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Will forest conservation areas protect functionally important diversity of fungi and lichens over time?

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Abstract Incorporating functional values in biodiversity monitoring systems could add novel perspectives of the status of biodiversity in conservation areas. Stable frequencies of large foliose nitrogen-fixing cyanolichens likely have positive effects on the nitrogen budget of forests and provide food, material and shelter for invertebrates, gastropods and birds. Stable volumes of deadwood and frequencies of associated fungi provide an important supporting function for ecosystem services such as nutrient cycling, carbon storage and soil formation. Based on regional monitoring data from boreal old-growth forest nature reserves and key habitats, we tested for changes in the frequency of various functionally important substrates and species over time. We detected significant reductions in the frequency of indicator cyanolichens occurring on deciduous trees already after 10 years in key habitats, despite non-significant changes in their host substrates. Frequencies of indicator pendulous lichens *Alectoria sarmentosa* and *Bryoria nadvornikiana* had also decreased in key habitats, despite overall stable volumes of large conifer host trees. Lichen reductions were more pronounced in the smaller key habitats compared to the larger formally protected nature reserves, likely due to degrading fragmentation and isolation effects. In contrast to these lichens, the average frequencies of old-growth forest indicator fungi decaying coniferous deadwood and common fungi on deciduous trees

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(*Fomes fomentarius*) and coniferous trees (*Fomitopsis pinicola*) remained unchanged. The studied cyanolichens and fruiting fungi generally had similar extinction rates over 10 years, whilst only cyanolichens had substantially lower colonization rates. Amid a severely fragmented landscape, conservation areas seem to struggle in preserving some of the basic old-growth forest values.

Introduction

Environmental managers are under increasing pressure to monitor the effectiveness of different conservation areas in safeguarding biodiversity (Geldmann et al. 2013). This is because international biodiversity conservation strategies rely heavily on protected areas and other complementary set-aside conservation areas (e.g., the Convention on Biological Diversity and the EU Habitat Directive). Conservation areas are also the foundation on which regional conservation strategies are built, where their basic role is to represent the biodiversity of the region and protect both natural values and ecosystem services from the processes that threaten their existence (e.g., Brooks et al. 2004; Rodrigues 2006; Jenkins and Joppa 2009; Butchart et al. 2010). A recent systematic review highlighted that evidence remains limited and inconclusive concerning the impact of protected areas on habitats and different taxonomic groups, although more positive than negative results generally are reported in the literature (Geldmann et al. 2013). The latter authors further highlight that there is very little quantitative understanding of the conditions (e.g., management regimes, types of conservation areas) under which protected areas succeed or fail to deliver conservation outcomes. Moreover, biodiversity in conservation areas have rarely been linked to the range of functions the organisms perform in communities and ecosystems; i.e., their functional values and ecosystem services (functions or processes directly beneficial to humans) (Chan et al. 2006; Egoh et al. 2007).

Forests provide a wealth of goods and services to society that is largely dependent on functions performed by organisms (Millennium Ecosystem Assessment 2005; Cardinale et al. 2011; Gamfeldt et al. 2013). Recent studies show that higher species diversity promotes a range of ecosystem functions under both experimental conditions (Balvanera et al. 2006; Cardinale et al. 2011) and in forest ecosystems at scales relevant to management (Gamfeldt et al. 2013). Given the typically high biodiversity in forest conservation areas, one may hypothesize that these areas also support a greater functional diversity, defined as 'the value and range of those species and organismal traits that influence ecosystem functioning' sensu Tilman (2001). For instance, higher levels of multiple ecosystem functions are found in forests with more tree species (Gamfeldt et al. 2013). The presence of large and old trees in conservation areas do not only regulate climate, soil conditions and water regimes, but also provide supporting services such as photosynthesis, soil formation, nutrient cycling and habitat for flora and fauna (e.g., Lindenmayer et al. 2012). Dead trees influence nutrient cycling, carbon storage and soil formation (Janisch and Harmon 2002), and provide habitat and food for a diversity of forest-dwelling organisms (Stokland et al. 2012; Siitonen 2001), and has therefore been defined as an indicator for supporting ecosystem services in Swedish forests (Hansen et al. 2014). Still,

the flow of ecosystem functions is complex and may not always align well with high biodiversity and biodiversity conservation goals (e.g., Chan et al. 2006; Wardle and Jonsson 2010). High species richness may not directly translate to high functional diversity, if there is a high degree of redundancy in the community (Díaz and Cabido 2001). Hence, the composition and abundance of the species in the community will also determine functional values. Incorporating functional values in existing conservation area biodiversity monitoring would, nevertheless, add novel perspectives on the status of biodiversity.

One way to incorporate functional values is to group and monitor species by their functional traits, which directly link the organisms' performance to environmental conditions (Violle et al. 2007). Response traits determine how organisms respond to environmental factors (e.g., epiphytic lichen growth form or photobiont type in relation to bark properties and stand structure) and effect traits influence ecosystem functioning (e.g., lichen photobiont type influencing photosynthesis and nitrogen fixation) (Lavorel and Garnier 2002; Díaz and Cabido 2001; Violle et al. 2007). A functional response-and-effect group (or guild) is a collection of organisms with similar suites of co-occurring traits, and with subsequent similar responses to environmental factors and effects on ecosystem functions (e.g., de Bello et al. 2010). By examining changes in the relative frequency of individuals belonging to various functional groups (e.g., saprotrophic fungi causing rot in coniferous logs) or single functionally important species, the maintenance of biodiversity is also linked to its functionality (e.g., deadwood decomposition).

In this study, we investigated which changes in the frequency of various functionally important substrates and species that have taken place after 10 years, in 15 boreal forest nature reserves and 17 key habitats in central Sweden. We hypothesized that changes in frequencies of substrates and species may be more pronounced in small key habitats compared to larger nature reserves, due to small population sizes and degrading effects of fragmentation in small and isolated habitats (Fedrowitz et al. 2012; Nordén et al. 2013). We aimed to test which quantitative changes that have occurred for five structural components (i) large old trees, (ii) total tree volumes, (iii) tree species richness, (iv) deadwood, and (v) tree sapling regeneration, and several species groups or species (vi) indicator species of old-growth forests (vii) old-growth forest indicator cyanolichens occurring on deciduous trees, (viii) two old-growth forest indicator pendulous lichens on coniferous trees, (ix) old-growth forest indicator and common saprotrophic fungi decaying coniferous deadwood, and (x) common parasitic and saprotrophic fungi on deciduous trees (*Fomes fomentarius*) and coniferous trees (*Fomitopsis pinicola*). We also tested which stand and substrate factors that affect changes in the frequency of these species and groups of species. Lastly, we provided colonisation and extinction rates for functional groups and individual species, which represent important population-level data needed when modelling population viability of organisms.

Materials and methods

The study forests and field work

The boreal forest landscape in the study region in central Sweden (counties of Dalarna and Gävleborg, about 100 km around 61.18°N, 15.12°E) is strongly influenced by modern forestry, and characterized by even-aged monocultures of conifers, few old trees, and low amounts of deadwood. Old-growth forest remnants are typically few and small, occurring

isolated in a matrix of managed forests. As part of a biodiversity monitoring programme of fragmented forests of high conservation value, we surveyed a random set of 15 formally protected nature reserves (average size 58 ha and median size 13 ha) and 17 key habitats (average size and median size 6 ha) of old-growth forest dominated by Norway spruce (*Picea abies*) and with Scots pine (*Pinus sylvestris*) and deciduous trees as subordinate species (Table 1, Online Resource 1a). In Fennoscandian and Baltic forests, small-scaled hotspots of biodiversity (i.e., key habitats) are set aside from forestry as an essential complementary component of biodiversity conservation (Timonen et al. 2010). The Swedish key habitat inventory is one of the world's largest conservation inventories ever conducted, with approximately 87,000 key habitats (mean size 4.6 ha) inventoried and delineated (Nitare 2011). Key habitats are hotspots for deadwood, species richness, and a number of red-listed species (Timonen et al. 2011).

All surveys were conducted in 1998–2000 and repeated after 10 years in 2009–2011 in the months August–October. No weather anomalies were recorded. Prior to the field work, north–south and west-east linear transects were drawn on maps of the entire area of the nature reserve or key habitat to form a transect grid, based on a random starting distance (obtained by multiplying a random number between 0 and 1 with the distances between transects, T) from the western-most point and with distances between transects (T) proportional to the total forest area expressed in m^2 (A); i.e., $T = (A/8)^{1/2}$. Permanent north–south or west-east linear transects were randomly established along the longest length of the each conservation area and marked with aluminium poles. The 14 m wide linear transects started and ended at the borders, and were divided into 10 m segments. In conservation areas smaller than 3 ha every other segment was surveyed throughout the entire transect length. If the distance between transects (T) was greater than 60 m (i.e., when the area is >3 ha) only 30 m before and 30 m after each grid intersection point was surveyed, creating gaps in the surveyed linear transects. The distance between the central points of the surveyed 60 m segments equalled the distance between transects (T). A total of 892 segments were surveyed in reserves, comprising on average 6 % of the total reserve area. A total of 698 segments were surveyed in key habitats, comprising on average 17 % of the total set-aside area. On each segment, living and dead trees were measured and surveyed for associated fungi and lichens. Tree species, diameter at breast height (DBH; diameter 1.3 m above ground) and height was registered for large old living trees considered to be of high conservation value. We defined large old trees as: living birch (*Betula* spp.) with a DBH ≥ 30 cm, goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) with a DBH ≥ 10 cm, all other deciduous tree spp. with a DBH ≥ 15 cm, and coniferous trees with a DBH ≥ 35 cm. All dead standing trees with a DBH ≥ 15 cm, as well as cut stumps (diameter at cut surface ≥40 cm) and natural stumps <1.3 m in height, were also

Table 1 Basic data on the study forest nature reserves and key habitats and survey effort

Type of conservation area	No. of areas	Size (ha)	No. of belt transects	No. of transect segments	Transect area (ha)	No. of circular plots	Circular plot area (ha)
Nature reserves	15	57.7 ± 103.4	3.9 ± 0.9	59.5 ± 41.1	0.8 ± 0.6	5.7 ± 4.5	0.09 ± 0.07
Key habitats	17	5.6 ± 4.5	4.1 ± 1.6	40.6 ± 14.3	0.6 ± 0.2	3.7 ± 1.0	0.06 ± 0.02

Showing the number of conservation areas surveyed and mean values with ± standard deviations

measured and surveyed for fungi and lichens. All logs, i.e. fallen dead trees, with a diameter ≥ 10 cm at the thickest end were surveyed, if their thickest end was situated within the segment. We registered tree species and measured total length and diameter at the thickest and thinnest end for each log.

To obtain a more detailed quantitative description of the forest stand structure and tree regeneration; i.e., total tree volumes and species richness (DBH $\geq$ 10 cm), number of saplings and sapling tree species richness (DBH < 10 cm), circular sample plots with a radius of 7 m were placed at the centre points of every other grid intersection and marked with an aluminium pole, comprising on average 4 circular plots per conservation area (Table 1). A total of 85 and 63 circular plots were surveyed in reserves and key habitats, respectively. Tree species and DBH were registered for all living trees ≥ 1.3 m in height. Trees with a DBH < 4 cm were all recorded as 2 cm DBH.

The volume of living trees was estimated based on DBH and height, using height functions according to Söderberg (1992). Broken stem and stump volumes were calculated as a cylinder. Log volume equations were based on diameters at the thickest and thinnest ends and length, using Smalian's formulae (Smalian 1837).

Study species and functional groups

On each substrate located within the transect segments, we registered the presence of a subset of fungi and lichens that indicate high conservation values and old-growth such as long-term continuity of old trees and deadwood, and naturalness of the forest (Table 2). These indicator species (two bryophytes, 14 lichens and 16 wood fungi) were also used during the key habitat inventory (e.g., Norén et al. 1995; Nitare 2000). We focused on indicator species as a group, since there is no single species that alone would be a good indicator for the total species pool (Halme et al. 2009; Junninen and Komonen 2011) and functional diversity, and because the frequencies of individual species were generally low (Table 2, Online Resource 1b). From the indicator species surveyed, we distinguished two groups of species with similar suites of co-occurring functional traits and associations with a specific substrate type: (i) photoautotrophic foliose cyanolichens occurring on living deciduous trees, and (ii) saprotrophic fungi decaying coniferous deadwood. Cyanolichens have a cyanobacterium (*Nostoc*) as photosynthesizing partner, contributing to the photosynthesis and the nitrogen budget of forest ecosystems through nitrogen fixation (Antoine 2004; Sillett and Antoine 2004). These relatively large foliose lichens also provide shelter and food for invertebrates, as well as nesting materials for birds (Sillett and Antoine 2004). Their conservation status is strongly linked to the status of large old deciduous trees, the disappearance of old-growth forests, and changes in tree species composition (Gärdenfors 2010). Wood-decaying saprotrophic fungi play a fundamental role in forest nutrient cycling (Junninen and Komonen 2011; Heilmann-Clausen et al. 2015), influencing carbon storage and soil formation. They enhance habitats for a succession of other fungi and organisms (Ottosson et al. 2014; Heilmann-Clausen et al. 2015). Their conservation status is strongly linked to the availability and quality of deadwood, and the disappearance of old-growth forests (Gärdenfors 2010; Junninen and Komonen 2011).

We also registered the presence of three perennial polyporous fungi that are common in the boreal forest: *F. fomentarius* on deciduous trees, and *F. pinicola* and *Trichaptum abietinum* associated with coniferous trees and deadwood. Although they may occasionally occur on other tree species, *F. fomentarius* is mostly associated with birch trees *Betula* spp. and *F. pinicola* and *T. abietinum* with Norway spruce *P. abies* in the studied forests. These three species were sufficiently frequent to be analyzed individually as (i) a common

Table 2 Descriptive data of the study species and functional groups, including data on colonisation and extinction rates

Scientific name	Organism description including fruit-body lifespan for fungi	Host substrate preference	Ecology	Functional group	Occupied stands 1st survey	Occupied stands 2nd survey	No of records 1st survey	No of records 2nd survey	No of records ha^{-1} 1st survey	No of records ha^{-1} 2nd survey	Area-relative Ext rate	Area-relative Col rate
Fomes fomentarius	Polyporous perennial fungi	Deciduous	Parasitic/saprotrophic	PD	31	33	300	346	13.477	15.544	0.180	0.135
Fomitopsis pinicola	Polyporous perennial fungi	Coniferous	Parasitic/saprotrophic	PC	29	32	157	190	7.053	8.535	0.090	0.180
Trichaptum abietinum	Polyporous perennial fungi	Coniferous	Saprotrophic	WD	31	32	189	169	8.491	7.592	0.180	0.135
Phellinus viticola (NT)	Polyporous perennial fungi	Coniferous	Saprotrophic	WDI	19	21	52	62	2.336	2.785	0.225	0.314
Leptogium saturninum	Foliose cyanolichen	Deciduous*	Epiphytic	CB	14	13	90	40	4.043	1.797	0.090	0.045
Parmeliella triptophylla	Foliose cyanolichen	Deciduous*	Epiphytic	CB	11	11	76	56	3.414	2.516	0.090	0.090
Phellinus nigrolimitatus (NT)	Polyporous perennial fungi	Coniferous	Saprotrophic	WDI	6	9	24	19	1.078	0.854	0.090	0.225
Nephroma bellum	Foliose cyanolichen	Deciduous*	Epiphytic	CB	9	8	46	24	2.066	1.078	0.090	0.045
Lobaria pulmonaria (NT)	Foliose cyanolichen**	Deciduous*	Epiphytic	CB	8	7	61	41	2.740	1.842	0.045	0.000
Leptoporus mollis (NT)	Polyporous annual fungi	Coniferous	Saprotrophic	WDI	2	6	4	7	0.180	0.314	0.045	0.270
Phellinus pini (NT)	Polyporous perennial fungi	Coniferous***	Parasitic/saprotrophic	NA	2	6	5	8	0.225	0.359	0.090	0.135
Collema subnigrescens (NT)	Foliose cyanolichen	Deciduous*	Epiphytic	CB	5	5	30	19	1.348	0.854	0.045	0.045

Table 2 continued

Scientific name	Organism description including fruit-body lifespan for fungi	Host substrate preference	Ecology	Functional group	Occupied stands		No of records		No of records ha^{-1}		Area-relative	
					1st survey	2nd survey	1st survey	2nd survey	1st survey	2nd survey	Ext rate	Col rate
Phellinus ferrugineofuscus (NT)	Polyporous perennial fungi	Coniferous	Saprotrophic	WDI	8	5	16	7	0.719	0.314	0.270	0.090
Anastrophyllum hellerianum (NT)	Bryophyte	Deciduous*	Saproxylic deadwood	NA	6	4	24	12	1.078	0.539	0.135	0.045
Nephroma parile	Foliose cyanolichen	Deciduous*	Epiphytic	CB	8	4	25	9	1.123	0.404	0.270	0.090
Phellinus chrysoloma (NT)	Polyporous perennial fungi	Coniferous	Parasitic/ saprotrophic	NA	8	4	15	5	0.674	0.225	0.225	0.045
Antrodia pulvinascens (NT)	Polyporous annual to perennial fungi	Deciduous	Saprotrophic	NA	0	3	0	5	0.000	0.225	0.000	0.135
Fomitopsis rosea (NT)	Polyporous perennial fungi	Coniferous	Saprotrophic	WDI	3	3	9	5	0.404	0.225	0.045	0.045
Inonotus rheades	Polyporous annual fungi	Deciduous	Saprotrophic	NA	4	3	11	5	0.494	0.225	0.135	0.090
Asterodon ferruginosus (NT)	Corticoid annual fungi	Coniferous	Saprotrophic	WDI	3	2	4	2	0.180	0.090	0.045	0.045
Climacocystis borealis	Polyporous annual fungi	Coniferous	Parasitic/ saprotrophic	NA	1	2	2	2	0.090	0.090	0.045	0.090
Collema spp.	Foliose cyanolichen	Deciduous*	Epiphytic	CB	8	2	33	2	1.482	0.090	0.359	0.090
Lobaria scrobiculata (NT)	Foliose cyanolichen	Deciduous*	Epiphytic	CB	2	2	4	3	0.180	0.135	0.045	0.045
Nephroma resupinatum	Foliose cyanolichen	Deciduous*	Epiphytic	CB	2	2	4	2	0.180	0.090	0.090	0.090

Table 2 continued

Scientific name	Organism description including fruit-body lifespan for fungi	Host substrate preference	Ecology	Functional group	Occupied stands		No of records		No of records ha⁻¹		Area-relative	
					1st survey	2nd survey	1st survey	2nd survey	1st survey	2nd survey	Ext rate	Col rate
Cladonia parasitica (NT)	Fruticose lichen	Coniferous	Saproxylic deadwood	NA	4	1	53	1	2.381	0.045	0.135	0.000
Collema furfuraceum (NT)	Foliose cyanolichen	Deciduous*	Epiphytic	CB	0	1	0	2	0.000	0.090	0.000	0.045
Cystostereum murraii (NT)	Corticoid perennial fungi	Coniferous	Saprotrophic	WDI	1	1	1	1	0.045	0.045	0.000	0.000
Neck era pennata (NT)	Bryophyte	Deciduous*	Epiphytic	NA	1	1	2	3	0.090	0.135	0.000	0.000
Phellinus populicola (NT)	Polyporous perennial fungi	Deciduous*	Parasitic/saprotrophic	NA	1	1	1	1	0.045	0.045	0.045	0.045
Trichaptum laricinum (NT)	Polyporous perennial fungi	Coniferous	Saprotrophic	WDI	1	1	6	1	0.270	0.045	0.000	0.000
Artomyces pyxidatus (NT)	Annual coral fungi	Deciduous*	Saprotrophic	NA	1	0	3	0	0.135	0.000	0.045	0.000
Collema flaccidum	Foliose cyanolichen	Deciduous*	Epiphytic	CB	1	0	1	0	0.045	0.000	0.045	0.000
Collema subflaccidum (EN)	Foliose cyanolichen	Deciduous*	Epiphytic	CB	1	0	1	0	0.045	0.000	0.045	0.000
Hericium coralloides (NT)	Annual coral fungi	Deciduous*	Saprotrophic	NA	1	0	1	0	0.045	0.000	0.045	0.000
Nephroma laevigatum (VU)	Foliose cyanolichen	Deciduous*	Epiphytic	CB	1	0	1	0	0.045	0.000	0.045	0.000
All indicator species pooled				WDI, CB, NA	33	31	605	344	27.179	15.454	2.920	2.156
Wood decaying indicator saprotrophic fungi on coniferous deadwood		WDI			23	25	116	104	5.211	4.672	0.764	0.988

Table 2 continued

Scientific name Organism description including fruit-body lifespan for fungi	Host substrate preference	Ecology	Functional group	Occupied stands		No of records		No of records ha^{-1}		Area-relative	
				1st survey	2nd survey	1st survey	2nd survey	1st survey	2nd survey	Ext rate	Col rate
Nitrogen fixing foliose cyanolichens on deciduous living trees			CB	20	18	372	198	16.712	8.895	1.258	0.584

The fungi and lichens recorded in transects, the organism type, associated host substrate type, ecology, functional group (*NA* no applicable functional group except the indicator group), the number of occupied forest conservation areas, the total number of records, the number of records per hectare, and the number of extinction and colonisation events per hectare recorded after 10 years in reserves and key habitats pooled. Red-list status in brackets according to Artdatabanken (2015). * Excluding *Betula* spp. ** *Lobaria pulmonaria* is a cephalolichen composed of both an ascomycete, a green algae (*Dictyochloropsis*), and a cyanobacteria (*Nostoc*) but was included in the cyanolichen group. *** *Pinus sylvestris*. Sorted in order of frequency in the 2nd survey. Data from pendulous lichens in circular plots are not included in the Table

parasitic and saprotrophic fungi on deciduous trees (*F. fomentarius*), (ii) a common parasitic and saprotrophic fungi on spruce trees (*F. pinicola*), and as (iii) a common saprotrophic primary fungi decaying spruce deadwood (*T. abietinum*). *F. fomentarius* and *F. pinicola* are important tree-mortality agents and saprotrophic fungi that influence forest structure and succession, e.g. influencing deadwood dynamics, creating habitat and canopy gaps for several other organisms. *T. abietinum* is an important primary species with a large effect on the succeeding fungal communities in decaying Norway spruce logs (Ottosson et al. 2014). We registered only one occurrence of each species on each substrate, even if several fungal sporocarps or lichen boles were present.

In the first quadrant surveyed of each circular plot, we registered the number of Norway spruce trees occupied by two indicator pendulous lichens *Alectoria sarmentosa* and *Bryoria nadvornikiana*. These pendulous lichens are abundant in boreal old-growth forest canopies and play important functional roles (Esseen et al. 1996). They indicate conifer old-growth forest continuity, provide shelter and food for canopy-living invertebrates, winter forage for reindeer (Kivinen et al. 2010), as well as nesting materials for birds and critical fodder for overwintering passerine birds (Pettersson et al. 1995).

Statistical analysis

We used paired t-tests to test for significant changes in mean frequencies in reserves and key habitats after 10 years. We used Wilcoxon paired tests to examine differences between the groups' mean ranks for non-normally distributed data. We tested for (i) volumes of large old coniferous and deciduous trees (m^3 ha^{-1}), (ii) total tree volumes (m^3 ha^{-1}, DBH $\geq$ 10 cm), (iii) tree species richness (number of tree species with a DBH $\geq$ 10 cm per circular plot), (iv) volume of deadwood (m^3 ha^{-1}, all with a DBH or thicker-end diameter $\geq$10 cm), (v) number of tree saplings (young trees) per hectare ($\geq$1. 3 m height and DBH < 9 cm), (vi) sapling species richness per circular plot, (vii) number of Norway spruce trees occupied by *A. sarmentosa* and *B. nadvornikiana* per hectare, (viii) total number of old-growth forest indicator species per hectare, (ix) number of indicator cyanolichens on deciduous trees per hectare, (x) number of saprotrophic indicator fungi on coniferous deadwood per hectare (xi) number of *F. fomentarius* on deciduous trees per hectare, (xii) number of *F. pinicola* on coniferous trees per hectare, and (xii) number of *T. abietinum* on coniferous deadwood per hectare.

If a significant change in the mean frequency of a functional group or species was detected (only significant negative mean changes were detected in the study), we performed additional analyses aiming to identify the variables that explained the probability of the change. As above, we hypothesized that declining frequencies of the species and groups of species may be more pronounced in key habitats compared to larger formally protected nature reserves. The richness and composition of bryophytes and lichens have been shown to differ between key habitats and reserves (Perhans et al. 2007), but the capacity of smaller key habitats to maintain their original species composition and support species persistence over time remains unknown (Timonen et al. 2011). We propose that increasing volumes of large old host trees will have a positive influence on the frequency of the species over time (e.g., Esseen et al. 1996; Lie et al. 2009; Fedrowitz et al. 2012).We used general linear models GLMs) to predict mean frequency changes over 10 years based on (i) conservation area type (reserve versus key habitat), (ii) conservation area size (hectares), (iii) the mean volume of living host trees per hectare based on both surveys, (iv) the change in the volume of living host trees per hectare over 10 years, and (v) the change in the volume of large coniferous trees (DBH $\geq$ 35 cm) per hectare over 10 years. For

cyanolichens, we examined volumes of *Populus tremula* (DBH $\geq$ 15 cm) and *Salix caprea* (DBH $\geq$ 10 cm) in segments. For pendulous lichens, we examined volumes of large old *P. abies* trees (DBH $\geq$ 35 cm) in circular plots. Changes in the volume of large canopy trees of shade tolerant Norway spruce could potentially reduce the light availability within the forests (i.e., act as a proxy for changes in light availability). Given that many lichens are sensitive to light availability (Gauslaa et al. 2007; Ellis 2012), we hypothesized that changes in the volume of large old conifer trees may influence lichen frequencies over time. No explanatory variables were strongly correlated. Candidate models were evaluated using corrected Akaike's Information Criteria (AICc), allowing us to determine which models, and hence predictors, were best supported by the data (Burnham and Anderson 2002). We report the difference in AICc (ΔAICc) between the candidate models and the null model. For ΔAICc $\leq$ 2, the level of empirical support for the candidate model is higher than for the null model (Burnham and Anderson 2002). The regressions were done in R 3.2.2 (R Development Core Team 2013).

As an additional measure of functionality, area-relative colonization and extinction rates were calculated for all individual species and functional groups within segments by dividing the number of colonizations and extinctions per conservation area and 10-year period with the area inventoried (ha^{-1}). Colonisation and extinction data has rarely been published for cryptogamic species but provide important population-level data needed when modelling population growth or decline of organisms (e.g., Akçakaya and Sjögren-Gulve 2000). It is important to notice that rates for fungi only refer to colonization and extinction rates of fungi that have been successful in sexual reproduction and formed sporocarps (fruiting bodies), which could be considered a proxy for fitness. High quality conservation areas will likely function as source habitats with growing populations, if colonisation rates are greater than extinction rates, or vice versa for low quality areas.

Results

Functionally important forest structures

The study forests largely maintained important key structures over the 10 year study period, as surveyed in transect segments (Fig. 1a) and circular plots (Fig. 1b). The mean volume of large conifers (DBH $\geq$ 35 cm) increased from 71 to 82 m^3 ha^{-1} in reserves, whilst no significant volume change was detected for key habitats. The mean volume of birch trees *Betula* spp. had near-significantly (P $\leq$ 0.055) decreased in circular plots in both reserves and key habitats, whilst volumes of deciduous trees excluding birch trees had increased slightly in reserves from 19 to 21 m^3 ha^{-1} (Fig. 1b). The mean number of saplings underwent a near-significant decline (P = 0.057) from 92 to 80 saplings ha^{-1} in reserves (Fig. 1b). The mean tree species richness per circular plot did not change over time for saplings with a DBH < 10 cm (mean both surveys reserves = 0.72 and key habitats = 0.96, $t_{dfs\ =\ 14,16} \leq -1.0$, P $\geq$ 0.332) or trees with a DBH $\geq$ 10 cm (mean both surveys reserves = 0.76 and key habitats = 1.11, $t_{dfs\ =\ 14,16} \leq 0.43$, P $\geq$ 0.672). Mean volumes of standing deadwood had increased in key habitats (Fig. 1a).
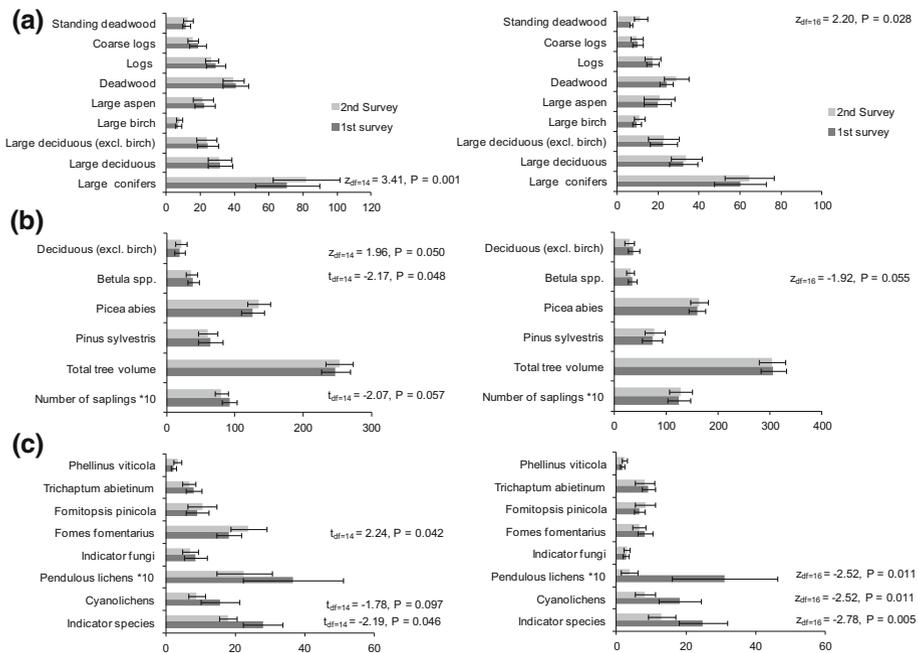
Fig. 1 Mean volumes of different structural variables per hectare based on **a** transect segments and **b** circular plots, in nature reserves (*left panel*) and key habitats (*right panel*) in the 1st and 2nd surveys; the *bars* represent the standard errors. **b** Also includes number of saplings per hectare, divided by 10. Tree diameters as described in the method section, and coarse logs with a thickest-end diameter >25 cm. Mean frequency of functionally important species and species groups (**c**), expressed as the number of occupied substrates per hectare on transect segments (except pendulous lichens inventoried in a quadrant of circular plots) in reserves (*left panel*) and key habitats (*right panel*) in the 1st and 2nd surveys; the *bars* represent the standard errors. The frequency of pendulous lichens per hectare was divided by 10 in order to be displayed in the same graph. Paired *t* test or Wilcoxon z-test statistics are given for near significant and significant variables with P < 0.1

Functional groups and species

The total mean frequency of indicator species decreased significantly in reserves and key habitats over 10 years (Fig. 1c). Frequencies of cyanolichens on deciduous trees and pendulous lichens on *P. abies* trees decreased significantly in key habitats, whilst no such significant reduction was detected for nature reserves (Fig. 1c). The mean frequency of *F. fomentarius* increased in reserves, but no significant change in mean frequency was detected for other fungi (Fig. 1c). This reduction in lichen frequencies but not fungi was reflected in the lower mean colonisation rate of 0.045 colonisations per hectare for individual cyanolichens compared to 0.124 colonisations per hectare for individual indicator fungi (Table 2). In contrast, average extinction rates were more similar with 0.097 extinctions per hectare for cyanolichens and 0.090 extinctions per hectare for individual saprotrophic fungi.

From the GLM, the probability of an increasing mean frequency of cyanolichens was higher in conservation areas with lower mean volumes of host trees and increasing host tree volumes over time (Table 3). The change in host tree volume was a significant

Table 3 Set of candidate models (ΔAICc ≤ 4) ranked by Akaike weights (AIC wt, the relative likelihood of the model given the data) for mean frequency changes of cyanolichens and pendulous lichens in nature reserves and key habitats after 10 years

Functional group	Model	Intercept	Conserv. area (reserve)	Average volume host trees	Change in volume deciduous host trees	Change in volume large old conifers	Conserv. area size	df	AICc	ΔAICc	AIC wt	Model output			Adj. R^2
												df	F	P	
Cyanolichen	1			−0.12 (0.07)	0.82 (0.39)*			4	61.2	0.00	0.26	2.29	4.45	0.02	0.30
	2	−0.33 (0.11)			0.93 (0.39)*			3	61.7	0.45	0.23	1.30	5.63	0.02	0.18
	3	−0.42 (0.13)			0.94 (0.39)*	0.59 (0.51)		4	62.9	1.67	0.13	2.29	3.49	0.04	0.23
	4	−0.02 (0.21)		−0.14 (0.07)				3	63.3	2.04	0.11	1.30	3.90	0.06	0.14
	5	−0.13 (0.23)		−0.11 (0.07)	0.84 (0.39)*	0.40 (0.52)		5	63.4	2.15	0.10	3.28	3.13	0.04	0.30
	6	−0.10 (0.22)	0.14 (0.21)	−0.12 (0.07)	0.84 (0.39)*			5	63.5	2.31	0.09	3.29	3.07	0.04	0.29
	7	−0.13 (0.27)		−0.12 (0.07)	0.84 (0.39)*		0.04 (0.08)	5	63.8	2.54	0.07	3.28	2.98	0.05	0.29
	8	−0.39 (0.15)	0.12 (0.21)		0.95 (0.40)*			4	63.9	2.71	0.07	2.29	2.92	0.07	0.20
	9	−0.39 (0.22)			0.94 (0.40)*		0.03 (0.09)	4	64.2	2.96	0.05	2.29	2.78	0.08	0.19
Pendulous	1	−2.07 (0.65)	1.68 (0.94)		NA			3	158.2	0.00	0.26	1.30	3.17	0.09	0.10

Table 3 continued

Functional group	Model	Intercept	Conserv. area (reserve)	Average volume host trees	Change in volume deciduous host trees	Change in volume large old conifers	Conserv. area size	df	AICc	ΔAICc	AIC wt	df	F	P	Adj. R²
Null model	2	−1.28			NA			2	159.0	0.77	0.18	2			
	3	−12.41 (8.38)	2.03 (0.98)*	8.95 (7.23)	NA			4	159.2	0.98	0.16	2.29	2.38	0.11	0.14
	4	−1.71 (0.86)	2.07 (1.14)		NA		−0.26 (0.41)	4	160.4	2.20	0.09	2.29	1.75	0.19	0.11
	5	−2.04 (0.71)	1.70 (0.98)		NA	−0.26 (2.43)		4	160.8	2.61	0.07	2.29	1.54	0.23	0.10
	6	−6.52 (8.32)		4.60 (7.30)	NA			3	161.0	2.80	0.06	1.30	0.40	0.53	0.01
	7	−1.60 (0.89)			NA		0.15 (0.36)	3	161.4	3.16	0.06	1.30	0.18	0.67	0.01
	8	−1.37 (0.62)			NA	0.59 (2.45)		3	161.4	3.16	0.05	1.30	0.06	0.81	0.00
	9	−11.56 (9.24)	2.16 (1.14)	8.34 (7.79)	NA		−0.10 (0.43)	5	161.9	3.74	0.04	3.28	1.55	0.22	0.14
	10	−12.66 (8.75)	2.00 (1.00)	9,14 (7.50)	NA	0.32 (2.45)		5	162.0	3.79	0.03	3.28	1.54	0.23	0.14

Explanatory variables tested were conservation area type (reserve as a reference), average volume of suitable host trees from the 1st and 2nd survey (m³ ha⁻¹), changes in the volume (m³ ha⁻¹) of suitable deciduous host trees from the 1st and 2nd survey (only applicaple for cyanolichens), changes in the volume (m³ ha⁻¹) of large old coniferous trees from the 1st and 2nd survey, and conservation area size (ha). Estimates (±SE) of variables included in each model are presented and the significance of individual variables are marked * for P < 0.05. Model outputs and adjusted R² values are presented. No significant models were found for pendulous lichens (the null model was included among candidate models)

explanatory variable included in all three top models (ΔAICc $\leq$ 2) for changes in the mean frequency of cyanolichens ($t_{df = 31} > 2.133$, P < 0.042). The mean host tree volume was near-significant in one of the top models ($t_{df = 31} = -1.709$, P = 0.098) and the change in volumes of large old coniferous trees was included in one of the top models but not significant ($t_{df = 31} = 1.138$, P = 0.264). The reserve type and conservation area size were included as positive but non-significant effects on increasing mean frequencies of cyanolichens in four separate models with ΔAICc $\leq$ 4 (Table 3). No environmental variable explained the probability of an increasing mean frequency of *A. sarmentosa* and *B. nadvornikiana* (Table 3). In fact, the null model was included in the top models with ΔAICc $\leq$ 2. We did not test which substrate factors that influenced the observed decline in the total mean frequency of indicator species (including all indicator species in Table 2; Fig. 1b), given that this group includes both epiphytic and saproxylic species associated with both deciduous and coniferous trees.

Discussion

Declining lichen epiphytes despite stable state of large old host trees

Large old trees are rapidly declining in many parts of the world with serious implications for ecosystem integrity and biodiversity (e.g., Lindenmayer et al. 2012). Conservation areas play a key role in ensuring a supply of large old trees of different tree species (Jönsson et al. 2009; Hedwall and Mikusiński 2015). However, even with stable or increasing volumes of large old trees over 10 years, we detected significant reductions in associated cyanolichens and pendulous lichen frequencies in conservation areas, particularly in key habitats compared to reserves. A decline of cyanolichens was also evident by low colonization rates, in comparison to their generally higher extinction rates. Increased local extinctions in small and isolated old-growth forest fragments have been reported for infrequent deciduous epiphytes in other studies, and have similarly been explained by low colonization rates as well as increased tree-fall rates near clearcut edges (Roberge et al. 2011; Fedrowitz et al. 2012). In fact, both stochastic extinctions from standing living trees and deterministic extinctions caused by tree fall have important implications for the metapopulation ecology of cyanolichens (Snäll et al. 2005a; Öckinger and Nilsson 2010; Fedrowitz et al. 2012). Many of the studied cyanolichens require a continuous availability of large old aspens *P. tremula*, which small and isolated reserves and key habitats may not be able to sustain over time (Fedrowitz et al. 2012). Our study showed that cyanolichens may decline in key habitats despite stable volumes of large old *P. tremula* and *S. caprea*, whilst increasing volumes of these host trees generally counteracted declines over time. Temporal studies of old-growth pendulous lichen dynamics are lacking. However, edge effects and low availability of large old trees has been found to reduce pendulous lichen biomass (Esseen et al. 1996; Essen 2006). Reductions of pendulous lichen frequencies were more pronounced in key habitats compared to reserves, but we did not capture any effect of the volumes of large old *P. abies* host trees. It is important to acknowledge that reductions may also be related to external uncontrolled factors, like climate-induced effects. Concerning negative fragmentation effects, however, large formally protected nature reserves serve as controls for key habitats.

Many old-growth forest indicator lichens are sensitive to habitat quality factors like humidity and light availability (Gauslaa et al. 2007; Ellis 2012). Lichen declines in our

study may partly be a result of the current successional trajectories of the forests, where fire suppression and historical human interventions have improved conditions for late-successional *P. abies* at the expense of early-successional deciduous trees (e.g., Jönsson et al. 2009). Increasing volumes of large over-shading *P. abies* trees may potentially have reduced the canopy openness and light availability over time in the studied forests, which has been shown to have a negative effect on lichen cover (Jüriado et al. 2009) and richness (e.g., Kuusinen 1994; McCune et al. 2000; Löbel et al. 2006; Moning et al. 2009; Marmor et al. 2012). It has been suggested that stand succession may create a bottleneck in epiphyte richness during a mature closed-canopy phase, prior to a more open old-growth forest phase characterised by greater canopy gaps and openings (Sillett et al. 2000). It can be argued that lichen declines in our study were therefore an effect of the natural dynamics of the ageing stands. However, we did not have access to very long-term forest stand data to evaluate the role of canopy openness and succession. Changes in the volume of large old coniferous trees (as a proxy for light availability) were not a significant environmental variable for lichen frequency changes over 10 years.

Low lichen colonization rates have been explained by increased landscape-level fragmentation and loss of suitable old-growth habitat (Snäll et al. 2005), lichen dispersal limitations (Snäll et al. 2005), competition from bryophytes and large foliose lichens resulting in over-growth of smaller lichens and impaired establishment (Armstrong and Welch 2007), and gastropod grazing on *Lobaria* (Asplund et al. 2010). The availability and quality of the habitat may also have changed substantially over longer time scales, resulting in delayed species extinctions ('extinction debt' sensu Tilman et al. (1994). Such an extinction debt has been documented for lichens in northern Swedish boreal forests (Berglund and Jonsson 2005) and for epiphytic lichens in Scotland (Ellis and Coppins 2007). Although the time period of this study was sufficient to observe epiphytic lichen declines and within the estimated generation times for some cyanolichens (Larsson and Gauslaa 2011), it still represents a very short time window in forest development. Hence, even more long-term empirical studies and simulations are needed to disentangle some of the processes that determine both lichen and fungal viability in conservation areas over time.

Stable state for saprothropic and parasitic wood fungi and deadwood

Stable volumes of deadwood and frequencies of associated saprotrophic fungi, as well as parasitic *F. pinicola* and *F. fomentarius*, indicates that the conservation areas protected many important forest habitats and functions provided by these fungi. In contrast to lichens, the studied fungi generally did not have lower colonisation rates than extinction rates of fruiting fungi over 10 years (with the exception of parasitic and saprothropic *Phellinus chrysoloma*). Although not studied specifically, the stable state for wood fungi was likely the result of the stable deadwood volumes at levels of 20–40 m^3 ha^{-1}, considered as a rough threshold level for sustaining red-listed polypore species—and, consequently, for the possibility of achieving the maximum number of species at a particular forest type—in mature *P. abies* forests (Junninen and Komonen 2011). For comparison, the average amount of deadwood in natural old-growth *P. abies* forests is around 60–120 m^3 (Siitonen 2001). Similar to epiphytic lichens, the persistence of wood fungi is determined by a combination of substrate and stand-level factors as well as factors relating to the surrounding landscape matrix, such as proximity and extent of clear-cuts and old-growth forest habitat (e.g., Snäll and Jonsson 2001; Aune et al. 2005; Nordén et al. 2013).

Stable state for the majority of the key structures

As discussed above, volumes of key structures such as large old trees and deadwood was stable or increasing over the 10 year study period. This was similar to results from a recent large-scale study of protected forests in Sweden, where the number of large trees and the volume of hard deadwood, including both standing and downed wood, have more than doubled over 60 years (Hedwall and Mikusiński 2015). They also found that the overall tree species richness was stable over time, whilst there was an indication of a shift towards the late successional *P. abies* among the largest trees with a DBH $\geq$ 35 cm (Hedwall and Mikusiński 2015). The observed absence of changes in the frequency and species richness of saplings (DBH < 10 cm) in our study indicated that the recruitment of a variety of trees was constant over time, and this is also in accordance with trends recorded over 60 years in protected areas (Hedwall and Mikusiński 2015). The stable state of light-demanding and disturbance-favoured species like *P. tremula*, *S. caprea*, and *P. sylvestris* is somewhat surprising since one could expect these species to decline in the absence of disturbance (Hedwall and Mikusiński 2015). In our study, however, we detected a significant reduction in the volume of *Betula* spp. over time. Volumes of standing deadwood increased in key habitats, indicating that the input of deadwood is probably in increasing extent based on trees dying standing (e.g., snags comprised 33 % of the deadwood volume in the 1st survey compared to 41 % in the 2nd survey in key habitats). This is likely the result of (i) the relatively high basal area within forests and increasing volume of large old *P. abies*, yielding increased competition and tree mortality, and (ii) development of late successional gap dynamics due to fungi, insects and wind as mortality agents of old trees (McCarthy 2001; Edman et al. 2007).

Implications for forest functional values and conservation

The combined value of the studied lichens and fungi as old-growth forest indicators and fundamental regulators of forest ecosystem functions makes them particularly suitable species for following trends in forest ecosystem health (Nitare 2000; Dahlberg et al. 2010; Heilmann-Clausen et al. 2015). In old-growth forests where they are abundant, indicator cyanolichens and pendulous lichens can greatly affect nitrogen fixation and nutrient cycles (Esseen and Renhorn 1998; Antoine 2004), as well as microclimates and habitats of other forest-dwelling organisms (Pettersson et al. 1995; Gunnarsson et al. 2004; Sillett and Antoine 2004; Asplund et al. 2010; Kivinen et al. 2010). Taken collectively with other studies (e.g., Esseen et al. 1996; Fedrowitz et al. 2012), our results suggest that basic lichen functions may not be sufficiently protected in conservation areas over time if declines are not halted or reversed. This was particularly evident for smaller key habitats. However, the ecosystem-level input and ecological importance of these functions, in relation to a reduction in lichen frequency, remains to be quantified and tested experimentally.

The stable state of deadwood and wood fungi represent an important supporting function for ecosystem services such as nutrient cycling, carbon storage and soil formation (Janisch and Harmon 2002; Heilmann-Clausen et al. 2015). For example, the saprotrophic old-growth fungi observed in our study may serve to maintain lower decomposition rates and subsequently ensure the longevity of ecological legacies such as deadwood in conservation areas (Jacobs and Work 2012). As with lichens, the ecosystem-level input and

ecological importance of these fungal-driven functions remains to be quantified and tested experimentally.

Several conservation actions can be used to mitigate declining abundances of epiphytic lichens in conservation areas over time. Based on our results, it is important to increase the availability of large old *P. tremula* and *S. caprea* to counteract cyanolichen declines, in both nature reserves and smaller key habitats. This can be achieved by (i) decreasing ungulate browsing pressures on deciduous saplings (e.g., Kouki et al. 2004), (ii) partial cutting of shade-tolerant *P. abies* trees to alleviate competition and extend the life of individual deciduous host trees (Nordén et al. 2012), and (iii) leaving uncut buffers of 50–100 m around smaller conservation areas to alleviate adverse edge effects (Essen 2006; Roberge et al. 2011). Our results suggest that conservation areas do protect tree species richness of regenerating trees over 10 years. In greater detail, Hedwall and Mikusiński (2015) showed that also deciduous tree recruitment was protected over 60 years in conservation areas. Such a recruitment of a variety of tree species over time is important for future generations of epiphytic organisms. However, our results showed that lichen colonisation rates need to increase above extinction levels (more than double for cyanolichens) to prevent further declines. This likely requires new policies and practices that conserve large old trees in the wider landscape (i.e., increasing host-tree connectivity) by managing trees and forests on much longer time scales than is currently practiced (Lindenmayer et al. 2014), where prolonged rotation times allow more time for lichen colonization and growth (Esseen et al. 1996; Essen 2006), by retaining large old trees during management operations (Rudolphi et al. 2014), and by protecting and restoring places where they are most likely to develop (Lindenmayer et al. 2014).

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