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Multiple-use forests and reindeer husbandry – Case of pendulous lichens in continuous cover forests

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A R T I C L E I N F O

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A B S T R A C T

Competition for land use between forestry and reindeer husbandry has been debated in northern Finland, particularly due to the possible adverse effects of forestry on the availability of forage resources for reindeer. In an attempt to achieve a better reconciliation of these land uses, as well as to promote multiple forest use, we studied the effects of 37 stand-, plot-, and tree-level variables on pendulous lichens (*Alectoria* sp., *Bryoria* sp. and *Usnea* sp.), and compared two methods of continuous cover forestry (CCF) on pendulous lichen occurrence in Finnish Lapland.

The main findings of the study indicate that the number of years after cutting, and the trunk diameter increase the probability of pendulous lichen occurrence. The highest probability of pendulous lichen occurrence by tree species was achieved in Norway spruce (*Picea abies* (L) Karst), and by area, in the southern and western parts of the study area. Of the two CCF methods studied – small gap cutting and selection cutting – the former was slightly more successful in maintaining pendulous lichens, especially in southern and western Lapland. In addition, the ground lichen coverage indicating the degree of xeric features of the stand reduced the probability of pendulous lichen occurrence. Furthermore, we compared our data with reference material, and found that the CCF stands of the present study maintained more pendulous lichens than managed young thinning stands, but less than managed mature even-aged forests.

This study shows that in order to better reconcile forestry and reindeer husbandry in a reindeer herding area, the larger trees should be saved, and the cutting cycle should be kept as long as possible. In addition, lichen-rich areas should be excluded from logging, and the access of reindeer to those areas should be secured. Of the two CCF methods studied, small gap cutting could be a viable method in reconciling forestry and reindeer husbandry, as well as the multiple use of forests, in that it allows to keep at least parts of the forest intact for a longer period of time, which advances the growth of pendulous lichens. Selection cutting, in turn, affects the whole area, and removes the large trees, which are advantageous for pendulous lichens.

1. Introduction

Land use between forestry and reindeer husbandry has been a source of dispute for over a hundred years in Finnish Lapland (Turunen et al., 2020). Both livelihoods are vital and economically important to the region, and their reliance on partly the same forest resources almost inevitably leads to some degree of disagreement. Most of the disputes between reindeer herders and forest owners have arisen out of the reduction, decline and fragmentation of reindeer pastures through intensive forestry practices. In addition to forestry, other land use modes (e.g., tourism, energy production, agriculture, mining, traffic and other infrastructure), a high number of reindeer, the lack of seasonal reindeer pasture rotation, and increasing climate-change induced competition between lichens and other, faster-growing species, such as shrubs, have reduced the amount of high-quality lichen-rich pastures in Finnish Lapland (Turunen et al., 2009; Akujärvi et al., 2014; Kumpula et al., 2020). Similar problems have been experienced in Canada (Stevenson and Coxson, 2003) and northern Sweden (Kivinen et al., 2010).

Both forestry and reindeer husbandry have changed considerably due to modernization since the mid-20th century. The changes have included a shift from a subsistence economy to a financial economy, and a rapid technical development (Kivinen et al., 2010; Horstkotte et al.,

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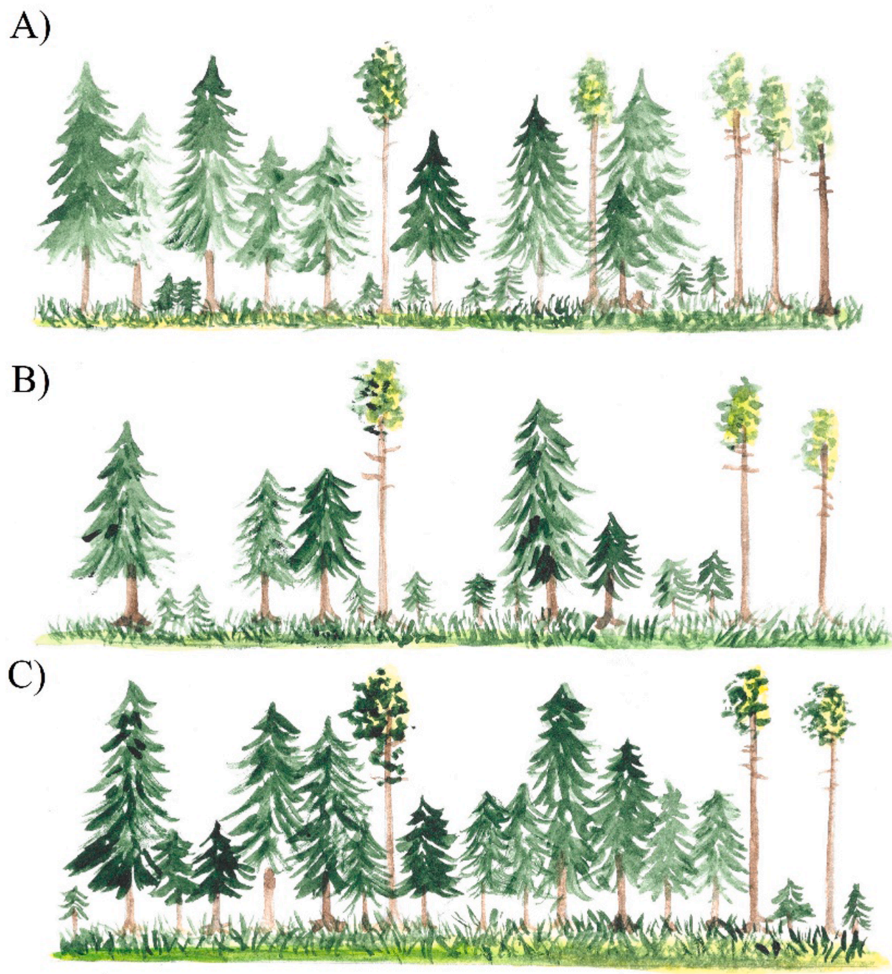

Fig. 1. Schematic illustration of the concept of selection cutting before cuttings (A), after cuttings (B) and 10–20 years after cuttings (C). Illustration: Jonna Hänninen (2021).

2011). The modern silviculture has brought about a structural and functional change in boreal forests, leading to a younger age distribution of trees and a change in tree species composition. Almost all forest practices, such as forest road building, soil preparation, fertilization, and ditching, have an impact on the reindeer grazing areas. In Finland, the proportion of old-growth forests, which are critically important forage sources for reindeer, has decreased by 43% from the 1950s to 2020 (Natural Resources Institute Finland, 2022). The changes in forests have significantly modified reindeer herding practices, and foraging in lichen-rich old-growth forests has been gradually replaced by supplementary winter feeding of reindeer.

One of the biggest problems caused by forestry on reindeer husbandry is its damaging effect on the winter forage sources for reindeer; both terricolous ground lichens, and epiphytic lichens that grow on tree trunks and branches (Dettki and Esseen, 1998; Kivinen et al., 2010; Kumpula et al. 2019). The rejuvenation of forests, in particular, is harmful for lichens, since many lichen species favor old-growth forests (Esseen et al., 1996; Kuusinen and Siitonen, 1998; Peura et al., 2018). Our study focuses on epiphytic pendulous lichens, such as *Alectoria* sp., *Bryoria* sp. and *Usnea* sp, which are bottleneck resources for reindeer during late winter, when the digging conditions are challenging (Helle et al., 1979; Kumpula et al., 2020). The access of reindeer to these winter forage resources is critically important particularly during winters of exceptionally difficult snow conditions (thick snow cover, ice formation on snow), such as the winter 2019–2020 in Northern Fennoscandia.

The occurrence of pendulous lichens and the availability of their habitat are affected by the age of the forest stand: Their species diversity is the highest in stands over a hundred years old (Esseen et al., 1996). Therefore, the abundance of pendulous lichens is usually higher in old-growth forests compared to younger ones. In addition, pendulous lichens grow most abundantly in stands on the most fertile soils (Jaakkola et al., 2006), and their amount is higher in structurally complex forests than in simple ones (Dettki and Esseen, 1998), even though there are some recent opposing results from Goward et al. (2022). Therefore, the basal area, i.e. stand density, and the spatial structure of the stand have been shown to have an impact on the amount of pendulous lichens, since those factors increase the availability of suitable habitats (Dettki and Esseen, 1998; Dettki et al., 2000; Jaakkola et al., 2006; Horstkotte et al., 2011). Due to the amount of habitat (growing substrate), pendulous lichens are usually most abundant in biomass-rich spruces (Esseen et al., 1996; Jaakkola et al., 2006).

The Reindeer Husbandry Act (848/1990) of Finland obliges the State authorities to consult the representatives of reindeer husbandry when planning measures concerning State lands have a substantial effect on the practice of reindeer husbandry. Reconciliation of reindeer husbandry and forestry has an impact on the operations of both: While the status of reindeer husbandry in land use planning has improved, the profitability of forestry has decreased through taking the obligations of reindeer husbandry into account. Along with the goals of increasing the multiple-use of forests, finding solutions for combining forestry and reindeer husbandry within the same forest – ones that minimize the potential harm of different forest uses, while guaranteeing the economic

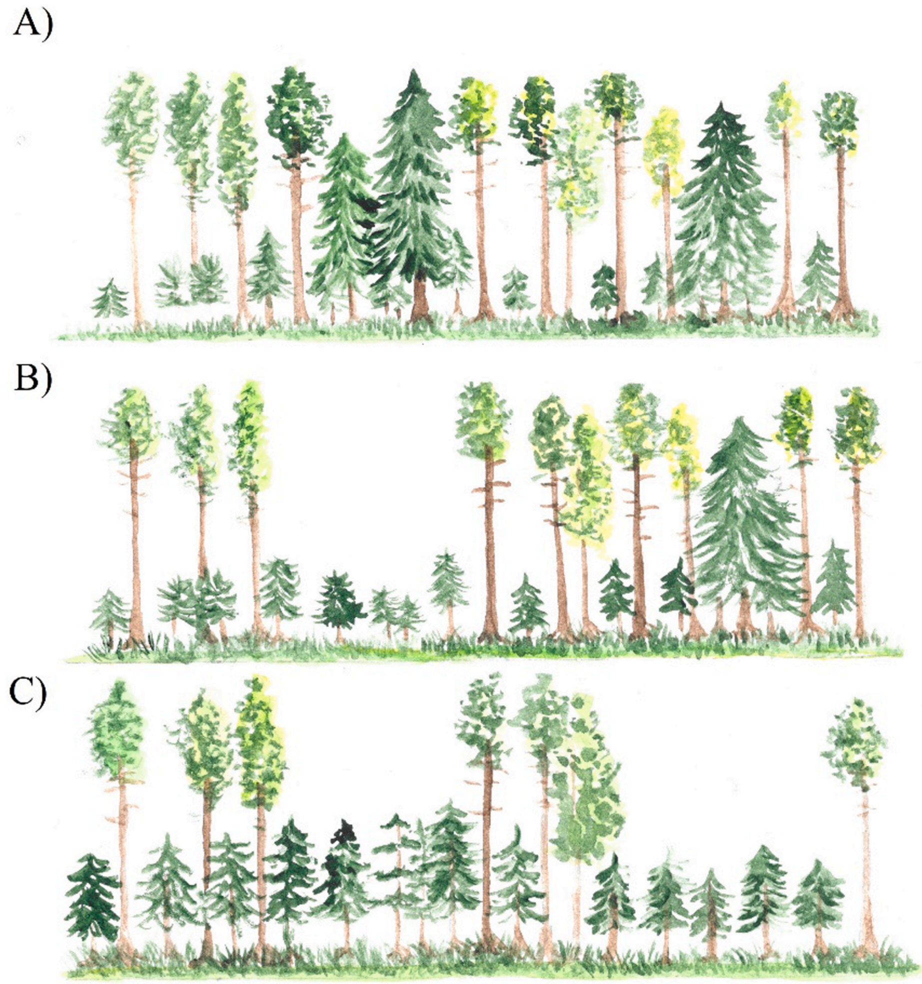

Fig. 2. Schematic illustration of the concept of small gap cutting before cuttings (A), after cuttings (B) and 10–20 years after cuttings (C). Illustration: Jonna Hänninen (2021).

result and the functioning of the ecosystems – is of central importance (Turunen et al., 2020). Optimally, multiple use of forests – in which forestry and reindeer husbandry could co-exist with recreation, tourism, hunting, and berry and mushroom gathering – could benefit all these livelihoods and activities within the same area. In addition, multiple-use forests could offer benefits for biodiversity, carbon sequestration and other ecosystem services (Miina et al., 2020).

Development towards more sustainable forestry measures has taken place recently through the introduction of the CCF (continuous cover forestry) methods (e.g. Valkonen, 2020). CCF can be defined as forestry in which no clear-cutting is conducted, and a large number of trees are left for the purpose of maintaining other forest ecosystem services (Valkonen et al., 2010). Given its potential for improved biodiversity and carbon sequestration (Nolet et al., 2018; Peura et al., 2018; Eyvindson et al., 2021), CCF is considered more multifunctional than methods that are based on even-aged forest stands (Pukkala et al., 2011; Valkonen, 2020).

The most common methods of CCF are selection cutting (Fig. 1) and small gap cutting (Fig. 2). The difference between these two methods is in their starting point: in selection cutting, attention is focused on a single tree and its environment, whereas in small gap cutting, attention is directed at small areas to be cut (see also Valkonen et al., 2010). Before the reformation of the Forest Act in 2014 (Forest Act, 1093/1996), these methods were prohibited by Finnish law, which explains why relatively little experience has been gained so far with CCF in Finland (Valkonen, 2020). After that, it has subsequently become more common to use these methods.

Because in the reconciliation of reindeer husbandry and forestry it is crucial to save lichen pastures, and since clear-cutting has been shown to be harmful to lichens (Ranlund et al., 2018; Rudolphi and Gustafsson, 2011), it is interesting to study how lichens respond to the clear cutting-free CCF-methods in reindeer herding areas. Kumpula et al. (2019) have stated that the development of CCF, and its more extensive use, would benefit reindeer husbandry in the long term, particularly through better maintenance of lichens (e.g. Dettki and Esseen, 1998; Stevenson and Coxson, 2007).

The relationship between forestry and the abundance of lichens has previously been studied for example in northern Sweden and North America (Rominger et al., 1994; Esseen and Renhorn, 1998; Dettki et al., 2000; Coxson et al., 2003; Stevenson and Coxson, 2004; Stone et al., 2008; Goward et al., 2022). Most of these studies are short-term ones, conducted in restricted locations and focusing mainly on terricolous lichens. Only a few studies have examined the impacts of CCF on pendulous lichens: Both selection cutting and small gap cutting were shown to be advantageous for the maintenance of the lichens studied (Stevenson and Coxson, 2003; Stevenson and Coxson, 2004; Stone et al., 2008). Hardly any information exists on the long-term impacts or potential benefits of CCF on pendulous lichens. The present study expands on previous studies by both covering a wider area and by shedding light on potential longer-term impacts through examining the responses of pendulous lichens to the use of CCF methods 12 to 35 years after cutting in different parts of Finnish Lapland.

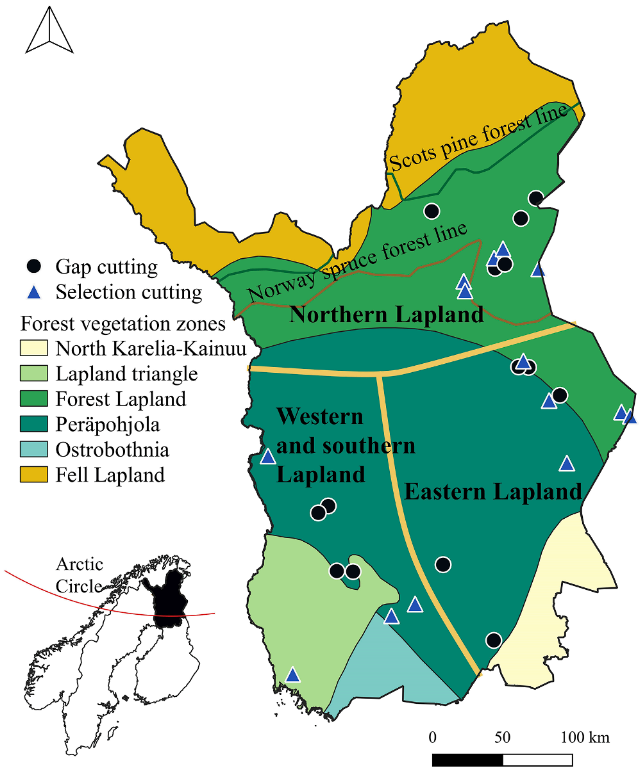

Fig. 3. Location of the study area, forest vegetation zones and the locations for the study stands and cutting methods. The study area was divided into three geographical sections (northern, eastern, and western/southern Lapland) as indicated by the yellow lines. Map: © Taru Rikkonen, Arctic Centre, University of Lapland 2021. Data: © National Land Survey 2021, © Finnish Environmental Institute 2021.

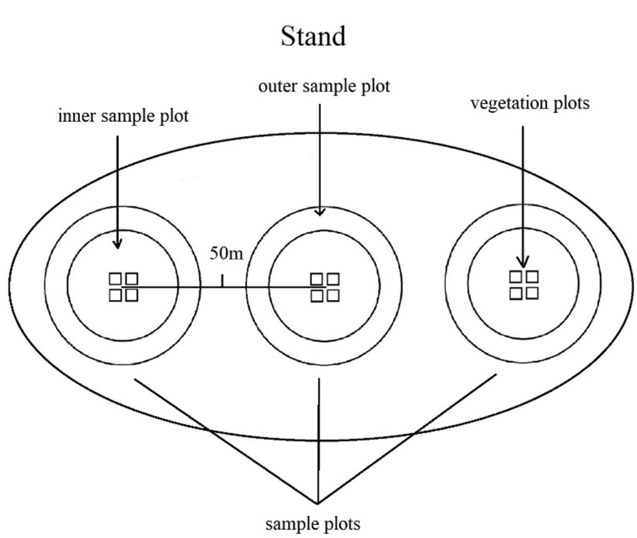

Fig. 4. The configuration of the sample plots. Each stand (n = 28) included three sample plots, which consisted of inner and outer sample plots, and four vegetation plots. The sample plots were located 50 m apart from each other. There were four vegetation plots (1 m^2) at the center of each sample plot. The sizes of the sample plots varied by the number of trees found from the stand. The target number of trees for three sample plots was to be around 100, and the target for one sample plot was 30 to 35 trees. The maximum radius of the outer sample plot was 35 m, and the radius of the inner sample plot was determined by the radius of the outer sample plot (Appendix part A: Table A.1).

This study aims to examine (1) what are the effects of stand-, plot- and tree-level variables on pendulous lichen occurrence, (2) what are the effects of selective and small gap cutting on pendulous lichen occurrence and (3) how the amount of pendulous lichen in CCF forests differ from a reference material gathered in managed even-aged forests. Based on the previous studies, we hypothesize that the age of the tree, the basal area of the stand, and the number of years after cutting increase the abundance of pendulous lichens. We further expect that the highest amounts of pendulous lichens can be found on fertile soils that mainly occur in southern and western parts of Finnish Lapland. Although our study site is partly located north of the polar timberline of Norway spruce (Fig. 3), we expect that the highest abundance of pendulous lichens is found on spruces. By answering these questions, we aim to find out if CCF can be used in multiple-use forests to better reconciliate reindeer husbandry and forestry in Finnish Lapland.

2. Material and methods

2.1. Study area

The study area is located in Finnish Lapland, which is the largest and northernmost province of Finland, located between the 66 and 70 north latitudes (Fig. 3). The majority of the area of Lapland is located north of the Arctic Circle and characterized by a cold and harsh climate (Tikkanen, 2005). The area belongs to the snow forest climate, which is characterized by humid and cold winters (Köppen, 1936; Peel et al., 2007). The area's climatic conditions are regulated by its northern location and the impact of the Arctic Ocean, the Gulf Stream, the Scandinavian mountains and the Asian continent (Autio and Heikkinen, 2002). The average temperature of Lapland varies between 3 °C and −3 °C. Due to the low temperature, the climate is quite moist, average annual precipitation varying between 400 and 650 mm. The climate of the northern Lapland is more oceanic, whereas the eastern parts of the area are characterized by a more continental climate.

More than half of Lapland is highlands (over 200 m above sea level) (Johansson & Kujansuu, 2005). Most of the bedrock belongs to the Fennoscandian shield, which mostly comprises Archaean and early Proterozoic rock types, such as migmatite-granitoid areas with greenstone belts and mica-schist-paragneissic areas, with additions of volcanic and sedimentary rocks (Korsman et al., 1997). More than half of the soil cover area is moraine, and other common soil types include peat, crag and rocks, as well as sand and gravel.

As one goes northward, the climate cools down and the growing season shortens, causing a typical zoning effect on vegetation (Heikkinen, 2005). Lapland belongs to the Central Boreal and North Boreal vegetation zones (Ahti et al., 1968), and the forest stands studied are located in Lapland triangle, Ostrobothnia, Peräpohjola and Forest Lapland forest vegetation zones (Kalela, 1961; Ahti et al., 1968; Kontula and Raunio, 2019).

The dominant species of the boreal vegetation zone are Scots pine (*Pinus sylvestris*, L.) and Norway spruce (*Picea abies* (L.) Karst) (Heikkinen, 2005). In the southern part of Lapland, the vegetation is more fertile, and the forest cover is denser, whereas in the northern parts of the area, the forest cover is thinner and the growth of trees slower (Kalliola, 1973). Some plant or tree species even disappear completely when they reach their northern limit of distribution. At the same time, southern species are being partially replaced by northern species, but in a way that the biota as a whole becomes poorer further north. One of the most significant features of Forest Lapland and the areas north of it is that the Norway spruce has not yet spread to the whole area at all (Fig. 3). In Forest Lapland and Peräpohjola, the majority of forests are mature or old-growth forests, characterized by lichen-rich areas important to reindeer, while young, growing forests and logging areas dominate the southern part of the region (Kumpula et al., 2019).

The province of Lapland covers approximately 30% of Finland, but only 3% of the country's inhabitants live there (National Land Survey

Table 1
Descriptive statistics for stand-, plot- and tree-level variables tested in the models.

Stand-level variables, n = 28	**Mean**	**Median**	**Range**
Years from cutting	21.5	20	12–34
Number of stems 2019	673	627.8	157.9–1769.9
Basal area 2019, m^2	12.2	12.3	2.3–28.4
Timber volume 2019, m^3	80.0	78.5	11.2–229.8
Number of logs 2009	162.0	132.3	0–668.8
Number of stems 2014	590.9	523.3	32.9–1769.9
Basal area 2014, m^2	10.6	11.03	0.9–26.5
Timber volume 2014, m^3	53.1	51.6	3.1–153.2
Number of logs 2014	104.7	78.7	0–509.6
Number of stems 2009	345.4	331.9	0–1062.0
Basal area 2009, m^2	7.8	8.5	0–23.7
Timber volume 2009, m^3	32.5	30.2	0–88.2
Number of logs 2009	51.3	39.3	0–183.9
Examination plot-level variables, n = 84			
Coverage of *Sphagnum* species, %	0.79	0	0–27.75
Coverage of other moss species, %	68.6	80	4.25–98
Coverage of ground lichen species, %	8.72	3	0–53.75
Coverage of litterfall and lying dead wood, %	19.17	10	1.25–74.5
Coverage of bare humus soil, %	0.7	0	0–23.75
Coverage of exposed mineral soil, %	0.07	0	0–2.75
Coverage of bare stones, %	1.05	0	0–23
Coverage of stumps, lying and standing dead wood, %	0.95	0	0–12
Coverage of *Vaccinium myrtillus,* %	4.66	2.625	0–20.5
Coverage of *Vaccinium vitis-idaea,* %	13.82	9.875	1.5–43.75
Coverage of *Vaccinium uliginosum*, %	1.54	0	0–28.25
Coverage of *Empetrum nigrum,* %	10.57	5.625	0–38.75
Coverage of *Calluna vulgaris,* %	6.52	0	0–51.25
Coverage of *Rhododendron tomentosum,* %	0.95	0	0–10
Coverage of grasses and sedges, %	0.62	0	0–7.5
Coverage of other vascular plants, %	0.24	0	0–8.75
Coverge of *Betula nana*, %	0.01	0	0–1
Coverage of cutting residue, %	0.08	0	0–3
Stoniness, cm.	21.41	16	3–70
Humus coverage, mm.	32.02	28	9.75–113.25
Tree-level variables			
The thickness of the bark, mm., n = 934	11.09	10	1–47
The age of the tree, y., n = 194	68.02	61	17–250
Trunk diameter (d1.3), mm., n = 934	150.9	137	42.5–438
Crown height, dm., n = 933	105	100	11–236

Finland, 2021). Lapland belongs to the reindeer management area, and most of this area is classified as forestry land, which is mainly state-owned. This area varies from boreal coniferous forests to subarctic downy birch forests, marshes and riversides (Kalliola, 1973). Both reindeer husbandry and forestry use the same areas, with the exception of the Sámi home region, in which forestry is restricted, and nature protection areas, in which forestry is prohibited. Reindeer herds usually utilize different pasture areas according to the seasons.

2.2. Sampling design and data preparation

The data were collected in pine-dominated forest stands that were randomly selected from among about a thousand experimental stands for CCF in the forestry area of Lapland (Fig. 3). The CCF methods used were selection cutting (Fig. 1) and small gap cutting (Fig. 2). The cuttings were conducted by Metsähallitus Forestry Ltd (responsible for the management of the state-owned commercial forests in Finland) during the period from 1985 to 2007. The study sites had been laser scanned and partly measured in advance, and the data were supplemented with fieldwork that was carried out during the snow-free periods in 2019 and 2020. The descriptive statistics from 2009 and 2014 were calculated using the KPL program (Heinonen, 1994) that yields tree- and timber-level data of a sample plot. With this program, it is possible to compute the length of the tree, timber volume, basal area and number of logs, 5 or 10 years before the tree-ring dating. The data included 28 stands, half of which (14) were stands where gap cuttings were carried out, and half where selection cuttings were used (Fig. 3). In each stand three sample plots were positioned, and thus, our analysis is based on 84 sample plots in total (Fig. 4; Table 1). The stands were located in three different geographical regions: northern Lapland (n = 10), eastern Lapland (n = 10) and western and southern Lapland (n = 8) (Fig. 3) that were fixed prior statistical analyses.

The location of the first sample plot of each stand studied was randomly positioned on the map prior to the fieldwork. The second plot of the stand was located 50 m north of the first sample plot, and the third one was located again 50 m north of the second one (Fig. 4). The sizes of the sample plots were determined by the number of trees found in the stand. The number of trees in one sample plot was supposed to be between 30 and 35, and the aim was to have at least a hundred trees in the study stand (3 plots). All stems over 4.5 cm DBH (diameter breast height) were considered as trees. The stand-level tree data consisted of all trees inside the 84 sample plots, 3015 trees in total. In addition, each sample plot was divided into two sections, here referred to as outer and inner sample plots (Fig. 4). Hence the sample plots could not overlap, the maximum radius of the outer sample plot was 25 m, and the radius of the inner plot was determined by the radius of the outer plot (Appendix part A: Table A.1).

The outer sample plot was established in order to record stand-level data, such as the number of stems, basal area, number of logs, and timber volume. The inner sample plot was to be at least 1/3 of the area of the outer plot, and it was established inside the outer plot in order to get more detailed data on the trees (e.g. age), and for the assessment of the pendulous lichens. The age of the sample trees was measured by counting the annual rings in a sample cored with an increment borer from the trunk at breast height. The thickness of the bark was measured from the sample cored for the annual ring measurements. The trunk diameter of each sample tree was measured by taking two diameter measurement at a 90-degree angle at breast height. The crown height was measured using the Haglöf Vertex instrument for measuring height, angle and distance. The tree-level data consisted of all trees inside the inner sample plots, resulting in 934 trees in total, of which 81.9% were pines, 9.2% were deciduous trees, and 8.9% were Norway spruce. In addition, every tree in the inner sample plot was divided into three different height sections (parts of the trunk) for the evaluation of pendulous lichen occurrence.

The amount of pendulous lichens in every tree of the inner sample plot was assessed. All "beardlike" lichens – which practically means the genera *Bryoria, Alectoria* and *Usnea* – were taken into account. The amount of pendulous lichens was assessed according to Kumpula et al. (2006), where the amount of lichens is estimated in the branches and the trunk of the tree, in different parts of the trunk: lower part < 2 m; middle part = 2–5 m; upper part > 5 m. The amount of lichens was assessed in the following abundance classes: 0 = no lichens (no pendulous lichens are observed at a brief glance); 1 = short pendulous lichens or sheaths of lichens are abundant, with a maximum length of one centimeter (Appendix part A: Fig. A.1a); 2 = pendulous lichens are observed almost entirely in long-growing form or in sheaths, length about two to five centimeters (Appendix part A: Fig. A.1b); 3 = longish or long pendulous lichens or sheaths of lichen grow generally or throughout the tree (over five centimeters, often over ten centimeters) (Appendix part A: Fig. A.1c).

For the vegetation cover measurement, four vegetation plots (1 m × 1 m) were established in the middle of the inner sample plots (Fig. 4). In total, the vegetation cover was recorded from 336 vegetation sample plots, and the coverages were calculated as the averages of the four plots. The coverages of the ground layer were determined for mosses, ground lichens, soil, rocks and humus surface (Table 1). Coverage of vascular plants was recorded from the field layer. The stoniness, number of stumps and the amount of lying dead wood, and the amount of visible stones on the surface, were recorded from the entire inner sample plot.

Table 2
The variables selected to the model for abundance class at least 1. The estimate of continuous variables (years from cutting, basal area, coverage of ground liches, trunk diameter) points out, how much the probability of pendulous lichens changes, if that variable grows by one unit. The estimate of categorial variables (cutting method, region, part of the trunk, tree species) points out the difference in the probability of pendulous lichens compared to the control level. For all fixed effects presenting a categorical variable also tests for the other treatment categories vs. a reference category (*given in parenthesis*) are presented.

Variable	Estimate	Std. err.	df	t/Chi	p
Fixed effect					
Intercept	−4.459	2.327	1806	−1.916	0.056
Years from cutting	0.246	0.079	21	3.101	**0.005**
Basal area 2019	0.070	0.061	52	1.153	0.254
Cutting method (*gap cutting*)			1	6.996	**0.008**
selection cutting	−2.815	1.069	21	−2.634	**0.016**
Region (*East*)			2	12.421	**0.002**
north	−1.162	1.407	21	−0.825	0.418
south/west	4.578	1.702	21	2.689	**0.014**
Coverage of ground lichens	−0.028	0.013	52	−2.191	**0.033**
Diameter of the tree at breast height (trunk diameter)	0.018	0.001	884	14.015	**0.000**
Part of the trunk (*<2 m*)			2	35.217	**<0.001**
2–5 m	−0.767	0.788	1806	−0.973	0.331
>5 m	−4.355	0.874	1806	−4.985	**0.000**
Tree species (*Picea abies*)			2	77.397	**<0.001**
deciduous tree	−4.827	0.815	884	−5.913	**0.000**
Pinus sylvestris	−2.146	0.786	884	−2.730	**0.007**
Part of the trunk * region			4	46.652	**<0.001**
2–5 m * north	−1.077	0.274	1806	−3.924	**0.001**
>5 m * north	−1.118	0.308	1806	−3.633	**0.003**
2–5 m * south/west	−1.055	0.273	1806	−3.861	**0.001**
>5 m * south/west	0.314	0.318	1806	0.986	0.324
Region * Basal area			2	8.453	**0.015**
north * basal area	0.105	0.083	52	1.256	0.215
south/west * basal area	−0.144	0.089	52	−1.608	0.114
Part of the trunk * Tree species			4	152.246	**<0.001**
2–5 m* deciduous tree	4.219	0.843	1806	5.005	**0.000**
>5 m * deciduous tree	4.781	0.890	1806	5.370	**0.000**
2–5 m * Pinus sylvestris	0.819	0.770	1806	1.064	0.288
>5 m * Pinus sylvestris	1.043	0.851	1806	1.226	0.220
Region * Cutting method			2	9.210	**<0.001**
north * selection cutting	3.959	1.422	21	2.785	**0.011**
south/west * selection cutting	0.362	1.665	21	0.218	0.830
Random effects	Variance				
Stand	2.037				
Experimental plot	0.237				
Tree	2.517				
Dispersion parameter	0.495				

2.3. Statistical analysis

Four categories (0–3) were used in assessing the amount of pendulous lichens, and the interpretation was made in ordinal scale. Instead of an ordinal multinomial logistic mixed effects model, we computed three separate binomial logistic mixed effects models for the following response categories: abundance class at least 1 (including abundance classes 1–3: at least some pendulous lichens); abundance class at least 2 (including abundance classes 2–3: a high amount of pendulous lichens); and abundance class is 3 (a very high amount of pendulous lichens). The advantages of the separate models were: 1) different linear combinations of the explanatory variables had a significant contribution in different categories, and the coefficients of the same predictors different categories as well, and 2) the tools in the presentation of the predictions (effect plots) were more advanced in R statistical environment (R Core Team, 2018), compared to the tools for the multinomial mixed effects models available in R. The first response category (abundance class at least 1) included 59.3% of the data (parts of tree trunks), the second response category (abundance class at least 2) included 16.5% of the data, and the third category (abundance class 3) included 4% of the data.

The mixed model had to be used because the data were hierarchical (region, stand, plot, tree, part of the trunk). Region was considered as a fixed variable in the models. Each of the three logistic mixed effect models could be described as follows:

$$binomial(n_{ijkl}, \pi_{ijkl}) \quad (1)$$

$$logit(\pi_{ijkl}) = ln\left(\frac{\pi_{ijkl}}{1-\pi_{ijkl}}\right) = f(X_{ijkl}, \beta) + \mu_i + \mu_{ij} + \mu_{ijk} \quad (2)$$

where π_{ijkl} is the probability of the event, i.e. a certain amount (level) of pendulous lichens was found on the part of the tree trunk. Binomial (n,π) denotes the binomial distribution with parameters (n) describing binomial sample size, in our case the total number of parts of the tree trunks and π describing the proportion, or probability, of events, the occurrence of a certain observed level of pendulous lichens on the part of the tree trunk. $ln\left(\frac{\pi_{ijkl}}{1-\pi_{ijkl}}\right)$ is a logit link function and $f(X_{ijkl}, \beta)$ describes the linear function, similarly to the function that is presented above (formula 1). The random part of the model can be described as: μ_i denotes the variance of stand, μ_{ij} the variance of plot and μ_{ijk} the variance tree. The lowest level l denotes the part of the tree trunk.

The models were computed using the package MASS (Venables and Ripley, 2002) of R-software, with the function qlmmPQL, which is flexible and allows easy generation of prediction images with confidence intervals using the R software package Effects (Fox, 2003; Fox and Weisberg, 2019).

Three different models were made for the different abundance classes, and the variables were selected for them by being statistically significant main factors (main effect $p < 0.05$), or being part of statistically significant interactions. Model assumptions were verified by scrutinizing residuals and variance inflation factors (VIF, see Appendix part B). In order to evaluate this data and to compare it to normal managed even-aged forests, we used the inventory of pendulous lichens in study stands of Akujärvi et al. (2014) as a reference material. Pendulous liches were inventoried at the same time with other parameters on trees on sample plots described in Akujärvi et al. (2014) (Appendix part A: Table A.2).

3. Results

3.1. Model 1: Abundance class at least 1

The probability of finding at least some pendulous lichens (abundance class at least 1) was significantly influenced by the trunk diameter (Table 2; Fig. 5A) and the time (years) passed since cutting (Fig. 5B). When the trunk diameter exceeded 250 mm, the probability of finding pendulous lichens was almost 100%, and when 30 years had passed since cutting, the probability was almost 100% as well. In addition, the coverage of ground lichens seemed to reduce the probability of the presence of pendulous lichens (Fig. 5C). The basal area did not have a significant effect as a main factor, but in Northern Lapland it increased the probability of pendulous lichen occurrence (Table 2; Fig. 5D).

Of the categorial variables, the region, the tree species, and the part of the trunk had significant effects on the probability of pendulous lichen occurrence. Regional differences were significant between Eastern Lapland, and Western and Southern Lapland (Table 2, Fig. 5E). The highest probability of pendulous lichen occurrence was found in Southern and Western Lapland, with a probability of approximately 90%. The lowest probability (50%) was found in Eastern Lapland. The highest probability of pendulous lichens between the different tree species was achieved in Norway spruces, whereas in deciduous trees and Scots pines the probability was slightly lower (Table 2; Appendix part A: Fig. A.2a). The part of the trunk had a significant effect on the occurrence of pendulous lichens: The lowest parts and the middle parts (<2

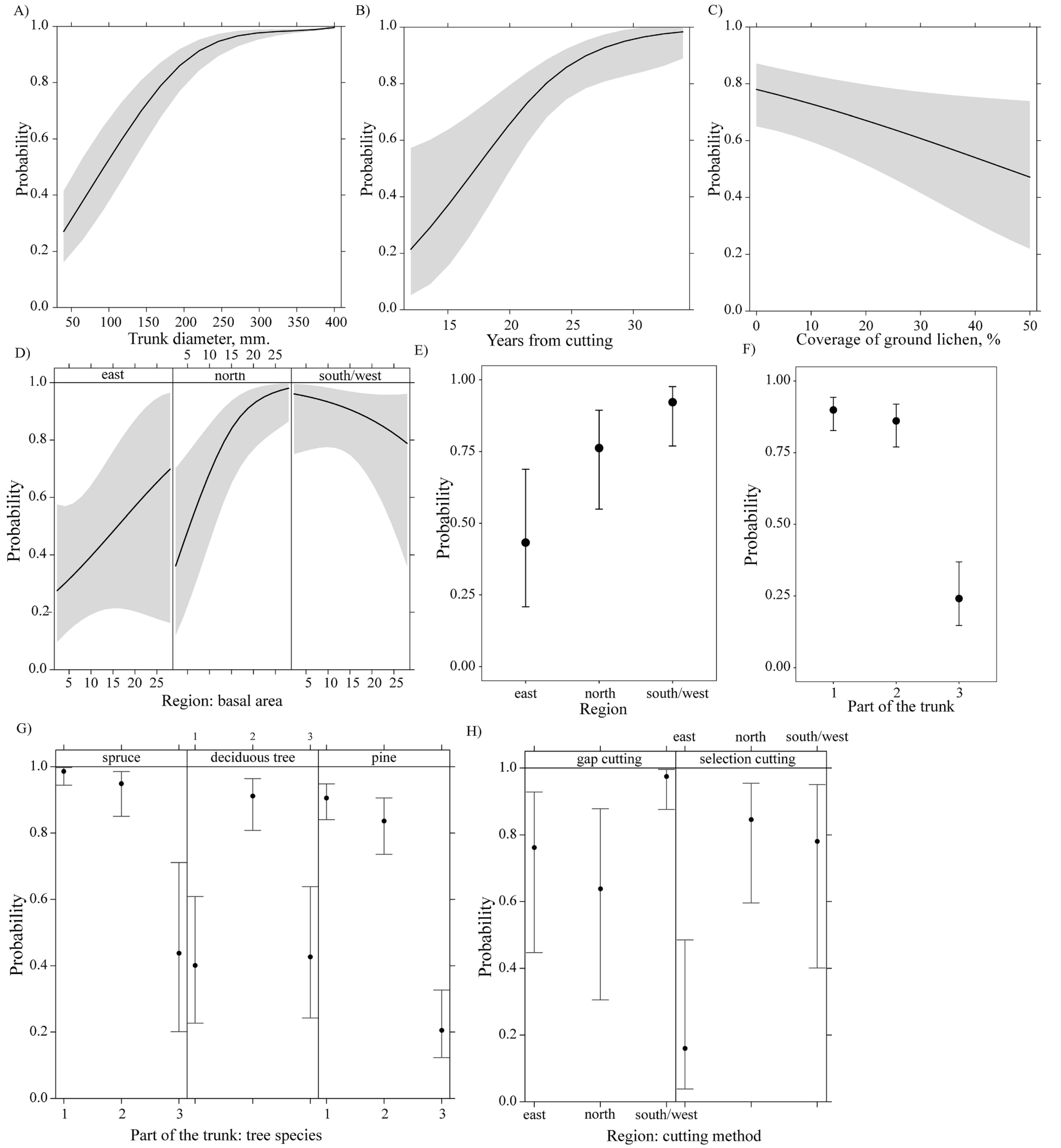

Fig. 5. Probability of pendulous lichen occurrence as predicted by model 1 (abundance class at least 1). Shaded areas or vertical bars indicate 95% confidence levels. A = impact of trunk diameter, B = impact of years from cutting, C = impact of the coverage of ground lichens, D = impact of the basal area in different regions, E = impact of the region, F = impact of the part of the trunk, G = impact of the part of the trunk on different tree species, H = impact of the cutting method in different regions.

and 2–5 m) of the trunk had clearly highest probabilities, whereas in the uppermost part (>5 m) the probability was significantly lower (Fig. 5F). Although the influence of the part of the trunk on the occurrence of lichens varied between regions (Table 2), the two lowest parts of the trunk (<2 m and 2–5 m) had the highest probability of pendulous lichen occurrence in all regions (Appendix part A: Fig. A.2b). The probability of pendulous lichen occurrence between the parts of the trunk varied between the tree species: In deciduous trees, the highest probability for pendulous lichen occurrence was clearly in the middle part (2–5 m), whereas in spruces, the highest probability was in the two lowest parts (<2 and 2–5 m) (Table 2; Fig. 5G). Also, pine seemed to display a similar trend as spruce, but it was not statistically significant.

The CCF cutting method (small gap cutting and selection cutting) as a main factor was not a significant variable, but the interaction with different regions was significant (cutting method * region interaction, Table 2; Fig. 5H). The highest probability for pendulous lichen

Table 3
The variables selected to the model for abundance class at least 2. The estimate of continuous variables (years from cutting, trunk diameter) points out, how much the probability of pendulous lichens changes, if that variable grows by one unit. The estimate of categorial variables (cutting method, region, part of the trunk, tree species) points out the difference in the probability of pendulous lichens compared to the control level. For all fixed effects presenting a categorical variable also tests for the other treatment categories vs. a reference category (given in parenthesis) are presented.

Variable	Estimate	Std. err.	df	t/Chi	*p*
Fixed effect					
Intercept	−10.790	2.051	1806	−5.262	**0.000**
Years from cutting	0.237	0.078	21	3.044	**0.006**
Cutting method (*gap cutting*)			1	1.400	0.237
selection cutting	−1.203	1.021	21	−1.179	0.252
Region (*East*)			2	13.662	**0.001**
north	0.140	0.987	21	0.110	0.889
nouth/west	4.151	1.213	21	3.423	**0.003**
Diameter of the tree at breast height (trunk diameter)	0.014	0.001	884	10.406	**0.000**
Part of the trunk (*<2 m*)			2	140.747	**<0.001**
2–5 m	5.854	0.495	1806	11.820	**0.000**
>5 m	3.150	0.481	1806	6.552	**0.000**
Tree species (*Picea abies*)			2	44.218	**<0.001**
deciduous tree	−6.036	0.941	884	−6.416	**0.000**
Pinus sylvestris	−2.053	0.482	884	−4.258	**0.000**
Part of the trunk * Area (*East*)			4	34.356	**<0.001**
2–5 m * north	−1.520	0.360	1806	−4.224	**0.000**
>5 m * north	−0.922	0.364	1806	−2.536	**0.011**
2–5 m * south/west	−2.151	0.392	1806	−5.495	**0.000**
> 5 m * south/west	−0.832	0.392	1806	−2.122	**0.034**
Part of the trunk * Tree species ()			4	80.647	**<0.001**
2–5 m * deciduous tree	3.326	0.911	1806	3.652	**0.000**
>5 m * deciduous tree	2.183	0.875	1806	2.495	**0.013**
2–5 m * Pinus sylvestris	−2.084	0.385	1806	−5.416	**0.000**
>5 m* Pinus sylvestris	−2.187	0.365	1806	−5.993	**0.000**
Region * Cutting method			2	19.507	**<0.001**
north * selection cutting	3.964	1.354	21	2.928	**0.008**
south/west * selection cutting	−2.828	1.624	21	−1.742	0.096
Random effects	Variance				
Stand	1.720				
Experimental plot	0.459				
Tree	4.046				
Dispersion parameter	0.315				

occurrence was found in small gap cutting in Southern and Western Lapland.

3.2. Model 2: Abundance class at least 2

The time (years) since cutting and the trunk diameter increased the probability of finding a high amount of pendulous lichens (abundance class at least 2) (Table 3; Fig. 6a-b). The probability was significantly higher when>30 years had passed since cutting, or when the trunk diameter exceeded 300 mm. Of the categorial variables, the part of the trunk, and the tree species were statistically significant variables (Table 3; Appendix part A: Fig. A.2c, A.2d). The probability of pendulous lichen occurrence was the highest in the middle part of the trunk (2–5 m), yet it still remained relatively low, being under 15%. The probability of pendulous lichen occurrence by tree species was clearly the highest in spruces, with a probability of ca. 30% (Table 3; Appendix part A: Fig. A.2d). The probability of pendulous lichen occurrence in pines and deciduous trees was very low, close to zero. The effect of the part of the trunk was remarkable on different tree species (Table 3; Fig. A.2e): middle part of the trunk (2–5 m) had clearly the highest probability of pendulous lichen occurrence in all tree species measured. However, the probability on the middle part of the trunk was clearly the highest in spruces, being more than 80%, while the probability of pendulous lichen occurrence on deciduous trees or on pines was less than 30%. In addition, in spruces, even the uppermost part of the trunk (>5 m), had a higher probability of pendulous lichen occurrence than other tree species in any part of the trunk. In all tree species, the lowest part (<2 m) had the lowest probability for pendulous lichen occurrence. The differences of the part of the trunk in different regions followed the same trend: in all regions the highest probability was found in the middle part of the trunk (Appendix part A: Fig. A.2f).

The cutting method was not a statistically significant main factor, but its regional differences were significant (Table 3; Fig. 6c). The highest probability was achieved in small gap cutting in Southern and Western Lapland. In Northern Lapland, on the other hand, selection cutting had the highest probability.

3.3. Model 3: Abundance class 3

There were so few observations in the abundance class 3 (a very high amount of pendulous lichens) (only 4%) that it did not warrant statistically sound interpretations. However, there was a trend towards increased probability of finding pendulous lichens in abundance class 3 in relation to the increase in trunk diameter (Table 4). Likewise, the part of the trunk -variable followed a trend similar to the other models: the middle part of the trunk (2–5 m) had the highest probability, but the probability was only 1% at maximum. Of the different tree species, Norway spruce had the highest probability, but also here the probability remained very low (∼1%).

4. Discussion

4.1. Variables influencing pendulous lichen abundance

Our results show that the most important factors affecting the occurrence of pendulous lichens in continuous cover forests in Finnish Lapland were the time passed since the cutting, and the size of the trunk (trunk diameter). Our study also indicated that pendulous lichens prefer fertile and mesic habitats, as the cover of ground lichens – an indicator of xeric soils – reduced the probability of pendulous lichen occurrence. A similar trend was also observed among the different regions: The highest probability of finding pendulous lichens was in the southern and western parts of the study area, which is most likely due to these parts of the area having more fertile and mesic soils when compared to the other parts. The habitat availability, measured as the basal area of the stand, increased the probability for pendulous lichen occurrence in the northern part of the study area. All these findings are in line with our hypotheses and previous studies (Dettki et al., 2000; Dettki and Esseen, 1998; Esseen et al., 1996; Horstkotte et al., 2011; Jaakkola et al., 2006; Lommi, 2011; Lundström et al., 2013).

Of the different tree species, Norway spruce (*Picea abies*) had the highest probability of pendulous lichen occurrence. This was also in line with the hypotheses, since spruces usually have more biomass and branches as a habitat for pendulous lichens than Scots pines (*Pinus sylvestris*) or deciduous trees. The difference between spruce and the other tree species was even larger when examining the occurrence of larger amounts of pendulous lichens. However, it needs to be acknowledged that part of the study area was located outside the northern forest line of Norway spruce, and that there were only 9% of spruces in the tree data. In addition, only 4% of the data had a very high amount of pendulous lichens (abundance class 3), which can explain the small number of variables that remained in the statistical model explaining the occurrence of this class.

When the different parts of the trunk were compared as a habitat for pendulous lichens, the highest probability of pendulous lichen occurrence was found in the middle part (2–5 m). This can most probably be explained by the fact that the competing factors, such as solar radiation and moisture, are in balance in the middle part of the tree, for the growth

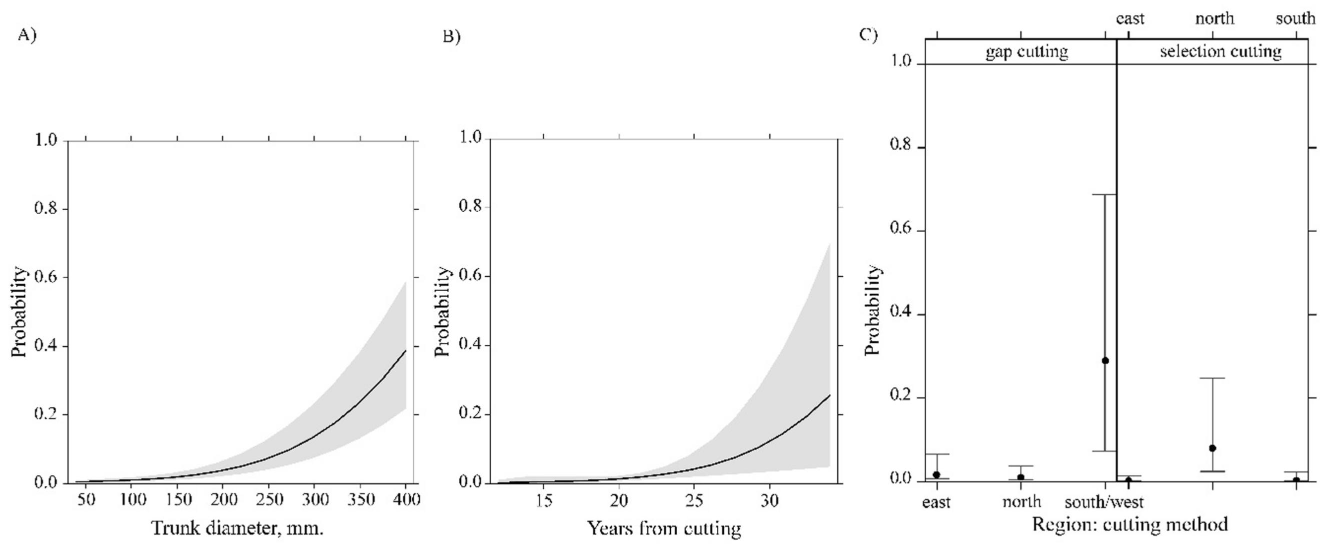

Fig. 6. Probability of pendulous lichen occurrence as predicted by model 2 (abundance class at least 2). Shaded areas or vertical bars indicate 95% confidence levels. A = effect of trunk diameter, B = effect of years from cutting, C = effect of the cutting method in different regions.

Table 4
The variables selected to the model for abundance class 3. The estimate of the continuous variable (trunk diameter) points out, how much the probability of pendulous lichens changes, if that variable grows by one unit. The estimate of categorial variables (part of the trunk, tree species) points out the difference in the probability of pendulous lichens compared to the control level. For all fixed effects presenting a categorical variable also tests for the other treatment categories vs. a reference category (given in parenthesis) are presented.

Variable	Estimate	Sts. err.	df	t/Chi	p
Fixed effect					
Intercept	−10.032	0.729	1814	−13.755	**<0.001**
Diameter of the tree at breast height (trunk diameter)	0.015	0.002	884	7.327	**<0.001**
Part of the trunk (*<2 m*)			2	535.819	**<0.001**
2–5 m	5.641	0.265	1814	21.284	**<0.001**
>5 m	3.926	0.259	1814	15.175	**<0.001**
Tree species (*Picea abies*)			2	41.131	**<0.001**
deciduous tree	−2.624	0.676	884	−3.884	**<0.001**
Pinus sylvestris	−3.793	0.597	884	−6.349	**<0.001**
Random effects	Variance				
Stand	3.231				
Experimental plot	0.002				
Tree	6.864				
Dispersion parameter	0.113				

of pendulous lichens (Jaakkola et al., 2006; Kumpula et al., 2009). In addition, there are less branches for lichens to grow in the lowest part of the tree, and that part is also easily accessible for reindeer forage.

4.2. How do pendulous lichens respond to the CCF methods?

The differences between the cutting methods were significant only between the regions; small gap cutting seems to be working better for pendulous lichens in southern and western Lapland, whereas in northern Lapland, selection cutting was slightly better for the maintenance of pendulous lichens. However, in northern Lapland, forests are naturally quite sparse, which means that the effect of different cutting methods can be quite similar, since cutting only a few trees can already make a gap.

Previous studies comparing the impacts of selection cutting and small gap cutting on the occurrence of pendulous lichens have produced variable results: It was shown that selection cutting saves some of the pendulous lichens better than small gap cutting, since the whole stand remains more covered (Stevenson and Coxson, 2003; Stone et al., 2008). On the other hand, another study by Stevenson and Coxson (2004) has indicated that small gap cutting is more applicable to pendulous lichen maintenance, since beside small gaps, un-managed forest patches are left on the site. The fact that in selection cutting the largest trees – the main habitat for pendulous lichens – are removed supports the observations (Stevenson & Coxson, 2004).

Even though we did not observe any large differences between the cutting methods, comparison of our results to the reference material is in line with the findings of Stevenson and Coxson (2004). The share of abundance class 1 was around 64% in the reference material (mature managed even-aged forests in Lapland, development class 4) (Appendix part A: Table A.2), and in abundance class 2 it was around 30%. In the present study however, the share of abundance class 1 was 42.8% and the share of abundance class 2 was 12.5%, leaving over 40% of the stands representing class 0 (i.e. no pendulous lichens). On the other hand, the share of abundance class 2 in young thinning stands (development class 2) in the reference material, was lower (1.4%) than in the present study (12.5%). Therefore, the present study shows, that there were less pendulous lichens in CCF-forests than in managed mature even-aged forests, but more than in young thinning forests.

4.3. Maintaining pendulous lichens in continuous cover forests

In order to maintain pendulous lichens in continuous cover forests and to improve the multiple use of forests, saving old trees should be favored, and the logging cycle should be kept as long as possible. This should be considered especially in selection cutting, where large and old trees are usually removed. Since small gap cutting saves patches of forests un-managed for a longer period of time than selection cutting, small gap cutting could therefore be a more efficient method for maintaining pendulous lichens. Similarly, small gap cutting showed good results in southern and western parts of Lapland in the present study. Small gap cutting could be favorable to reindeer husbandry in that it increases the amount of summer forage for reindeer, such as grasses and sedges, at least in the most nutritious soils (Bergstedt and Milberg, 2001; Tonteri et al., 2016).

The results also suggest that an increase of the basal area of the stand could benefit the growth of pendulous lichens, at least in the northern part of the study area. This should be taken into account in the planning process of areas where the main use of the forests is reindeer herding.

Fig. A.1. Examples of different abundance classes for pendulous lichens. A = Abundance class 1 (short lichens or sheaths of lichen are abundant, with a maximum length of 1 cm), B = Abundance class 2 (pendulous lichens are observed almost entirely in long-growing form or in sheaths, length about 2–5 cm), C = Abundance class 3 (longish or long lichens or sheaths of lichen grow generally or throughout the tree (over 5 cm, often over 10 cm long).

This is mainly due to the fact that, given their relatively short propagation distance, the growth and propagation rates of lichens are very slow: the propagation distance for pendulous lichens is averagely 200 m (Dettki et al., 2000). Because the propagation of pendulous lichens is dependent on the number of old-growth forest stands and tall trees, which are important sources of new lichens and lichen crumbs (soredíums) (Stevenson, 1988; Campbell and Coxson, 2001; Coxson et al., 2003), old, lichen-rich forests should be maintained adjacent to logging areas in order to ensure the propagation of pendulous lichens into young forests.

Stevenson et al. (2001) suggest that in order to secure pendulous lichens in commercial forests, a maximum of 30% of the trees should be cut in lichen-rich areas. This would be enough for increasing the solar radiation, which is favorable for lichen growth, while still maintaining enough habitats for pendulous lichens. Dettki and Esseen (1998) suggest to increase the compositional heterogeneity of the forest, which also would provide more habitats for pendulous lichens. Kumpula (2003) states that reindeer are able to graze in the treated forests as well, if the availability of pendulous lichens is secured. Reindeer herders have reported that when reindeer herding is practiced in an area, keeping the area forested would be the best regeneration practice, because it makes natural tree stand survival possible and results in fewer disturbances in the region (Turunen et al., 2020).

Although forestry presents one of the most significant threats to pendulous lichens (Jääskeläinen, 2011), the presence of reindeer, too, affects forest ecology and vegetation through selective grazing, trampling and fertilizing (Stark et al., 2003; Akujärvi et al., 2014; Santalahti et al., 2018; Pykälä et al., 2019). Reindeer grazing can change the composition structure and the abundance of vegetation, and accelerate soil processes including decomposition of dead organic material and nutrient cycling. Winter grazing by reindeer decreases the amount of terricolous and epiphytic lichens mostly in nutrient-poor lichen-rich habitats, including xeric, sub-xeric and barren forests (Stark et al., 2003; Akujärvi et al., 2014; Kumpula et al., 2019). Intensive summer grazing increases the amount of graminoids (Olofsson et al., 2001), and grazing and trampling can transform the lichen-rich biotopes into moss-dominated habitats.

4.4. Applying CCF in multiple-use forests

In forestry, the transition to CCF methods that preserve old trees could promote not only reindeer husbandry, but also other benefits provided by the forest, such as biodiversity and the ecosystem services (Miina et al., 2020; Valkonen, 2020). It is obvious that the production of all the ecosystem services cannot be maximized within the same forest, and that CCF alone cannot provide the conditions for all different land uses. In forestry planning, the best possible outcome for all actors involved should be sought. When choosing the forestry method, the purpose of the forests should be kept in mind, and the forest stand should focus on producing the kinds of services it is best suited for. Therefore, forestry methods should be varied, as no single method can be suitable for all purposes.

It is also worth considering that logging restrictions create economic losses for forestry. This can lead to forestry operating in a larger area in order to obtain the same amount of timber as in even-aged forestry. With more efficient forestry methods, larger areas would remain completely

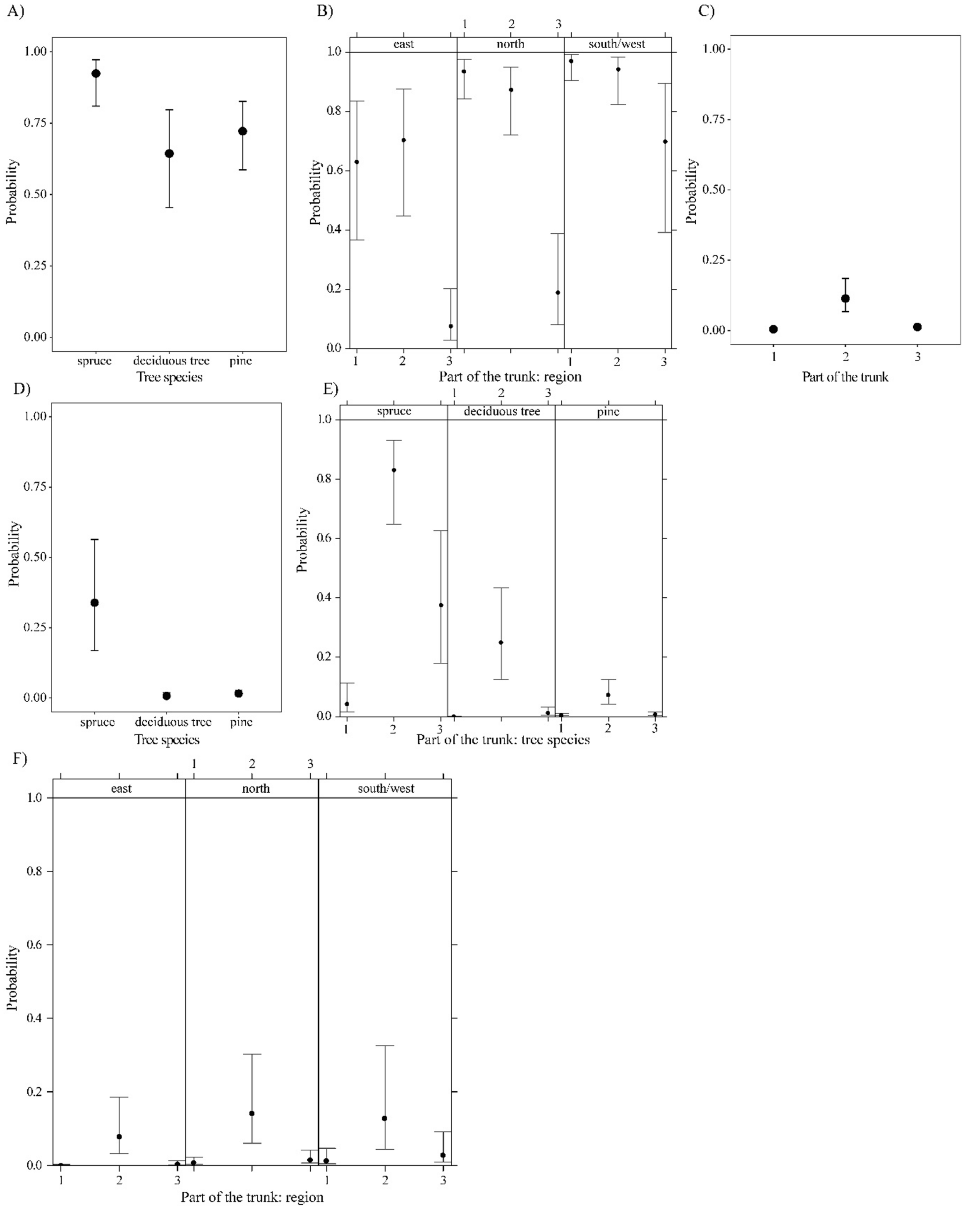

Fig. A.2. Probability of pendulous lichen occurrence as predicted by model 1 (abundance class at least 1): A = effect of different tree species, B = effect of the part of the trunk in different regions, and by model 2 (abundance class at least 2): C = effect of the part of the trunk, D = effect of the part of the trunk in different regions, E = effect of the part of the trunk on different tree species, F = effect of the tree species. Vertical bars indicate 95 % confidence levels.

Table A.1
The radius of the outer sample plot determined the radius of the inner sample plot. The outer plot was supposed to have about 100 trees.

Radius of the outer sample plot (m)	5	6	7	8	9	10	11	12	13	14	15
Radius of the inner sample plot (m)	2.9	3.5	4.0	4.9	5.2	5.8	6.4	6.9	7.5	8.1	8.7
Radius of the outer sample plot (m)	15	16	17	18	19	20	21	22	23	24	25
Radius of the inner sample plot (m)	8.7	9.2	9.8	10.4	11.0	11.5	12.1	12.7	13.3	13.9	14.4

Table A.2
The reference material from Akujärvi et al. (unpublished data), to compare present study data to normal managed even-aged forests. Pendulous lichens were inventoried at the same time with other parameters on trees on sample plots described in (Akujärvi et al., 2014). Development class 1 = stands in regeneration phase, development class 2 = young thinning stands, development class 3 = advanced thinning stands, development class 4 = mature stands (see also: Ylitalo, 2013).

Development class	Abundance class 0 (%)	Abundance class 1 (%)	Abundance class 2 (%)	Abundance class 3 (%)
1	58.7	39.1	2.3	
2	37.6	61.0	1.4	
3	2.1	80.9	17.0	
4	0.8	64.4	30.3	4.6

free of forestry use, than in CCF. In addition, the CCF methods seem to be reducing the long-term volume growth at least in spruce-dominated forests (Lundqvist, 2017; Hynynen et al., 2019). Furthermore, pressures towards forestry are rising from new energy productions, such as bioproduct mills, the increasing demand for wood-based products, as well as from the possible implementation of priced carbon storage. Regarding the present study, it has to be borne in mind that the oldest loggings examined in this study were conducted 35 years ago, which means that the long-term effects of CCF repetitive cuttings in CCF could not be monitored, and further studies are thus needed. On the other hand, relatively short cycles constitute the starting point for CCF, and therefore the basic maintenance of pendulous lichens should be achieved in other ways, e.g. through saving retention trees (Valkonen, 2020).

5. Conclusions

In order for forestry and reindeer husbandry to operate successfully in the same area, the growth and availability of pendulous lichens must be maintained, and the access of reindeer to this forage source should be considered already in the forestry planning phase. In addition, efforts should be made to save large trees in commercial forests, which is not automatically done in CCF. Also, the basal area of the stand should be kept as high as possible, as it can increase the habitat availability for pendulous lichens. Keeping the logging cycle as long as possible would also be favorable for the maintenance of pendulous lichens, but since CCF is based on relatively short logging cycles, the success of pendulous lichens in commercial forests should be maintained mainly by other means, such as saving retention trees. It would be particularly important to keep lichen-rich stands close to logging sites to allow the spreading of pendulous lichens into young stands.

CRediT authorship contribution statement

Taru Rikkonen: Formal analysis, Validation, Data curation, Investigation, Writing – original draft. **Minna Turunen:** Data curation, Writing – review & editing, Supervision. **Ville Hallikainen:** Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – review & editing, Supervision, Project administration. **Pasi Rautio:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Appendix Part A

Appendix Part B

The variance inflation factor (VIF) is a measurement of multicollinearity. The variance inflation factor for the j[th] predictor is determined as:

$$VIF_j = \frac{1}{1 - R_j^2}$$

where R^2 is the R^2-value obtained by regressing the j[th] predictor on the remaining predictors (Neter et al., 1983). Typically, the VIF value of 10 (Hair et al., 1998) or as low as 5 or 3 (Hair et al., 2021) have suggested to be the upper limit that should not be exceeded to avoid multicollinearity. In our case in all three models the VIF for the main effects varied from 1.0 to 1.44. The multicollinearity is a near-linear relation between the explanatory variables, leading to unstable parameter estimates (Crawley, 2007) and biased predictions as well.

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