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Continuous-cover forestry maintains soil fungal communities in Norway spruce dominated boreal forests

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ABSTRACT

Traditional clear-fell forestry greatly alters community structure and ecosystem function within boreal forests and alternative management practices may reduce these impacts. Continuous-cover forestry can maintain similar invertebrate and plant communities to unmanaged forest, but whether this extends to soil fungal communities remains unclear. Within four sites across the mid-boreal zone of Sweden, we conducted a comprehensive study to assess the impact of continuous-cover and clear-felling on soil fungi and chemical properties within Norway spruce dominated forests, using unmanaged forest as a control. We sampled soils for chemical properties (pH, carbon, nitrogen, C/N and Organic matter) and used both surveys of fungal fruiting bodies and state of the DNA metabarcoding techniques to assess treatment effects on soil fungal communities. We found that forest management practices had significant effects soil pH, C and C/N ratio and that continuous-cover forestry had more similar soil properties to unmanaged forest. Furthermore, the biodiversity of fruiting bodies, as expressed by species richness and Shannon's diversity index, was higher in continuous-cover forestry and unmanaged forest compared to clear-felled areas. However, the opposite was true for the diversity of soil fungal communities, which was probably due to the high level of disturbance in clear-felled areas, and thus, ample habitat for early successional colonisers and some remnants of mature forest communities. However, in agreement with predictions we found that the composition of both fruiting body and soil fungal communities broadly similar in continuous-cover and unmanaged forest, but fundamentally different to clear-felled areas. Consequently, our findings highlight that continuous-cover forestry is an alternative to conventional practise, maintaining communities associated with unmanaged forest and mimicking natural disturbance regimes.

1. Introduction

The boreal forest constitutes the largest terrestrial biome, covering 14 million km^2 around Canada, Russia and Fennoscandia (Burton et al., 2003) and representing one third of the terrestrial carbon stock in the world (Dunn et al., 2007). At present, two thirds of this surface is managed for wood production which accounts for 37% of the global wood supply (Gauthier et al., 2015). Since the 21st century, boreal forest has been increasingly acknowledged for the provision of multiple services that go beyond wood production to also include production of wild berries, mushrooms and lichens, which are also essential for many herbivores and omnivores (Granath et al., 2018; Strengbom et al., 2018). Maintaining these services and the conservation of associated communities are now recognised as important priorities for sustainable forest management in many regions (Kuuluvainen et al., 2015). For example, the Swedish forest act now states that timber production and biodiversity conservation are equally weighted goals in management. Development of sustainable forestry practises for boreal forests thus relies on evaluating the impact of different management options on not only timber production but also ecological values (Sylvie, 2009).

Clear-fell forestry is still the dominant harvesting practice used in boreal forests today, significantly altering biodiversity, ecosystem function and services (Burton et al., 2010; Gauthier et al., 2015; Gerasimov et al., 2012). These effects on biodiversity are often related to

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habitat loss and fragmentation as well as declines in habitat diversity (Fischer and Lindenmayer, 2007; Hasan et al., 2020; Puettmann et al., 2011). Earlier research has also shown that clear-fell forestry can have negative effects on forest ecosystems through the erosion of the soil organic layer and reducing soil nutrients and biodiversity (Laudon et al., 2011). In addition, forest ecosystems become less resilient after clear-cutting (Lavoie et al., 2019; Reyer et al., 2015), indicating that they could be more susceptible to future disturbances such as climate change. Thus, research into alternative forest management practices has recently gained much attention (Girona et al., 2018) and suggests that forest biodiversity would benefit from management strategies which better mimic natural disturbance regimes (Kuuluvainen, 2009; Martin et al., 2020).

Continuous-cover forestry has been proposed as a potential alternative to clear-fell forestry which better mimics small scale disturbance regimes typical of *Picea abies* (Norway spruce) dominated forests. This followed a trend of developing forest management practices that emulate natural disturbance, conserving forest communities while improving productivity (Muscolo et al., 2014; Vajari et al., 2012). Emulating natural disturbance regimes aims to maintain high species richness with forest communities by conserving both early- and late-successional species, as per the intermediate disturbance hypothesis (Osman, 2015). In continuous-cover forestry, 30–40% of the standing forest volume is harvested every 15–20 years, thus maintaining a continuous tree cover (Helliwell and Wilson, 2012). This results in a tree density that allows for natural regeneration and the continuous ingrowth of seedlings into the tree strata (Tahvonen and Rämö, 2016). As such continuous-cover forestry may be beneficial for species that are adapted to small scale disturbance and also provides higher habitat availability for species dependent on deciduous trees and mature forest structure (Calladine et al., 2015; Kuuluvainen et al., 2012; Pukkala et al., 2011). Accordingly, previous studies have shown that continuous-cover forestry maintains plant and invertebrate biodiversity (Peura et al., 2018) as well as a higher bilberry production and resistance against wind than clear-fell forestry (Pukkala, 2016, 2017; Pukkala et al., 2011). Furthermore, continuous-cover forestry may better preserve soil fungal communities, since labile carbon (C) from trees is the main source of C for these organisms (Peura et al., 2018).

Soil fungal communities are important mediators of biogeochemical processes and play crucial roles in the establishment of plant communities (Baldrian, 2016; Van Der Heijden et al., 2008). They are also regulators of plant productivity, especially in nutrient poor ecosystems where plant symbionts are responsible for the acquisition of limiting nutrients (Baldrian, 2016; Van Der Heijden et al., 2008). Fungi rely on carbon fixed by plants and have developed diverse metabolic processes that enable them to utilise many forms of organic nutrients for growth that plants themselves cannot easily access (Marzluf, 1981). For instance, mycorrhizal fungi, nitrogen-fixing bacteria and cyanobacteria are responsible for 80% of all nitrogen, and up to 75% of phosphorus, that is acquired by plants in boreal forests annually (DeLuca et al., 2002; Van Der Heijden et al., 2008). Thus, it is important to determine the extent to which forest different management practices can maintain soil fungal communities.

While fungal species richness and community composition is sensitive to meteorological and geographical factors more broadly, forest management practices including clear-fell forestry may cause changes in soil fungal communities by altering more subtle factors including soil chemical properties (Goldmann et al., 2015; Tedersoo et al., 2014). Recent studies demonstrated that more wood harvesting results in decreasing the diversity of ectomycorrhizal and wood-inhabiting species in the short-term (Tomao et al., 2020). One of the cornerstones in sustainable forestry is the effective conservation of soils (Hartmann et al., 2012), since soils bring essential ecosystem services such as decomposition and transformation in nutrient cycling (Dominati et al., 2010). Clear-fell forestry has been shown to impact a range of key soil chemical properties, many of which is important for soil fungal communities (Purahong et al., 2014). For instance, soil organic matter (SOM) is generally decomposed by soil fungi in boreal ecosystem, and thus, strongly affects fungal abundance (Sterkenburg et al., 2015). Soil pH also plays a strong role in shaping soil communities by influencing the solubility of metals, and nutrient- and carbon-availability (Rousk et al., 2009). While both mycorrhizal and saprotrophic fungi play crucial roles in the cycling of N and C respectively (Lindahl et al., 2007), they are also affected by N availability. For instance, Zheng et al. (2017) found that the ratios of ectomycorrhizal fungi to total fungi were clearly decreased after N fertilization. Therefore, variation in fungal community composition may be influenced by chemical changes to soils.

To address the potential impacts of continuous-cover forestry on soil fungal communities and soil chemical properties, we present a large-scale investigation combining next-generation sequencing (NGS) of soil fungi with visual assessment of fruiting bodies at four experimental sites throughout Northern Sweden. The main objectives of this study were: (i) to assess the effects of different forest management practices on soil chemical properties in relation to fruit-body biomass (abundance and dry weight) and fungal community composition, and (ii) evaluate the relationship between soil chemical properties and fungal community composition. To address these objectives, we hypothesize that (1) continuous-cover forestry would retain similar soil chemical properties, fruit-body biomass and fungal community composition to unmanaged forest than clear-fell forestry and (2) variation in fungal communities would be related to soil chemistry. By assessing the effects of forest management practices on soil fungal communities, this study supports the development of sustainable forest management practices to balance wood production and biodiversity conservation based on uneven-aged timber management in boreal ecosystems.

2. Materials and methods

2.1. Study sites and experimental design

To assess the impacts of clear-fell forestry and continuous-cover forestry on soil chemistry and fungal communities, we sampled homogeneous forest stands subjected to either clear-felling, continuous-cover forestry or no treatment (unmanaged forest) across four sites located in the mid-boreal zone of Sweden (Tvärålund, Sidensjö, Stugun, Kulbäcksliden) (Fig. 1). To broaden our inference space, we included four different sites to incorporate site heterogeneity resulting from variable historical differences, but also meteorological factors (Table 1). The sampling of continuous-cover forests and unmanaged forests was conducted within permanent plots 25 × 40 m set up by the Swedish University of Agricultural Sciences and Swedish Forest Agency as part of a long-term forestry experiment established in 2012. Prerequisites for the experiment were that stands had a suitable stand structure (i.e., uneven-aged), were dominated by Norway spruce as the main species (>70%) and had no recent logging activity (estimated stand ages ranged 80–150 years). The first round of harvesting was conducted in 2014–2015 using conventional harvester and forwarder machinery (Tvärålund and Kulbäcksliden; Komatsu 911.4 and Komatsu 860, Sidensjö; Eco-Log 560 and Log Max 5000, and Stugun; Ponnse Ergo and Ponsse Buffalo) along access corridors so that a 25 × 40 m plot was passed three times. Targeted trees were cut between corridors to reach the target of 30% of basal area removal. To allow comparison with the clear-fell forestry treatment, we set up comparable plots on clear-fells adjacent to the permanent experiment, which were within 350 m of the experimental plots. Tree removal was carried out between 2010 and 2014 and did not include stump harvesting but all clear-cuts were subjected to soil scarification. Following soil scarification, the clear-fell forestry areas at Tvärålund and Stugun were replanted with Norway spruce, while those at Sidensjö and Kulbäcksliden were replanted with *Pinus sylvestris* (Scots Pine). The mean elevation of the four sties ranges from 170 m to 345 m. The mean annual precipitation of the four sites ranges from 450 mm to 900 mm, while the mean temperature of the

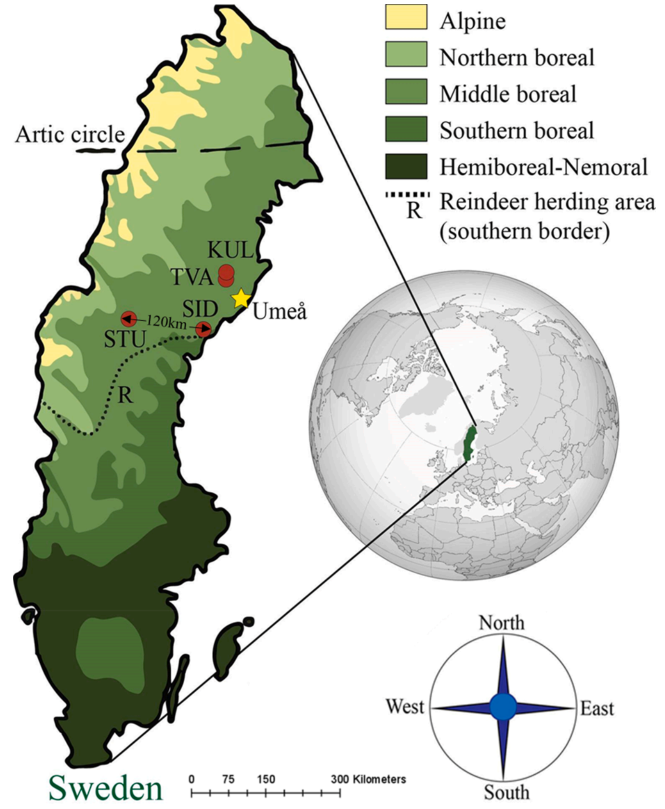

Fig. 1. The geographic locations of the four sites used to assess the impacts of forest management on soil fungal communities.

growing season (May to September in Northern Sweden) ranges between +10 °C and 14 °C. The four study sties were located on very similar soil types which were broadly classified as podzols (Troedsson and Wiberg, 1986). As such, the ground cover communities of sites were very similar, comprising of predominantly lingonberry (*Vaccinium vitis-idaea*) and bilberry (*Vaccinium myrtillus*) as well as some small birch and rowan trees.

2.2. Sampling

2.2.1. Soil sampling and chemical analyses

To assess the effects of forest management practices on soil chemical properties and fungal communities, we sampled 10 randomised square plots (1.25 m × 1.25 m) per treatment at each site, totalling to 120 samples (=3 forest managements × 4 sites × 10 randomised plots) during September 2018. After first removing the litter layer, three 10 cm depth soil cores with 2.5 cm diameter were taken from evenly spaced positions within each plot and pooled in a single plastic bag. We chose to sample to this depth in order to capture a greater section of the fungal diversity present, as ectomycorrhizal and arbuscular mycorrhizal are often distributed at different soil depths (Neville et al., 2002). Soil samples were immediately placed within a cooler after collection. The soil samples were then homogenized using a 2 mm sieve and divided into portions for soil chemical analysis and DNA sequencing. Two portions intended for pH and organic matter (OM) measurement were bench dried, a portion was frozen and freeze-dried for total C and N analysis and one last portion was frozen at −80 °C for DNA sequencing. The soil corer and all lab equipment were carefully sterilized with 20% bleach solution and rinsed between samples.

To determine soil pH, one gram of each soil sample was weighed into a 15 ml falcon tube and combined with 5 ml of 0.01 M $CaCl_2$ solution. The tubes were then vortexed and left to equilibrate for one hour before measurement on a pH meter (MP220, Mettler Toledo, Ohio U.S.). The C and N concentrations of freeze-dried and ground soil samples were measured using an isotope ratio mass spectrometer (DeltaV, Thermo Fisher Scientific, Bremen, Germany) coupled with an elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen Germany) as described by Werner, Bruch, and Brand (1999). Soil organic matter was measured by the optimized loss on ignition method (Hoogsteen et al., 2015). The soil samples were heated at 105 °C for 24 h and a 5 g subsample of each soil was transferred to a crucible and heated for six hours to reach 550 °C. The temperature was maintained 550 °C for six hours and then soils were re-weighed to calculate soil organic C.

2.2.2. Sampling of fungal fruit-bodies

Fruiting bodies were assessed to determine whether the broader findings from the sequencing data were also apparent in an important and easily observable component of the holistic soil fungal community. Moreover, as fungal communities above and below ground often differ (Cairney and Bastias, 2007), we included measurements of both in this study. To assess how forest management practices influenced fungal fruit-body abundance and composition, we revisited the randomized plots in the study sites during October 2018 and harvested all mushrooms within a 1.6 m^2 wooden frame. The sampled mushrooms were identified according to Swedish and international taxonomic literatures (Michell and Parker, 2006; Evans, 2007; Knudsen, 2004; Nylén, 1995; Bon, 1994; Lange, 1982; Cortin, 1991, 1995; Svrček et al., 1981; Nylén, 1985; Garnweidner et al., 1999; Hallingbäck, 1985) and several fungal database websites (International Mycological Association, n.d.; Swedish University of Agricultural Sciences, n.d.; Global Biodiversity Information Facility, n.d.; The Mushroom Research Foundation, n.d.; Jayasiri et al., 2015). After species identification, the fungal fruit-bodies were counted and dried at 50 °C for 72 h and weighed.

Table 1
The field survey of the three forest management practices in the four study sites.

Site	Elevation (m)	*Temperature (°C)	**Precipitation (mm)	FMP	Harvest year	Replanted
TVA	234	11.4	647	CF	2014	Spruce
				CCF	2015	–
				UF	–	–
KUL	174	11.4	647	CF	2010	Pine
				CCF	2014	–
				UF	–	–
SID	223	12	771	CF	2014	Pine
				CCF	2014	–
				UF	–	–
STU	323	12.2	525	CF	2014	Spruce
				CCF	2015	–
				UF	–	–

*Annual mean of Temperature(°C, Growing season, 2014–2018), **Annual mean of Precipitation(mm, 2013–2017), Replanted(Artificial Regeneration), FMP(Forest management practice), CF(Clear-fell forestry), CCF(Continuous-cover forestry), UF(Unmanaged forest).

2.3. DNA sequencing

The 120 soil samples intended for DNA sequencing were freeze-dried and were finely ground before DNA extraction. Fungal DNA amplicon libraries were prepared at the Uppsala Metabarcoding Laboratory (UMBLA) at the University of Uppsala, Sweden. Two hundred milligrams of each sample were extracted using a Machery-Nagel NucleoSpin ® Soil kit and DNA concentrations were measured using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific Inc, Wilmington, USA). The fungal-specific internal transcribed spacer 2 (ITS2) region was amplified using tagged gITS7 and ITS4 primers. The new primers gITS7 and ITS4 were produced to overcome strong bias against species with longer amplicons when amplifying entire ITS region (Ihrmark et al., 2012). The ITS4 primer was extended by a specific sample tag of eight bases, produced using BARCRAWL software (Frank, 2009). Polymerase chain reaction (PCR) was carried out on 9–12 ng of DNA for each sample in duplicate under the following conditions: 5 min at 95 °C, 22–29 cycles of (30 s at 95 °C, 30 s at 57 °C, 30 s at 72 °C), followed by 5 min at 95 °C. The amplified DNA was purified with the AMPure kit (Beckman Coulter Inc. Brea, CA) and then equal amounts of purified DNA from each sample duplicate were pooled prior to preparing amplicon libraries for sequencing. The amplified samples were then randomly divided into two amplicon libraries, each containing 60 samples, prior to Pacific Biology Sequel sequencing at SciLifeLab (www.scilifelab.se).

The SCATA pipeline was used to analyse and quality check soil fungal sequences (Brandström et al., 2011). To assure the quality of sequences, data were deleted with mean quality scores below 20 or with bases of equality lower than 3. Sequence data were then screened for the gITS7 primer and identity tags and reverse complemented if necessary. Sequences were compared for similarity, applying USEARCH as the search engine, requiring minimum match length of 85%. We followed single linkage clustering, with the maximum distance to the closest neighbour in USEARCH and it enabled to enter a cluster set of 1.5%. Singletons, samples with < 100 reads and samples with unmatched tags were removed from further statistical analyses. We discovered sequence errors in two tags (tag 25 and 26). Thus, the two samples for which these tags represented were removed and a total of 118 samples remained for subsequent statistical analyses. We annotated DNA-based Species Hypotheses (any species-level group of individuals that share a given set of observed characters; SHs) with above 10 reads using the mass BLASTer in UNITE and non-fungal SHs were removed (Kõljalg et al., 2013). Species hypotheses were assigned to species based on at least 98.5% similarity and a BLAST score of at least 400 to a sequence validated by professional taxonomists. We assigned SHs to genera, families or orders when identifying was not validated by references.

2.4. Data analysis

To address the first hypothesis that continuous-cover forestry would retain more similar soil chemical properties, fruit-body biomass and diversity and soil fungal diversity to unmanaged forest than clear-fell forestry, linear mixed effects models were applied to test for the effects of forest management treatments on each soil variable, diversity matrices and total fungal dry weight and abundance using the lmer function from the *lme4* package (Bates et al., 2015). Models included treatment as a fixed effect and site as a random effect to account for the effects of site on the response variables and statistical dependence among randomised plots within sites. Site was not fitted as a fixed effect, as we were interested in the general effects of forest management treatments across the landscape. Data were checked for the assumptions of normality and homogeneity of variances using the function qqnorm from the package stats (R Core Team, 2018) and the function plot from the package graphics (R Core Team, 2018), respectively. All soil variables were natural logarithm transformed, except soil pH that required a cube root transformation to meet model assumptions. Analysis of variance tables were returned from lmer models applying the anova function from the lmerTest package (Kuznetsova et al., 2017). The function lsmeans from the package lsmeans (Lenth, 2016) was conducted to extract model lsmeans and confidence intervals as well as perform Tukey's HSD pair-wise comparisons. To address the second hypothesis that variation in fungal communities would be related to soil chemistry, Pearson's product-moment correlations were also performed in R using cor.test function in corrplot and Hmisc package (R Core Team, 2018). To control for false discovery rate, Bon-ferroni correction was applied to correlation results (0.05/the number of correlations = 0.001, new significance level).

For multivariate analyses, the abundance and dry weight of fruiting body communities were square root transformed and individual species observations were standardised by the total abundance or dry weight of all species found in their respective plot. To compare the number of species are existed and how evenly they were distributed within treatments, community metrics (Shannon's diversity index and Margalef's species richness) were calculated in PRIMER software from the collected fruiting body communities and sequenced soil fungal communities. These metrics were used to test for the effects of forest management treatments on fungal diversity and correlate fungal diversity with soil chemical properties. Permutational multivariate analysis of variance (PERMANOVA) was applied on Bray-Curtis similarity matrices in PRIMER and PERMANOVA+ to test whether fruiting body community composition in abundance and dry weight data was affected by forest management treatments. The model included forest management treatment as a fixed effect, site as a random effect and was run for 999 permutations. Constrained canonical analyses of principal coordinates (CAP) was used to visualise significant effects of forest management treatments on fruiting body and soil fungal community composition. To determine the individual fungal taxa which contributed to significant differences between treatment groups, we calculated the contribution of each species to the dissimilarity between treatments, applying similarity percentage (SIMPER) analysis. SIMPER analyses were conducted on Bray-Curtis distance matrices generated from the square root transformed and standardised data. SIMPER analyses were performed for two comparisons based on significant results of PERMANOVA pair-wise comparisons: (1) continuous-cover forestry and clear-fell forestry; (2) unmanaged forest and clear-fell forestry in both fruiting body and soil fungal data.

Distance-based linear models (DistLM) were performed to test for relationships between soil chemical properties and fungal community composition. The DistLM models were conducted on Bray-Curtis distance matrices generated from the square root transformed and standardised data. The contribution of each soil variable on fungal community composition was estimated applying marginal tests to evaluate the statistical significance and percentage contribution of each soil variable taken alone. All univariate analyses were performed using the statistical package R version 3.4.3 (R Core Team, 2018), while multivariate analyses were conducted using PRIMER v.6.1.11 with the PERMANOVA+ add on (Anderson, 2017).

3. Results

3.1. Soil chemical properties, fruit-body biomass and fungal diversity

Soil chemical properties, fruit-body biomass and fungal diversity were strongly influenced by forest management practices (Table 2). We detected significant effects of forest management practice on soil pH, C, C/N, fruiting body abundance, dry weight, fungal diversity indices and species richness. The significant influence of forest management practice on soil pH and C/N was driven by two pair-wise differences (Tukey's Honest Significant Difference, HSD), where clear-fell forestry stands had a higher pH compared to continuous-cover and unmanaged forest areas but a lower soil C to N ratio. Regarding fruiting body diversity, clear-fell forestry stands had lower Shannon's diversity index compared to continuous-cover forestry and unmanaged forest and lower species

Table 2

The main effects and pair-wise comparisons of forest management practices on soil chemical properties and fruiting body biomass based on linear mixed effects models. For each test, the treatment least squares means, numerator and denominator degrees of freedom (df) as well as the F and P values are reported. Bolded p-values and least squares means with different letters indicate statistical significance at α = 0.05.

Dataset	Variable	$F_{(df)}$	P-value	Clear fell	Continuous cover	Unmanaged
Soil chemistry	pH***	$12.9_{2,114}$	**<0.001**	3.2^{a}	3.0^{b}	3.0^{b}
	Organic matter (% soil dry weight)	$2.2_{2,112}$	0.1119	14.9	13.5	17.5
	Carbon* (% soil dry weight)	$2.1_{2,112}$	**0.0131**	8.3^{a}	7.9^{a}	10.0^{a}
	Nitrogen (% soil dry weight)	$2.9_{2,112}$	0.0617	0.3	0.2	0.3
	Soil C to N ratio*** (%)	$8.4_{2,112}$	**<0.001**	29.7^{b}	34.1^{a}	32.3^{a}
Fruiting bodies	Dry weight (g)	$3.1_{2,68}$	0.0513	1.0	0.3	0.6
	Abundance**	$5.0_{2,68}$	**0.0097**	1.9^{b}	2.0^{ab}	2.7^{a}
	Shannon's Diversity Index***	$10.8_{2,113}$	**<0.001**	0.4^{b}	0.8^{a}	0.8^{a}
	Species richness***	$12.0_{2,113}$	**<0.001**	2.0^{b}	3.2^{a}	3.3^{a}
Soil fungi	Shannon's	$7.8_{2,115}$	**<0.001**	5.0^{a}	4.9^{b}	4.8^{b}
	Species richness***	$8.2_{2,115}$	**<0.001**	137.7^{a}	130.5^{b}	126.6^{b}

richness. In terms of soil fungal diversity, clear-fell forestry stands had higher Shannon's diversity index compared to continuous-cover forestry and unmanaged forest and higher species richness. Soil carbon and fruiting body abundance were also significantly influenced by forest management treatments. However, there were no significant pair-wise differences following Tukey's HSD adjustment.

3.2. DNA sequencing output

A total of 355,867 reads passing quality control (65% of the total number of reads) were clustered into 2,157 SHs and the mean of total reads per sample was 1,016 (Standard Deviation: 142). The five most abundant fungal SHs were *Penicillium austroafricanum* Houbraken & Visagie, *Hyaloscyphaceae* Nannf., *Oidiodendron pilicola* Kobayasi, *Luellia* K.H. Larss. & Hjortstam and *Solicoccozyma terricola* (T.A. Pedersen) A.M. Yurkov. These five SHs accounted for 9% of total SH's abundance (10,797 out of 119,848).

3.3. The influence of forest management practice on fruiting body and soil fungal communities

There was a significant interactive effect of forest management practice and site on the community composition of both fruiting bodies and the holistic soil fungal community (PERMANOVA; $P < 0.05$). After accounting for this effect of site on communities by fitting site as a random intercept, models showed that forest management practice had a significant effect on these communities across the landscape. Specifically, results showed that fruiting body (abundance and dry weight) and soil fungal community composition varied depending on forest management treatments (Appendix A) and continuous-cover forestry maintained similar fungal communities to unmanaged forest than clear-fell forestry. Fruiting body community composition in clear-felled areas significantly differed to continuous-cover ($P < 0.05$) and marginally with unmanaged forest areas ($P = 0.07$). Soil fungal community composition in clear-felled areas significantly differed to unmanaged forest ($P < 0.05$) and marginally with continuous-cover forestry ($P = 0.07$). Fruiting body and soil fungal communities showed distinct clusters in the Canonical Analysis of Principal coordinates (CAP). Fruiting body dry weight and abundance communities in continuous-cover forestry and unmanaged forest were more similar to each other, while clear-fell forestry tended to form a distinct group (Fig. 2a,b). However, regarding soil fungal communities, all three treatments appeared to be distinct from each other (Fig. 2c).

Similarity percentages (SIMPER) analyses in fruiting body abundance and dry weight revealed that 10 to 13 species, accounting for approximately 10% of all fruiting body species (120 species), contributed to half of the dissimilarity between treatment groups (Appendix 1a, b). Three fruiting body species (*Micromphale perforans* (Hoffm.) Gray, *Hygrophoropsis aurantiaca* (Wulfen) Maire, *Cortinarius sp* (Pers.) Gray) commonly influenced dissimilarities among the treatment groups in both fruit-body abundance and dry weight. In the fruiting body abundance between continuous-cover and clear-fell forestry, for instance, *M. perforans* was more common in continuous-cover forestry (35%) than in clear-fell (1%). *H. aurantiaca* and *Cortinarius sp* were more common in clear-fell forestry (5 and 7%, respectively) than in continuous-cover forestry (absent and 1%, respectively). *M. perforans* in fruiting body community composition was the most abundant species in both continuous-cover and unmanaged forest compared to clear-fell forestry.

SIMPER analyses in soil fungi showed that twenty-five species, accounting for 1% of all soil fungal species hypotheses (2,157 SHs), contributed 15% of the average dissimilarities (Appendix 1c). Three soil fungal species (*Piloderma sphaerosporum* Jülich, *Thelephora terrestris*, *Luellia* sp) were important drivers of differences in community composition between continuous-cover and clear-fell forestry and unmanaged and clear-fell forestry, contributing to a 2–2.3% dissimilarity between treatments. In the soil fungi between continuous-cover and clear-fell forestry, for example, *P. sphaerosporum* was more common in continuous-cover forestry (0.98%) than in clear-fell (0.22%). *T. terrestris* and *Luellia* sp were more common in clear-fell forestry (1.05% and 0.92%, respectively) than in continuous-cover forestry (0.1 and 0.61%). *P. sphaerosporum* was similarly abundant in both continuous-cover forestry and unmanaged forest (average abundance: 0.98% in continuous-cover forestry and 1.37% in unmanaged forest).

3.4. The influence of soil chemical properties on fruiting body and soil fungal communities

Distance-based linear models conducted on the fruiting body data (abundance only) revealed that, fruiting body community composition was significantly related to soil pH, organic matter and C to N ratio (Table 3). When all soil variables were included in the same model, soil pH was the variable with the highest explanatory value (3%) in fruiting body abundance and second highest (2.1%) in fruiting body dry weight. Soil C to N ratio explained the greatest degree of variation (2.2%) in fruiting body dry weight and second highest (2.9%) in fruiting body abundance. Moreover, soil organic matter was also found to be significantly associated with the fruiting body community composition when analysing the fruiting body abundance dataset (2.2%, $P = 0.03$). Based on the fruiting body abundance and dry weight community, soil C and N concentrations did not influence fruiting body community composition

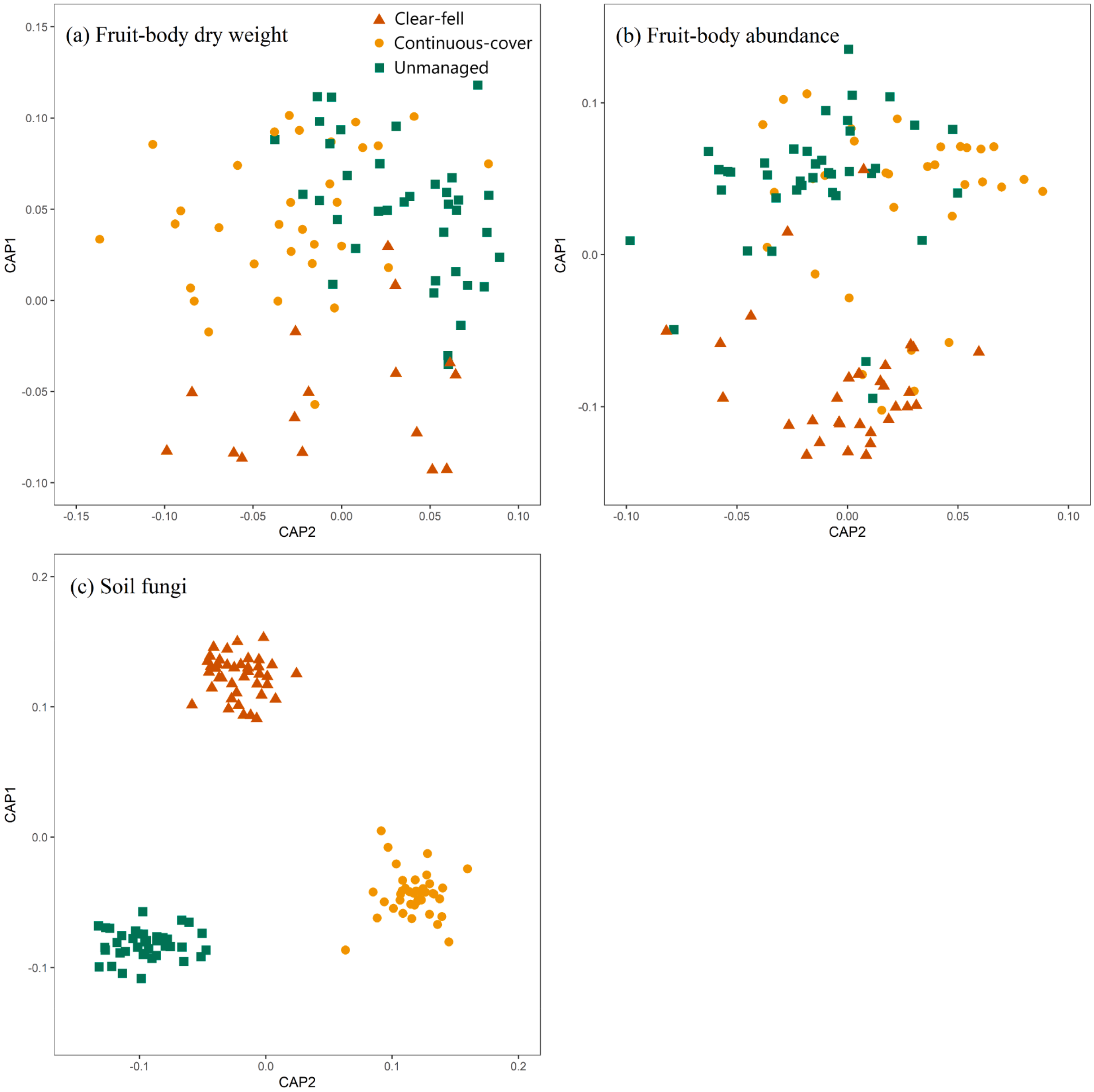

Fig. 2. Ordinations show that forest managements practices influence fungal communities. Constrained canonical analyses of principal coordinates (CAP) plot illustrating the effects of forest management practices on fruiting body and soil fungal communities. CAP1 and CAP2 represent axes through the multivariate space that best discriminate forest management practices. Plots are grouped by management practice using different symbols and colours.

in marginal tests although their ratio did (Table 3). Soil fungal community composition was significantly influenced by all soil chemical variables (pH, organic matter, C, N, C/N: $P < 0.002$). In accordance with results of fruiting bodies, soil pH and C/N were the variables with the highest explanatory value (pH: 6.1%, C/N: 4.5%). Similar to fruiting bodies, soil fungal community composition was also influenced by soil organic matter, C and N, which explained around 1.5 to 1.8% of variation each.

The linear regression models detected significant relationships between soil variables and soil fungal diversity indices (Table 4; Fig. 3). The soil pH was significantly and positively correlated with the soil fungal diversity index (Shannon, $R^2 = 0.34$; $p < 0.001$) and species richness (Margalef, $R^2 = 0.36$; $p < 0.001$). Soil C to N ratio was close to significant and negative correlation with soil fungal species richness ($R^2 = 0.21$, $p = 0.022$). Regarding fruiting body communities, there were no significant correlations with any of the soil chemical properties ($P > 0.05$).

4. Discussion

Given the key role that soil organisms play in regulating numerous ecosystem services, it is essential to develop more sustainable forest management practices that can effectively maintain these communities. In the last 15 years, it has been suggested that management practices which emulate natural disturbance regimes would benefit conservation in forests adapted to small scale disturbances (Kuuluvainen, 2009; Gauthier, 2009). Recently, Sterkenburg et al. (2019) found that tree retention can relieve the impacts of harvesting on ECM fungi. However, there is currently limited empirical evidence to assess if this is the case or not (Peura et al., 2018). In this study, we investigated whether continuous-cover forestry, as opposed to more conventional clear-fell forestry, can retain more similar soil chemical properties and fungal communities to unmanaged stands in Norway spruce dominated forests, and whether variation in soil fungal community composition results from management-induced changes to soil chemical properties. This

Table 3

Marginal test results of distance-based linear models indicating the influence of soil chemical properties on fruiting bodies (abundance and dry weight) and soil fungal community composition. The marginal tests showed how much variation each soil variable explains when considered alone. Bolded p-values indicate statistical significance at $\alpha = 0.05$.

Dataset	Variable	Pseudo-F	P-Value	Prop.
Fruiting body abundance	pH**	2.0	**0.002**	3.0%
	OM*	1.5	**0.033**	2.2%
	C	1.4	0.11	2.0%
	N	1.3	0.142	1.9%
	C/N**	1.9	**0.009**	2.9%
Fruiting body dry weight	pH*	1.4	**0.036**	2.1%
	OM	1.1	0.273	1.6%
	C	1.0	0.4	1.6%
	N	1.1	0.312	1.6%
	C/N*	1.4	**0.027**	2.2%
Soil fungi	pH***	7.3	**0.001**	6.1%
	OM***	2.0	**0.001**	1.8%
	N**	1.8	**0.002**	1.5%
	C***	2.1	**0.001**	1.8%
	C/N***	5.3	**0.001**	4.5%

P-value: ns > 0.05, *<0.05, **<0.01, ***<0.001.

Table 4

Pearson's product-moment correlation coefficients (r) between soil chemical properties and soil fungal community variables.

Fungal Community Variables	Correlation Matrix	Soil Variables		
		pH	Carbon	C/N
Fruiting bodies	Dry weight	−0.11 ^{ns}	0.16 ^{ns}	0.12 ^{ns}
	Abundance	−0.20 ^{ns}	−0.10 ^{ns}	0.10 ^{ns}
	Shannon's diversity index	−0.17 ^{ns}	0.01 ^{ns}	0.07 ^{ns}
	Species richness	−0.16 ^{ns}	−0.10 ^{ns}	0.04 ^{ns}
Soil fungi	Shannon's diversity index	**0.34****	0.03 ^{ns}	−0.17 ^{ns}
	Species richness	**0.36****	0.03 ^{ns}	*−0.21* ^{ns}

Significant alterations (adjusted P-value to 0.003) are shown in bold. Italic: significant ($P < 0.05$) before Bonferroni correction. ns(non-significant) > 0.003, *<0.003.

study represents the first assessment of the effects of even- and uneven-aged forest management systems on both fruiting body and soil fungal communities in a boreal ecosystem. Two key findings emerged. Firstly, we found that forest management treatments differently influenced soil chemical properties, fruiting body biomass and community composition of fruiting bodies and soil fungi. Specifically, the continuous-cover forestry treatment appeared more similar to unmanaged stands than clear-felled areas with respect to soil chemical properties, fruiting body abundance and soil fungal community composition. Secondly, we found that variation in fruiting body and soil fungal community composition exhibited a significant relationship with soil chemical properties, suggesting that community changes were at least in part influenced by chemical changes in soils. Our study demonstrates that continuous-cover forestry can broadly maintain similar fruiting body abundance, soil fungal communities and soil chemical properties to unmanaged forests.

4.1. Continuous-cover forestry maintains similar soil chemical properties and fungal communities to unmanaged forest

The results showed that continuous-cover forestry can retain similar soil chemical properties to that of unmanaged forest. There are likely many reasons for the milder effects of continuous-cover forestry on soil chemical properties, compared with clear-fell forestry. First, the removal of the majority of the stems in clear-felled areas has large effects on abiotic conditions such as moisture and sun influx compared to a partial cutting of 30%, and these changes may alter chemical processes in soils (Smenderovac et al., 2017). Clear-felling can also cause substantial disturbances to soil, induce soil erosion and affect nutrient cycling and water quality in forest ecosystems (Laudon et al., 2011). Further, the practice of soil scarification (as conducted in our clear cutting treatment) is known to increase nutrient mineralisation, which can result in nutrients being leached from the system (Persson and Wirén, 1995; Stenger et al., 1995). A complete harvest also cuts the photosynthetic input of trees to ectomycorrhizal fungi leading to the death of mycelia and thus, an initial release of carbon to soils (Jones et al., 2003). Indeed, we found that the mycorrhizal fungi *Piloderma sphaerosporum* with known associations with Norway spruce was much less abundant in clear-cuts than continuous-cover and unmanaged forest (Veselá et al., 2019). Further, the soil C to N ratio within the clear-felled areas was lower than in continuous-cover forestry and in unmanaged forest. This is in agreement with previous research demonstrating that the C to N ratio of soils following the death of fungal biomass is lower than in soils with fresh plant litter (Koide and Malcolm, 2009; Mouginot et al., 2014; Nilsson et al., 2012; Šnajdr et al., 2013). Thus, our finding of low C to N ratio in clear-fell forestry could be explained as the result of dead fungal biomass. Moreover, soil pH and C to N ratio are in inverse proportion to each other (Cabral, 2012), which explains the higher pH and lower C to N ratio in clear-fell forestry than unmanaged forest. Continuous-cover forestry and unmanaged forest did not significantly differ in any soil chemical variable, but clear-fell forestry differed to unmanaged forest in soil pH and C/N.

Diversity is an ecological indicator to monitor the impact of anthropogenic disturbances in forest ecosystems. Our results revealed that forest management practices had opposite effects on fruiting body compared with soil fungal diversity. While clear-felling clearly had a negative effect on fruiting body diversity, the soil fungal diversity was higher in clear-felled areas than in continuous cover and unmanaged forest. The explanation for these results is not obvious, but our results are in accordance with previous findings from other systems showing that fruiting body richness is lower in clear-fell forestry than continuous-cover forestry and unmanaged forest (Purahong et al., 2014). Although not measured directly in this study, part of these effects may be due to a lower input of coarse woody debris in clear-fell forestry (Purahong et al., 2014; Brunet et al., 2010). Around 40% of the 1800 red-listed fungi in Sweden are related to coarse woody debris (Sandström et al., 2015) and when it is removed, this could influence diversity of fruiting bodies (Purahong et al., 2014; Brunet et al., 2010). The reason for us finding of higher diversity of soil fungal richness in clear cuts than in unmanaged and continuous-cover forestry may result from the quite recent logging disturbance (<8 years ago) increasing suitable habitat for the colonization of generalist fungi, while retaining some of the species from more mature forests. For example, understory vegetation may become more diverse and abundant during the early stages of succession following clear-felling which, in turn, may provide additional habitat for their associated fungi (Fornwalt et al., 2018). Indeed, previous studies have shown that plant diversity is correlated with fungal richness (Gao et al., 2013; Peay et al., 2013). Soil scarification constitutes major disturbance to soils and increases small scale habitat heterogeneity (Girona et al., 2018). This increase in habitat heterogeneity may provide a more ideal environment for some fungi by increasing in soil moisture and temperature and by decreasing soil density (Eero and Lauri, 1994; Johansson et al., 2005; Lahde, 1978). Although the conclusions from the fruiting body collections should be conservative as we only sampled fruiting bodies once, the broader patterns from fruiting bodies resemble the patterns from the broader fungal communities present at each site, i.e. clear-felling had a strong effect on community composition while continuous-cover and unmanaged forest were similar. However, it is unclear how the diversity of soil fungal communities will change as the new rotation of trees develops.

Although the effects of silvicultural treatments on the diversity of fruiting body vs. soil fungal communities differed, we found consistent

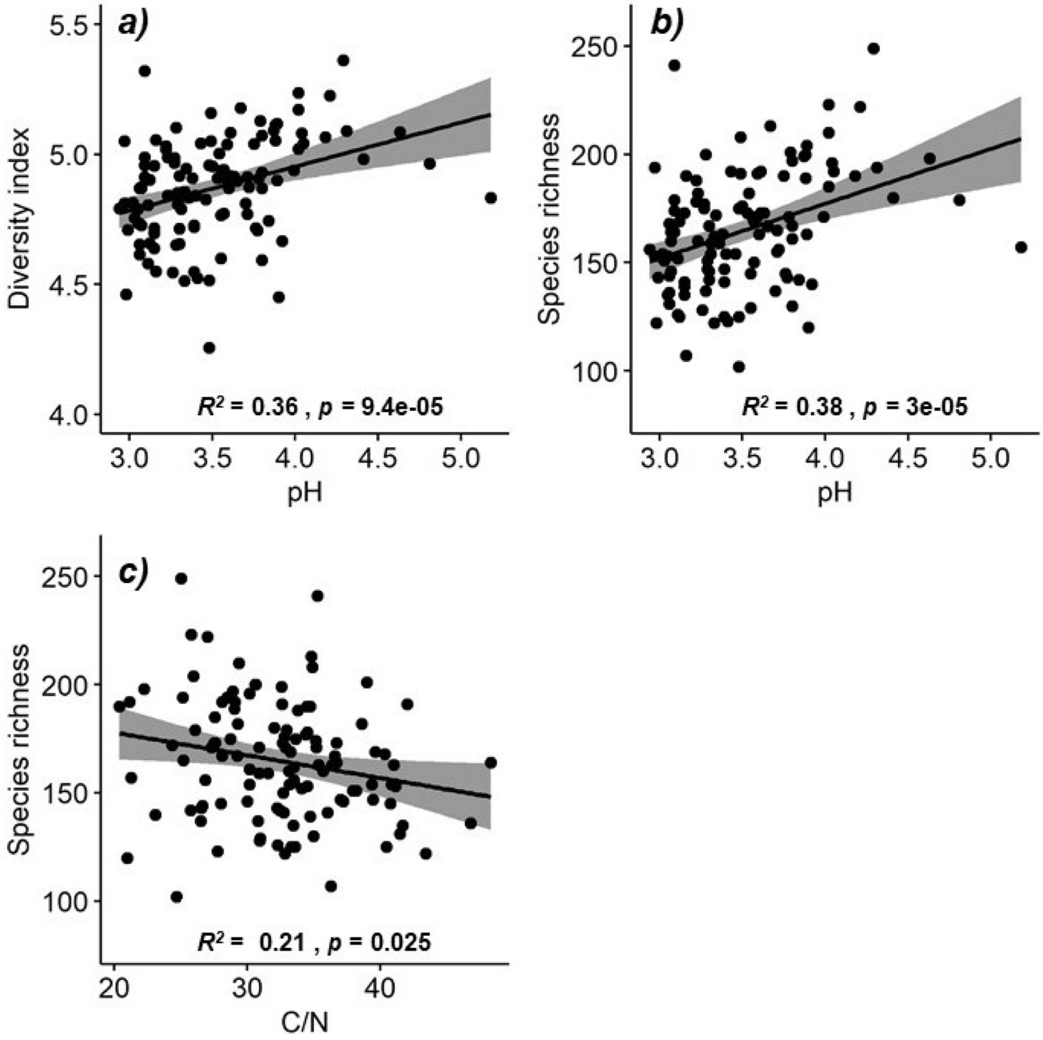

Fig. 3. Scatter plots of significant correlations between soil chemical properties (pH and C/N ratios) and soil fungal diversity (Margalef's species richness and Shannon diversity index).

support for the idea that management practices which mimic small scale disturbance have milder effects on soil communities. We found that the composition of both fruiting body and soil fungal communities in continuous-cover forestry was similar to unmanaged forest, while clear-felled area showed a vastly different composition. These results strongly support our hypothesis that continuous-cover forestry can maintain more similar fungal communities compared to unmanaged forest than clear-fell forestry. It is well known that fungal communities are extremely sensitive to changes in plant diversity and community composition (Goldmann et al., 2015) due to their close association with plants (Lauber et al., 2008). Clear-felling causes immediate changes to plant communities and soil ecosystems, while continuous-cover forestry maintains the majority of the standing forest volume after logging, providing continuous habitat for organisms adapted to more stable conditions and little disruption to the ecosystem. Our findings of consistent milder effects of continuous-cover forestry on the composition of fungal communities provide strong support for the idea that management practises mimicking small scale disturbance regimes could maintain a similar composition of organisms as would be present in unmanaged forests.

Clear-felled areas had a distinct fruiting body community composition to that of continuous-cover and unmanaged forest that had a greater abundance of generalist and wood decaying species. Three fungal species (*Micromphale perforans, Hygrophoropsis aurantiaca* and *Thelephora terrestris*) in the fruiting body community may represent species that are vulnerable or preferential to logging. A decomposing fungus *M. perforans*, which often arises from fallen needles of spruces and firs (Michael, 2013), was much more abundant in continuous-cover forestry and unmanaged forest stands than in stands that were clear-felled. This fungus utilises coniferous needles, predominantly from Norway spruce, as growing substrate and a higher abundance of this fungus in continuous-cover forestry is likely due to a continuous input of needle litter. In line with our findings of higher abundance of *M. perforans*, Purahong et al. (2014) showed that litter decomposition is faster in continuous-cover forestry and unmanaged forests compared to clear-cut. Furthermore, *H. aurantiaca* which is also a wood-decaying fungus was more abundant in clear-felled areas. This fungus is a habitat generalist and occur in mixed woodland, but is also common on open land such as heaths and grasslands (Kibby, 2012). It is typically associated with woody debris (Desjardin, 2015; Fransson et al., 2004) and are especially common on clear cuts with abundant logging residues (Toivanen et al., 2012). We found that *T. terrestris* was only present in clear-felled areas and completely absent in continuous-cover and unmanaged forest stands at all four study sites. *T. terrestris* is a pioneer species typically occuring after disturbance (Paul et al., 2008, Colpaert, 1999). Varenius et al. (2017) confirmed that regenerated stands would have a greater abundance of *T. terrestris* than old natural stands. For instance, a large amount of *T. terrestris* was observed in young stands of Douglas fir regeneration after clear-felling and wildfire (Twieg et al., 2007). Furthermore, *T. terrestris* frequently occurs on nursery-grown seedlings (Menkis et al., 2016) and could thus have been introduced to our clear-cuts with planted seedlings.

Three fungal species (*Piloderma sphaerosporum*, *Thelephora terrestris* and *Luellia* sp) in soil fungal community may also be the indicator species that are vulnerable or preferential to timber harvesting. *P. sphaerosporum* is a mycorrhizal fungus associated with Norway spruce dominated forests and becomes especially dominant in soil adjacent to heavily decayed logs (Mäkipää et al., 2017). It was much more abundant in continuous-cover forestry and unmanaged forest stands than clear-fell forestry. The combination of a continuous-cover forestry and unmanaged forest treatments retaining a forest cover and holding many old logs in later decaying stages has likely contributed to maintaining *P. sphaerosporum* in these forests. Furthermore, logs in the late stages of decay may bring a steady amount of moisture to the organic layer (Rajala et al., 2012) and it would provide a favourable habitat for some mycorrhizal species (Rajala et al., 2015). Thus, we show that continuous-cover forestry could maintain mycorrhizal fungi, which are responsible for the acquiring of scarce nutrients in boreal forests. *Luellia* sp, was more abundant in clear-fell forestry stands than continuous-cover forestry and unmanaged forest. *Luellia recondita* is associated mostly with Sidebells wintergreen (*Orthilia secunda*) a herbaceous plant common in woodland throughout Sweden and might be either ecto-mycorrhizal or saprotrophic (Malysheva et al., 2018). The clear-fell forestry treatment has a greater area of opened canopy so that weedier and earlier successional vegetation could establish and thus introduce plant-associated fungi. As mentioned above, *T. terrestris* is predominately associated with young regeneration stands such as clear-felling and with nursery grown seedlings.

Continuous-cover forestry is thought to be an alternative forest management practice to achieve the sustainable management of boreal forests (Girona et al., 2016; Girona et al., 2017). However, to better understand the biodiversity implications more efforts must be provided (Rosenvald and Lõhmus, 2008; Schuler, 2004). Taken together, we show that continuous-cover forestry can maintain some fungal species that are crucial to the functioning of boreal forests, such as *P. sphaerosporum* which is important mycorrhizal fungus and *M. perforans* which is important decomposer. Furthermore, we found that clear-cutting can generate the new dominant fungal species such as *H. aurantiaca*, *T. terrestris* and *Luellia* sp. Understanding ecological functions of fungal species that greatly contribute to dissimilarities among forest management treatments represents the key to unravel the potential impacts of forest management on ecosystem function.

4.2. Variation in soil fungal communities is related to soil chemical properties

We show that fruiting body and soil fungal community composition are sensitive to changes in soil chemical properties. This is in agreement with previous studies which show that fungal richness is related to abiotic factors including soil pH, moisture, temperature and N availability (Allison et al., 2007; Bi et al., 2011; Wang et al., 2015; Wardle and Lindahl, 2014). This is likely because fungi typically respond differentially to environmental factors according to their functional group and/or special traits (Crowther et al., 2014; Koide et al., 2014). For example, the mycelial growth of ecto- and ericoid-mycorrhizal fungi decreases with high nutrient availability, while the production of arbuscular-mycorrhizal fungi increases in more nutrient-rich soils (Nilsson et al., 2005). However, the percentage of variation in fungal community composition explained by soil chemical properties in this study was low. This suggests that other environmental variables such as sun exposure, soil moisture and habitat availability could also be drivers explaining this phenomenon.

5. Conclusion

Adapting silvicultural treatments to incorporate natural disturbance regimes will be critical for developing long-term sustainable management strategies to maintain the biodiversity and function of boreal forest ecosystems. Our findings provide strong support for the use of continuous-cover forestry maintain soil communities and chemical properties similar to that of unmanaged forests in boreal forest ecosystems. In terms of both soil fungal communities and chemical properties, the continuous-cover forestry treatment was consistently similar to unmanaged stands. This maintenance of soil fungal communities in forests managed with continuous-cover forestry likely derives from the combined effects of retaining similar properties in partially harvested stands and their effect on maintaining biotic (species associations) and abiotic conditions (micro-climate and soil chemistry). Future studies should be directed towards assessing temporal effects throughout the full rotation cycle to improve our understanding of the impact of forest management strategies on long-term biodiversity.

Credit authorship contribution statement

Conceptualization: JKS and EPA. Data curation: SK. Formal analysis: SK. Funding acquisition: JKS and EPA. Investigation: SK, JKS and EPA. Methodology: SK, JKS and EPA. Project administration: JKS and EPA. Resources: JKS and EPA. Software: Swedish University of Agricultural Science (SLU). Supervision: JKS and EPA. Validation: SK, JKS, EPA and MMG. Visualization: SK. Writing – original draft: SK. Writing – review & editing: JKS, EPA and MMG.

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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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118659.

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