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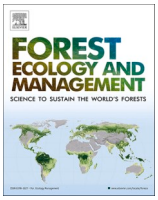

Bryophyte species composition at the stand scale (1 ha) – Differences between secondary stands half a century after clear-cutting and older semi-natural boreal forests

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ABSTRACT

A growing proportion of the boreal biome consists of managed even-aged secondary forest stands regenerated after clear-cutting. Many disturbance-intolerant species may not be able to recolonize or reach their original abundance in these stands before the next clear-cutting, potentially causing large-scale biodiversity losses. Boreal bryophytes (mosses and liverworts) include many species intolerant to clear-cutting, and at small spatial scales species richness and occupancy has been shown to remain changed in secondary stands half a century after logging. To assess if such persistent changes occur also at the stand scale, we listed and estimated cover of all bryophyte species in 1-ha plots, comparing 14 secondary stands originating from clear-cutting 40–60 years earlier with 14 older semi-natural stands. The large plots also made it possible to assess differences in occupancy and abundance for more bryophyte species than in previous studies. Species composition differed significantly for both mosses and liverworts, but unlike earlier studies, we could not detect any significant difference between stand types in species numbers. Thirteen species were significantly associated with semi-natural stands and the total cover of liverworts was less than half in secondary stands. Secondary stands had significantly fewer species typically occurring under shady conditions and/or mostly growing on "tree substrates" (dead wood and/or bases and stems of living trees). Ordination analysis further emphasized the importance of shade and suitable dead-wood substrates; the among-plot variation in bryophyte species composition was related to amount of coarse deadwood as well as to gradients from shady spruce dominated to open pine dominated stands and from polar- to equator-facing slopes. Besides lack of suitable habitat conditions in secondary stands, dispersal limitation may have caused a colonization time lag for some species. The clear importance of stand scale habitat conditions for bryophyte species composition calls for management adaptions to facilitate life boating and/or recolonization by ensuring availability of shade, coarse decomposing logs, and specific deciduous tree species (*Populus*, *Salix*, *Sorbus*) in secondary stands.

1. Introduction

After World War II, a forestry system based on even-aged stands created by clear-cutting has become dominant in the vast boreal biome (Östlund et al., 1997, Josefsson and Östlund, 2011, Bergeron and Fenton, 2012, Kuuluvainen et al., 2012). This management system was thoroughly implemented in the Nordic countries already from the 1950s (Axelsson and Östlund, 2001, Kouki et al., 2001), making the region uniquely well suited for studies on long-term consequences of such forestry. For example, a great majority of the Swedish forest land is now covered by even-aged secondary stands originating from clear-cutting after 1950. Additional areas have secondary forests resulting from clear-cutting predating 1950 or from afforestation of agricultural land or mires. The rest of the Swedish boreal forests consist of mature semi-natural stands affected by different degrees of earlier selective cutting. The less affected of these semi-natural forests support relatively many wood-inhabiting and late-successional organisms (Gustafsson et al., 2004, Stenbacka et al., 2010). However, because such forests are continuously clear-felled, Swedish boreal forests will in the future consist almost entirely of secondary even-aged stands or protected areas.

There are concerns that many native forest species will not be able to re-colonize the secondary even-aged stands quickly enough to maintain

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viable populations at a landscape level, considering that the stands are planned to be clear-cut again within 80–100 years (e.g. Botting and Fredeen, 2006). There is, however, a great deal of uncertainty about the magnitude of this problem and about which kinds of adjustments might be necessary regarding management of secondary stands, e.g. when thinning (Bauhus et al., 2009). Therefore, scientific knowledge on the biodiversity of this relatively new type of boreal forest is urgently needed, in particular about the later stages before next clear-cutting. Some progress has been achieved in later years through studies in this type of stands covering bryophytes (Dynesius et al., 2009, Schmalholz and Hylander, 2009, Rudolphi et al., 2011, Rudolphi and Gustafsson, 2011, Schmalholz et al., 2011, Dynesius, 2015, Paquette et al., 2016), vascular plants (Widenfalk and Weslien, 2009), lichens (Hilmo et al., 2009, Rudolphi and Gustafsson, 2011), beetles (Similä et al., 2002, Stenbacka et al., 2010, Johansson et al., 2016, Joelsson et al., 2018), and wood-inhabiting fungi (Junninen et al., 2006).

In boreal forests, mosses (Phylum Bryophyta) include hundreds of species, constitute a major component of the vegetation, and are key players in many ecosystem processes (Turetsky et al., 2012). Boreal liverworts (Phylum Marchantiophyta) are also species rich, but have low abundance (Botting and Fredeen, 2006) and most of them are restricted to microhabitats with low competition. These two major plant groups are often referred to as bryophytes (together with hornworts, Phylum Anthocerotophyta, absent from boreal forests). Mechanical disturbance during clear-cutting and site preparation (sometimes including harvest of stumps, tops and branches), together with the immediate and large changes in microclimate, inflict substantial changes in bryophyte communities. These initial changes include reductions in overall cover, local extinction of intolerant species (mostly liverworts), and colonization by disturbance-favored species (mostly mosses) (Hannerz and Hånell, 1997, Jalonen and Vanha-Majamaa, 2001, Fenton et al., 2003, Hylander et al., 2005, Nelson and Halpern, 2005). After clear-cutting, bryophyte communities slowly develop in the direction of those in the pre-logging stands, but at least for several decades cover and species composition differ considerably from what is found in older forests that have not been clear-cut (Botting and Fredeen, 2006, Åström et al., 2007, Baldwin and Bradfield, 2010, Schmalholz et al., 2011, Dynesius, 2015). In addition, commercial thinning of even-aged stands has been shown to set back this bryophyte succession (Dynesius, 2015). Previous studies of the short- and longer-term response of bryophytes to clear-cutting and subsequent even-aged forest management generally surveyed small plots of 0.03–2 m^2 (e.g. Hannerz and Hånell, 1997, Rambo and Muir, 1998, Jalonen and Vanha-Majamaa, 2001, Fenton et al., 2003, Nelson and Halpern, 2005, Botting and Fredeen, 2006, Baldwin and Bradfield, 2010, Baldwin et al., 2012), whereas a few studies surveyed areas up to 200–1000 m^2 (Hylander et al., 2005, Åström et al., 2007, Dynesius et al., 2009, Schmalholz et al., 2011). However, in the latter larger-scale studies only species presence was recorded, not cover.

In the present study, we compare boreal bryophyte communities in even-aged stands regenerated after clear-cutting 40–60 years earlier with older semi-natural stands similar to the stands that predated the even-aged stands. We do this at an unprecedentedly large spatial scale, approaching the size of a stand (survey plots of 10 000 m^2). We record not only presence/absence, but also abundance of every individual species. On the basis of this survey, we ask two main questions:

First, do bryophyte species composition and abundance differ between secondary and semi-natural stands at the 1-ha scale?

Second, do remaining differences in habitat conditions between the stand types allow sustained survival of species which colonized in response to logging and/or preclude the recolonization of other species which disappeared? We analyze this (i) by collecting data on current habitat conditions, (ii) by relating habitat conditions in study plots to overall species composition, (iii) by separately analyzing ecological subgroups of species based on environmental association (light, moisture, substrates), and (iv) by identifying the individual species that are significantly associated with either semi-natural or secondary stands.

We also discuss the potential role of dispersal limitation for a recolonization lag of species intolerant to clear-cutting. Finally, we use our results as a basis to suggest management measures in even-aged secondary stands, to mitigating negative effects of clear-cutting forestry on bryophyte diversity.

2. Methods

2.1. Study system

The study area extends across a 30 × 40 km forest landscape in the middle boreal zone (Ahti et al., 1968) of northern Sweden (64°05′ − 64°10′N, 19°05′ − 19°30′ E, for a map see Johansson et al., 2016). The area consists of a mosaic dominated by managed conifer-dominated forest stands and clear-cuts, but also includes mires and lakes. The most common conifers are native Norway spruce (*Picea abies)* and Scots pine (*Pinus sylvestris)*, but there are also some plantations of the non-native lodgepole pine (*Pinus contorta*). The by far most abundant broadleaved trees are birches (*Betula pubescens* and *Betula pendula*). Glacial till with relatively few boulders dominates.

The study was performed in two forest stand types; (i) stands that historically had not been clear-cut, but instead selectively logged on several occasions during the past c. 150 years ("semi-natural stands") and (ii) even-aged thinning-stage stands regenerated from clear-cutting 40–60 years before the study ("secondary stands"). About 40% of Sweden's boreal productive forest land is currently classified as thinning-stage forest (stands where most of the trees are ≥ 10 cm in diameter at breast height, but which are too young to be legally clear-cut; Swedish National Forest Inventory), and this forest type generally contain low volumes of thick-diameter dead wood (Fridman and Walheim, 2000).

The two most common forest site types (Arnborg, 1990) in the study plots are mesic and moist dwarf-shrub types with *Vaccinium myrtillus* as the dominant species in the field layer, and the more productive herb dwarf-shrub type with some meadow herbs and grasses.

2.2. Stand selection

We selected 14 secondary and 14 semi-natural stands based on the following criteria: (1) stand age according to the land-owner's database (secondary 40–60 years after clear-cutting or semi-natural ≥ 80 years old), (2) stand width of ≥ 200 m in all directions, and (3) mid-point located ≥ 500 m from the mid-point of any other study stand. The ground moisture and other factors not affected by logging history, but likely to affect bryophytes, were kept similar between the semi-natural and secondary forest stand groups (see Section 3.2). The secondary stands had an even-aged structure, and were checked on old aerial photos to ensure that they originated from clear-cuts. Nine of these secondary stands had been recently thinned (c. 3–5 years before the bryophyte survey). The semi-natural stands were less even-aged, and their mean dominant age varied from 80 to 130 years according to the landowner database.

2.3. Sampling procedure

A square plot of 1 ha was placed in the center of a relatively homogeneous part in each of the 28 stands. Within these plots, bryophytes were surveyed in September 17–18 2009 (two semi-natural, two secondary stands), May 28–31 2010 (six semi-natural, four secondary), and September 14–18 2010 (six semi-natural, eight secondary). Because most bryophyte species are found in specific types of microsites covering a small fraction of the area, the most efficient way to survey them is to spot and scrutinize such microsites and to record the species of more abundant habitats while moving between the microsites. In this way a list of bryophyte species was compiled for each 1-ha plot by a highly skilled field bryologist until no more species were found. The time spent in a plot therefore varied with habitat complexity. In addition, the cover

of each species in a plot was visually estimated. The following cover classes were used: a cover of < 1.5 dm^2 in a 1-ha plot was always set to 0.5 dm^2, then 2, 3, 4, 5, 10, 20, 30, 40 and 50 dm^2, then 1, 2, 3, 4, 5, 10, 20, 30, 40 and 50 m^2, and finally in 100 m^2 intervals from 100 m^2 upwards.

Basal area of living trees was measured using a relascope in the autumn of 2011. In each plot measurements were made from three points, from which the mean value (m^2 ha^{-1}) was calculated. To quantify the amount of dead wood, four transects (5 m $\times$ 50 m) were placed in the study plots in 2011, starting at the plot center and going in the four cardinal directions, so that 10% of the plot area was sampled. Within each transect, all logs, snags and stumps with a maximum diameter of $\geq$ 5 cm were included. In addition, for each dead wood object the base and top diameters and length were recorded as well as the degree of decomposition (soft and hard, see Table 1 for a definition). From these data, deadwood volumes were calculated using the conic-paraboloid formula (Fraver et al., 2007). The volume of coarse woody debris was then calculated as the sum of the volumes of all logs and snags with a maximum diameter $\geq$ 10 cm. The volume of fine woody debris was calculated as the volume of logs and snags with a maximum diameter $\geq$ 5 and $<$ 10 cm.

Slope, slope aspect, and latitude for each of the 28 plots were extracted from topographical maps and used to calculate potential annual direct incident solar radiation (PADIR) using equation 2 of McCune and Keon (2002). Data on altitude, tree height, and diameter at breast height were taken directly from the landowner database, and were for entire stands and not for the sampling plots specifically.

2.4. Taxonomy and nomenclature

Species level taxonomy and nomenclature follow Hodgetts et al. (2020). Because it was often too difficult to distinguish certain species reliably in the field, 18 combinations of species were treated as one species each (Appendix). Taxonomy on the family level and higher follows Goffinet et al. (2008) for mosses and Crandall-Stotler et al. (2008) for liverworts.

2.5. Classification of species into ecological subgroups

To analyze differences in community composition and their environmental correlates, all 154 species encountered in the study were classified according to their general association with level of moisture and light and according to the substrate they most commonly grow on in boreal Sweden (Appendix). A species was assigned to one group only in each classification. Levels of moisture and light were classified as high, intermediate or low. Generalist species were included in the intermediate category. The basis for the moisture and light classification was Ellenberg indicator values (Ellenberg et al., 1992) and data from Diekssen (2001) combined with information from a Swedish "ecological catalogue" (Hallingbäck, 1996) and recent Scandinavian floras (Damsholt, 2002, Hallingbäck et al., 2006, Hallingbäck et al., 2008). The starting point for the substrate affiliation classification was Dynesius et al. (2009) with the addition of data from Hallingbäck (1996) and the abovementioned Scandinavian floras. To ensure that the literature-based ecological classifications applies also to boreal Sweden, the classifications of each species were eventually checked and in a few obvious cases corrected by a skilled field bryologist with extensive experience from the region.

The light classification resulted in 39 low-light, 73 intermediate/generalist, and 42 high-light species (Appendix). The moisture classification gave 13 low-moisture, 111 intermediate/generalist, and 30 high-moisture species. No species was classified as being both low-light and low-moisture, but all eight other combinations were present. Substrate affiliation was classified into five categories: undisturbed ground (70 species), disturbed ground (30 species), tree substrates (tree bases and stems, dead wood; 28 species), boulders (20 species), and dung and carcasses (6 species).

2.6. Data analyses

Differences in species composition between the 14 semi-natural and the 14 secondary stands were tested with the Multi-Response Permutation Procedure (MRPP). Non-metric Multidimensional Scaling (NMS) ordination was performed to get a visual overview of the among-stand variation in species composition and the relationships between this variation and 10 habitat factors (PADIR; basal areas of all trees, spruce, pine, and broadleaves; volumes of fine deadwood, coarse deadwood, hard logs, soft logs, and stumps). One semi-natural and one secondary stand were excluded from the NMS analysis, because some habitat data were missing from them (see footnotes in Table 1). In MRPP and NMS, Sörensen's (=Bray-Curtis) distance measure was used. The species composition analyses were performed once with untransformed and once with fourth root-transformed cover data. The transformation reduces the influence of very abundant species in the analyses, but the results were similar and we only present results for untransformed data. In the NMS, we chose 250 runs with real data and 2-dimensional solutions. Differences between stand types in cover and species numbers of species groups and of cover of individual species were tested using the Mann-Whitney's *U* test. The affinity of individual species to either semi-natural or secondary stands was determined using Indicator Species Analysis (Dufrêne and Legendre, 1997) and the untransformed cover data. Mann-Whitney U-tests were run in IBM SPSS Statistics 20 and MRPP, Indicator species and NMS analyses in PC-ORD 5.33.

3. Results

A total of 154 bryophyte species (101 mosses and 53 liverworts) were found in the 28 one-hectare study plots. The mean number of species per 1-ha plot was 35 for mosses (range 22–57) and 18 for liverworts (range 10–26). Mean total cover was 92% for mosses (median 95%; among-plot range 50–99%), but only 0.26% for liverworts (median 0.15%, range 0.016–1.1%). For a large majority of species, cover was very low (Appendix). For example, the median cover of the species within each 10,000 m^2 plot ranged from 0.05 to 1.5 m^2 among the 28 plots (mean median cover was 0.38 m^2). There were, however, some highly abundant mosses; *Pleurozium schreberi* (45% mean cover in the 28 plots) and *Hylocomium splendens* (18%). The most abundant liverwort covered a two orders of magnitude smaller area (*Barbilophozia lycopodioides*, 0.13%), but it still contributed half of the total liverwort cover.

3.1. Comparison of species composition and abundance between secondary and semi-natural stands.

In the semi-natural forest plots 126 of the 154 bryophyte (liverworts + mosses) species in the study were recorded and the plots in secondary stands held 124 species (Appendix). More than 60% of the species (96 species) were found in both stand types. The 58 species found in one stand type only were infrequent and 38 of them were found in one plot only, 12 in two plots, six in three plots and two in four plots (the moss *Tetraplodon angustatus* and the liverwort *Nyholmiella obtusifolia*, Table 2).

According to the MRPP analysis, bryophyte species composition differed significantly between secondary and semi-natural stands (A=0.0456, p=0.024). Accordingly, the overlap between secondary and semi-natural stands in ordination space was relatively small (Fig. 1). Axis 1 in the NMS ordination represented 69% of the variance in the original distance matrix and axis 2 represented 24%. The final stress was 10.3 after 57 iterations, which is reasonably good.

The bryophyte cover was lower in secondary stands (mean=89.2%, SD=13,2%, range 50.4–98.8% *vs* mean=95.7%, SD=4.0%, range 85.3–99.4%; p=0.050), but bryophyte species richness was very similar (mean=53.9, SD=11.6, range 32–79 species in secondary stands *vs* mean=52.1, SD=11.1, range 35–75 species in semi-natural; p=0.667,

Table 1
Habitat properties of the study plots in secondary stands 40–60 years after clear-cutting and older semi-natural stands. Tree height and diameter are from the stand data base of the forest company Sveaskog and are for whole stands, not for the 1-ha plots.

	Mean		Median		Range	
	Semi-natural	Secondary	Semi-natural	Secondary	Semi-natural	Secondary
Dead wood (m^3/ha) †						
Coarse wood*	9.30	2.90	6.89	2.39	0.85–37.61	0.16–6.84
Fine wood**	0.40	1.15	0.33	1.09	0.09–0.96	0–2.43
Soft logs***	2.08	0.60	1.76	0.18	0.05–8.23	0–3.80
Soft stumps***	0.91	1.48	0.94	1.06	0.14–1.74	0.30–3.37
Hard logs***	2.23	2.12	1.21	2.14	0–7.58	0–4.39
Hard stumps***	0.29	1.32	0.09	0.60	0–2.05	0.01–5.39
All dead wood	10.90	6.89	8.81	7.64	1.95–39.53	1.85–12.08
Basal area (m^2/ha) ††						
All trees	31	26	31	28	22–41	15–31
Spruce	20	12	20	10	7.7–40	1–28
Pine	8.7	13	8.7	11	0–22	0–29
Birch	2.0	1.0	1.7	0.5	0–6.7	0–2
Other deciduous trees	0.2	0.2	0	0	0–1	0–2.3
Tree diameter at breast height (cm)	24.5	17.5	24.6	18.4	20.8–29.8	12.0–21.5
Tree height (m)	18.2	14.6	17.5	14.8	15.7–22.3	10.3–19.9
PADIR (MJ cm^{-2} $year^{-1}$)	0.50	0.53	0.51	0.53	0.40–0.54	0.46–0.57

†Dead wood with a maximum diameter ≥ 5 cm; dead wood was not measured in one secondary plot, i.e. n=13 for dead wood volumes in secondary stands.
††Basal area was not measured in one semi-natural plot, i.e. n=13 for basal area in semi-natural stands.
*Maximum diameter ≥ 10 cm; includes logs and snags only, stumps are excluded.
**Maximum diameter 5–9.9 cm; includes logs and snags only, stumps are excluded.
***Soft dead wood is the more decomposed (decay stage 4–6) and hard dead wood the less decomposed (decay stage 1–3) according to Olsson and Jonsson (2010).

Mann-Whitney U-tests). Likewise, liverwort cover was clearly lower in secondary stands, whereas liverwort richness was only slightly and statistically insignificantly lower (Fig. 2A–B). For mosses, no clear difference in cover or richness was found between stand types. The moss class Polytrichopsida (hair-cap mosses and allies) had a clearly higher cover and species richness in secondary stands (Fig. 2C–D). Almost all of the 10 species from this class found in the study had higher plot occupancy and cover in secondary stands and four of them significantly so (Table 2, Appendix). In contrast, the moss class with highest cover and species number (Bryopsida) showed no clear difference between stand types, although they covered a close to significantly smaller area in semi-natural stands (Fig. 2C–D). Species richness and cover of Sphagnopsida (peat mosses) was remarkably similar in secondary and semi-natural stands (Fig. 2C–D). No statistically significant differences in species number were found for the four major orders of Bryopsida (Hypnales, Dicranales, Bryales, Splachnales), the major order of liverworts (Jungermanniales), or the major families within Jungermanniales (Scapaniaceae, Cephaloziaceae, Calypogeiaceae, Jungermanniaceae).

3.2. Comparison of habitat factors between secondary and semi-natural stands.

The altitude ranged from 205 to 313 m a. s. l. and was very similar in the two stand types (mean 265 and 270 m). Likewise, the mean potential solar radiation (PADIR) was almost identical in semi-natural and secondary study plots (Table 1).

There was a clear difference in amount of dead wood substrate suitable for specialized bryophytes, with a 3.5 times higher mean volume of soft (i.e. more decomposed) logs in semi-natural than in secondary stands (Table 1). Secondary stands had a higher volume of cut stumps and fine woody debris, but there was also a considerable number of mostly relatively decomposed cut stumps in the semi-natural stands (Table 1), resulting from previous selective logging. Total basal area of living trees was 16% lower in the secondary than in the semi-natural study plots. The tree-species composition also differed, with more spruce and deciduous trees in semi-natural stands and more pine in secondary stands (Table 1). The proportion of pine in the secondary stands in our study is representative for Swedish boreal thinning-stage forests, whereas spruce proportion was higher and proportion of broadleaves lower than average (comparison with data from the Swedish National Forest Inventory).

3.3. Species composition and habitat factors

In the NMS ordination, the secondary stands had higher scores on axis 1 and lower scores on axis 2 than the semi-natural stands (Fig. 1). Axis 1 was most strongly correlated to basal area of spruce (r=−0.75, Pearsońs correlation), total basal area (r=−0.60) and basal area of pine (r=0.57), and is thus associated with a gradient from dense stands with a lot of spruce (low scores) to less dense pine dominated stands (high scores). Axis 2 was instead strongly correlated to PADIR (r=−0.67), and is thus associated with a gradient from polar-facing (high scores) to equator-facing (low scores) slopes. Both axes were relatively strongly associated with the amount of coarse deadwood (Fig. 1; r=−0.48 and r=0.57, respectively) and soft logs (r=−0.38 and r=0.48).

Seven species (the mosses *Dicranum majus, Hylocomiastrum umbratum, Sphagnum girgensohnii, Sphagnum quinquefarium;* the liverworts *Lophocolea heterophylla, Lophozia ciliata, Obtusifolium obtusum*) were strongly negatively correlated to axis 1 in the NMS (both r and Kendall's tau < -0.4; r for some of the species are found in Table 2). A negative correlation with axis 1 indicate an affinity to stands with high tree basal area in general and high spruce basal area in particular (Fig. 1), and thus shady conditions. It also indicates an affinity to coarse and soft deadwood (Fig. 1). Two of the three liverwort species are specialized to grow on downed logs (*L. ciliata* and *L. heterophylla*), supporting the relationship to deadwood of axis 1. Six of the seven species belong to the low-light ecological group in our classification (Appendix), supporting the relationship between axis 1 and shade.

3.4. Comparison of ecological subgroups between secondary and semi-natural stands

The species subgroup that grow mainly on tree substrates (tree bases and stems, dead wood) was less species rich and had lower cover in secondary stands, although the difference in cover was not statistically significant (Fig. 3). Conversely, disturbed ground species had higher

Table 2
Bryophyte species differing significantly in their relationship to (i) secondary stands regenerated after clear-cutting 40–60 years before the study and to (ii) older semi-natural forests that have been subjected to selective cuttings only. Differences were assessed by comparing mean species cover in the two forest types and by indicator species analysis using data from 14 stands of each kind (1-ha plots). Significant p-values are highlighted (bold). The species are classified into three classes of light availability and three classes of moisture according to the habitats in which they most frequently occur in the region. In the same way each species is assigned one substrate, i.e. the most common substrate on which they grow in the region. To illustrate the species' relationships to the major gradients in species composition, their linear correlation coefficients with the axes of a NMS ordination (Fig. 1) are listed. Axis 1 is negatively correlated with canopy shading and deadwood availability, whereas axis 2 is negatively correlated with potential solar radiation input (PADIR) and positively correlated with deadwood availability.

Species	Habitat subgroup†		Substrate subgroup	Number of stands		Cover per plot (m^2 ha^{-1})‡			Indicator values		NMS ordination	
	Light	Moisture		Secondary	Semi-natural	Secondary Mean	Semi-natural Mean	p+	IV	p	Axis 1	Axis 2
MORE IN SEMI-NATURAL FORESTS												
Liverworts												
Barbilophozia lycopodioides	1	2	Undisturbed ground	14	14	6.12	20.6	0.064	77.1	**0.0496**	−0.23	0.10
Lophozia ciliata	1	2	Tree substrates	3	7	0.0011	0.011	0.056	45.5	**0.047**	−0.54	0.36
Lophoziopsis longidens	2	2	Tree substrates	8	14	0.032	0.071	**0.001**	68.9	**0.031**	−0.44	0.01
Neoorthocaulis attenuatus	2	2	Tree substrates	8	14	0.022	0.040	**0.009**	64.6	0.099	−0.38	0.16
Ptilidium pulcherrimum	2	2	Tree substrates	14	14	1.41	4.12	0.075	74.5	**0.030**	−0.10	0.43
Sphenolobus minutus	2	2	Boulders	5	10	0.005	0.11	**0.018**	68.4	**0.019**	−0.27	0.02
Mosses												
Dicranum majus	1	2	Undisturbed ground	14	14	18.2	205	**0.030**	91.8	**0.003**	−0.58	0.69
Dicranum montanum	2	2	Boulders	6	12	0.053	0.084	**0.033**	52.5	0.116	−0.46	−0.12
Hylocomiastrum umbratum	1	2	Undisturbed ground	1	6	0.21	330	**0.030**	42.8	**0.034**	−0.45	0.69
Hylocomium splendens	2	2	Undisturbed ground	14	14	1132	2471	**0.010**	68.6	**0.0058**	−0.76	0.36
Nyholmiella obtusifolia	2	1	Tree substrates	0	4	0	0.0057	**0.034**	28.6	0.102	0.10	0.30
Ptilium crista-castrensis	1	2	Undisturbed ground	14	14	133	295	**0.004**	68.9	0.128	−0.44	0.34
Sphagnum quinquefarium	1	2	Undisturbed ground	3	9	0.64	53.9	**0.015**	63.5	**0.014**	−0.46	0.70
MORE IN SECONDARY STANDS												
Liverworts												
Scapania irrigua	2	2	Disturbed ground	10	4	0.42	0.03	**0.011**	66.7	**0.009**	0.45	−0,14
Mosses												
Ceratodon purpureus	3	1	Disturbed ground	10	6	0.38	0.005	**0.050**	70.5	**0.030**	0.40	−0.23
Pohlia nutans	2	2	Disturbed ground	14	14	1.30	0.39	**0.042**	76.7	**0.018**	0.48	−0.27
Polytrichum commune + jensenii + swartzii	2	2	Undisturbed ground	14	14	1150	515	0.088	69.1	**0.044**	−0.18	−0.71
Polytrichum juniperinum	3	2	Undisturbed ground	14	13	12.1	2.24	**<0.001**	84.4	**<0.001**	0.26	−0.29
Polytrichum strictum	3	2	Undisturbed ground	8	2	8.44	0.714	**0.041**	52.7	**0.029**	0.31	−0.08
Racomitrium microcarpon	3	1	Boulders	14	11	3.89	1.25	**0.018**	75.7	**0.013**	0.47	−0.20
Splachnum sphaericum	2	2	Dung/Carcass	8	3	0.0064	0.0011	**0.043**	49	0.064	0.24	−0.11
Tetraplodon angustatus	2	2	Dung/Carcass	4	0	0.0014	0	**0.034**	28.6	0.099	0.46	−0.18

†1=low; 2=intermediate or generalist; 3=high.
+Mann Whitney U test.
‡Mean cover was calculated using all 14 plots of each kind, i.e. also those where the species was absent.

cover and richness in secondary stands, but the difference in richness was not statistically significant. Species having undisturbed ground as their main substrate covered about 90% of the forest floor, but represented less than half of the species present in a 1-ha plot. Neither cover nor species richness differed significantly between secondary and semi-natural stands for this group, for boulder species, or for species growing on dung and carcasses (Fig. 3).

The cover of species classified as occurring mainly under dry conditions was significantly higher in secondary stands, whereas the richness difference was small and statistically insignificant (Fig. 4A–B). In contrast, cover and richness of "wet species" did not differ in any consistent nor significant way. The cover of species with no clear association with high or low moisture was significantly lower in secondary stands, whereas the species richness of this group was almost identical in the two stand types (Fig. 4A–B). Cover of "dry species" and "wet species" was less than 0.15% in both stand types, i.e. the intermediate/generalist group dominates totally.

Species classified as occurring mainly under shaded conditions had lower richness and cover in secondary stands, whereas species associated with high light levels had higher cover and richness (Fig. 4C–D). The cover of light-demanding species was, however, very low in both stand types, less than 1%. Both species number and cover of species with no clear association with high or low light levels were higher in secondary stands, but neither of the differences were statistically significant.

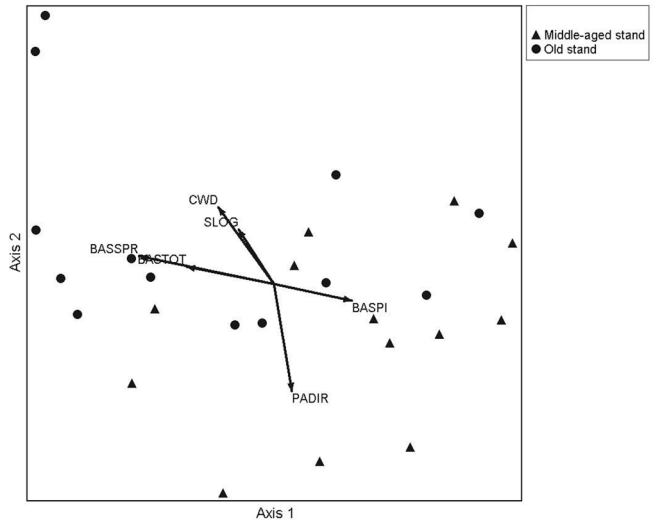

Fig. 1. NMS ordinations of the bryophyte community of 1-ha plots in 13 secondary stands 40–60 years after clear-cutting and in 13 older semi-natural stands that had never been clear-cut. The ordinations are based on untransformed cover data and include all bryophyte species encountered in the plots. Arrows indicate habitat factors that correlated well ($r^2 > 0.20$) with at least one of the ordination axes. *BASTOT*=basal area of all trees, *BASSPR*=basal area of spruce, *BASPI*=basal area of pine, *CWD*=volume of coarse logs and snags, *SLOG*=volume of soft (more decomposed) logs, and *PADIR*=potential annual direct incident solar radiation (related to slope and slope aspect). Volume of stumps, volume of hard (little decomposed) logs, volume of fine woody debris, and basal area of broadleaved trees correlated only weakly ($r^2 < 0.10$), and are thus not shown.

3.5. Individual species' affinity to secondary or semi-natural stands.

Twenty-two bryophyte species were significantly associated with either secondary (eight mosses, one liverwort) or semi-natural stands (seven mosses, six liverworts) according to indicator species analysis and/or to significant differences in cover between the two forest types (Table 2). Seven of these 22 species appeared in all 28 plots and thus differed in cover only. Species that grow mostly on tree substrates (tree bases and stems, dead wood) were only represented among the 13 species associated with semi-natural forest, whereas species associated with disturbed ground or specialized to grow on dung or carcasses were only found among the secondary forest species. Four of the nine secondary forest species were classified as species mostly growing in full light, whereas none of them are in the "shade-associated" species group (Table 2).

The nine species contributing most to the lower richness of tree substrate species in secondary stands (Fig. 3A) were liverworts mainly growing on relatively shaded logs on the ground (*Blepharostoma trichophyllum, Fuscocephaloziopsis affinis/lunulifolia, Lepidozia reptans, Lophozia ciliata, Lophoziopsis longidens, Lophozia longiflora, Neoorthocaulis attenuatus*) and mosses growing as epiphytes on the bark of non-birch broadleaves (*Lewinskya speciosa* and *Nyholmiella obtusifolia*).

4. Discussion

Below, we discuss how the differences in bryophyte species composition between secondary and semi-natural stands could be explained by differences in habitat conditions and by a recolonization lag. Finally, we discuss why we found so small differences in species richness compared to earlier studies.

4.1. Direct measurements of differences in habitat conditions.

Among-plot variation in species composition correlated with tree basal area (a proxy for canopy density and composition), potential incoming solar radiation, and amount of coarse woody debris and of soft (i.e. more decomposed) logs (Fig. 1). These correlations are most likely the results of the sensitivity to microclimate of many bryophyte species as well as of variation in amount of decomposing wood, potentially excluding some dead-wood species from the stands having least of this substrate (e.g., Hofmeister et al., 2015, Táborská et al., 2020). Could these factors also cause differences in bryophyte communities between semi-natural and secondary stands, i.e. do they differ between the two forest stand types? Indeed, volume of coarse dead wood was more than three times higher in semi-natural than in secondary stands (Table 1), reflecting the long period after clear-cutting with small trees and therefore low or no input of coarse dead-wood (Fridman and Walheim, 2000, Stenbacka et al., 2010). Concerning microclimate, the tree canopy is a main factor providing ground-level shade, and both total tree basal area and proportion of Norway spruce was lower in the secondary stands (Table 1). For a given diameter, Norway spruce has a considerably higher leaf area than the pioneer tree Scots pine (Goude, 2016) and thus provides more shade. The importance of spruce is further corroborated by bryophyte species composition in our study being more strongly correlated with basal area of spruce than with total basal area (Fig. 1). In line with these results, Paquette et al. (2016) demonstrated an important role of tree species composition for bryophyte communities in Canadian boreal secondary forests and emphasized the need to investigate the functional mechanisms behind this role (see also Barbier et al., 2008).

4.2. Differences in habitat conditions indicated by bryophyte subgroups

Differences in richness and cover of species subgroups add further detail to the role of the current habitat conditions in maintaining the differences in the bryophyte species composition between secondary and semi-natural stands. Solar light, including UV-radiation, is the most obvious habitat factor that changes abruptly after clear-cutting and, as previously mentioned, canopy shading was still lower in secondary stands. Clear-cutting also changes temperature and air moisture regimes dramatically. Many species associated with shade go locally extinct (e.g. Hylander et al., 2005), and in our study the cover of the "shade species" group was still reduced by two thirds and species numbers by almost a quarter in secondary stands (Fig. 4C-D; Table 2). Light-demanding species instead colonize clear-cuts and in our study they still remained more than twice as abundant and c. 50% more species rich in secondary stands (Fig. 4C-D, Table 2). Our results conform well to the findings of Baldwin and Bradfield (2010), who surveyed much smaller plots, that richness of open-canopy species was higher and abundance of closed-canopy species was lower in stands 25–49 years after clear-cutting of temperate rainforests in British Columbia.

Hylander et al. (2005) found that bryophyte species growing on convex substrates such as tree trunks, tree bases, downed logs etc. were more negatively affected by the immediate (2.5 years) effects of clear-cutting than others. Species growing on tree substrates are thus particularly sensitive to the microclimatic changes brought by clear-cutting. In our study, half of the species in this group was classified as low-light species, half as intermediate and none as associated with full light. The significant difference in species richness for the tree substrate species subgroup (Fig. 3A) and the significant association of five of its species to semi-natural forests (Table 2) may thus not only be maintained by differences in substrate availability, but also by the difference in shading (Táborská et al., 2020). Lower richness of species associated with tree substrates (tree bases and stems, dead wood) in clear-cuts and second-growth has been documented in several previous studies using smaller study plots (Dynesius and Hylander, 2007, Åström et al., 2007, Schmalholz et al., 2011, Baldwin et al., 2012, Dynesius, 2015).

Colonist species take advantage of the disturbed ground on clear-cuts and rapidly increase in both cover and richness (Dynesius and Hylander, 2007, Åström et al., 2007, Baldwin and Bradfield, 2010, Baldwin et al., 2012). For example, members of the class Polytrichopsida (hair-cap

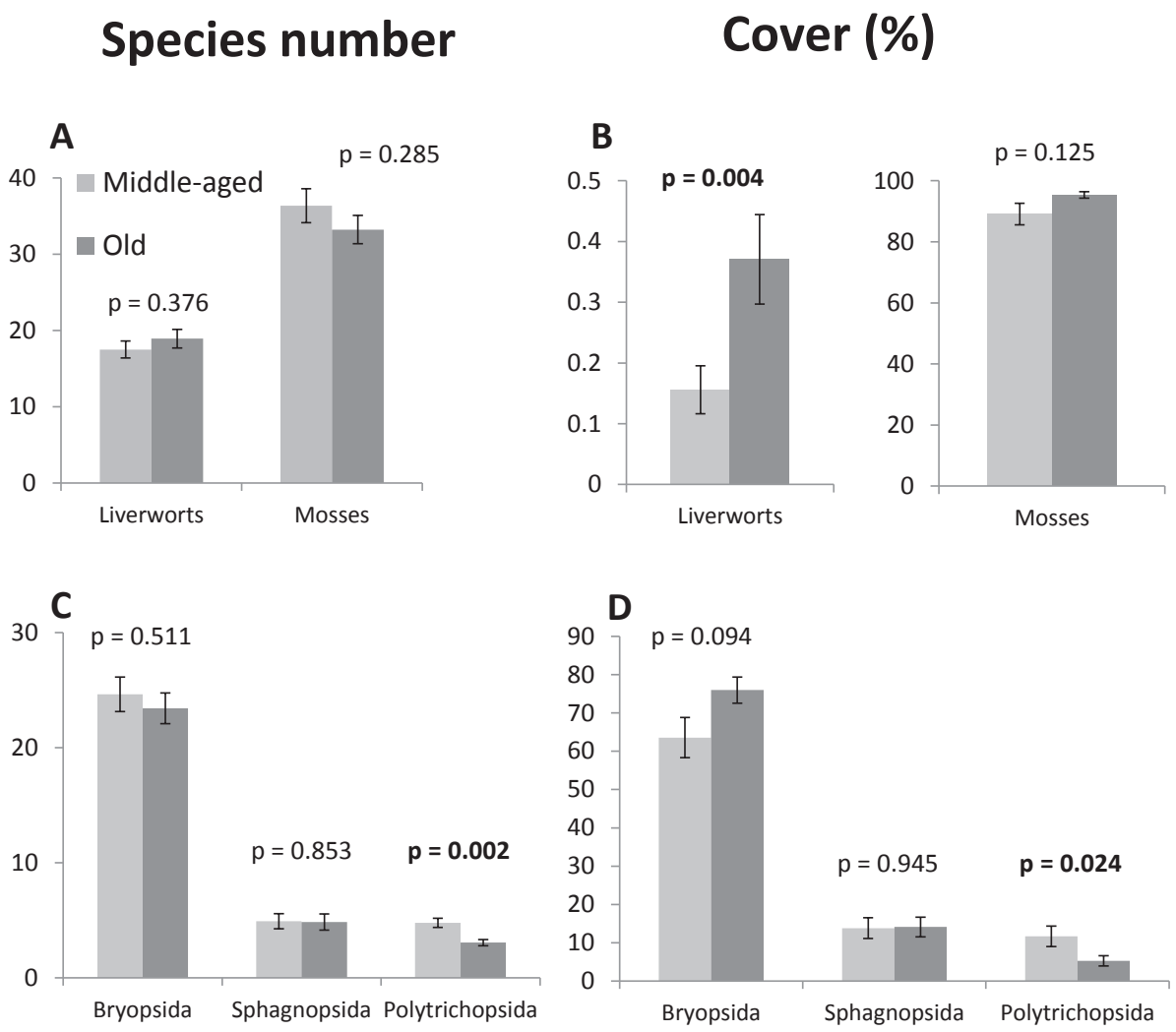

Fig. 2. Differences in species number (A, C) and cover (B, D) in 1-ha plots between secondary stands 40–60 years after clear-cutting and older semi-natural stands that have never been clear-cut. *A–B* The two bryophyte phyla present in boreal forests. *C–D* The three major taxonomic classes of mosses. *p*-values are from Mann-Whitney U-tests (n=14).

mosses and allies, Fig. 2 C-D) are known to be favored by disturbances (Hannerz and Hånell, 1997, Botting and Fredeen, 2006, Schmalholz and Hylander, 2009, Baldwin and Bradfield, 2010). A majority of the secondary stands (9 out of 14) in our study had been commercially thinned c. 3–5 years before the bryophyte survey, causing ground disturbance. In contrast, the semi-natural forests had not been thinned for a long time, the most recent being c. 15–20 years ago in some stands. The recent disturbance in secondary stands is most likely a main reason for their higher cover and richness of disturbed-ground species (Fig. 3). This effect of recent thinning was also shown by Dynesius (2015).

None of the moisture-based species groups differed in species richness between secondary and semi-natural stands (Fig. 4A). There was, however, turnover within groups caused by differences in light availability. The wet group consisted of 30 species, and 90% of these grow on the ground, a substrate buffered against desiccation (Hylander et al., 2005). This buffering may explain the richness similarity between stand types. Instead there was a turnover from low-light "wet species" (e.g. *Pseudobryum cinclidioides*) in semi-natural forests to species of open wetlands (e.g. *Aulacomnium palustre)* in secondary stands. The "dry species" group consisted of 13 species only, and in secondary stands there were no species growing on stems of non-birch broadleaves (*Orthotrichales* mosses, which were present in semi-natural stands), but instead there was a higher occupancy of ground-living "dry species" associated with high light (e.g. *Polytrichum piliferum* and *Racomitrium microcarpon*). Although species richness differences were not related to moisture class, bryophyte cover differences were (Fig. 4 B). These cover differences were, however, mostly driven by two individual species, the common feather moss *Hylocomium splendens* and the above-mentioned high-light species *R. microcarpon* (Table 2). Many other species in the respective moisture groups showed cover differences in the opposite directions (Appendix).

4.3. Earlier studies advocating an important role of differences in habitat conditions

Microclimate and substrate limitation have earlier been advocated as mechanisms behind differences in boreal bryophyte communities with different histories. Åström et al. (2007) found that differences in bryophyte communities between young secondary and older semi-natural stands were smaller in polar-facing than in equator-facing slopes and explained this with the smaller difference in solar radiation between these stand types in polar-facing slopes. Studying a chronosequence of southern boreal spruce-dominated stands presumed to have regenerated after clear-cutting, Schmalholz and Hylander (2009) found that species composition and cover of bryophytes as well as canopy cover in 0.1 ha plots changed rapidly up to stand ages of 30–40 years, but then

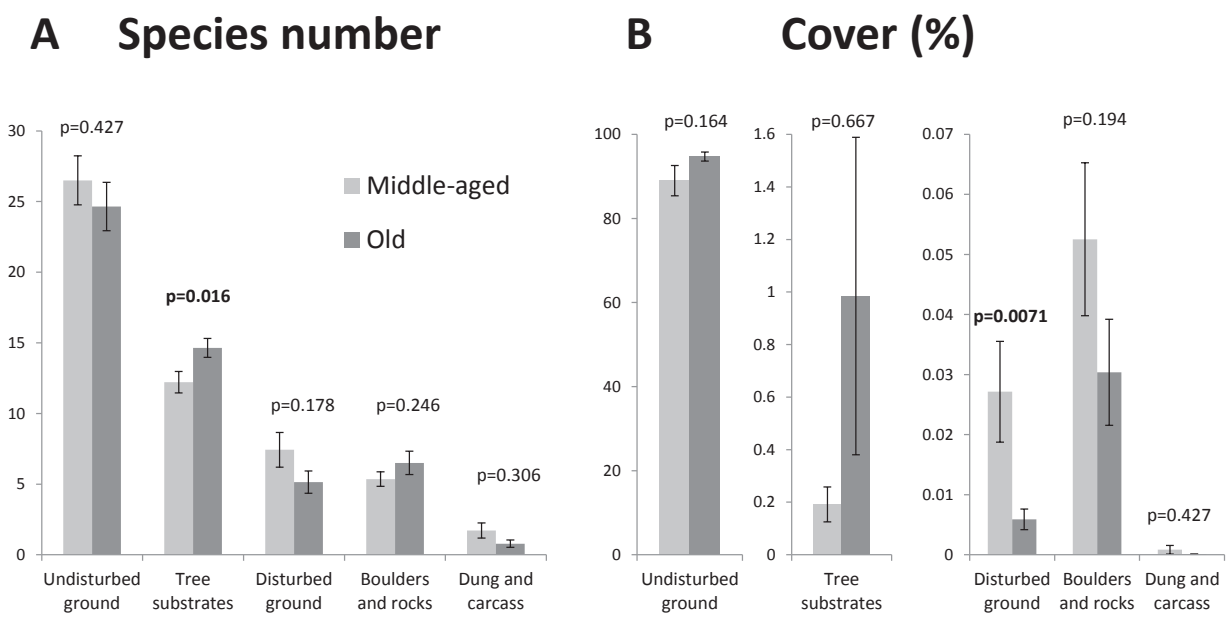

Fig. 3. Differences in species number and cover in 1-ha plots between secondary stands 40–60 years after clear-cutting and older semi-natural stands that have never been clear-cut. The species are divided into subgroups according to the most common substrate they grow on in north Swedish forests. The tree substrates subgroup includes species mostly growing on bark of standing trees, on tree bases, on stumps, and/or on downed dead logs. Note that cover spans five orders of magnitudes among groups. *p*-values are from Mann-Whitney U-tests (n=14).

remained approximately the same up to 96 years. They concluded that microclimate rather than substrate abundance drives bryophyte succession, a conclusion that was shared by Åström et al. (2007) and Dynesius et al. (2009) for species living on dead wood. Focusing on red-listed species only, Rudolphi and Gustafsson (2011) made a detailed comparison between 30 and 70 year old secondary stands and older semi-natural stands. They found lower numbers of red-listed species in secondary stands and, in contrast to the abovementioned authors, they attributed this to substrate limitations rather than microclimatic differences.

4.4. Recolonization lag

Differences in bryophyte communities between semi-natural and secondary stands might also be explained by a recolonization time lag caused by dispersal limitation. There is mixed evidence on how important dispersal limitation is in forest bryophytes and there is most likely a large variation among species. In a study of primary colonization of boreal land uplift islands, Tiselius et al. (2019) found that dispersal limitation at the landscape scale may occur in species which have a low total output of spores in the landscape because they rarely produce sexual spores and have low regional abundances. The regional spore rain of such species may be so sparse that it results in a colonization lag when suitable conditions appear. Liverworts have generally low abundances (Fig. 2 B) and some of the liverwort species in the present study that appear less in secondary stands (Table 2) rarely produce sexual spores (*Barbilophozia lycopodioides, Lophozia ciliata, Lophoziopsis longidens*; Damsholt, 2002). Dispersal limitation also at the stand scale have been indicated in studies of bryophyte recolonization after clear-felling of Tasmania's southern forest dominated by Eucalyptus, having a bryophyte species pool totally different from the boreal (Baker et al., 2013; 2018). Bryophyte recolonization in boreal forests does not, however, appear to be limited by distance to nearby propagule sources. Hylander (2009) found that bryophyte species that are known to be negatively affected by clear-cutting had, half a century after clear-cutting, recolonized secondary stands equally well (or poorly) at all studied distances (10, 20, 40, and 80 m) from the nearest former clear-cut edge. This lack of effect of distance was evident for several of the species found to have recolonized poorly in our study (Table 2), surprisingly also including species having relatively low abundances and rarely reproducing sexually (e.g. the liverwort *Lophoziopsis longidens)* and therefore being more dependent on short-distance dispersal by vegetative propagules.

4.5. Small difference in bryophyte species richness

The small and statistically insignificant differences in species richness between secondary stands and older semi-natural forests (Fig. 2A) are in contrast to the lower richness in secondary stands found in earlier studies, in particular for liverworts (e.g. Botting and Fredeen, 2006; Dynesius, 2015). We assume that the small richness differences between stand types in our study is caused by (i) a more intense management history in our semi-natural stands resulting in a more impoverished bryophyte assemblage before clear-cutting and (ii) a smaller difference in canopy shading. To check these assumptions, we compare our data with data from the 0.1 ha non-riparian plots in boreal Sweden of Dynesius (2015). Liverwort species richness was not higher in the 10 times larger plots of semi-natural forest in the present study, indicating a considerably poorer liverwort flora. Was the shading difference smaller? Indeed, in the previous study the spruce basal area in semi-natural stands was 220% higher and the total basal area 60% higher than in secondary stands, whereas in the present study the corresponding differences were only 70% and 20%, respectively. These observations further emphasize the importance of the magnitude of differences in habitat factors between semi-natural and secondary boreal forest stands in explaining differences in bryophyte assemblages between these stand types.

5. Implications for forest management

Our results show that some ecological subgroups of bryophytes still have significantly depressed species numbers 40–60 years after clear-cutting. This result is particularly alarming considering (i) the large area sampled in each stand (1 ha), approaching the size of managed forest stands, (ii) the already impoverished bryophyte flora and relatively low volume of deadwood of the semi-natural reference stands in

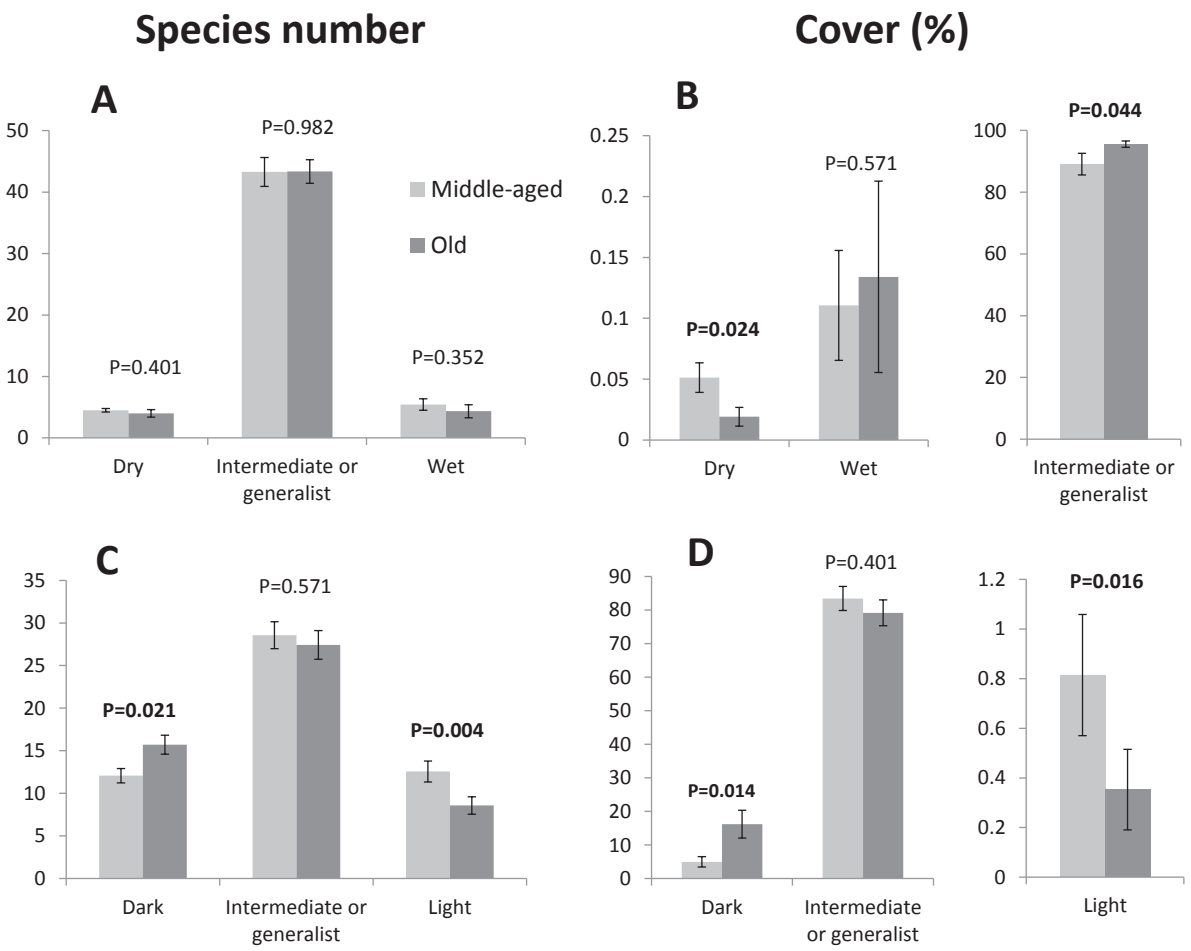

Fig. 4. Differences in species number and cover in 1-ha plots between secondary stands 40–60 years after clear-cutting and older semi-natural stands that have never been clear-cut. Species habitat subgroups are defined according to level of moisture (*A–B*) and level of light (*C–D*) were species most commonly grow. Generalist species are included in the intermediate group. *p*-values are from Mann-Whitney U-tests (n=14). Note that cover of dry, wet and light species are very low.

the study, and (iii) the few decades left before next clear-cutting. In forestry-dominated boreal landscapes the population sizes of many species, in particular species typical of shaded environments and of tree-related substrates, risk becoming severely reduced. Intensified forestry practices to produce bioenergy replacing fossil fuels, e.g. harvest of logging residues (tops, branches, stumps) and recycling of the wood ash from this combustion, further reduce the populations of some of these species (Åström et al., 2005, Schmalholz and Hylander, 2011, Dynesius, 2012, Andersson et al., 2017). These negative impacts taken together pinpoints the need of long-term retention of older forests in managed landscapes to preserve source populations of species susceptible to harvesting impacts (e.g., Boudreault et al., 2018). Climate warming makes this even more important.

It might be argued that clear-cutting forestry mimics natural disturbances and the following succession, and that the effects on bryophyte biodiversity therefore should be limited. However, empirical studies show that bryophyte communities in stands developing on former clear-cuts differ from those in stands with their origin in natural disturbance (e.g. Schmalholz et al., 2011; Paquette et al., 2016). Schmalholz et al. (2011) found that c. 40 years after disturbance by clear-cut logging, by forest wildfire, and by outbreak of spruce budworm, species richness was similar but species compositions were distinct among the three stand types. Stands regenerating from clear-cuts had many forest floor bryophytes, but a composition of woody-debris species most distant from mature forests. The small recovery of the bryophyte flora of boreal middle-aged secondary stands found over a period of 15 years by Dynesius (2015) lends little hope for a considerable recovery until next clear-cutting. Similarly, in a chronosequence study, Schmalholz and Hylander (2009) recorded only minor changes in bryophyte species composition between 30 and 96 years old south-boreal stands regenerated after clear-cutting.

To mitigate the negative long-term stand-level effects on bryophyte biodiversity of boreal clear-cutting forestry, thoughtful and forward-looking conservation measures are needed. Already, much effort is put into making clear-cuts less clear, i.e. leaving tree groups and solitary trees as well as leaving and creating deadwood (e.g. Rudolphi et al., 2014). These measures will make future secondary stands somewhat less hostile to bryophytes associated with shade and tree substrates. To further improve this function, broad-leaved trees with higher bark pH (e.g. *Populus, Salix, Sorbus*) should be prioritized for retention (habitat for specialized bryophyte epiphytes), and the unlogged retention patches should include coarse deadwood and provide maximum shade (dense tree cover, polar-facing slopes). When regenerating with pine it would also be advisable to plant some patches with spruce or other strongly shading tree species, e.g. around retention patches and in polar-facing areas. Beware, however, that there are other disfavored organism groups that need sunlight, e.g. many wood-inhabiting insect species (Jonsell et al., 1998). Finally, greater care to preserve existing deadwood should be taken during soil scarification after clear-cutting.

To improve conditions in future mature stands developing from today's middle-aged secondary ones, measures must be taken in connection to thinning operations (Bauhus et al., 2009). The measures should aim at preserving shade, partly decomposed dead wood, and large deciduous trees other than birch. Patches with dominance of strongly

shading trees, such as spruce, may be left un-thinned. Logs that are already lying on the ground should be protected and new coarse logs be created. In addition, during thinning some stumps should be cut higher than normal (c. 0.5 m). Such stumps will not be so easily overgrown by ground vegetation (Dynesius et al., 2010), but will still be low enough to be relatively moist, and thus serve as substrate for some dead wood bryophytes. To optimize the benefit to bryophytes, retention of un-thinned patches should not be located to equator-facing slopes and deadwood creation should be primarily directed towards highly shaded sites. The growth and survival of broadleaved trees of the genera *Populus, Salix* and *Sorbus* should be favored by the felling of nearby competing conifers.

Thinking outside of the clear-cutting forestry box, a way to safeguard forest organisms adapted to shade is to implement uneven-aged forestry with late successional tree species such as Norway spruce in parts of boreal landscapes. It has already been shown that uneven-aged spruce silviculture benefits beetle biodiversity (Hjältén et al., 2017). This forest management method would likely also provide permanent habitats for the shade-bryophytes that we have shown are disfavored by clear-cutting forestry, but this still needs to be studied scientifically. To benefit deadwood species, it is of course necessary to ensure the availability of this substrate also in uneven-aged forestry.

CRediT authorship contribution statement

Mats Dynesius: Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing. **Jörgen Olsson:** Conceptualization, Methodology, Writing - review & editing. **Joakim Hjältén:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Therese Löfroth:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Jean-Michel Roberge:** Conceptualization, Methodology, 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.

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Appendix A. Supplementary material

Appendix. A list of the 154 species found in the study grouped according to their taxonomical affiliation. For each species the following data is given: (i) substrate category, (ii) moisture category (iii) light category, (iv) occupancy, (v) percentage cover, and (vi) indicator value.

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