

Article

The Potential of Production Forests for Sustaining Lichen Diversity: A Perspective on Sustainable Forest Management

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Abstract: There is a critical gap in our knowledge about sustainable forest management in order to maintain biodiversity with respect to allocating conservation efforts between production forests and set-asides. Field studies on this question are notably scarce on species-rich, poorly detectable taxon groups. On the basis of forest lichen surveys in Estonia, we assessed the following: (i) how much production stands contribute to maintaining the full species pool and (ii) how forest habitat conditions affect this contribution for habitat specialist species. The field material was collected in a “semi-natural forestry” system, which mitigates negative environmental impacts of even-aged forestry and forestry drainage by frequently using natural regeneration, tree retention, and low intensity of thinnings. We performed standard-effort surveys of full assemblages of lichens and allied fungi (such as non-lichenized calicioid and lichenicolous fungi) and measured stand structure in 127 2 ha plots, in mainland Estonia. The plots represented four management stages (old growth, mature preharvest forests, clear-cut sites with retention trees, and clear-cut sites without retention trees). The 369 recorded species represent an estimated 70% of the full species pool studied. Our main finding was that production forests supported over 80% of recorded species, but only one-third appears tolerant of management intensification. The landscape-scale potential of production forests through biodiversity-friendly silviculture is approximately twice as high as the number of tolerant species and, additionally, many very rare species depend on setting aside their scattered localities. The potential is much smaller at the scale of individual stands. The scale effect emerges because multiple stands contribute different sets of sensitive and infrequent species. When the full potential of production forests is realized, the role of reserves is to protect specific old-growth dependent taxa (15% to 20% of the species pool). Our study highlights that production forests form a heterogeneous and dynamic target for addressing the biodiversity conservation principle of sustainable forest management.

Keywords: biodiversity conservation; epiphytes; even-aged forestry; forest set-asides; habitat specialist species; life-history traits; mixed-species forests; retention forestry; silviculture; threatened species

1. Introduction

Sustainable forest management (SFM) is a central politically-accepted concept that links forestry with broader issues of land use in the framework of sustainable development [1]. SFM was introduced to address the multiple trade-offs between different forest-related goals and time frames, and one of its major issues is how to allocate forest land for production, ecological services, and human environment. Maintaining biodiversity is a major goal (a principle) of SFM, and there is a broad consensus, after nearly 30 years of focused research, that following this principle requires combining forest protection,

improving and mitigating forest management techniques, and effective landscape planning [2,3]. Despite such an understanding and several political and market mechanisms to enforce SFM [4], forest biodiversity continues to decline even in those regions that have a strong political commitment to SFM, such as the European Union [5].

A critical gap in knowledge about maintaining forest biodiversity along with other forest use is how to allocate conservation efforts between production forests and set-asides of different type and size [6–8]. This gap remains partly rooted in incomplete knowledge on most forest organisms and their responses to management practices [9], which weakens conservation arguments in stakeholder processes and, specifically, makes these dependent on approaches to the precautionary principle [10]. A promising approach is to define a set of well-studied “focal” taxa with different habitat requirements for forest landscapes [11], however, its effectiveness to protect full biodiversity still has to be demonstrated [12]. Another caveat is the prevalence of simplistic study methods or reporting [9]. For example, a common focus is to compare “managed” vs. “unmanaged” forests (e.g., [13]) or limited biodiversity metrics such as stand-scale species richness [14], instead of explicitly documenting the conditions created by different management techniques and their effects on different parts of species pools at the landscape scale required for SFM. The uncertainties related to such gaps of knowledge remain greatest for the most species-rich and poorly detectable taxon groups.

In this paper, our main aim is to characterize, in operational terms for SFM, the ecological composition of lichens (lichenized fungi) in forest landscapes. We build on nearly 20 years of research on biodiversity in Estonian forests where we have used standard sampling designs to test the responses of species and assemblages to various influences of even-aged forestry (e.g., [15–18]). The Estonian context is suitable for general insight because it has, until recently, adopted a “semi-natural forestry” approach, which mitigates environmental impacts of even-aged forestry and forestry drainage by frequently using natural regeneration, tree retention, and low intensity of thinnings [19,20]. In addition to relatively intact species pools, a semi-natural context reveals species that depend on naturally developing forests (strict protection) from those, which are restricted to such forests only because of inadequate habitat provision in production stands [11,17,21]. In addition, Estonia has a recent history of land abandonment and wetland drainage processes, which has created extensive new forests with informative species assemblages for understanding dispersal limitation as opposed to habitat provision [22]. Variability in habitat conditions also includes local acceptance of natural disturbances, such as wildfire, which is followed by restricted salvage logging [23].

Forest lichens are a diverse, highly specialized taxon group [24–26], which provide a valuable study system for SFM. Functionally, lichens play important roles in water and nutrient cycling, and provide forage and habitat to many other organisms [27,28]. The diversity of lichens in the forest is mostly supported by stand structures, dynamics, and heterogeneity. Most important stand structures include live trees of different species and age classes, standing and fallen dead trees of all decay stages and sizes, and windthrows and other disturbed sites; their habitat values are further modified by stand age and microclimatic conditions (e.g., [15,25,29,30]). Several forest-dwelling lichen species have also limited dispersal capacity and low population recovery or colonization rates after human induced disturbance [25,29]. As a result, lichen assemblages and individual species are sensitive to various forestry interventions, specifically to changes in within-stand heterogeneity, substrate persistence and microhabitat fluctuations, ecosystem heterogeneity across landscapes, and forest fragmentation [25,29,31]. Under unfavorable conditions, such as even-aged forestry systems based on a few commercially profitable tree species and short rotation times, many lichen populations decline and can eventually go extinct [32–35]. And, vice versa, there is a potential to actively restore lichen diversity through interventions that (re)create limiting habitat conditions, but such research is only emerging and, to date, has been mainly restricted to assessments of partial cutting [36].

There have been two historical approaches to sensitivity of lichen species pools to human-caused land cover change. A North-European school built upon the early 20th century works of botanist Kaarlo Linkola [37] who distinguished the following four types of tolerance in plants: hemerophobic

(sensitive to various human activities), hemeradiaphoric (tolerate weak or moderate activity), apophyte (preferring moderately changed sites), and hemerophilic species (spreading with humans, e.g., weeds and cultivated plants). The Linkola's system was used by Finnish lichenologists Räsänen [38,39] and Koskinen [40]. The latter reported hemeradiaphory to be the dominant tolerance type among epiphytic lichens (49% of species) and hemerophoby to be rare (1.3% of species). In recent times, hemerophobic taxa have been proposed as criteria for assessing naturalness of forests, however, the proposed species among an Estonian list of macrolichens formed 26% of all forest-dwelling species [41]. Independently, an English school developed in the middle of the 20th century with the works by Francis Rose [42] who distinguished a subset of sensitive forest species that have both specialized habitat requirements and poor dispersal abilities. He proposed "indices of ecological continuity" based on such species. This fueled research on forest continuity requirements in many lichen groups (e.g., [43–48]), which, however, are prone to misinterpretation due to confounding effects of other habitat qualities [15]. Therefore, the historical approaches to lichen species sensitivity increasingly developed toward explaining old-growth affinity of certain species, instead of asking how to conserve whole species pools in human-influenced landscapes, which is a question more relevant to the biodiversity maintenance principle of SFM.

In this paper we reformulate the issue of lichen species sensitivity to forestry as follows: What is the full potential of forest stands managed for timber production to host lichen assemblages that occur in natural ecosystems? This question focuses on factors supporting landscape-scale species pools for a set of stands, in contrast to previous attention on species richness variation at the scale of individual stands (e.g., [49–52]). We answer this question based on our extensive stand-scale data, which reveals both among-plot variation, different forest ecosystems, and the total species pool in Estonian forests. We provide a categorization of the species pool by management sensitivity (tolerance), combining historical classifications [37,40] with a general approach to distinguish species whose viability in production forestry depends on the techniques used (e.g., [53]), and resolving the joint issue of poor data on extremely rare species. We then re-analyze the plot-scale assemblage data to indicate how species of different tolerance are distributed in relation to management regimes and key factors, and whether indicator species can be used to reveal broader assemblages. Our main hypothesis is that intensified forestry reduces species pools of production forests both in terms of stand-scale (alpha) and among-stand (beta) diversity, which is revealed by a proportionately larger share of management-sensitive species at the landscape than stand scale. Finally, we discuss how SFM approaches could be improved, including specific approaches on old-forests species, rare species, and using "focal" species [54] to guide the management.

2. Materials and Methods

2.1. Study Area

The study was carried out in the mainland of Estonia (Figure 1), which is situated in the European hemiboreal vegetation zone. The topography is mostly of glacial origin. i.e., flat and undulating moraine plains as well as glaciolacustrine plains with abundant clayey deposits and extensive postglacial paludification. The mean air temperature is 17 °C in July and −6 °C in January; the average precipitation is from 600 to 700 mm year^{−1}. Forests naturally cover ca. 85% of the Estonian land area [55]; the actual cover of forest land (including clear-cuts) is 51%, but only 1% are old natural stands [56].



Figure 1. Location of the study sites in Estonia.

Our study system included 127 forest stands distributed among the following five common forest site-type groups (sensu [57]): (1) 35 dry boreal forests (mostly *Vaccinium vitis-idaea* type) on higher fluvioglacial landforms and till mounds with podzols (pH_{KCl} 3.5 to 5.0) where the top layer is periodically dry and ground water deeper than 2 m; (2) 24 meso-eutrophic forests (mostly *Oxalis* type) on till mounds or rolling plains with podzols or stagnic Luvisols (pH_{KCl} 3.2 to 4.2) where ground water is usually deeper than 2 m; (3) 26 eutrophic boreo-nemoral forests (mostly *Aegopodium* type) predominantly on undulating sandy till plains with favorably moist (in springtime anaerobic) Gleyic Cambisols or Luvisols (pH_{KCl} 4.7 to 6.5) almost lacking organic horizon; (4) 20 mobile-water swamp forests on thin seasonally flooded Eutric histosols and Fluvisols with a peat layer >30 cm (pH_{KCl} 5.0 to 6.5) in lowlands and valleys along rivers or around bogs; (5) 24 artificially drained swamp forests (*Oxalis* type, originating from type 4, see [16]) on well decomposed peat soils (pH_{KCl} 4.0 to 6.5). The dry boreal stands were dominated by Scots pine (*Pinus sylvestris*) (Figure 2a–c); the other sites hosted conifer/deciduous mixtures with Norway spruce (*Picea abies*) (Figure 2d–e) or, in some *Oxalis* type stands, with Scots pine. All the stands were situated in contiguous lowland forest landscapes (only two plots >100 m a.s.l.); cultivated land covered on average only 5% of the land area within 1 km radius.



Figure 2. The habitats studied. Left column: *Pinus sylvestris* sites, dry boreal old-growth (a); mature paludified stand regenerating after surface fire (b); retention-cut with soil scarification (c). Right column: *Picea abies* mixed wood on fertile soils, old-growth swamp of >300 year continuity, trees 160 years old (d); boreo-nemoral mature stand, 90 years old, unthinned and dead-wood rich (e); and boreo-nemoral retention cut left to natural regeneration (f). Photo credits: R. Rosenvald (c) and authors (a,b,d–f).

The core of this study system (Figure 1, forests and cutovers) was an established blocked design (116 stands in 29 blocks) that explores forest biodiversity along with post-harvest succession and management approaches (e.g., [15,17,58]). Each block comprised four stands of a fixed set of management stages of the same site type as close as possible on the landscape (<18 km with two exceptions). The management stages were: (i) old growth (most trees 100 to 180 years, coniferous >125 years old, stand ages up to at least 300 years); (ii) mature production forests (hereafter “mature managed”, 65 to 95 years old, both recently thinned and un-thinned, most documented to be secondary stands of clear-cut origin); and cutovers (usually 3 to 7 years post-harvest, range 4–19 years) of

two types—(iii) with retention trees (“retention cuts”, on average $20\text{ m}^3\text{ ha}^{-1}$ of live retention trees, range $2\text{--}69\text{ m}^3\text{ ha}^{-1}$), and (iv) without retention trees (“clear-cuts”). Most cutovers were naturally regenerating, and soil scarification had been practiced in only four dry-boreal stands.

To increase the species pool addressed, we supplemented the block design with 11 stands of comparable site types, which have been surveyed by the same observer and the same methods [18]. Two stands were old eutrophic boreo-nemoral stands and nine stands were post-wildfire stands in Scots pine-dominated dry boreal or paludified (*Polytrichum* and *Vaccinium*) sites (documented by [23,59], respectively). In six wildfire stands (three naturally regenerating and three salvage logged with $10\text{ m}^3\text{ ha}^{-1}$ live tree retention), the initial surveys four years post burn were repeated five years later and both of these surveys have been included in this paper; three other wildfire sites were older burns (last fire 15 to 20 years ago). Before burning, the sites had been 70- to 100-year-old pine dominated stands with a history of moderate thinning. We included these as distinct sets of mature managed or retention cut stands among the dry boreal forests, which typically have fire-driven disturbance regimes also under natural conditions in Estonia [60].

2.2. Lichen Surveys and Lab Work

The fieldwork followed a common standard field protocol for fixed-area-fixed-effort survey [18]. In each study stand, a 2 ha plot was delineated on the map without prior knowledge of the lichens present. The same field observer (author PL) surveyed the lichen assemblages (the block design plots from 2006 to 2009 and additional plots in 2010 and 2015). All lichens, lichenicolous, and allied saprotrophic fungi (i.e., species traditionally treated by lichenologists) were searched for in each plot during 4 h. All substrates 0 to 2 m from the forest floor were checked with the primary aim of finding as many species as possible (i.e., the observer allocated the effort to check diverse microhabitats in the whole plot). The substrates included freshly fallen branches and canopies of fallen trees, which alleviates the undersampling of canopy-inhabiting taxa, e.g., [61,62]. According to critical assessments of our survey method, the 133 surveys included here collectively capture ca. 70% of the species pool of the studied habitats [18]. At plot level, >70% lichen species present are typically listed in the 4 h survey time (>50% in the most species-rich old boreo-nemoral forests, [59]); 2–3 h are required to reliably compare species composition of plots for overall differences, and at least 3 h for poorly detectable species subsets to become comparable with well detectable subsets [18].

For each lichen species in each survey, all substrate types were recorded (ground; different woody substrates as combinations of tree species, type, decay stage of wood, and surface, e.g., bark or wood of live trees). Plot-scale abundance of each species was scored based on the number of records (i.e., discrete patches in the case of ground lichens or occurrences on distinct substrate entities, such as a tree trunk [63]) as follows: 1, one record; 2, two to five records; 3, six to 15 records; 4, 16 to 100 records; 5, >100 records (dominant species). Where necessary, lichen specimens were collected for further identification in the laboratory where microscopy, color spot tests, and standard thin-layer chromatography were used. Some species groups were treated collectively in the field and in the analyses including *Cetrelia cetrarioides*/*C. olivetorum*/*C. monachorum*; *Cladonia arbuscula*/*C. mitis*; *Lecanora compallens*/*L. stanislai*; and *Parmelia ernstiae*/*P. serrana*. The nomenclature follows [64]. Vouchers of notable species are deposited in the lichen herbarium of the University of Tartu Natural History Museum (TU). Life history traits of the lichen species detected have been compiled according to Estonian, Scandinavian, and British lichen key books [65–68] and in some cases research literature to specify the green algal symbionts (e.g., [69,70]).

Within each 2 ha study plot, the habitat structure was measured along four 50 m straight, spaced-out sampling lines following the methods of [19]. This included line-intersect measurements of downed woody material, logs ≥ 10 cm in diameter at intersections along the whole line, and fine woody debris (0.3 to 9.9 cm in diameter) at six 1 m sections established at 10 m intervals. Strip transects to both sides of the sampling line were used for standing trees (live and dead standing trees ≥ 10 cm DBH) and tree regeneration and shrubs (<10 cm DBH). Decay stage (a five-point scale; [19]) of standing dead

trees was assessed at breast height, and decay stage of logs and fine woody debris was recorded at the intersection with the line. The volume calculations used circular cross-sections of the woody items as approximations.

2.3. Categorizing Lichen Taxa by Tolerance of Forest Management Disturbance

In our study, the basic effects of even-aged forestry were included by the management stages sampled: they distinguished post clear-cut, tree-retention and rotation-aged production stands, and, as a proxy of long-term strict protection, old growth (Section 2.1). The cutover surveys were purposefully carried out a few years after the harvest, to include the period when most lichen die-off related to canopy loss had happened [71]. The sampled mature managed forests were all within ± 10 years of the official rotation ages of the Estonian forests, which generally exceed those optimizing economic income alone [72]. Additionally, our production forests were mixed stands (except some pine sites where other tree species are lacking due to natural soil conditions), and the tree retention volumes exceeded the $5 \text{ m}^3/\text{ha}$ required by the Estonian Forest Act. Therefore, we interpreted the contrasts between clear-cuts versus retention cuts, and between mature stands versus old-growth stands as a potential to mitigate immediate clear-cutting effects and practice even-aged forest management (as opposed to forest protection), respectively.

On the basis of such interpretation, we constructed a decision tree to categorize each species into one of four basic management-tolerance categories (Figure 3). We used the following three analytical approaches: comparisons of relative frequencies of occurrence, formal indicator species analyses (ISA) [73], and validation based on Estonian casual records and the literature (notably in the case of rare species for which the two former approaches could not be applied). For ISA, we distinguished two broad groups of forest ecosystems (pine forests vs. mixed forests, based on NMS, see below) combined, first, by three management stages (old growth, mature managed stands, and cutovers). We ran another ISA to check whether some species attained significant indicator value for old growth if the forest ecosystems were pooled (Table S1).

As shown in Figure 3, the categories included: (1) management-tolerant species, species that inhabit diverse production-forest habitats, and thus have high likelihood of retaining viable populations under various forest management schemes. Here, we included common canopy-inhabiting species having multiple records both in mature managed and retention-cut stands, given that these can be underrecorded in ground surveys; (2) old-growth dependent species, species having all or most of their populations in old-growth stands, despite the minor share of such stands remaining (Section 2.1). Rare species only found in one to three old-growth stands in our material (never elsewhere) were only retained in this category if their old-growth affinity was confirmed based on all other Estonian records in herbaria and literature (as databased in eBiodiversity as of 15 September 2019, elurikkus.ee); (3) management-sensitive species, species not qualifying under categories one to two, but either having statistically significant preference to old stands (3a, rotation-age sensitive), highly varying in occurrence among the three management stages in production forests (3b, \geq five-fold variation in presence or $>10\%$ presence vs. absence, species sensitive to stage modifications in even-aged management), or infrequent substrate-specific species (3c, sensitive to substrate loss); and (4) unknown sensitivity, rare and infrequent species that did not meet any of the above-listed criteria.

We made three exceptions when applying the criterion 3b (Figure 3). The lichenicolous fungus *Epicladonia sandstedei* was moved to the “widespread” category (1a), because its low frequencies can be attributed to poor detectability in the field. Another lichenicolous fungus, *Tremella hypogymniae* was recategorized as “unknown” (criterion 4b) because we considered the fact that all its sparse records were from retention-cut plots most likely a sample error. *Sarea resinae*, an otherwise widespread species (1a), was listed as sensitive based on criterion (3b) considering its absence in cutover sites (it thus depends on spruce trees in close-canopy stands, note that spruce is seldom retained at harvest due to its poor survival [74]).

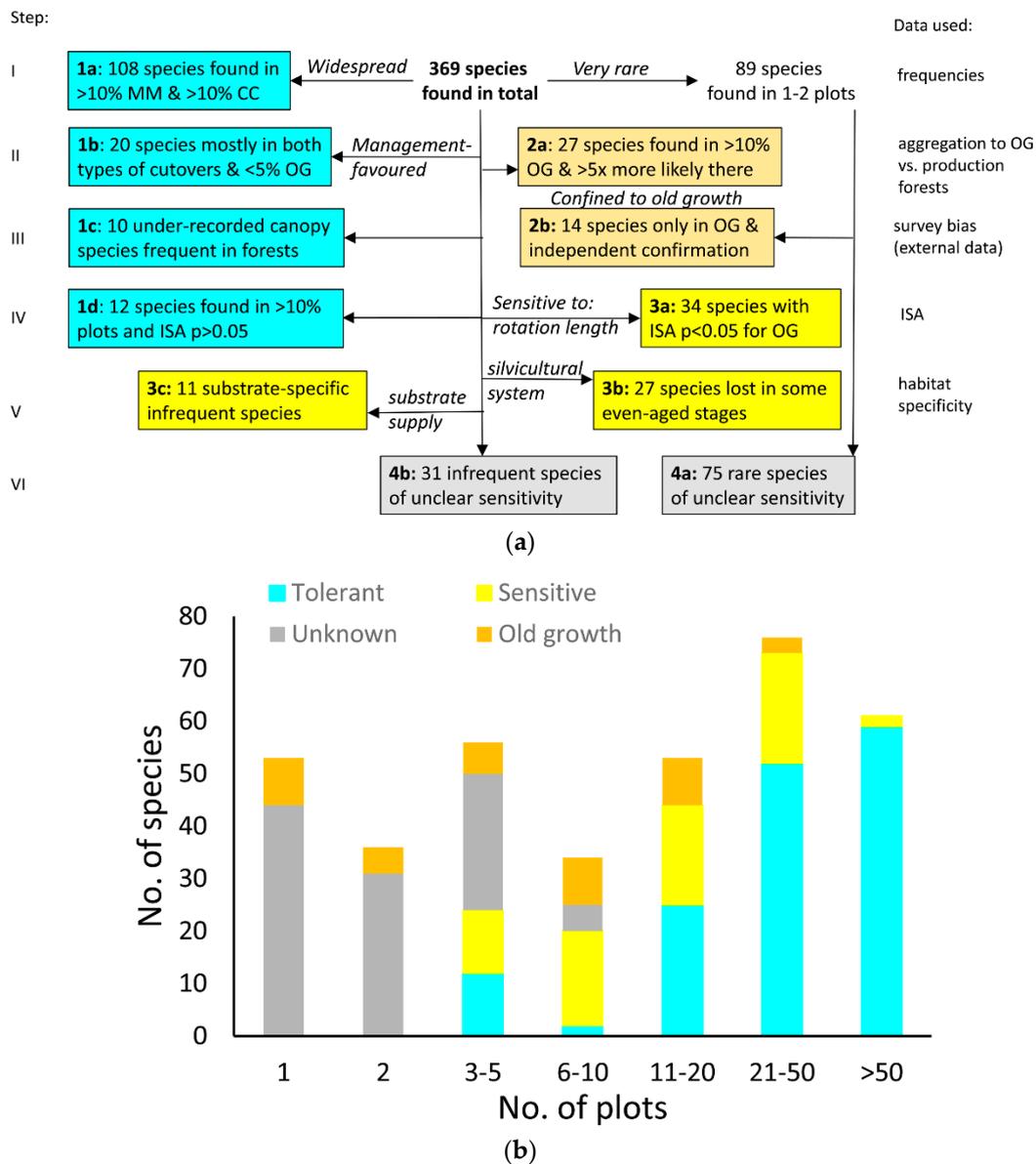


Figure 3. Management-tolerance categorization of lichen species: The decision tree (a) and frequency distributions (no. of 2 ha plots with occurrences) of the species by the tolerance categories (b). Abbreviations: CC, clear-cuts; ISA, indicator species analysis; OG, old growth; and MM, mature managed forests.

2.4. Statistical Analysis

At the 2 ha plot scale, we tested the effects of management stage on the mean species richness by species sensitivity groups using Factorial ANOVA and post-hoc Tukey HSD-tests in STATISTICA v7.0 (StatSoft, Inc., Tulsa, OK, USA). To additionally explore the information value of indicator species, we related the numbers of recorded woodland key-habitat species (based on the Estonian official list [75]) to the numbers of sensitive and unknown species (categories 3 and 4 above).

We visualized compositional differences in lichen assemblages using non-metric multidimensional scaling (NMS) based on the Sørensen dissimilarity index in PC-ORD vers. 6.07 [76]. The species matrix (233 species; species recorded in 1 to 4 plots omitted) comprised species abundance class in each plot. We ran the ordination in the medium autopilot mode (200 runs with real data and 200 with randomized data, stability criterion 0.00001), accepting a two-dimensional solution based on the mean

stress value with real data (<13.5). We distinguished 22 habitat combinations of plots (four forest management types, five site types, wildfire sites separated). Nine potentially important structural variables (density of snags, live nemoral broad-leaved trees, trees with DBH >30 cm per ha, Shannon diversity of live trees and fine woody debris, volume of logs and fine woody debris, density of tree regeneration >1.3 m tall) were also included in the environmental matrix to explore their correlations with the ordination axes formed. Snags and logs refer to items at least 10 cm in diameter (coarse woody debris). Nemoral broad-leaved trees include *Acer*, *Fraxinus*, *Quercus*, *Tilia*, and *Ulmus* that are all near their northern natural distribution border in Estonia.

We additionally tested the impact of forest management stage on the assemblage composition using multi-response permutation procedures (MRPP). This procedure tests whether Sørensen (Bray–Curtis) distances among predefined classes exceed those resulting from random assignment of sample units to those classes, and it has the advantage of not requiring distributional assumptions that are seldom met with ecological assemblage data. The dataset of forest site types was pooled to test a general impact of four management types, but it was also confirmed for mixed forests and pine-dominated forests separately.

3. Results

3.1. Management Tolerance Distribution of the Lichen Species Pool

We found 369 taxa of lichenized, lichenicolous, and saprophytic fungi traditionally treated by lichenologists from the 133 study plots (Table S1). The 31 old-growth plots hosted 312 species, 38 mature managed plots 267 species, 35 retention-cuts 259 species, and 29 clear-cut plots 226 species. The total species numbers in individual site types ranged from 30 (*Vaccinium*-type) to 119 species (eutrophic boreo-nemoral sites). One-fourth of the species pool were found in one (53 species) or two plots (36 species) only. The most frequent species were *Hypogymnia physodes* and *Cladonia fimbriata* (found in all plots), *Parmelia sulcata* (132), and *Placynthiella icmalea* (129 plots).

We categorized a total of 150 species (41% of the recorded species pool) as management-tolerant (hereafter, tolerant) and most of these as widespread (29%, Figure 3a). Additionally, a small group of canopy-dwellers (3%, e.g., macrolichens *Anaptychia ciliaris*, *Physconia distorta*, and *Ramalina fraxinea*, and microlichens *Athallia cerinella*, *A. holocarpa*, and *Gyalolechia flavorubescens*) were apparently widespread as well, but underrecorded with our field methods. Indicator species analysis (ISA) further distinguished 12 less frequent species (3%), which were equally distributed among the management stages, although some are substratum specific (e.g., *Psilolechia clavulifera* on windthrows and *Lecidea erythrophaea* on old deciduous trees). Only 20 tolerant species (5%, including three widespread species *Peltigera didactyla*, *Placynthiella oligotropha*, and *P. uliginosa*) were obviously management-favored, preferring clear-cuts.

We found 41 species (11% of the recorded species pool) confined to old growth stands (hereafter, old growth species). Several such species were frequent in some old-growth plots (*Alyxoria varia*, *Arthonia leucopellaea*, and *Reichlingia leopoldii*), and 22 of the 27 species meeting criterion 2a (Figure 3a) had also statistically significant indicator value for old growth (ISA, $p < 0.05$, Table S1). In contrast, 14 species were found both in very few stands and as single records only (e.g., *Chaenotheca subroscida*, *Coenogonium luteum*, *Collema nigrescens*, and *Microcalicium arenarium*).

One-fifth of the recorded species pool comprised species, which in production forests only inhabited specific, potentially vulnerable successional stages or substrates (hereafter, sensitive). Sensitive species had a wide frequency variation (Figure 3b) indicating that they can be frequent in suitably managed landscapes. The largest group of sensitive species (34 species, 9%) has statistically significant preference for old growth (criterion 3a) and is potentially sensitive to lowering rotation age. These include, for example, *Arthonia vinosa*, *Bacidia laurocerasi*, *Biatora chrysantha*, *Chaenotheca brachypoda*, *C. chrysocephala*, *Multiclavula mucida*, *Mycoblastus sanguinarius*, *Parmeliopsis hyperopta*, and *Usnea dasypoga*. Regarding other successional stages, we found no species that regularly occurred on clear-cuts, while being absent from retention-cuts. We distinguished 11 species (3%) whose presence even in the Estonian moderately

managed forests strictly follows specific substrate supply, so that they tend to be more frequent in old parks (e.g., old broad-leaved trees for *Chaenotheca phaeocephala* and *Pertusaria flavida*) or woodland key habitats (e.g., *Leptogium saturninum* on old aspen trees).

Finally, management tolerance of 106 species remained unclear but most such species, 75 species (20% of the recorded species pool), were very rare in our sample (Figure 3b). Four less rare species have never been recorded in harvested sites in Estonia, thus being candidates for the sensitive category (*Bryoria implexa*, *Cheiromycina petri*, *Fellhanera gyrophorica*, and *Veizdaea aestivalis*).

At the 2 ha plot scale, the number of species of the four tolerance categories varied depending on the management stage (factorial ANOVA, tolerance \times management interaction $F_{9516} = 5.5$, $p < 0.001$ and the main effect of management stage $F_{3516} = 30.9$, $p < 0.001$, Figure 4). The most informative pattern in this variation was that the mean richness of sensitive species followed the severity gradient of management intervention, although differences between old-growth and mature managed stands appeared statistically marginal (Tukey test, $p = 0.057$) and such species were so infrequent on cutovers that retention-cuts rather resembled clear-cuts ($p = 0.946$). The share of sensitive species as compared with tolerant species varied almost 50-fold among plots, 15% to 48% in old-growth plots, 4% to 37% in mature managed stands, 5% to 24% in retention cuts, and 1% to 15% in clear-cuts. Expectably, the mean number of tolerant species was similar among the treatments (Tukey post-hoc test, $p = 0.58$); old-growth species had highest richness in old growth stands (Tukey test $p < 0.01$ and no difference in richness among other treatments $p = 0.98$); and unknown species were too rare to draw conclusions (Figure 4).

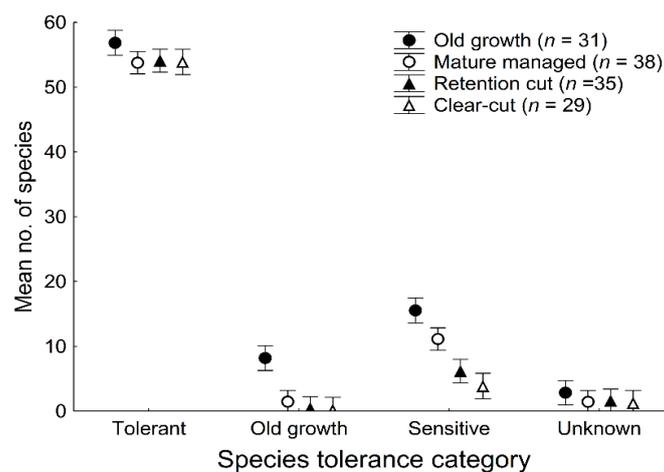


Figure 4. Mean number of lichen species in 2 ha plots by species' management tolerance and management stage; the whiskers are 95% confidence intervals.

3.2. Forest Lichen Assemblages in Relation to Environmental Factors

NMS ordination revealed distinct lichen assemblages in all mixed forests versus pine-dominated sites (Axis 1) ranging from cutover to mature to old-growth stands (Axis 2, Figure 5a). The MRPP tests confirmed these management-stage differences ($p < 0.01$ for all pair-wise comparisons, Table S2). Most stand-structural variables varied along Axis 2 ($r^2 \geq 0.2$, details in Table S3), reflecting the loss of tree-related structures and only an increase of fine woody debris on the cutovers of the even-aged forestry system. Importantly, our species categorization of management tolerance closely followed these assemblage patterns, with an intermediate position of old-forest preferring sensitive species between tolerant and old-growth species (Figure 5b). A few sensitive species by criterion 3b (successional transitions) clustered together with tolerant species (Figure 5b, lower part); these species (*Bacidina chlorotricula*, *Cladonia furcata*, and *C. crispata*) can inhabit current clear-cuts but appear to require specific conditions there. Because our ordination excluded rare species, it was not useful for analyzing

most unknown species, however, a mostly aspen-inhabiting microlichen *Bacidia polychroa* (unknown) distinctly clustered near the sensitive category (Figure 5b, the “4b” label on the left).

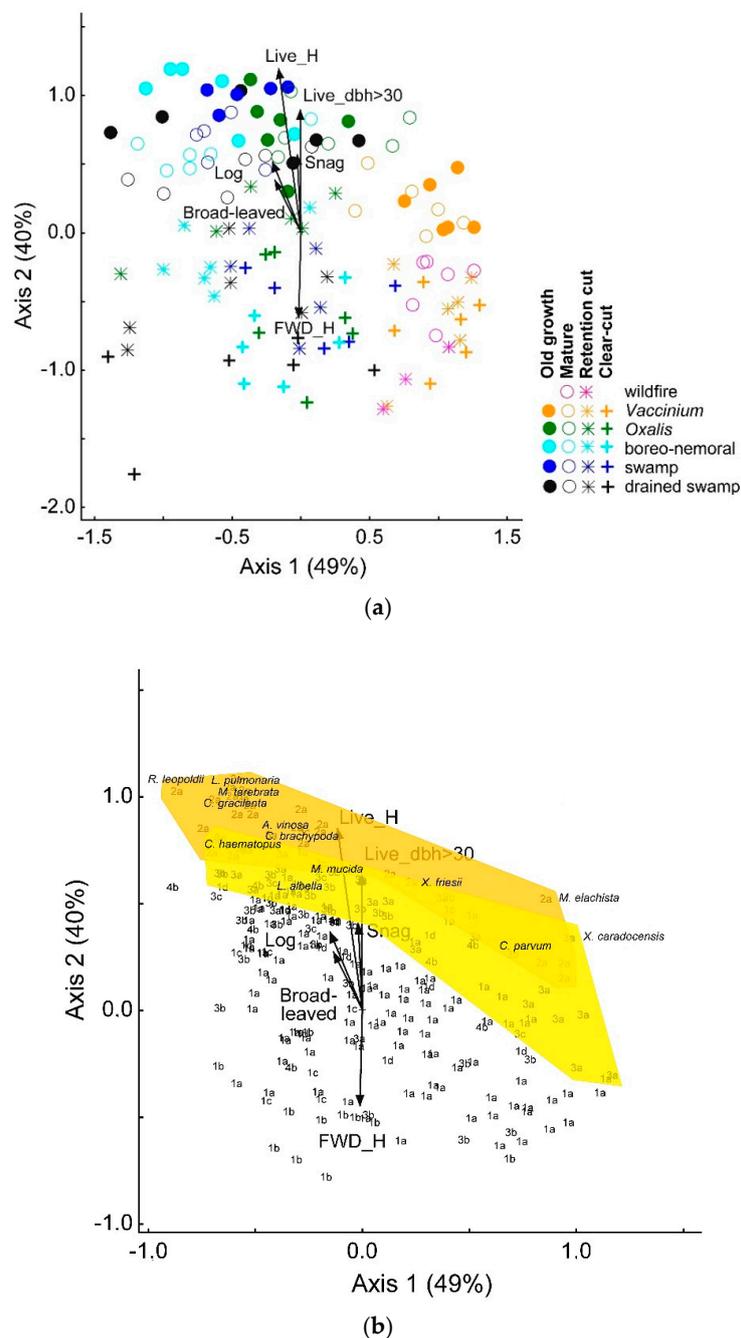


Figure 5. Nonmetric multidimensional scaling ordination diagram of lichen assemblages by forest habitat (a) and species centroids in the same ordination space (b). The arrows denote forest structural variables correlated with the axes ($r^2 \geq 0.2$): “Broad-leaved”, density of overstorey nemoral hardwoods; “Live dbh > 30”, density of trees with diameter at breast height >30 cm; “Live_H”, Shannon diversity of overstorey live trees; and “FWD_H”, Shannon diversity of fine woody debris. Snag abundance was measured as no. of trunks ha^{-1} ; abundance of logs (fallen or felled trunks ≥ 10 cm in diameter), and fine woody debris (<10 cm) as $\text{m}^3 \text{ha}^{-1}$. Graph (b) depicts species mostly at the scale of the tolerance category (cf. Figure 3a); colors indicate the space inhabited by old-growth species (orange, category 2a) and sensitive old-forest preferring species (yellow, category 3a), with species examples given.

A more direct contribution of stand structures on lichens of different management tolerance was revealed by analyses of actual substrate records. Expectably, the share of old-growth species and sensitive species was reduced on structures retained on cutovers, however, we noticed that this reduction also included a large loss of unknown species and was severest on dead-wood substrates (Figure 6). Considering the general scarcity of snags and live nemoral broad-leaved trees, their contribution to host such lichens appeared remarkable in old and mature stands. Live nemoral broad-leaved trees were also valuable post-harvest as compared with the whole species richness of nontolerant species found on live retention trees (Figure 6).

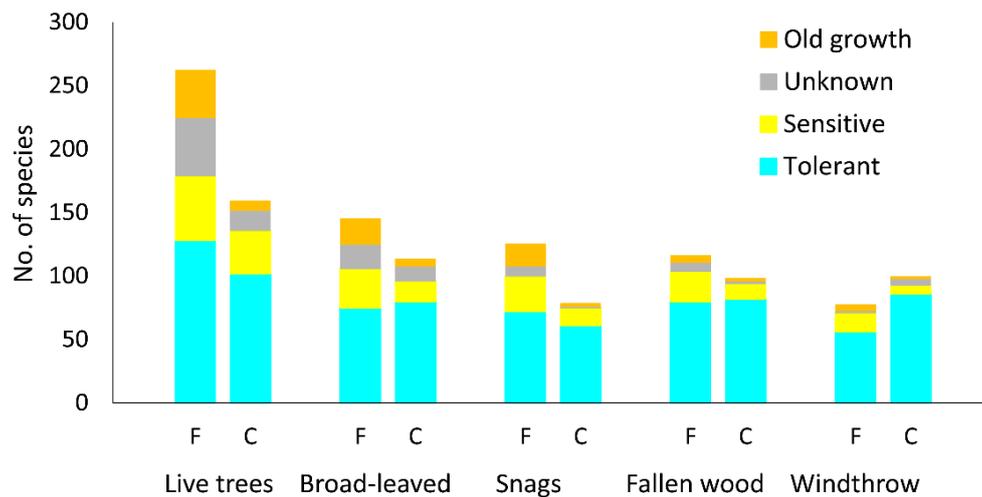


Figure 6. Total no. of lichen species by tolerance categories detected on five substratum types in old and mature forests (F, $n = 64$ plots) and cutovers (C, $n = 61$ plots). Note that live trees in cutovers refer to green-tree retention, and nemoral broad-leaved trees (*Acer*, *Fraxinus*, *Quercus*, *Tilia*, and *Ulmus*) are a subset of all live trees. In total, 330 species are included (95% to 99% in categories tolerant, sensitive, and old growth; 70% of unknown); those recorded but not included on the graph inhabit other substrates. See Figure 3 for the categorization.

Per every woodland key-habitat (WKH) species recorded in a plot there were several sensitive and unknown species present. However, the indicator quality of WKH species appeared best in mature managed stands, whereas they were poor in old-growth plots and relatively uninformative in retention-cut sites having none versus one to two WKH species (Figure 7).

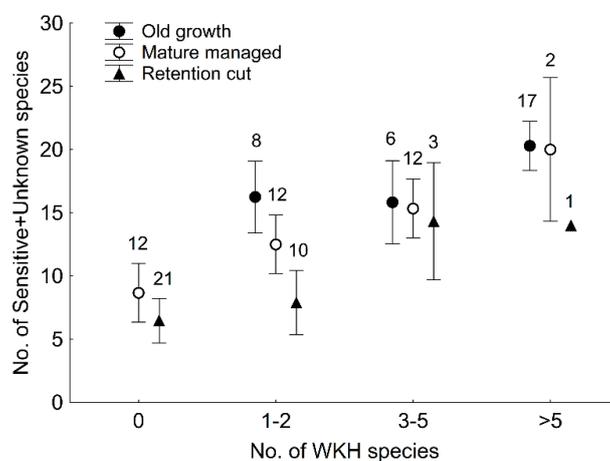


Figure 7. Mean numbers ($\pm 95\%$ CI) of sensitive and unknown species recorded per study plot depending on the number of woodland key habitat (WKH) species and forest management stage.

3.3. Life History Traits

Across recorded species, 70% were crustose, 75% had trebouxoid green algae as a photobiont, 87% had the ability of sexual (or mixed) dispersal, and 57% contained lichen substances (Table 1, Table S1). Differences in the distribution of these major traits among management tolerance categories were relatively small. Microlichens were most frequent among sensitive species, and particularly among inhabitants of retention trees and snags. Cyanolichens formed a minor part of all four tolerance categories. However, trentepohlioid algal symbionts (i.e., *Ulvophyceae*) were more common among old-growth species (24%, e.g., in genera *Arthonia*, *Alyxoria*, *Coenogonium*, *Opegrapha*, and *Pyrenula*); in other categories they formed <10%. The fact that lichen substances were less common among species grouped as “unknown” (in 40%) was apparently due to 25 species of lichenicolous and saprotrophic fungi in this category, while other categories only had four to 10 such species.

Table 1. Distribution of major life-history traits among the 369 lichen species in management-tolerance categories (Table S4 specifies their occurrence at plot level).

Tolerance	No. of Species									
	Thallus Type		Photobiont				Dispersal Mode		Lichen Substance	
	Macro-Lichens	Micro-Lichens	Trebouxio-Phyceae	Ulvophyceae	Cyano-Bacterium	Not Lichenized	Vegetative Only	Sexual or Mixed	Yes	No
Tolerant	59	91	130	7	5	8	19	131	104	46
Old growth	10	31	22	10	5	4	4	37	21	20
Sensitive	14	58	54	6	2	10	8	64	43	29
-retention	10	40	39	6	2	3	7	43	31	19
-snag	0	10	6	0	0	4	1	9	6	4
-ground	4	8	9	0	0	3	0	12	6	6
Unknown	27	79	70	7	4	25	16	90	43	63
Total	110	259	276	30	16	47	47	322	211	158

Note: Subgroups of the sensitive category refer to species' main substrate in the current dataset, and there is no species overlap among subgroups. The subgroup “ground” combines species growing on soil, logs, and stumps.

4. Discussion

4.1. The Lichen Diversity Potential of Production Forests

In production forests, certain lichen species and groups have been used to analyze specific limiting factors, such as old deciduous trees or stands in conifer-based forestry systems [51,77,78]; standing dead trees [15]; historical landscape connectivity [79]; and habitat functions of retention trees, buffer strips, and logging residues (e.g., [35,80]). Due to the vast fieldwork effort needed, stand-scale assessment of full assemblages has been rare [49,51,52,81], usually focusing on species richness rather than composition, and unrelated to species pool.

We compiled an extensive dataset on full assemblages to address this gap of knowledge. Our analyses demonstrate two expectable, but poorly documented broad patterns for forest conservation biology: (i) production forest stands vary widely in how much they host local forest species pools even in a single jurisdiction (cf. [81] for a between-region comparison), and (ii) this variation is at least partly due to the presence of management sensitive species and assemblages. For SFM, we interpret such biodiversity variation related to species sensitivity as the “potential” of production forests (both at stand and landscape scales) to achieve biodiversity conservation goals through management. Thus, based on actual species list, we can specify parts of the biota to be targeted: sensitive species by forest managers, old-growth species by reserve managers, and unknown species by the research community. Conceptually, targeting (the most) sensitive species is compatible with Lambeck’s treatment of “focal” species [54], but mapping of the whole species pool makes the approach more flexible. For example, political, administrative and owners’ decisions on different levels can determine what part of the sensitive species pool is addressed in production forests versus set-asides and at which spatial scale, and new research can add species targets from among currently unknown species.

Before elaborating lichen targets for SFM in terms of assemblages, species, ecological, and socioeconomic conditions, we critically review the distribution of species among management tolerance categories. Biodiversity sampling in limited areas overestimates the share of common species in the species pool (criteria 1a and 1c in our study, Figure 3a), since adding effort reveals increasingly rare species that also tend to be less tolerant of intensive silviculture. Low abundance *per se* can predispose populations to local extinction [82,83] and at least 16% of rarely found species in our study were additionally old-growth dependent (criterion 2b, note that the rest were labelled unknown). A rough correction to the observed management-tolerance proportions can be calculated based on the estimated 30% of the species pool not present in our sample [18] and the proportions in the lowest well-studied frequency class (Figure 3b, species found in six to 10 plots). Such calculation indicates a total species pool of ca. 530 species, with 30% tolerant, 30% sensitive, 16% old-growth, and 24% unknown species. If the latter comprises three-quarters of rare species (as in our sample), the true share of both tolerant and sensitive lichens should be around one-third of the total forest species pool in Estonia. Thus, a landscape-scale potential of production forests is to double the number of species sustained in intensive forestry systems (tolerant only) and, additionally, to contribute to the conservation of rare species (see below). Importantly, the stand-scale potential is smaller (given numbers of sensitive species <40% of tolerant numbers); this highlights a scale effect due to the fact that multiple stands contribute beta diversity, different sets of sensitive and infrequent species.

4.2. Reconceptualizing Old-Forest Lichens

Our research links a species-pool perspective on old-forest affinity of species with the practical task of conserving old-forest specialist species. Our Estonian study system has helped to replace a dichotomy between “old-forest species” vs. generalist species with a more nuanced assessment of habitat conditions present in a particular landscape matrix outside old-growth patches (e.g., [15,17]). We remind that most forest species have evolved in naturally dynamic landscapes where structural legacies blur clear segregation of biotic assemblages by successional stage at least throughout close-canopy stands [84]. Thus, the species currently found mostly in old forests represent an ecological continuum where one can distinguish at least four groups; this also reconciles different views on SFM versus forest protection by highlighting, simultaneously, the large number of species to be addressed, the high protection value of old growth, and the importance of close-to-nature silviculture in the matrix. In the Estonian lichen species pool, we can distinguish: (i) an estimated >15% of strictly old-growth dependent species, which in the current even-aged silvicultural setting are targeted by strict forest reserves [60] but some might be also conserved by introducing low-intensity selection cutting systems [59]; (ii) old-growth preferring species, which formed slightly less than half of all sensitive species, i.e., probably another 15% of the species pool. For these species, habitat conditions currently only develop in mature stands but, again, improved silviculture might create some of these conditions also in younger stands; (iii) species confined to old-forest legacies, another subset of sensitive species, which are now addressed mostly through retention forestry practices (e.g., [23,71,85]). Such species might comprise 3% to 5% of the species pool (we made no separate assessment but old-forest microhabitats dominated for the species distinguished by criterion 3c); and (iv) rarities concentrating to old growth through stochastic population and habitat processes, primarily because their colonies and substrates have much slower turnover times without harvest entries. Such rare species form an unspecified proportion of the total pool of unknown species, which may not require specific old growth structures and microclimate but have a higher probability of occurring there. Substrate turnover, as a limiting factor, also requires additional research; so far, we have documented, for example, how extensive loss of preharvest dead wood is masked by harvest-created dead wood in clear-cuts [86].

Adding up these proportions provides an estimate remarkably similar to a German assessment of >40% of epiphytic forest lichens being “bound to old-growth forests” and ca. 10% (also mostly old-growth dependent) being already extinct [87]. The extinction fact highlights that there is also a time factor involved. Production forests may become increasingly impoverished over subsequent

rotations and, conversely, lichen populations may seem viable in production forests where management has only recently intensified [88,89]. We recall that our study was carried out in contiguous forest landscapes on long-term forest lands. Small woods within agricultural landscapes may be further impoverished also in Estonia, specifically when these are new forests recently developed after land abandonment. In brief, we suggest that different estimates of old-forest lichen biota, ranging from the 1% “hemerophobic” epiphytic species in Finland in the 1950s [40] to >40% currently in Germany [87], largely reflect management intensities, not differently adapted species pools, at least in the European boreal and temperate forests. In other words, they reflect how much of the production-forest potential has been lost in different forest regions.

4.3. Addressing Rare Species in Forest Landscapes

Compared to their species richness, rare species (by localities and abundance) receive little attention as biodiversity targets of SFM as compared with old-growth and other high conservation-value forests and with habitat-providing structures, such as dead wood and retention trees (cf. [9,90,91]). Our key finding was that rare lichens (often also ecologically poorly known, criterion 4b) formed an astounding 20% of all recorded lichen species, and their true proportion is probably even larger in the unrecorded part of the species pool. Due to their few localities and poor knowledge, rarities may be the first to go extinct (often unnoticed) in intensive silviculture. Therefore, we propose that rare species form a distinct goal for biodiversity conservation in production forests—to identify, maintain, and enhance their localities, which may be critical for the whole population. Such a goal is shared with the reserve network goals across landscapes, and its distinct feature is that the focus of managers should be primarily on acquiring spatial information for planning. In this respect, it resembles the concept of woodland key habitats, which were originally suggested for cost-effective protection specifically of habitats of threatened species in Northern Europe [92]. However, key habitats were then adopted as a main policy instrument for habitat protection in production forests, including an interpretation (also in the case of lichens) that their main role is to complement forest reserves with habitats not protected in sufficient amount (e.g., [93]). These developments received both theoretical criticism [94,95] and field demonstration on lichens [33,89] that such small fragments cannot sustain viable populations in the long term.

We propose that the protection of rare species localities must stay in the toolkit of SFM and, perhaps, return to the root of the woodland key habitat concept and to the debate on whether indicator species can effectively reveal sites hosting threatened species [81,96,97]. Our answer to this question is a cautionary “yes”, given that the effort required to census rarities is much larger than available for most surveys. Our 4 h survey effort typically captures only 5% to 10% of occurrences of lichen species in a 2 ha plot, i.e., there can be viable populations even when the survey reveals only single records [59,98]. However, the detection of sites hosting multiple unknown species by key-habitat indicator species varied among management stages, for example, it was almost uninformative in the case of old-growth stands that are anyway most convenient to identify by stand structure (Figure 7). There is an urgent necessity to refine methods of mapping rare species’ localities in production forests [99,100], given also that forest certification schemes (such as FSC) actually oblige the certificate holders to do so [101].

5. Conclusions

Our study indicates that production forests form a heterogeneous and dynamic target for addressing the biodiversity conservation principle of SFM. Lichens have a role to play in this exercise globally, given their high diversity in forests, and specifically the number of management-sensitive and rare species. Our study constitutes one approach to simplifying the vast information on regional species pools for strategic understanding of the biodiversity conservation principle.

In practice, trade-offs involved in SFM are becoming more acute due to the globally growing demand for forest products and related intensification of silviculture on the one hand, and environmental degradation and climate change on the other hand [102,103]. In this setting, there must be next steps to

rapidly operationalize strategic reassessments of the biodiversity principle for management planning. On the basis of the original field data, and supported by other research on lichens and their habitats, we have compiled a preliminary list of “focal” lichen species *sensu* Lambeck [54], for planning and monitoring certain critical habitat qualities across multiple scales, from large forest reserves to the preservation of individual substrate items (Table 2, Figure S1).

Although our focal species list is directly applicable to the current even-aged forestry system in Estonia, its principles could be used more widely. One is that the number of species should stay manageable. Table 2 includes 2% of the Estonian forest lichen species; in a similar vein, we have proposed four focal polyporous fungi among ca. 230 known in Estonia [17]. Secondly, focal species selected based on sensitivity can be used for several planning purposes, depending on spatial allocation of conservation efforts and management changes. For example, some old-growth epiphytes (including *Lobaria pulmonaria* and *Menegazzia terebrata* on our list) can have viable populations also outside reserves in the case of low-intensity, continuous-cover forestry [104]. The delicate balance of habitat provision in such management systems is prone to even small (for example, market driven) intensity changes that can unexpectedly become threatening to small or slowly recovering populations. Hence, reserve networks should be planned with a “buffering” function also for those species that in a given time may seem to have viable populations throughout landscapes.

Table 2. Proposed focal lichens and allied fungi for guiding sustainable forest management (based on even-aged forestry system) and forest reserve management in Estonia.

Species (Ecological Group)	Limiting Process	Proposed Target	References
Old-Growth dependent species in protected forests			
<i>Lobaria pulmonaria</i> (epiphytic macrolichen)	Dispersal/establishment	Spatio-temporal connectivity of nemoral broad-leaved trees and aspen in reserves	[42,77,96,105–108]
<i>Menegazzia terebrata</i> (epiphytic macrolichen)	Air moisture and quality	Hydrologically intact semi-open moist and wet forests	[16,105,109,110]
<i>Chaenotheca gracilentia</i> (epixylic microlichen)	Microhabitat	Supply of shady moist microhabitats on dying and uprooted old trees in reserves	[15,43,50,105]
<i>Xylopsora friesii</i> (epiphytic/epixylic microlichen)	Disturbance regime	Conifer forests with continuity of small-scale disturbances and slow-grown old trees	[46,111]
Species sensitive to reduced rotations and functioning of mature production stands			
<i>Arthonia vinosa</i> (epiphytic microlichen)	Microhabitat and –climate	Mature species-rich moist and wet forests	[16,42,46,81,105]
<i>Chaenotheca brachypoda</i> (epiphytic/epixylic microlichen)	Microhabitat	Supply of senescent trees with bark and wood crevices in close-canopy stands	[15,43,50,105]
<i>Chaenothecopsis haematopus</i> (saproxylic calicioid fungus)	Fungal tree pathogens	Soft exposed wood on deciduous trees that die standing	[15,43,112]
<i>Calicium parvum</i> (epiphytic microlichen)	Pine management	Landscape-scale continuity of mature pine stands	[15,88,105]
<i>Multiclavula mucida</i> (epixylic basidiolichen)	Full decay cycles of fallen trees	Supply of well decayed large trunks in close-canopy stands	[105]
Species dependent on retention forestry			
<i>Lecanora albella</i> (epiphytic microlichen)	Late-successional tree species	Supply of mid-aged or old nemoral broad-leaved trees in close-canopy stands	[59]
<i>Leptogium saturninum</i> (epiphytic macrolichen)	Stable pool of mature aspens	Stand-scale continuity of mature aspen trees hosting the lichen	[105,113]

Note: See Figure 5b for habitat positions of the selected species in the assemblage ordination space.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/10/12/1063/s1>, Table S1: Species list, Table S2: Results of MRPP test, Table S3: Pearson and Kendall correlations of structural variables with ordination axes, Table S4: Mean number of species per 2 ha plots, and Figure S1: Photos of proposed focal lichen species.

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