatened (NT) and three species as Vulnerable (VU). Red-listed species were found in kelo, harvester created and

burned deadwood, while no red-listed species were found in old deadwood. *Cladonia parasitica*, *Erastia ochraceolateritia*, *Phellodon secretus* and *Tricholoma matsutake* were only found in one sample each. The red-listed species found in kelo were not found in any other substrate types, but because of the limited amount of data, no statistical analysis could be performed.

Table 1: Red-listed species found and occurrence in different substrate types.

Scientific name	Red-list category	Kelo	Old	Harvester created	Burned
<i>Cladonia parasitica</i>	NT	1			
<i>Dacrymyces ovisporus</i>	DD			3	
<i>Erastia ochraceolateritia</i>	NT			1	
<i>Femsjonia peziziformis</i>	DD			1	2
<i>Gloeodontia subasperispora</i>	NT	2			
<i>Hertelidea botryosa</i>	NT	11			
<i>Leptoporus erubescens</i>	NT			2	
<i>Microcalicium ahlneri</i>	NT	3			
<i>Phellodon secretus</i>	VU				1
<i>Rhodonina placenta</i>	VU			2	4
<i>Skeletocutis kuehneri</i>	NT			9	
<i>Tricholoma matsutake</i>	VU				1

4. Discussion

The main findings in this study are that (1) pine deadwood of different qualities hosted unique assemblages of wood-inhabiting fungi. (2) Kelo had a lower α -diversity and γ -diversity compared to all other substrate types, but hosted unique and red-listed species not found on other substrate types. Sun exposure and ground contact did not have a significant impact on either assemblage composition or species richness. There are several studies that explore the unique habitat that kelo pine provides (Niemelä et al. 2002; Santaniello et al. 2017; Larsson Ekström et al. 2023). However, there are not many studies that explore fungal species diversity through eDNA metabarcoding in kelo specifically, which the results in this study provide.

4.1 Deadwood type

Previous studies have shown that deadwood type influence species composition and richness (Santaniello et al. 2017; Kunttu et al. 2018; Larsson Ekström et al. 2024). Assemblage composition was significantly different for all substrate types when tested with a PERMANOVA. A likely reason for the differences in assemblage composition between harvester created and burned deadwood is that there is a larger variation in species found on harvest created deadwood. Prescribed burning can lead to a homogenisation of assemblage composition (Larsson Ekström et al. 2024), possibly because less variation within the substrate type can be found in burned deadwood compared to unburned deadwood. Performing a Multivariate homogeneity of groups dispersion (betadisper) test as well could, however, provide more insight as to how they differ.

Old deadwood and kelo hosted distinct species assemblages and because of the differences in physical characteristics, the assemblage composition in old deadwood will not become more like kelo. Old deadwood will break down and decompose long before it becomes similar to kelo, because of the differences in life history of the tree (Niemelä et al. 2002).

In this study, kelo differentiates from all other substrate types by having a significant lower species richness on substrate level. This result is not surprising, because kelo is in many respects an inhospitable (but unique) environment for fungi (Niemelä et al. 2002). Kelo is highly resistant against decay because it is rich in resin and after standing for many years exposed to the elements, only eroded heartwood remains of the once living tree (ibid). Even if many fungal species cannot be found on kelo, both Larsson Ekström et al (2023) and Nirhamo et al.

(2024) found the highest species richness of lichenised fungi on kelo. Kelo provides a favourable surface area for lichens, possibly because the longevity of the substrate enables colonization of lichen that usually need a long time to establish.

Not only the quality type of the deadwood influence species assemblages of wood-inhabiting fungi. A study from the same area found that the deadwood quality is of importance, and that the position of the deadwood (standing or lying) affects species assemblages as well (Larsson Ekström et al. 2023). I only used quality as grouping factor in the statistical analyses, rather than quality and position. This decision was made to reduce the number of factor levels and simplify the model structure. If both quality and position would be used instead, it would result in a high number of categories with relatively few replicates in each. By focusing on quality, I could detect overall patterns in species composition and richness between substrate types, which is the primary aim with this study. Future studies with larger sample sizes could explore more factors to explore influences on fungal diversity.

4.2 Microclimatic impact

Microclimatic variables were not found to have a significant impact on species composition and richness. Even if no significant impact was found, microclimatic conditions of a substrate are of importance when studying fungal communities. A factor that can affect the results when studying fungal communities through DNA sequencing is where on the substrate the samples are collected and how many samples that are collected from each substrate (Kubartová et al. 2012). Each substrate was sampled at the same distance from the bottom part two times at opposite sides, which resulted in that the same area of the wood were sampled between all deadwood types. If more samples were collected from each substrate, a larger part of the fungal community could be found and microclimate could be explored on a finer scale, possibly finding clearer connection between microclimate and species composition.

Another explanation as for why microclimatic variables did not have a significant impact, could be the type of forest the samples were collected from. Sampled deadwood were all from Effaråsen, a forest area dominated by Scots pine with stands that are more or less thinned out. This creates a forest environment that in general is more open compared to if the substrates were found in a full-storied spruce forest. An example of this is fallen kelo trees found in spruce-dominated heath forests host an essentially different fungal community compared to kelo found on drier sites (Niemelä et al. 2002).

4.3 Red-listed Species

A number of interesting and rare species were found in the samples collected in Effaråsen. The red-listed species identified were not concentrated to one type of deadwood but found in all substrate types except old deadwood. These species were only found in a few samples each, which means that it is not possible to say based on the results that one substrate type hosts more red-listed species compared to another. Four species (*Cladonia parasitica*, *Erastia ochraceolateritia*, *Phellodon secretus* and *Tricholoma matsutake*) were only found in one sample each. *Phellodon secretus* is a rare fungus (classified as VU) with a unique ecology. It can be found in gaps under pine logs, preferably in strongly decayed wood or rootstocks of kelo pine (Niemelä et al. 2003). It is mycorrhizal, but is dependent on pine deadwood for development of their fruiting bodies (ibid). This species is threatened by clearcutting and other types of forest management and by the limited amount of suitable deadwood (SLU Artdatabanken 2025).

Another red-listed species found that is classified as vulnerable is *Rhodonía placenta*. It is a saprotrophic wood-living fungi that is dependent on a continuity of large logs (SLU Artdatabanken 2020). It is threatened by the limited number of suitable substrates, and harvesting of old pine forests (ibid). The last species found in this study that is classified as vulnerable are *Tricholoma matsutake*. This Species is a mycorrhizal fungi that can be found in old pine forests growing on dry, nutrient poor soils (SLU Artdatabanken 2025). It is rarely found in forests with an age lower than 100 years, and the main threat is a decrease of suitable habitat caused by harvesting of old pine forests (ibid). It is hard to explain why it was found in a burned log, because it is a soil-living mycorrhizal fungi and is not dependent on deadwood.

Many of the red-listed species found in this study are highly specialised and strongly associated to the environment they are found in. It is not possible to say if it has significant meaning, but it is still interesting that all red-listed species found on kelo were only found on kelo substrates. Species identification through eDNA metabarcoding has a lot of applications in future ecological studies. To increase the gain from these studies, more knowledge is needed in species identification through DNA to be able to match to collected data from different environments. In this study, 33.4% of the ZOTUs could be identified to species level. If more species could be identified to species level, we could learn more about species-specific ecology.

4.4 Conclusion

To be able to sustain a high fungal species diversity in managed forest landscapes, rich amounts of deadwood with different qualities is crucial for successful conservation and restoration efforts. It is of importance that management practices lead to an increased and steady supply of new deadwood, because substrates break down over time. This would lead to an increased availability of suitable substrates for a high number of species, but it is not enough for all fungal species. Rare fungal species associated with kelo pine are at risk of extinction if no measures are taken to allow creation of new pine deadwood with kelo properties. Indeed, a prerequisite for creation of new kelo pine is that pines are allowed to reach an older age than achieved in a rotation period. Because of the time it takes for creation of new kelo pines, existing kelo needs to be protected and act as “lifeboats” until new suitable substrates are created. Management practises such as prescribed burning can destroy existing kelo, reducing the already limited number available. At the same time, an increased use of fire is necessary for creation of future kelo pine. This must be taken into consideration when planning for prescribed burning. In areas that have a lot of kelo, it may be more suitable to use alternative methods such as spot burning or girdling to avoid unnecessary loss of substrates that are vital for wood-inhabiting fungi and other organisms.

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Popular science summary

Dead trees may seem lifeless, but they are just as important as living trees for a wide variety of species. A big threat to forest biodiversity in Sweden is the lack of deadwood available for all these species that depend on it for survival. Many species of fungi live in deadwood, and the species that you may find in a dead tree depend on several things, such as the tree species, the surrounding climate, how far the wood has decayed, and how big the piece of wood is.

A special type of pine deadwood is called kelo pine, which are pines that died long ago but because of their durability do not break down easily. These trees are common in untouched, natural pine forests and are important for specialised fungal species. But in today's managed forests, trees are usually harvested before they become that old, which means new kelo trees cannot form. Because of this, it is now more important than ever to study the fungal communities that live in kelo wood, to find out whether these fungi can survive in other kinds of deadwood, or if they are at risk of disappearing along with the increasingly rare kelo trees.

By collecting sawdust from pine deadwood, I investigated how fungal communities differ between different types of deadwood by using a method called DNA metabarcoding. This method allows detection of multiple fungal species through their DNA in the collected sawdust, making it possible to compare which fungal species that live in different types of deadwood, and how many different species are present.

The results were that fungal communities differ between different types of deadwood. Each deadwood type hosted its own fungal community, while sun exposure and how much the wood touched the ground did not have a noticeable effect on species found. Kelo had fewer detected species overall, but it included rare and threatened species that were not found in other deadwood types.

In summary, this study supports earlier findings that show how kelo pine is important for unique fungal species, and that it is important to preserve this increasingly rare substrate in order to keep our forests rich in species in the future.

Appendix 1

<i>Predictors</i>	Sum		
	<i>Incidence Rate Ratios</i>	<i>CI</i>	<i>p</i>
(Intercept)	14.97	13.92 – 16.11	<0.001
orderchange [CR]	1.42	1.30 – 1.56	<0.001
orderchange [Old]	1.41	1.24 – 1.62	<0.001
orderchange [BURN]	1.62	1.45 – 1.81	<0.001
Random Effects			
σ^2	0.15		
τ_{00} Stand	0.00		
ICC	0.01		
N_{Stand}	24		
Observations	490		
Marginal R^2 / Conditional R^2	0.172 / 0.176		

Figure 7: Results for GLMM with sum of species as response variable and substrate type as predictor variable. Intercept=kelo, orderchange=substrate type and CR=harvester created.

Appendix 2

<i>Predictors</i>	Sum		
	<i>Incidence Rate Ratios</i>	<i>CI</i>	<i>p</i>
(Intercept)	14.49	13.02 – 16.13	<0.001
orderchange [CR]	1.46	1.27 – 1.68	<0.001
orderchange [Old]	1.55	1.27 – 1.88	<0.001
orderchange [BURN]	1.79	1.36 – 2.37	<0.001
Sun exposure [Shaded]	0.92	0.75 – 1.12	0.384
Sun exposure [Sunny]	1.14	0.97 – 1.34	0.104
orderchange [CR] × Sun exposure [Shaded]	1.07	0.84 – 1.35	0.579
orderchange [Old] × Sun exposure [Shaded]	0.89	0.63 – 1.26	0.510
orderchange [BURN] × Sun exposure [Shaded]	1.03	0.72 – 1.46	0.889
orderchange [CR] × Sun exposure [Sunny]	0.92	0.74 – 1.13	0.402
orderchange [Old] × Sun exposure [Sunny]	0.84	0.62 – 1.15	0.282
orderchange [BURN] × Sun exposure [Sunny]	0.79	0.57 – 1.09	0.148
Random Effects			
σ^2			
τ_{00} Stand	0.00		
N _{Stand}	24		
Observations	485		

Figure 8: Results for GLMM with sum of species as response variable and substrate type and sun exposure as predictor variables. Intercept=kelo, orderchange=substrate type and CR=harvester created.

Appendix 3

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	Sum	
		<i>CI</i>	<i>p</i>
(Intercept)	12.87	9.41 – 17.60	<0.001
orderchange [Old]	1.64	1.10 – 2.45	0.015
Ground contact	1.00	1.00 – 1.01	0.087
orderchange [Old] × Ground contact	1.00	0.99 – 1.00	0.218
Random Effects			
σ^2			
τ_{00} Stand	0.00		
N_{Stand}	22		
Observations	97		

Figure 9: Results for GLMM with sum of species as response variable and substrate type and ground contact as predictor variables. Intercept=kelo, orderchange=substrate type and CR=harvester created.

Appendix 4

Table 2: ZOTUs identified to species level and their occurrence in different substrate types.

Scientific name	Harvester created	Kelo	Old	Burned
<i>Oidiodendron griseum</i>	13	12	4	36
<i>Hypochnicium albostramineum</i>	4	0	0	11
<i>Hamamotola lignophila</i>	132	0	0	56
<i>Sistotrema brinkmannii</i>	30	0	0	4
<i>Symbiotaphrina microtheca</i>	120	38	8	46
<i>Talaromyces rademirici</i>	23	0	4	42
<i>Peniophorella praetermissa</i>	57	0	2	50
<i>Vexillomyces palatinus</i>	115	1	6	12
<i>Lapidomyces epipinicola</i>	19	1	0	6
<i>Lecidea nylanderii</i>	6	1	0	4
<i>Unilacryma unispora</i>	18	0	0	6
<i>Phialocephala melitaea</i>	30	26	25	4
<i>Botryobasidium obtusisporum</i>	25	2	1	16
<i>Tremella encephala</i>	154	0	0	30
<i>Carcinomyces polyporinus</i>	32	0	7	34
<i>Exophiala abietophila</i>	43	0	0	3
<i>Hyphodiscus hymeniophilus</i>	52	0	0	11
<i>Phaeotremella foliacea</i>	24	0	0	5
<i>Cladonia sulphurina</i>	1	2	5	0
<i>Dacrymyces subarcticus</i>	0	15	1	1
<i>Tubulicrinis medius</i>	0	11	4	0
<i>Ascocoryne albida</i>	58	31	6	26
<i>Globulicium hiemale</i>	0	12	1	0
<i>Phialocephala virens</i>	0	30	1	0
<i>Microcalicium ahlneri</i>	0	5	0	0
<i>Xylopsora friesii</i>	0	23	1	0
<i>Gorgoniceps viridula</i>	4	1	3	0
<i>Phialemonium atrogriseum</i>	0	1	0	0
<i>Mollisia cinerea</i>	4	1	1	1
<i>Cistella acuum</i>	2	0	0	0
<i>Tubulicrinis borealis</i>	24	0	19	0
<i>Dacrymyces capitatus</i>	32	0	0	28
<i>Pseudomerulius aureus</i>	1	0	0	0
<i>Mycocalicium subtile</i>	32	0	0	8
<i>Syzygospora alba</i>	6	0	0	6
<i>Symbiotaphrina microtheca</i>	37	0	0	11
<i>Itersonilia pannonica</i>	1	0	0	0

Scientific name	Harvester created	Kelo	Old	Burned
<i>Imshaugia aleurites</i>	6	1	1	0
<i>Amyloenasma allantosporum</i>	10	0	5	0
<i>Unilacryma bispora</i>	5	2	3	10
<i>Placynthiella dasaea</i>	8	6	2	2
<i>Tubulicrinis subulatus</i>	0	0	9	0
<i>Skvortzovia furfuracea</i>	0	1	10	1
<i>Mycena laevigata</i>	0	0	4	0
<i>Stereum sanguinolentum</i>	82	0	0	36
<i>Vexillomyces verruculosus</i>	41	0	1	25
<i>Capturomyces luteus</i>	43	3	0	9
<i>Heterophaeomoniella pinifoliorum</i>	10	0	0	0
<i>Lachnellula resinaria</i>	17	1	0	5
<i>Sydowia polyspora</i>	91	4	1	12
<i>Umbelopsis changbaiensis</i>	1	0	0	0
<i>Variabilispora flava</i>	27	0	0	3
<i>Phaeotremella skinneri</i>	41	0	0	10
<i>Leptoporus erubescens</i>	2	0	0	0
<i>Cyberlindnera jadinii</i>	6	0	0	0
<i>Lapidomyces aloidendricola</i>	10	2	0	2
<i>Dacrymyces lacrymalis</i>	12	0	0	27
<i>Mrakia frigida</i>	8	1	0	3
<i>Hyphoderma setigerum</i>	9	0	0	7
<i>Hypochnicium wakefieldiae</i>	1	0	0	0
<i>Exidia saccharina</i>	10	0	0	18
<i>Sarea difformis</i>	0	6	0	0
<i>Hertelidea botryosa</i>	0	11	0	0
<i>Hypocenomyce scalaris</i>	0	9	1	0
<i>Dacryonaema rufum</i>	0	2	0	0
<i>Gloeophyllum sepiarium</i>	6	0	0	1
<i>Naganishia albida</i>	46	0	0	3
<i>Hypogymnia physodes</i>	14	0	1	3
<i>Cerinomyces tortus</i>	45	0	16	0
<i>Skeletocutis kuehneri</i>	9	0	0	0
<i>Lactarius rufus</i>	3	0	0	0
<i>Piloderma sphaerosporum</i>	2	0	0	0
<i>Oidiodendron chlamydosporicum</i>	3	0	0	0
<i>Fuscidea pusilla</i>	4	0	0	0
<i>Lophium mytilinum</i>	6	0	0	0
<i>Tympanis pini</i>	6	0	0	9
<i>Trichaptum fuscoviolaceum</i>	2	0	0	5

Scientific name	Harvester created	Kelo	Old	Burned
<i>Laccaria trichodermophora</i>	10	0	0	1
<i>Diatrype stigma</i>	1	0	0	0
<i>Phlebiopsis gigantea</i>	17	0	0	4
<i>Penicillium decumbens</i>	1	0	0	0
<i>Pichia holstii</i>	18	0	0	15
<i>Hypholoma capnoides</i>	12	0	0	2
<i>Taphrina carpini</i>	4	0	0	0
<i>Filobasidium magnum</i>	7	0	0	0
<i>Naganishia diffluens</i>	10	0	0	0
<i>Trapeliopsis flexuosa</i>	7	3	0	3
<i>Xylographa soralifera</i>	0	1	0	0
<i>Trechispora byssinella</i>	2	0	0	0
<i>Phaeococcomyces eucalypti</i>	1	0	0	0
<i>Amyloporia sinuosa</i>	16	1	3	6
<i>Filobasidium wieringae</i>	13	0	0	0
<i>Lecidea hypopta</i>	4	0	0	1
<i>Rhodosporidiobolus colostri</i>	5	0	0	0
<i>Umbelopsis ramanniana</i>	1	0	0	0
<i>Nodulosphaeria thalictri</i>	1	0	0	0
<i>Cladonia rangiferina</i>	4	0	1	0
<i>Hypomyces albidus</i>	1	0	0	0
<i>Capronia epimyces</i>	11	0	0	4
<i>Leucosporidium intermedium</i>	1	0	0	0
<i>Lophodermium pinastri</i>	2	0	0	0
<i>Trichoderma viride</i>	4	0	5	1
<i>Sugiyamaella paludigena</i>	6	3	15	2
<i>Pseudevernia furfuracea</i>	2	0	0	0
<i>Scheffersomyces ergatensis</i>	9	0	5	2
<i>Dacrymyces ovisporus</i>	3	0	0	0
<i>Aphanocladium album</i>	2	0	0	0
<i>Spirographa fuisporella</i>	3	0	0	0
<i>Neosetophoma guiyangensis</i>	2	0	0	0
<i>Alternaria tenuissima</i>	1	0	0	0
<i>Skeletocutis amorpha</i>	2	0	0	0
<i>Pseudoplectania lignicola</i>	2	0	0	0
<i>Nothophaeomoniella ekebergiae</i>	7	0	0	0
<i>Botryobasidium tubulicystidium</i>	0	2	0	0
<i>Sistotremastrum suecicum</i>	1	8	17	0
<i>Rhodonina placenta</i>	2	0	0	4
<i>Suillus variegatus</i>	2	0	0	2
<i>Cerinomyces borealis</i>	5	0	10	0

Scientific name	Harvester created	Kelo	Old	Burned
<i>Acrodontium simplex</i>	1	0	0	0
<i>Alutaceodontia alutacea</i>	0	0	2	0
<i>Athelia decipiens</i>	2	0	4	5
<i>Ceratosporella novae-zelandiae</i>	0	0	6	0
<i>Pholiota chocenensis</i>	1	0	0	0
<i>Infundichalara microchona</i>	3	0	0	4
<i>Pseudogymnoascus pannorum</i>	0	1	0	0
<i>Talaromyces minioluteus</i>	0	1	0	0
<i>Atrozythia lignicola</i>	0	4	0	0
<i>Sorocybe oblongispora</i>	0	1	0	0
<i>Colacogloea philyla</i>	0	1	0	0
<i>Exophiala nidicola</i>	1	0	0	0
<i>Phlebia lilascens</i>	8	0	0	0
<i>Skeletocutis papyracea</i>	4	0	0	0
<i>Lophium arboricola</i>	3	0	0	1
<i>Violella fucata</i>	4	1	0	0
<i>Gyromitra tianshanensis</i>	8	0	0	24
<i>Peniophora pini</i>	3	0	0	10
<i>Cephalotheca foveolata</i>	1	0	0	0
<i>Piskurozyma arborea</i>	1	0	0	0
<i>Cerinomyces lipoferus</i>	10	0	0	1
<i>Dacrymyces fennicus</i>	4	0	4	6
<i>Cryptodiscus pini</i>	1	0	1	3
<i>Helicogloea dryina</i>	12	0	3	0
<i>Candida parapsilosis</i>	2	0	0	0
<i>Micarea fallax</i>	1	0	2	0
<i>Botrytis caroliniana</i>	2	0	0	0
<i>Ditiola haasii</i>	2	0	2	4
<i>Mucronella calva</i>	4	0	0	1
<i>Phaeosclera dematioides</i>	4	0	0	2
<i>Amylokenasma grisellum</i>	2	0	0	0
<i>Mycoblastus affinis</i>	0	2	1	0
<i>Pezoloma ericae</i>	1	0	0	0
<i>Pleotrichocladium opacum</i>	1	0	0	0
<i>Skeletocutis mopanshanensis</i>	1	0	0	0
<i>Cladophialophora laricicola</i>	2	0	5	0
<i>Crumenulopsis pinicola</i>	24	0	0	48
<i>Grosmannia cucullata</i>	2	0	0	0
<i>Phellinus viticola</i>	0	1	0	0
<i>Exobasidium maculosum</i>	2	0	0	0
<i>Sidera lunata</i>	1	0	1	0
<i>Micarea misella</i>	7	0	2	0

Scientific name	Harvester created	Kelo	Old	Burned
<i>Trichoderma deliquescens</i>	2	0	0	0
<i>Goffeuzyma gastrica</i>	1	0	0	0
<i>Phlebia radiata</i>	3	0	0	1
<i>Peniophorella pallida</i>	0	1	4	0
<i>Cryptodiscus tabularum</i>	0	2	0	0
<i>Alternaria oregonensis</i>	1	0	0	0
<i>Phialocephala sphaeroides</i>	1	0	0	0
<i>Xenasmatella vaga</i>	0	0	3	0
<i>Erastia ochraceolateritia</i>	1	0	0	0
<i>Cordana pauciseptata</i>	0	0	1	0
<i>Propolis farinosa</i>	1	1	0	0
<i>Vishniacozyma victoriae</i>	3	0	0	0
<i>Cryptococcus festucosus</i>	3	0	0	0
<i>Pseudogymnoascus pannorum</i>	0	1	0	0
<i>Gorgoniceps aridula</i>	1	0	0	0
<i>Taphrina tormentillae</i>	3	0	0	0
<i>Penicillium glabrum</i>	2	0	0	0
<i>Trichoderma parapiluliferum</i>	1	0	0	0
<i>Cystobasidium laryngis</i>	3	0	0	0
<i>Phlebia livida</i>	2	0	0	0
<i>Botryobasidium laeve</i>	2	0	0	0
<i>Femsjonia peziziformis</i>	1	0	0	2
<i>Cyniclomyces guttulatus</i>	1	0	0	0
<i>Tubulicrinis accedens</i>	0	1	3	0
<i>Dacryonaema macrosporum</i>	0	0	1	0
<i>Tausonia pullulans</i>	2	0	0	1
<i>Sistotrema oblongisporum</i>	0	0	0	1
<i>Exobasidium woronichinii</i>	0	1	0	0
<i>Exophiala xenobiotica</i>	0	1	0	2
<i>Amorphotheca resinae</i>	0	1	0	0
<i>Candida nitratophila</i>	0	0	0	1
<i>Gyromitra venenata</i>	0	0	0	3
<i>Lecanora pulicaris</i>	0	0	0	1
<i>Graphilbum fragrans</i>	0	0	0	2
<i>Sporidiobolus salmonicolor</i>	0	0	0	3
<i>Cuniculitrema polymorpha</i>	0	0	0	2
<i>Trichomonascus apis</i>	0	0	0	1
<i>Mariannaea camptospora</i>	0	0	0	2
<i>Xylographa rubescens</i>	0	1	0	0
<i>Archaeorhizomyces borealis</i>	0	0	0	1
<i>Tylospora fibrillosa</i>	0	0	0	2
<i>Orbilina eucalypti</i>	0	0	0	1

Scientific name	Harvester created	Kelo	Old	Burned
Metarhizium anisopliae	0	0	0	1
Piloderma olivaceum	0	0	0	1
Umbelopsis dimorpha	0	0	0	1
Exophiala lignicola	0	0	0	2
Marquandomyces marquandii	0	0	0	1
Penicillium brevicompactum	0	0	0	2
Pachyramichloridium pini	0	0	0	1
Capronia villosa	0	0	0	1
Mortierella basiparvispora	1	0	0	1
Cabalodontia subcretacea	0	0	1	0
Terfezia pini	0	0	0	1
Tomentella coerulea	0	0	0	1
Botryobasidium subcoronatum	0	0	2	1
Kuraishia capsulata	0	0	0	1
Placynthiella icmalea	0	0	0	1
Oidiodendron majus	0	0	0	1
Graphilbum furuicola	1	0	0	1
Basidiopycnis hyalina	1	0	0	3
Tricholoma matsutake	0	0	0	1
Metapochonia suchlasporia	0	0	0	1
Talaromyces rugulosus	0	0	0	1
Paramyrothecium roridum	0	0	0	1
Phellodon secretus	0	0	0	1
Ischnoderma benzoinum	0	0	0	1
Beauveria bassiana	0	0	0	1
Lichenomphalia umbellifera	0	1	1	0
Cladonia parasitica	0	1	0	0
Hyphodontia abieticola	0	0	1	0
Aphanobasidium pseudotsugae	0	0	1	0
Coniophora arida	0	2	0	0
Chionosphaera cuniculicola	2	0	0	0
Nothophaeomoniella ekebergiae	0	1	0	0
Biatora troendelagica	0	1	0	0
Tylospora asterophora	1	0	0	0
Mucor abundans	1	0	0	0
Cylindrocarpostylus gregarius	1	0	0	0
Stropharia hornemannii	1	0	0	0
Ophiostoma tingens	1	0	0	0
Ceratocystiopsis minuta	2	0	0	0
Gloeodontia subasperispora	0	2	0	0
Entomortierella beljakovae	1	0	0	0

Scientific name	Harvester created	Kelo	Old	Burned
<i>Vishniacozyma europaea</i>	1	0	0	0
<i>Phialocephala glacialis</i>	1	0	0	0
<i>Inocybe relicina</i>	1	0	0	0
<i>Desmazierella acicola</i>	1	0	0	0
<i>Volutella ciliata</i>	1	0	0	0
<i>Galerina camerina</i>	0	0	1	0
<i>Colacogloea fennica</i>	0	0	1	0
<i>Blastobotrys indianensis</i>	0	0	1	0
<i>Cladonia mitis</i>	0	0	1	0
<i>Cystocoleus ebeneus</i>	1	0	0	0
<i>Inocybe giacomii</i>	1	0	0	0
<i>Spegazzinia parkeri</i>	1	0	0	0
<i>Colacogloea hydrangeae</i>	1	0	0	0
<i>Cetrariella delisei</i>	1	0	0	0
<i>Lachnellula fuscousanguinea</i>	1	0	0	0
<i>Calicium trabinellum</i>	1	0	0	0
<i>Hypomyces ochraceus</i>	1	0	0	0
<i>Agyrium rufum</i>	2	0	0	0
<i>Neonectria tsugae</i>	1	0	0	0
<i>Cystofilobasidium capitatum</i>	1	0	0	0

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