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Species richness of epiphytic lichens in coniferous forests: the effect of canopy openness

Liis Marmor[1,*], Tiiu Tõrra[1], Lauri Saag[1,2] & Tiina Randlane[1]

[1)] *University of Tartu, Institute of Ecology and Earth Sciences, Lai Street 40, Tartu 51005, Estonia (*corresponding author's e-mail: marmor@ut.ee)*
[2)] *Estonian Biocentre, Riia 23b, Tartu 51010, Estonia*

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Epiphytic lichen communities were studied in old coniferous forests across Estonia to find out the effect of site openness on the lichen species richness. All lichen species were recorded on the basal 2 m of 105 *Picea abies* and 105 *Pinus sylvetsris* trunks. The canopy openness readings were taken with a spherical densiometer around every sampled tree. The number of species on the trunks of both tree species increased significantly with increasing canopy openness. Nine lichen species, e.g. *Cladonia cenotea*, *Lecidea nylanderi*, *Platismatia glauca*, were significantly favoured by higher light availability, and only one species, *Coenogonium pineti*, by lower light availability. The results demonstrate that in the coniferous forests higher light availability supports higher species richness of epiphytic lichens on the lower trunk of trees.

Introduction

Light availability is one of the important factors affecting lichens as well as other photosynthesising organisms. It is known that low light availability limits lichen growth, whereas excessive light can cause photoinhibition and quicken the dehydration of thalli (Green *et al.* 2008, Palmqvist *et al.* 2008). Measurements have shown that the photosynthetic capacity (e.g. Palmqvist & Sundberg 2000, Lange *et al.* 2004, Lakatos *et al.* 2006) and light response curves (e.g. Green *et al.* 1997, MacKenzie *et al.* 2001, Barták *et al.* 2005, Piccotto & Tretiach 2010) vary considerably between lichen species. Transplantation experiments have proven a contrasting response of selected lichen species to the increased light availability in forest edges (Stevenson & Coxson 2008, Jansson *et al.* 2009), which can be related to varying light and humidity preferences among the species. As fatal desiccation risk increases with excessive radiation, Gauslaa *et al.* (2006) emphasised the importance of balance between light availability and desiccation risk to lichen species occurrence, in an old-forest lichen. The studies carried out on a community level indicate that higher light availability favours higher lichen species richness (Fritz & Brunet 2009) and cover (Jüriado *et al.* 2009) in deciduous forests. Lichen studies in wooded meadows have shown that lichen diversity is higher in managed open habitats, which can be related to better light conditions (Leppik & Jüriado 2008). Increasing light availability has also been considered a major factor affecting vertical changes in the lichen communities in

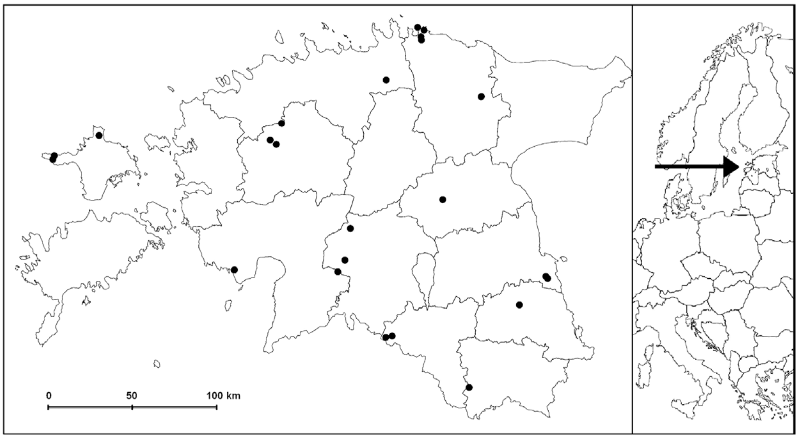

Fig. 1. Locations of the study sites in Estonia.

tree canopies (e.g. Coxson & Coyle 2003, Sillet & Antoine 2004).

Information about the effect of light on the epiphytic lichen diversity in coniferous forests is sparse, although these forests represent the majority of forests in the boreal and hemiboreal vegetation zones. The importance of light on the epiphytic lichens in coniferous forests has been discussed in several ecological studies (e.g. Coote *et al*. 2008, Hilmo *et al*. 2009, Nascimbene *et al*. 2009), but rather few measurements of light conditions were carried out (e.g. Hauck & Meissner 2002, Gauslaa *et al*. 2006, 2007, Coxson & Stevenson 2007). Knowledge about the effects of light availability on lichen diversity and the presence of individual lichen species may be useful for interpreting the results of different ecological and bioindicational studies. The present study focuses on the effects of canopy openness on the epiphytic lichens growing in old coniferous forests with different canopy density. We hypothesise that more lichen species prefer higher canopy openness resulting in increasing species richness with increasing light availability.

Material and methods

Study area

The study was carried out in Estonia. The mean annual temperature in the area is ca. 5 °C (the monthly means vary from –6 to 16 °C), and the mean annual precipitation ca. 630 mm (http://www.emhi.ee). About half of the territory of the country is covered by forests. The Estonian forests belong to the hemiboreal subzone of the boreal forest zone, lying in the transitional area where the southern taiga forest subzone changes into the spruce–hardwood subzone (Ahti *et al*. 1968, Laasimer & Masing 1995). The conifers *Pinus sylvestris* (hereafter pine) and *Picea abies* (hereafter spruce) are the dominating tree species, *Betula pendula* being the most abundant deciduous tree.

In order to minimise the effects of forest history and management on the epiphytic lichens, old stands without any signs of management were selected for the study. Most of the studied forests have a long continuity, as the respective areas appear as forests already on the 17th century maps. The study sites are scattered across the country (Fig. 1), being situated mainly in nature protection areas and woodland key habitats.

Field methods

The fieldwork was carried out in 2008–2009. The spruces and pines were both studied at 21 forest sites; in most cases the sites of the two studied tree species were located in the same place. Five spruces and/(or) five pines were sampled at every site, i.e. in total 210 trees were examined. The trees were selected randomly within a 50-m radius plot; only trees with > 50 cm circumference were included. The presence of all lichen species was recorded on the basal 2 m of the tree trunks. Some specimens were collected for later identification under a microscope and using spot tests. If necessary, thin layer chromatography was used for identifying secondary compounds in crustose lichens. A spherical densiometer was used for estimating the light availability to epiphytic lichens. According to Korhonen *et al.* (2006), a densiometer serves as a compromise between measurement speed and accuracy; when testing a densiometer in spruce-pine forests they did not find statistically significant differences from control values. We measured the canopy openness (percentage of open sky) 0.8 m from the trunk at a height of ca. 1 m for all sampled trees. The readings were taken in every four cardinal direction, with back towards the tree. Based on the four readings, the mean canopy openness was calculated for every tree, and was later used in the statistical analyses. As higher lichen species richness has been described previously on older trees (e.g. Lie *et al.* 2009, Marmor *et al.* 2011), we included tree age as an additional variable in this study. The age of trees was determined with an increment borer; the core samples were taken at a height of 1.3 m. In three cases, it was impossible to count the growth rings.

Statistical analyses

The relationship between canopy openness and lichen species richness on the tree trunks was evaluated using Pearson's correlation. In addition, general linear model (GLM) type III decomposition was used for estimating the effects of canopy openness and tree age on the lichen species richness. GLM (test of all effects) with a logit-link function was used to find out the effect of canopy openness on the occurrence of lichen species; tree species was added as a categorical factor (this analysis was done jointly for the two tree species). STATISTICA 7 was used for the statistical analyses.

Results

Lichens were observed on 105 spruces and 105 pines. Altogether 74 lichen species were found in the study, 59 of them on spruces and 59 on pines (Table 1). The most frequent species were, in the order of descending frequency, *Hypogymnia physodes*, *Cladonia coniocraea*, *Lepraria incana*, *Cladonia digitata*, *Parmeliopsis ambigua* and *Chaenotheca chrysocephala*. The mean canopy openness of the sampled trees varied from 10% to 36% (mean 21%) in spruces, and from 4% to 55% (mean 27%) in pines. The age of spruces varied from 36 to 217 (mean = 123 years), and the age of pines from 87 to 295 (mean = 167 years). Canopy openness affected the lichen species richness on the tree trunks (Table 2); in spruces, tree age also had a significant effect, species richness being higher on older trees. The results of the Pearson correlation analyses verified the positive effect of light availability on the number of lichen species growing on the trunks (Fig. 2). The presence of the following lichen species was significantly higher with higher canopy openness: *Cladonia cenotea*, *C. digitata*, *Imshaugia aleurites*, *Lecidea nylanderi*, *Lepraria jackii s. lato*, *Ochrolechia microstictoides*, *Parmeliopsis ambigua*, *P. hyperopta*, and *Platismatia glauca*. Only one species, *Coenogonium pineti*, was significantly favoured by lower canopy openness.

Discussion

The relatively low light availability under forest canopies may limit photosynthesis and, thus, the growth of lichen thalli (Green *et al.* 2008, Palmqvist *et al.* 2008). This study confirms that higher light availability favours higher species richness of epiphytic lichens in coniferous stands, at least on the basal 2 m of the trunks. The lichen species richness increased significantly with increasing canopy openness on both studied phorophytes, spruce and pine (Pearson's $r = 0.36$; Fig. 2). The effect of canopy openness remained significant in type III GLM, with tree age as a covariate (Table 2).

Barkman (1958) stated that most foliose and fruticose lichens are photophilous. This is in accordance with our results that revealed a significant positive effect of higher canopy openness on the occurrence of nine lichen species (marked in Table 1), whereas only one species, *Coenogonium pineti*, was significantly favoured by lower canopy openness. This species and

Table 1. Frequencies (percentage of occurrences) of the lichen species on the studied trees (n = 105 for both tree species). Species preferring higher canopy openness (according to GLM), are marked with an asterisk (*) and species preferring lower canopy openness with '°'.

Lichen species	*Pinus sylvestris*	*Picea abies*	Lichen species	*Pinus sylvestris*	*Picea abies*
Arthonia leucopellaea	12	32	*Hypogymnia tubulosa*	5	2
Arthonia mediella	0	1	*Imshaugia aleurites**	22	3
Arthonia vinosa	1	1	*Lecanactis abietina*	10	41
Biatora efflorescens	3	6	*Lecanora conizaeoides*	1	8
Biatora helvola	1	1	*Lecanora expallens*	0	10
Bryoria capillaris	19	17	*Lecanora norvegica*	2	0
Bryoria fuscesens	5	0	*Lecidea leprarioides*	0	2
Calicium viride	0	9	*Lecidea nylanderi**	59	36
Chaenotheca chrysocephala	36	63	*Lecidea turgidula*	3	1
Chaenotheca ferruginea	51	37	*Lepraria incana*	69	92
Chaenotheca furfuracea	0	10	*Lepraria jackii s. lato**	25	5
Chaenotheca stemonea	4	5	*Lepraria lobificans*	0	1
Chaenotheca trichialis	3	5	*Loxospora elatina*	38	30
Chrysothrix chlorina	0	4	*Micarea elachista*	12	1
Chrysothrix flavovirens	21	7	*Micarea hedlundii*	2	0
Cladonia bacilliformis	6	1	*Micarea melaena*	58	3
*Cladonia cenotea**	51	20	*Micarea prasina s. lato*	18	33
Cladonia chlorophaea	6	5	*Mycoblastus sanguinarius*	2	0
Cladonia coniocraea	82	80	*Ochrolechia alboflavescens*	1	1
Cladonia cornuta	1	1	*Ochrolechia androgyna*	0	2
*Cladonia digitata**	96	58	*Ochrolechia microstictoides**	8	12
Cladonia fimbriata	37	25	*Opegrapha vulgata*	0	1
Cladonia norvegica	4	0	*Parmelia saxatilis*	1	1
Cladonia ochrochlora	19	10	*Parmelia sulcata*	5	7
Cladonia parasitica	1	0	*Parmeliopsis ambigua**	85	34
Cladonia polydactyla	1	2	*Parmeliopsis hyperopta**	41	2
Cliostomum griffithii	1	2	*Pertusaria amara*	0	7
Cliostomum leprosum	2	0	*Pertusaria coccodes*	0	2
Coenogonium pineti°	15	10	*Platismatia glauca**	30	7
Evernia divaricata	0	1	*Pseudevernia furfuracea*	4	0
Evernia prunastri	0	2	*Pycnora sorophora*	1	0
Haematomma ochroleucum	1	0	*Pyrrhospora quernea*	0	2
Hypocenomyce anthracophila	1	0	*Ramalina thrausta*	0	1
Hypocenomyce friesii	9	3	*Trapeliopsis flexuosa*	3	0
Hypocenomyce scalaris	47	4	*Usnea filipendula*	1	3
Hypogymnia farinacea	1	0	*Usnea hirta*	3	0
Hypogymnia physodes	85	85	*Vulpicida pinastri*	14	0

Nomenclature mostly follows Randlane *et al.* (2011).

Table 2. Effects of canopy openness and tree age on lichen species richness, as indicated by GLM.

	P. abies (n = 104)				*P. sylvestris* (n = 103)			
	df	Type III SS	F	p	df	Type III SS	F	p
Intercept	1	16	2	0.14	1	248	34	< 0.0001
Canopy openness	1	54	8	< 0.01	1	100	14	< 0.001
Tree age	1	141	20	< 0.0001	1	5	1	0.40

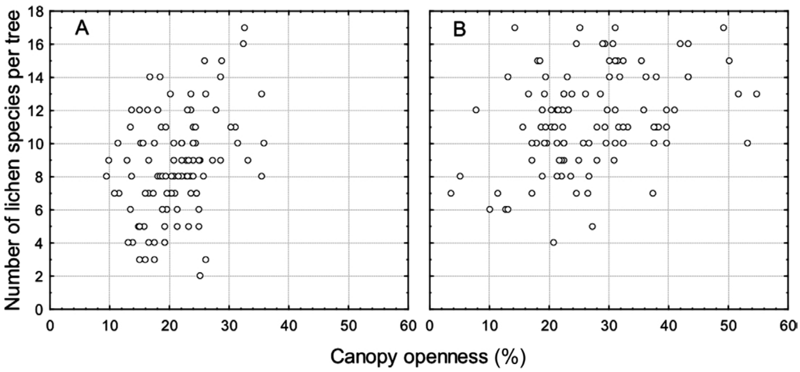

Fig. 2. Correlations between canopy openness and lichen species richness on the trunks of (**A**) spruces, and (**B**) pines. In both cases, Pearson's $r = 0.36$, $n = 105$, $p < 0.001$.

few more microlichens are more abundant under a dense canopy also in deciduous woodlands (Leppik *et al.* 2011). In general, the lichen diversity on old broad-leaved trees in wooded meadows is lower in overgrown habitats with reduced light levels (Moe & Botnen 2000, Leppik & Jüriado 2008, Leppik *et al.* 2011). Moe and Botnen (1997) concluded that many species growing on tree trunks are favoured by the well-lit conditions in open wooded habitats. The studies in deciduous forests have also indicated a positive impact of light on the epiphytic lichen communities (Fritz & Brunet 2009, Jüriado *et al.* 2009).

Previous measurements of light availability in coniferous forests have shown a positive effect of light on selected lichen species: for example, on the growth rates of *Lobaria pulmonaria* (Gauslaa *et al.* 2006, Coxson & Stevenson 2007), and the cover of *Platismatia glauca* (Hauck & Meissner 2002); the latter species is photophilous also according to the present study. The lichens growing on the lower part of the tree trunks in relatively dense coniferous forests experience rather low light availability that limits the growth of thalli (Gauslaa *et al.* 2007). Hilmo *et al.* (2009) associated the sparse lichen cover in the lower canopy of mature spruce plantations with reduced light availability. Gauslaa *et al.* (2007) suggested that poor light conditions are an additional reason for the lack of old-forest lichens in the forest landscapes dominated by young dense stands. The preference of many species for higher canopy openness indicates that selective thinning may improve the habitat conditions for epiphytic lichens in dense, managed plantations.

However, it has to be stressed that the present study only comprises lichens growing on the basal 2 m of tree trunks, the height usually surveyed in lichenological studies, and it remains unknown whether the total lichen diversity on trees, from the base to the top, depends on habitat openness. It is known that many species are more frequent above the height of 2 m (e.g. McCune *et al.* 2000, Fritz 2009, Marmor *et al.* 2010). Vertically-improving light conditions are regarded among the main causes for the vertical changes in the lichen communities in tree canopies (Sillet & Antoine 2004). For example, *Imshaugia aleurites*, a species favoured by higher light availability (Table 1), is most frequent at the height of 6–10 m from the ground on the pines in the Estonian coniferous forests (Marmor *et al.* 2013). Light availability near the ground is especially important for those species absent or infrequent higher up in the canopy. For example, the two *Cladonia* species (*C. cenotea* and *C. digitata*) that were significantly favoured by higher light availability in the present study are associated with tree bases (Holien 1997).

Our analysis underlines the importance of collecting data on the site openness in studies of the ecology of forest lichens. As canopy openness is one of the important factors affecting species richness and composition of epiphytic lichens, the possible effect of light should be considered when interpreting the effects of other variables, such as forest management, in ecological studies. According to Gauslaa and Solhaug (1996), some indicator lichens of long forest continuity, especially within the *Lobarion* community, cannot thrive in high-light conditions, which may be detrimental to the remaining lichen thalli at clear-felling sites. At the same time, in poor light availability the limiting effect of light may mask the effects of other variables; for example, Nascimbene *et al*. (2009) found that tree age affected the lichen cover in relatively open stands, whereas no effect was revealed in dense stands.

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