


Lichen communities on *Populus tremula* are affected by the density of *Picea abies*

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Abstract

Questions: Aspen (*Populus tremula*) is declining in the old-growth forests of boreal Fennoscandia. This threatens the numerous taxa that are dependent on old aspens, including many epiphytic lichens. Potential methods to aid epiphytic lichens on aspen are centered around treatments which affect the density of Norway spruce (*Picea abies*). In this study, we investigated how epiphytic lichen communities on aspen are affected by the variation of spruce density in the immediate vicinity of the focal aspen.

Location: Southern boreal forests in Finland.

Methods: We recorded the occurrence of lichens from 120 aspens in 12 semi-natural forest sites. We used spruce basal area as the measure for spruce density. The selected aspens represented a gradient in spruce basal area in the vicinity of the aspen from 0 to 36 m²/ha. We also measured other tree- and stand-level variables that are known to influence lichen occurrence.

Results: Lichen communities on aspen were affected by spruce density, stand age and bark pH. Both lichen species richness and the richness of red-listed species were highest at an intermediate spruce density, and both increased with stand age. Lichen species richness was higher when bark pH was lower. Additionally, community composition was influenced the most by spruce density, followed by bark pH.

Conclusions: Our study highlights the detrimental effects of high spruce density on lichen diversity on aspens. This is caused by high spruce density resulting in low light availability. Lichen diversity on aspens was highest when spruce density was intermediate. Spruce thinning in aspen-rich old-growth forests can be helpful in ensuring the long-term persistence of old-growth lichens on aspen in protected forests.

KEYWORDS

Biodiversity, boreal forests, community ecology, cyanolichens, epiphytic lichens, European aspen, Norway spruce, old-growth forests, protected areas, red-listed species, succession

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1 | INTRODUCTION

European aspen (*Populus tremula*) is a keystone species of the boreal forests of Fennoscandia (Kivinen et al., 2020). It is also the primary substrate for many epiphytic lichens (Kuusinen, 1994; Kuusinen, 1996a; Jüriado et al., 2003; Tarasova et al., 2017). The abundance of aspen is declining in many protected forests of boreal Fennoscandia (Hardenbol et al., 2020). The epiphytic lichens of old-growth aspens in protected forests are threatened both by the loss of suitable host trees (Snäll et al., 2005) and the encroaching of Norway spruce (*Picea abies*) which increases shading (Jönsson et al., 2017). However, the situation may be ameliorated with conservation measures that reduce spruce encroachment and promote aspen recruitment (Nordén et al., 2012; Johansson et al., 2013; Hämäläinen et al., 2020), but their effects are insufficiently known.

Aspen hosts a rich lichen flora (Kuusinen, 1994; Tarasova et al., 2017). The lichen assemblages on aspens are unique in comparison to other widespread tree species in boreal Fennoscandia, which is in large part due to the relatively high bark pH of aspen (Kuusinen, 1996a). A crucial aspect of the lichen flora of aspens is cyanolichens, which prefer substrates with high pH and are primarily inhabitants of old-growth forests (Kuusinen, 1996b; Hedenäs & Ericson, 2000; Rikkinen, 2015). Aspen is host to many red-listed lichens, most of which are inhabitants of old-growth forests (Pykälä et al., 2019).

Forest succession causes many changes in forest habitats, which then affect lichen communities (McCune, 1993; Ellis, 2012). In boreal forests of Fennoscandia, spruce is the dominant species in the late-successional phases of many forest types (Angelstam & Kuuluvainen, 2004; Lilja et al., 2006). Spruce has been considered to promote favorable conditions for old-growth specialist lichens on aspen (Hedenäs & Ericson, 2004; Ylisirniö & Hallikainen, 2018), which require moist, shaded habitats (Kuusinen, 1994; Kuusinen, 1996b; Gu et al., 2001; Belinchón et al., 2017). However, old-growth specialists on aspen may also be hindered by low light availability (Renhorn et al., 1997; Gauslaa et al., 2006; Gauslaa et al., 2007; Gustafsson et al., 2013). Thus, there are contradictory results regarding the effects of spruce, and more studies are required to clarify this issue.

Aspen is a pioneer species, and hence its persistence in protected forests is at risk. Since the early 20th century, the formation of aspen-rich forests has been low due to reduced forest fire frequency and forestry practices that disadvantage aspen (Kouki et al., 2004; Lankia et al., 2012). The established aspens in protected forests are gradually reaching the end of their life span, and there is very little new aspen recruitment because of closed-canopy conditions and browsing pressure (Hardenbol et al., 2020; Komonen et al., 2020). Consequently, aspen is declining rapidly in old-growth forests (Kouki et al., 2004; Hardenbol et al., 2020). This puts the numerous species dependent on old-growth aspens under serious threat (Kouki et al., 2004).

The long-term persistence of epiphytic lichens in protected forests relies on a continuous supply of suitable host trees (Snäll et al., 2005). The decline of old, large aspens has repeatedly been identified as a threat to epiphytic lichens (Hedenäs & Ericson, 2004; Snäll et al., 2005; Jönsson et al., 2017). Furthermore, the encroachment

of spruce during succession may reduce light availability and thus affect lichens negatively (Jönsson et al., 2017). These problems may be alleviated with conservation measures (Johansson et al., 2013). Spruce thinning in aspen-rich stands promotes aspen recruitment, which ultimately increases the continuity of old, large aspens (Hämäläinen et al., 2020). Spruce thinning may also directly aid epiphytic lichens by increasing light availability (Nordén et al., 2012). Still, there is insufficient knowledge on how such treatments may affect lichens on aspen.

The purpose of this study was to evaluate how lichen communities on aspen are affected by variation in spruce density. The influence of spruce density was investigated together with important environmental variables that are known to influence the structure of epiphytic lichen communities. We obtained tree-level community data from 12 mature or old-growth semi-natural boreal forest sites that had variation between and within them in the density of spruce. We examined a gradient from the absence of spruce to the total dominance of spruce. Specifically, this study sought to answer the following question: how does spruce density in the vicinity of an aspen affect lichen species richness, the richness of red-listed lichens, and lichen community composition on the aspen?

2 | METHODS

2.1 | Study sites and trees

We collected the data from 12 sites in the southern boreal zone in Finland (Appendix S1). The altitude of the sites was 80–180 m. The mean annual temperature of the area is 4°C and the annual precipitation is 690 mm. The region was exposed to moderate sulfur deposition during the 20th century, but current sulfur pollution is low (Anttila & Tuovinen, 2010). Nitrogen deposition is circa 3–4 kg ha⁻¹ year⁻¹ (Salemäa et al., 2020). The study sites consisted mostly of mesic forests and to a lesser degree of herb-rich forests, with a few study trees being located in patches of sub-xeric forests. In this region, mesic and herb-rich old-growth forests are usually dominated by spruce, while sub-xeric forests are usually dominated by *Pinus sylvestris*. Aspen is regularly present in all these forest types, but less abundantly in sub-xeric forests. All the study sites were protected areas, with four national parks, five old-growth forest reserves and three Natura 2000 sites.

The study sites were chosen using the following criteria: the sites had to (a) be located within 200 km of the city of Jyväskylä for logistic reasons; (b) contain mature or old-growth semi-natural forests; (c) have a high number of aspen; and (d) have variation within and among them in the density of spruce in the vicinity of aspens. Due to the last criterion, the study sites contained different types of forest habitats in various successional stages. The youngest sites were in the mature stage (about 75–100 years; Angelstam & Kuuluvainen, 2004) and dominated by even-aged deciduous trees with a low density of spruce. The oldest sites were well in the old-growth stage (>125 years), being characterized by a dominance of spruce and

an uneven-aged structure caused by gap dynamics (Kuuluvainen & Aakala, 2011).

The number of study trees per site was 10–14 except for the four smallest sites where it was 6–7. We spent two days at most study sites, and one day at the smallest sites. The number of trees surveyed in each site was based on how many trees we were able to survey in the time spent there. Since the inventory of aspens may be challenging due to its aggregated distribution (Maltamo et al., 2015), we headed into zones with a high presence of aspen based on prior knowledge or examination of satellite images. We considered any encountered aspen a potential study tree, if it met the following criteria: (a) minimum diameter at breast height (dbh) 30 cm; (b) alive; (c) upright; and (d) at least 30 m away from any forest edge. If there was at least one other aspen within 30 m of the encountered aspen, we chose one of them using a random number generator. We always left a gap of at least 50 m between the study trees.

We aimed to cover the gradient of spruce density comprehensively. Therefore, as an additional criterion of tree selection, we ignored aspens with a level of spruce density in its vicinity that was overrepresented in the data in favor of underrepresented levels of spruce density, until all levels of spruce density were equally represented.

2.2 | Data collection and analysis

On each study tree, we surveyed all epiphytic lichens up to two meters. If needed, we collected samples for identification in the laboratory with microscopy and chemical spot tests. Lichen nomenclature followed Pykälä et al., (2021). "*Lecanora allophana* agg." may have included poorly developed other species of *Lecanora* aside from *L. allophana*, such as *L. argentata*, *L. populicola* and *L. chlarotera*.

We used basal area as the measure for tree density. We measured the basal area of spruce (spruce density) surrounding the study aspen with a relascope. The relascope method is based on point sampling alias variable radius sampling (Kangas, 2006). The most distant trees that are included are large trees about 30 m from the sampling point. We similarly measured the basal area of aspen (aspen density) and the total basal area of all tree species (total tree density).

We measured canopy openness by taking photographs of the canopy around the study tree with a camera (Nikon D90) equipped with a 24 mm lens (24–120 mm f/3.5–5.6G ED-IF AF-S VR Nikkor, Nikon, Japan). We took four photographs per tree, one toward each cardinal direction. The photographs were taken with the camera in a vertical position and the lower edge of the view parallel with the ground at eye level. Meanwhile, the upper edge of the view was slightly above the highest point of the sun. We calculated the portion of open sky pixels in the images using the program ImageJ. The measure for canopy openness was the average portion of open sky pixels across the photographs (Oldén et al., 2017).

We took a core drill sample of the largest spruce, or pine if there were no large spruces, within 20 m of the study tree. We did not drill aspens, because they are usually not suitable for core drilling

(Lankia et al., 2012). However, the age of the cored tree likely was close to the age of the study tree, because both the study trees and the cored trees represented the largest size class at the stand. We counted the number of growth rings on the core drill samples to estimate stand age at the location of each study tree. In four cases, this method produced an anomalously low stand age value, i.e. significantly lower than was expected from the appearance of the stand in the field and when compared to other measurements of the study site. In these cases, the value used for stand age was the lowest measured stand age of the study site, the anomalies excluded. In one study site, Vaarunvuori, core drilling was not possible because of a lack of suitable trees. The stand age of this study site was obtained from Metsähallitus, the national forest administration.

We determined the bark pH of the study trees by collecting bark samples from the southern face of the boles from a height of 1.5–2 m. We broke the bark samples into tiny pieces and placed 3 g of bark pieces in 37 ml of distilled water for 24 hrs, after which we measured the pH of the solution using a standard pH meter (Kusinen, 1994).

Finally, we also measured dbh of the study trees.

2.3 | Statistical analyses

We examined the relation of environmental variables to patterns of lichen species richness and the richness of red-listed species with generalized linear mixed models with a Poisson distribution using the function *glmer* from the package *lme4* (Bates et al., 2015). The fixed effects were spruce density, aspen density, total tree density, stand age, canopy openness, bark pH and dbh. In data exploration, the responses to spruce density appeared non-linear, and thus the quadratic term of spruce density was added. Stand identity was used as a random effect. We compared models with all possible combinations of the fixed effects and selected the model with the lowest AIC (Akaike information criterion) value to be the final model. This was done using the function *dredge* from the package *MuMIn* (Barton, 2019).

We examined the effects of environmental variables on community composition with a canonical correspondence analysis (CCA) using the function *cca* from the package *vegan* (Oksanen et al., 2019). The CCA was based on the presence/absence of the species on the study trees. Only species with at least three occurrences were included. We ranked the importance of environmental variables in affecting community composition using the function *ANOVA.cca* from the package *vegan*. First, we ranked the variables based on their marginal effects. Then, we examined the conditional effects of the variables by first adding the variable with the highest marginal effect, and then the rest of the variables in descending order based on their marginal effects. With this method, we could test how much new information was added by introducing more variables. Variables with non-significant *p*-values were excluded from the final CCA (ter Braak & Verdonschot, 1995).

We also did species-specific analyses about how the environmental variables affected species occurrences based on presence/absence data. We did these analyses with generalized linear mixed

models similar to those used in the species richness analyses, model selection based on AIC values included, but with a binomial distribution. The species-specific analysis was done only on species with at least seven observations. We performed all statistical analyses using R version 3.6.1 (R Core Team, 2019).

3 | RESULTS

The gradient of spruce density was covered extensively and for the most part evenly. Values of spruce basal area from 0 to 36 m²/ha were included (Appendix S2). We observed a total of 85 lichen species including 15 red-listed species (Appendix S3) on the 120 surveyed trees, with an average of 13.2 species and 1.3 red-listed species per tree (Table 1). The best model for lichen species richness included spruce density, the quadratic term of spruce density, stand age and bark pH. These effects were included in the ten most parsimonious models (Appendix S4). The association with lichen species richness was statistically significant for all the fixed effects (Table 2, Figure 1). The final model for the richness of red-listed species included spruce density, the quadratic term of spruce density and stand age, and these variables were included in the ten most parsimonious models (Appendix S4). The association with the richness of red-listed species was statistically significant for the quadratic term of spruce density and stand age (Table 2, Figure 2). The final models explaining the richness of all lichen species and that of the red-listed species did not include canopy openness, tree size, aspen density or total tree density.

In the community composition analysis, the marginal effects of aspen density and total tree density were non-significant, and thus they were omitted from the final CCA (Table 3). The variable that affected community composition the most was spruce density, followed by bark pH (Table 3). The first axis of the CCA was

mainly correlated with spruce density, and the second with bark pH (Figure 3). Spruce density and bark pH were the variables most often associated with species occurrences also in the species-specific analyses. The number of species associated with spruce density was 16, mostly explained by the quadratic term, while 16 species were associated with bark pH, mostly negatively (Table 4, Appendix S3).

4 | DISCUSSION

Spruce density had a significant effect on lichen species richness, the richness of red-listed species and community composition. The response of lichen species richness and the richness of red-listed species to spruce density was hump-shaped, as both were highest at an intermediate spruce density. Stand age affected lichen species richness and the richness of red-listed species, and bark pH affected lichen species richness and community composition.

Tree size (dbh) is important for lichen communities (Fritz et al., 2009; Moning et al., 2009; Jönsson et al., 2011). In our study, however, its importance was low, probably because we only studied large (dbh >30 cm) aspens. Likewise, canopy openness is often significant for lichen communities (Gustafsson & Eriksson, 1995; Moning et al., 2009; Jönsson et al., 2011), but much less so in our study. Our measurement of canopy openness was probably suboptimal in explaining light availability from the perspective of epiphytic lichens: it emphasized more distant trees, whereas spruce basal area emphasized nearby trees.

4.1 | Stand age

Lichen species richness increased with stand age (70–226 years). Aspens may live for up to about 200 years (Lankia et al., 2012). Thus,

TABLE 1 Summary of site-specific results. All values except the number of study trees are site-specific averages

Site name	Lichen species richness	Red-listed species	Spruce density	Stand age	pH	dbh	Canopy open-ness	Aspen density	Total tree density	No. of study trees
E-Konnevesi	15.8	1.5	12.1	129	6.12	52	6.62	4.5	24.2	12
Isojärvi	13.8	0.9	22.3	111	5.97	46	6.08	5.0	30.3	12
Kirkkokangas	13.0	1.8	26.7	129	6.02	57	6.21	0.7	31.7	6
Kotinen	16.2	2.4	20.1	147	5.82	47	4.31	6.8	36.3	14
Kuoppa-aho	11.5	1.1	20.8	131	5.82	48	5.92	3.7	30.1	10
Kuusimäki	12.3	1.3	25.8	160	6.05	63	4.84	4.3	35.6	12
Kuruvuori	12.4	0.0	5.4	103	5.84	46	7.4	5.7	24.9	7
Linnansaari	9.6	0.8	4.9	91	5.6	52	5.56	7.8	27.5	12
Pyhä-Häkki	15.9	2.3	21.9	167	5.67	49	6.4	3.3	32.9	13
Tieransaari	12.7	0.8	1.0	129	5.93	58	6.97	2.0	23	6
Vaarunvuori	11.8	0.3	2.2	95	5.44	49	5.17	6.7	23.3	6
Vuorilampi	10.3	0.6	19.1	101	5.78	45	5.82	3.1	32.7	10
Whole study	13.2	1.3	16.4	128	5.84	51	5.86	4.7	30.1	120

Abbreviation: dbh, diameter at breast height.

TABLE 2 Generalized linear mixed model (GLMM) results for lichen species richness and the richness of red-listed species. The environmental variables were centered for the GLMMs

	Estimate	SE	z-value	p-value
Species richness				
Intercept	2.6707	0.0550	48.593	<0.001
Spruce density	-0.0093	0.0038	-2.449	0.014
Spruce density ²	-0.0012	0.0003	-3.706	<0.001
Stand age	0.0025	0.0009	2.783	0.005
pH	-0.2006	0.0605	-3.316	<0.001
Red-listed species				
Intercept	0.4447	0.1314	3.384	<0.001
Spruce density	0.1808	0.0112	-3.398	0.106
Spruce density ²	-0.0036	0.0011	1.617	<0.001
Stand age	0.0083	0.0023	3.593	<0.001

assuming that the measured stand age corresponded to aspen age, lichen richness on aspens would seem to increase continuously until the death of the aspen. Lichen richness generally increases with tree and stand age (Lie et al., 2009; Nascimbene et al., 2009; Ellis, 2012). As trees and forest stands age and grow, they: (a) offer more space for epiphytes; (b) have been available for lichen dispersal units for a longer time; and (c) their bark becomes more heterogeneous (Snäll et al., 2003; Ellis, 2012).

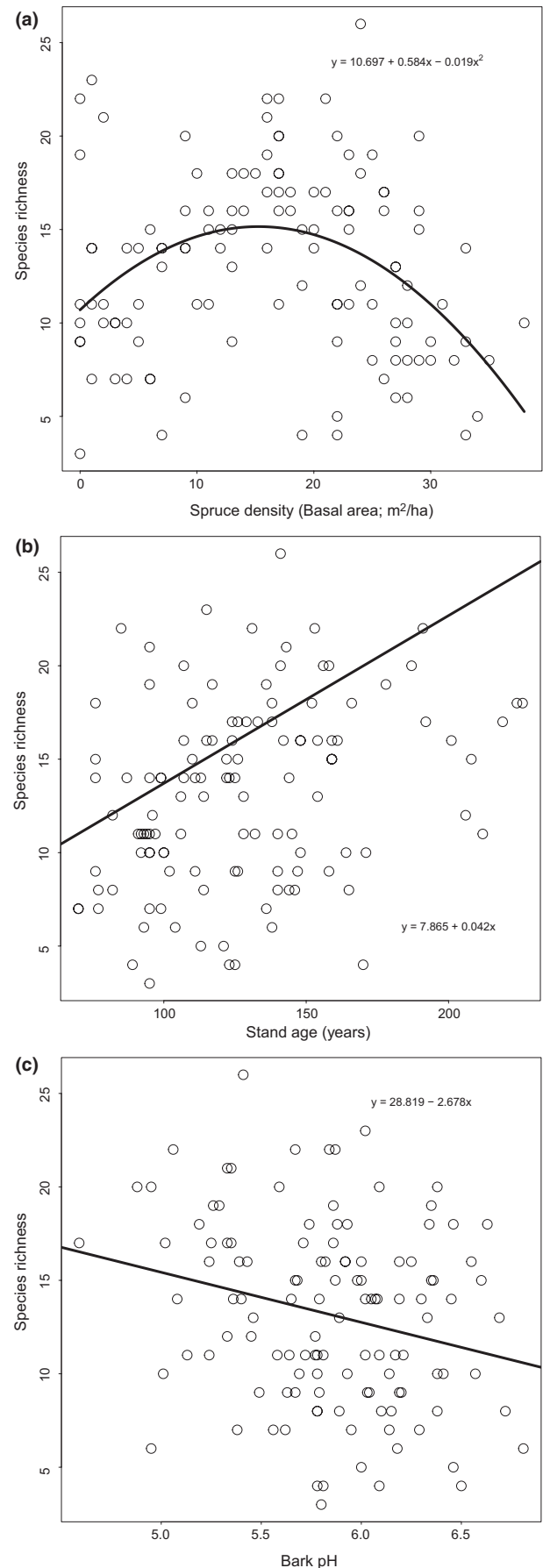
The relationship between the richness of red-listed species and stand age was clear in our study. Almost all observed red-listed species are old-growth specialists, and thus expected to occur predominantly in old stands. Species that are restricted to old-growth forests have faced significant habitat loss, and their populations have declined steeply, and they have become red-listed (Pykälä, 2004; Pykälä et al., 2019). In our study, the occurrence of red-listed species was very likely in stands older than 150 years: 93% of the aspens in such stands hosted at least one and 75% hosted at least two red-listed species.

4.2 | Spruce density

Spruce density affected the richness of all lichens and that of red-listed species, as well as lichen community composition. Spruce density is linked to two crucial factors: stand age and light availability.

Spruce density increases in succession (Lilja et al., 2006; Shorohova et al., 2011). Indeed, low spruce density was found only in younger stands, whereas older stands had an intermediate or high spruce density (Appendix S5). Thus, it remains unclear

FIGURE 1 The response of lichen species richness to: (a) spruce density; (b) stand age; and (c) bark pH. The fitted regression lines or curves are based on parameters produced by simple regression analyses. As such, these graphs are not fully correspondent with the results of the generalized linear mixed model



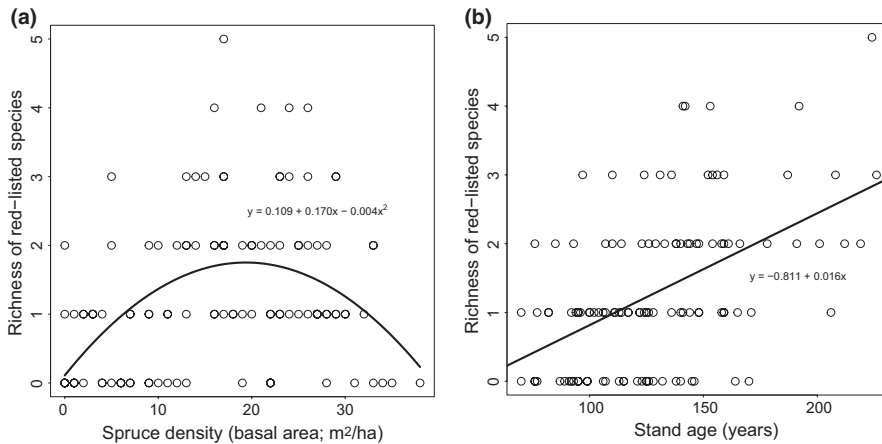


FIGURE 2 The response of the richness of red-listed species to: (a) spruce density; and (b) stand age. The fitted regression lines or curves are based on simple regression analyses. As such, these graphs are not fully correspondent with the results of the generalized linear mixed model

whether the lower lichen richness in stands with low spruce density was caused entirely by stand age or partially by spruce density per se. High spruce density results in low light availability (Messier et al., 1998; Sonohat et al., 2003), and decreasing light availability has negative effects on lichen species richness (Gustafsson & Eriksson, 1995; Moning et al., 2009; Jönsson et al., 2011). Thus, high spruce density caused low lichen richness due to low light availability. In the stands with an intermediate spruce density, neither low stand age nor low light availability limited lichen richness. Therefore, the highest lichen richness was found at an intermediate spruce density. The same pattern was also observed for red-listed species, although their richness peak was at slightly higher spruce density.

An intermediate spruce density was found in stands with notable tree mortality and within aspen aggregations. Tree mortality opened the canopy and increased light availability, and most likely thus benefited lichens. In aspen aggregations (Maltamo et al., 2015), spruce density is inevitably lower. Light availability (Messier et al., 1998) and tree-level connectivity (Belinchón et al., 2017; Gu et al., 2001) are likely to be higher in aspen aggregations. In our analyses, aspen density had no effect, but it still is possible that lichen richness is higher on aspens in aspen aggregations than on lone aspens. Lichen occurrence on aspens may also be affected by the total population size of aspens in the focal forest (Hedenås & Ericson, 2008).

Red-listed species showed no preference toward any environmental variables that indicated high shadiness, such as high spruce density or low canopy openness. Old-growth epiphytes on aspen are often alluded to favor moist and shaded habitats (Kuusinen, 1994; Kuusinen, 1996b; Gu et al., 2001; Belinchón et al., 2017). In this study, they were favored by intermediate conditions (see also Gauslaa et al., 2006). Most of the red-listed species were cyanolichens, which (possibly along with some other old-growth lichens, e.g. Esseen et al., 1981) may prefer more closed conditions than other epiphytic lichens (McCune, 1993). Indeed, the richness of red-listed species peaked at a slightly higher spruce density than total lichen species richness, although this may also be explained by the higher affinity of red-listed species to high stand age. Still, the

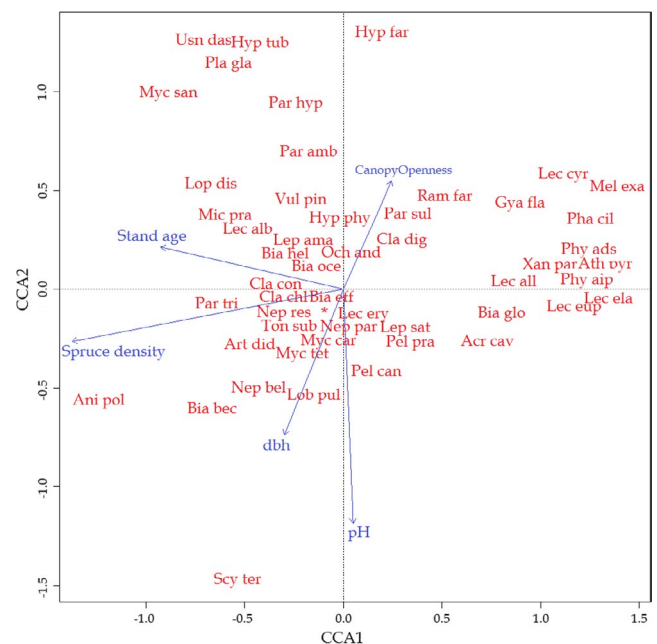


FIGURE 3 The ordination graph created with canonical correspondence analysis, which describes species' responses to the environmental gradients. Only species with at least three observations were included in the ordination analysis. The species' name abbreviations consist of the first three letters of the generic and the specific names. Full species names are found in Appendix S3. The asterisk near the center of the graph is where three taxa, *Phl arg*, *Myc epi* and *Lepraria*, were clumped very closely

richness of red-listed species was low in the most closed conditions. Therefore, there is need for caution when some lichens are claimed to require shaded conditions.

Humidity and shading both increase with a more closed canopy, but they may have conflicting effects on lichens. Some old-growth lichens, such as cyanolichens, are both favored by higher humidity (McCune, 1993; Ellis & Coppins, 2006) and disfavored by low light availability (Renhorn et al., 1997; Gauslaa et al., 2006; Gauslaa et al., 2007). Thus, optimal conditions may consist of both high humidity and light availability. This combination is rare in relatively

TABLE 3 The marginal effects of the environmental variables in the canonical correspondence analysis

	df	χ^2	F	p-value
Spruce density	1	0.121	5.46	0.001
pH	1	0.075	3.36	0.001
Stand age	1	0.047	2.12	0.007
dbh	1	0.041	1.87	0.012
Canopy openness	1	0.040	1.78	0.026
Aspen density	1	0.035	1.56	0.053
Total tree density	1	0.027	1.21	0.202
Residual	112	2.484		

Note: The variables are ranked based on their χ^2 values, which describe how strong an effect the variable had on community composition.

TABLE 4 Summary of the species-specific analyses, showing the number of species that had a statistically significant association with each environmental variable

	Positive	Negative	Quadratic term	Total
Spruce density	0	4	12	16
Bark pH	2	14		16
Stand age	7	1		8
Canopy openness	5	2		7
dbh	4	2		6
Aspen density	3	0		3
Total tree density	2	0		2

Note: Information about which species were affected by which environmental variables is found in Appendix S3. dbh, diameter at breast height.

dry climates (e.g., Finland), and for example cyanolichens are more abundant in oceanic regions (Rikkinen, 2015). Intermediate canopy-closure, where neither humidity nor light availability is at an intolerable level (*sensu* Gauslaa et al., 2006), may provide the most favorable conditions for many old-growth lichens in this region.

4.3 | Bark pH

This study highlighted the high variability of bark pH on aspen (see also Kuusinen, 1994). Lichen species richness was higher on aspens with lower bark pH. This is puzzling since high bark pH is acknowledged as a key factor for the lichen flora of aspens (Kuusinen, 1996a). We found 14 species to be linked to low bark pH, while only two species were linked to high bark pH. Many cyanolichens had a slight preference toward high bark pH. The lichens that favor high bark pH may have been particularly sensitive to and thus suffered from past sulfur deposition without having recovered yet (see Weldon & Grandin, 2021).

Spruce has acidifying effects on its surroundings (Lindroos et al., 2011). Therefore, we hypothesized that a high density of spruce may reduce the bark pH on aspen either via the soil (see e.g., Gustafsson & Eriksson, 1995) or the dripzone effect (see Goward & Arsenault, 2000). However, the result was the opposite, as aspen bark pH was positively correlated with spruce density (Appendix S6). However, the correlation was weak, so there was probably no causative connection between aspen bark pH and spruce density.

4.4 | Implications for conservation and management

Species that are dependent on old-growth aspens are threatened by the rapid decline of aspen in protected forests (Kouki et al., 2004; Hardenbol et al., 2020). One way to improve the long-term persistence of aspen in protected forests is to reduce spruce density in aspen-rich stands, which can improve aspen recruitment (Hämäläinen et al., 2020). Our study indicated that the reduction of spruce density should not have negative effects on lichen communities on aspen; rather it may increase lichen species richness due to increased light availability (see also Nordén et al., 2012). Red-listed species would most likely not be negatively affected either. Effects of spruce thinning on lichen communities on aspen should be confirmed with an experimental study. Importantly, spruce thinning is ultimately pointless if the successful recruitment and thus the continuity of aspens is not ensured. Therefore, browsing pressure (Komonen et al., 2020) should also be addressed. Finally, the decline of aspens in protected forests has been remedied in the managed landscape by retaining aspens in loggings (Gustafsson et al., 2020; Lundström et al., 2013). The lichen diversity of retained aspens is very likely to be reduced if, once the forest regenerates, they are surrounded by a high density of spruces, which is a typical situation for managed forests.

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AUTHOR CONTRIBUTIONS

JP and AN had the idea for the study; all authors contributed to the study design; data were collected by AN; sample analysis was done by AN, along with JP for species identification; statistical analysis was done by AN and AK; the paper was written by AN, edited by AK and commented by JP and PH.

DATA AVAILABILITY STATEMENT

The data that were collected for this study and used in the analyses can be found in Appendix S7.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Location of the study sites on a map of southern Finland.

Appendix S2. A histogram showing coverage of the spruce density gradient.

Appendix S3. List of the species observed in the study.

Appendix S4. Results of model selection.

Appendix S5. The relationship between spruce density and stand age.

Appendix S6. A matrix of the correlations between the environmental variables.

Appendix S7. Data used in the study.

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