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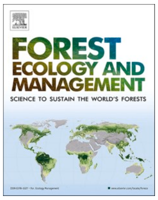

Influence of canopy structure and light on the three-dimensional distribution of the iconic lichen *Usnea longissima*

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ABSTRACT

Forest canopies modify microclimates and create habitats for nonvascular epiphytes, but we need to better understand the mechanisms regulating their vertical and horizontal distributions. Here we examine how canopy structure and light environment influence the 3D distribution of *Usnea longissima*, the world's longest lichen, and associated with old-growth forests. We quantified forest structure, vertical profile of light (PPFD transmittance fraction), and horizontal as well as vertical distribution of the lichen in a 1 ha plot dominated by *Picea abies*. The forest had a multi-layered canopy with mortality driven by small-scale gap dynamics. The population size of the lichen had an approximate log-normal distribution with host trees showing strong clustering. The lichen extended up to mid-canopy and had a rather sharp upper limit. Population size increased with DBH and upper limit but did not correlate with basal area. The vertical profile of light was steeper in dead than in live trees, with the lichen occurring in a zone with low-intermediate light. The horizontal distribution was linked to the vertical distribution through short-distance asexual dispersal. The lichen's 3D distribution was shaped by various interacting functional mechanisms. Its absence from the upper canopy was mainly explained by sensitivity to high light when desiccated and limited capacity for upward migration. The population dynamics was driven by source trees hosting large populations in mid-canopy. The lichen's strong association with humid, old-growth forests is explained by narrow niche preferences and dispersal limitation, and not by slow growth. Protection of multi-layered forests with long continuity of tree cover is needed to secure substrates and suitable microclimates for development of viable lichen populations. Our study highlights that the 3D distribution of lichens in forest canopies is driven by forest dynamics, canopy structure, microclimate, and lichen functional traits.

1. Introduction

The architecture of forest canopies creates habitats for canopy-living organisms, drives energy exchange and modifies microclimates in forests (Lowman and Rinker, 2004; Nakamura et al., 2017; De Frenne et al., 2021). Canopy access by rope climbing, fixed infrastructure, and mobile aerial platforms (Anderson et al., 2015; Cannon et al., 2021) has significantly increased our understanding of the distributions of vascular (e.g., Mendieta-Leiva and Zotz, 2015; Nakanishi et al., 2016; Ishii et al., 2018; Zotz et al., 2021) and nonvascular epiphytes (lichens and bryophytes; e.g., Sillett and Antoine, 2004; Williams and Sillett, 2007; Ellis, 2012; Miller et al., 2017; Shen et al., 2018). Epiphytic lichens have several ecosystem functions in forests and influence hydrology, carbon uptake, nutrient cycling, and biodiversity (Asplund and Wardle, 2017; Porada et al., 2018; Porada and Giordani, 2022). These lichens are sensitive to environmental disturbance and are useful indicators of forest ecosystem integrity and global change (Ellis, 2019; Esseen et al., 2022). We need to understand the mechanisms shaping their 3D distribution within canopies to develop effective management strategies that can secure the diversity and function of epiphytic lichens in forest ecosystems.

Lichens are poikilohydric with metabolic activity regulated by water from rain, dew, and humid air and by morphological and anatomical water storage traits (Gauslaa, 2014). Functional groups and lichen species show niche differentiation along vertical, horizontal and temporal scales in forests (McCune, 1993; Antoine and McCune, 2004; Sillett and Antoine, 2004; Ellis, 2012). The mechanisms driving the distribution of lichens in canopies result from interactions among

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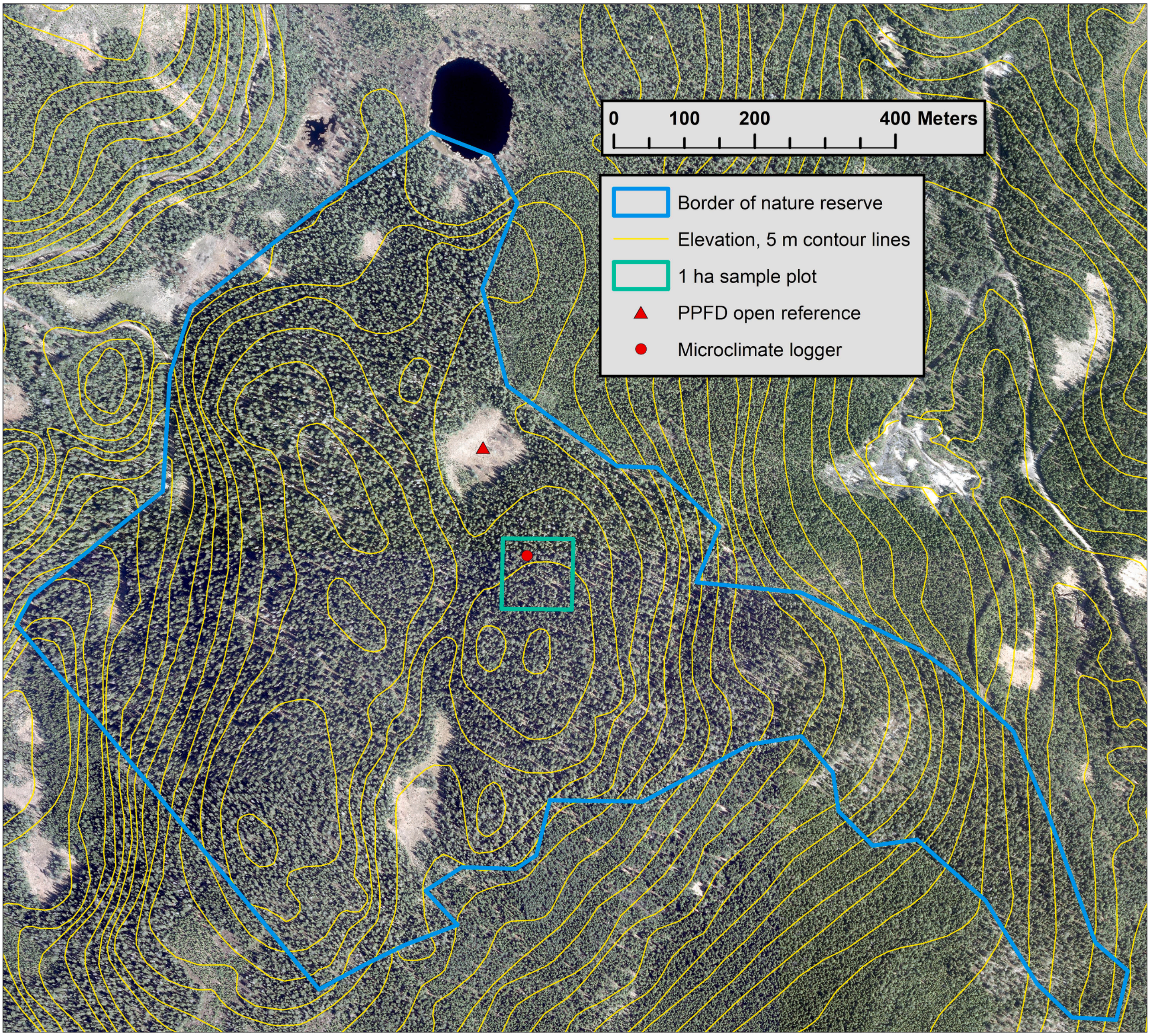

Fig. 1. Map over Edsbodskogen nature reserve, with the studied 1 ha plot, position of the microclimate logger and the reference PPFD sensor in an open wetland.

gradients in light, moisture, temperature, throughfall chemistry, disturbance, and lichen functional traits.

The vertical gradients in microclimate are steeper than horizontal gradients and have received more attention. Many studies have documented the vertical distribution of different lichen functional groups (e.g., McCune, 1993; McCune et al., 1997; Campbell and Coxson, 2001; Benson and Coxson, 2002; Coxson and Coyle, 2003; Hilmo et al., 2013; Li et al., 2015). Various hypotheses have been proposed for vertical distribution of lichens, including moisture and stand age gradients (McCune, 1993), light availability (McCune et al., 1997), vapor pressure deficit (Rambo, 2010), herbivory (Asplund et al., 2010), sun-screening pigments (Färber et al., 2014) and hydration traits (Esseen et al., 2017). The gradients in moisture and light play key roles for epiphyte distributions within canopies as lichen growth is linked to the duration of hydration periods during daylight (Palmqvist, 2000). These gradients interact with lichen functional traits that influence hydration status and productivity (Coxson and Coyle, 2003; Gauslaa, 2014; Esseen et al., 2015; Ellis et al., 2021). The vertical gradient in light can be divided into three zones (Parker, 1997; Parker and Brown, 2000): (1) A 'bright' zone in upper canopy with high direct light and little variation in light transmittance, (2) A 'transition' zone from upper to lower canopy with large variability in transmittance, and (3) a 'dim' zone in lower canopy with low transmittance and little variability. Lichens are often exposed to higher light than at light saturation of photosynthesis, with species differing in the ability to tolerate high light stress (Beckett et al., 2021). Färber et al. (2014) showed that the functioning of species-specific sunscreening fungal pigments that protect the underlying algae to high light shape the vertical gradient of pendulous lichens in boreal forests. Dark lichens with melanins tolerate high light and dominate the upper canopy, whereas pale ones with usnic acid (like *Usnea* spp.) dominate the lower canopy. However, we lack detailed information on how old-growth associated lichens respond to the complex light environment within canopies.

Studies of horizontal distribution of lichens in landscapes and forest stands have focused on edge influence (Esseen and Renhorn, 1998; Kivistö and Kuusinen, 2000; Rheault et al., 2003; Hilmo et al., 2005), gaps (Benson and Coxson, 2002; Bartemucci et al., 2022), canopy openness (Goward et al., 2022) as well as patch size and isolation (Kruys and Jonsson, 1997; Johansson et al., 2012; Cardós et al., 2016). Esseen (2019) studied distribution of pendent lichens in a forest-wetland mosaic and suggested that the same mechanisms drive horizontal and vertical niche differentiation in these lichens. Yet, quantification of the 3D distribution of old-growth forest lichens is still rare (Miller et al., 2017; Benesperi et al., 2018).

Here we examine how the 3D distribution of the iconic lichen *Usnea longissima* Ach. is linked to canopy structure and light environment in an old *Picea abies* forest (Norway spruce, henceforth spruce) in Sweden. This lichen occurs in the northern hemisphere (Clerc, 2011) and may reach a length of several meters, constituting the longest lichen in the world. It is suitable for studying niche specialism in lichens for several reasons: (1) Its unique morphology and preference for the lower canopy in boreal forests enable quantification from the ground (Esseen et al., 1981), (2) Its distribution is strongly linked to climate at global, regional and local scales (Gauslaa et al., 2007; Smith et al., 2016; Eriksson et al., 2018; Strother et al., 2022), and (3) It is associated with old-growth spruce forests in Europe (Esseen et al., 1981; Gauslaa, 1997, Josefsson et al., 2005) and a flagship species for conservation of biodiversity in boreal forests (Esseen et al., 1992). *Usnea longissima* is extinct or endangered in European countries and red-listed as vulnerable as well as protected by law in Sweden (SLU, 2020). Our objective was to identify the functional mechanisms that shape the lichen's 3D distribution within canopies. We address the following questions: (1) How is occurrence and horizontal distribution of the lichen coupled to host tree characteristics, forest structure and spatial distribution of trees? (2) How is population size and vertical distribution coupled to host tree characteristics and vertical profile of light on live and dead trees? and (3) Is the horizontal distribution of the lichen linked to its vertical distribution?

2. Materials and methods

2.1. Study area

The study was done 2018–2019 in Edsbodskogen nature reserve (N63°4′19″, E18°6′39″), located close to the High Coast World Heritage Site in the middle boreal zone, north-eastern Sweden (Fig. 1). The reserve has an area of 82 ha and is located 11 km from the Bothnian Sea on a hill at 225–350 m a. s. l. The bedrock is mostly composed of nutrient poor granite. Temperature and precipitation data from Västmarkum, 8 km northwest of the site, were downloaded from the Swedish Meteorological and Hydrological Institute (SMHI, 2022) for the period 1996–2020. The climate was slightly oceanic with a mean annual temperature of 3.6 °C; monthly mean temperatures ranged from −6.0 °C in January to + 15.3 °C in July. Mean annual precipitation was 785 mm (range 522–1226 mm), of which c. 35 % was snow.

The forest was dominated by spruce and had long continuity of canopy cover. The oldest trees reached an age of ~ 150–200 years. No traces of forest fires or other stand-replacing disturbances were found. However, the forest was probably more open in the past due to grazing by cattle and selective logging, evidenced by the presence of old stumps and scarcity of logs in late decay stages. Edsbodskogen is one of the richest *U. longissima* sites in Sweden, with ~ 300 host trees, due to its location on a hill in a region with elevated precipitation, high air humidity and frequent fog. The epiphyte community was luxuriant and dominated by chlorolichens. The most common fruticose species were *U. dasopoga* (Ach.) Nyl.), followed by *Alectoria sarmentosa* (Ach.) Ach. and *U. longissima. Usnea dasopoga* and *A. sarmentosa* reached higher up in the canopy than *U. longissima*, ~15–20 m and ~ 13 m, respectively. *Bryoria* was only abundant in upper canopy and included *B. capillaris* (Ach.) Brodo & D. Hawksw., *B. fuscescens* (Gyeln.) Brodo & D. Hawksw., and *B. nadvornikiana* (Hoffm.) Brodo & D. Hawksw. The dominating foliose lichens were *Hypogymnia physodes* (L.) Nyl., *H. tubulosa* (Schaer.) Bitter, and *Platismatia glauca* (L.) W.l. Culb. & C.F. Culb.

2.2. Sample plot

The initial survey of the lichen was facilitated by that 210 host trees had been marked with a yellow PVC band in 2001 (Anon., 2015). We searched through 6–8 ha for three days and recorded the positions of host trees with a Garmin GPSMAP 64st. A polyester band with the number of the tree was tied on a lower branch. We mapped the trees in ArcGis 10.3 and located a 100 m × 100 m plot in the area with highest numbers of host trees, at an elevation of 330–340 m a. s. l. (Fig. 1). The plot was marked out using a Suunto mirror compass and measurement tapes.

2.3. Forest structure and composition

We made a detailed map of all live and dead trees with DBH ≥ 5 cm. The mapping was done separately in 100 subplots (10 m × 10 m). We placed out measurement tapes along the sides of the subplot and measured the distances to the trees with a Vertex IV ultrasound instrument (Haglöf, Sweden). One person held a transponder at the centre of each tree at 1.3 m above ground, while the other person measured the shortest distance (i.e., perpendicular to the measurement tape) to the western side of the plot (y-axis) with the Vertex held at the same height. This procedure was repeated for all trees in the subplot. We then measured the distances to each tree from the southern side (x-axis), with the Vertex placed at the previously recorded distances. The Vertex has a resolution of 1 cm and an accuracy of 1 % and operates even if the target tree is hidden by undergrowth. However, we estimate that the maximum positional error was ~ 20 cm, due to minor variations in topography. We recorded species, DBH, vitality (VIT; live, dead) and height of stem breaks for all trees. We also measured the height (HEIGHT) of all host trees with the Vertex.

2.4. Population size

We made a total census of the horizontal and vertical distribution of *U. longissima* on all trees. The 'population size' (POP) was measured as the summed length of all thalli, along the main branches (Esseen et al., 1981); the number of thalli cannot be counted without using destructive sampling (Gauslaa, 1997; Gauslaa et al., 1998). Total thallus length was estimated in 1-m vertical sectors on each tree, from ground level to the uppermost occurrences. The height of a thallus refers to its attachment point on a branch and was measured with a 5-m or a 10-m extendable aluminium pole (see below). The estimates were done by naked eye and binoculars (8 X) from all sides of the trees. They were done in days with sunny or partly cloudy weather with little wind, when the thalli were dry, as thallus length vary with RH (Rolstad and Rolstad, 2008). Finally, the height of the lowest (LOWER) and highest positioned thallus (UPPER) was measured to the nearest 0.1 m.

2.5. Vertical light profiles

The vertical profile of photosynthetic photon flux density (PPFD) was measured for 39 live and nine dead trees with large *U. longissima* populations, constituting 75 % of total POP. We used two LI-250A Light Meters, each equipped with a LI-190R Quantum Sensor, LI-COR Biosciences GmbH, Bad Homburg, Germany. One sensor was placed on top of an extendable (2–10 m) telescopic pole (Nestle Telefix, Gottlieb NESTLE GmbH, Dornstetten, Germany). The pole was placed on the side of the tree with the largest POP and positioned vertically (with a bubble level) within or just outside the crown, where it could be extended up to a height of 10 m, close to the thalli. The mean distance from the stem was 1.3 m (range 0.7–2.4 m). All cardinal directions were represented, but > 50 % were eastern. The other sensor was used as open sky reference and placed horizontally with a bubble level on a 2-m tripod in the middle of a nearby 1.2 ha open wetland (Fig. 1). PPFD was measured during days with an overcast sky (to exclude direct light) as a 15 s average at 1-m vertical intervals from 2.0 to 10.0 m, with a simultaneous reading of the reference sensor. A final second reading was taken at 2 m to assess the variation. PPFD transmittance fraction was calculated as the ratio of PPFD at each height to PPFD at the reference (Messier and Puttonen, 1995). An instantaneous measure of PPFD fraction on overcast days correlates strongly with mean daily PPFD fraction during the growing season (Parent and Messier, 1996; Lieffers et al., 1999). The difference in PPFD fraction was on average ~ 0.02 between the two measurements at 2 m.

2.6. Microclimate

The temporal variation in PPFD, RH and air temperature (TEMP) was monitored from 1 October 2017 to 24 September 2019 with a Hobo H21-USB Micro Station datalogger, Onset Corporation, USA. We used a Hobo 12-bit Temperature/Relative Humidity Smart Sensor placed within an unaspirated radiation shield, and a Hobo S-LIA-M003 PAR sensor. Data were logged at 10-minute intervals. The sensors were positioned on a pole 3 m above ground in the middle of a small gap surrounded by host trees (Fig. S1).

2.7. Data analysis

The statistical analyses were done with R version 4.1.2 (R Core Team, 2022). We calculated basal area (BAS) from DBH of all trees in the plot, and in a 10-m radius around each tree. We then calculated mean (±1 SE) of DBH, HEIGHT, POP, LOWER and UPPER by VIT, and evaluated differences between live and dead trees with Student's t-tests. POP was log-transformed in these tests. POP was also pooled over all 1-m vertical sections in the trees.

The spatial distribution of trees was analysed with Ripley's (homogeneous) *K*-function and nearest neighbour statistics (Baddeley et al., 2016). The theoretical *K*-function (Ripley, 1981) is defined as the expected number of other trees within radius *r* of a randomly chosen tree, divided by the density of trees per unit area. The corresponding empirical *K*-function was used to test whether the pattern of the trees followed a homogeneous Poisson point process (CSR, complete spatial randomness). We first calculated this *K*-function for all spruces, by applying an isotropic edge-correction algorithm. We then applied Besag's *L*-function ($L(r) = \sqrt{K(r)/\pi}$) (Besag, 1977), which transforms the theoretical Poisson *K*-function for CSR to a straight line, and plotted the empirical centred version of the *L*-function ($\widehat{L}_{obs}(r) - r$) against *r*. Finally, we tested the hypothesis of CSR against the alternative hypothesis of clustering by applying a (slightly conservative) one-sided global envelope test using the *L*-function (Baddeley et al., 2014; 2016). The test was performed using 19 simulations, giving a significance level of 5 %. The null hypothesis of CSR was rejected if any value of the empirical centred *L*-function was above the global envelope.

We also used the *L*-function to test whether the locations of host trees were CSR. However, this analysis did not consider that the spatial distribution of host trees was conditional upon the locations of the spruces. Based on Esseen (1983) and Lione and Gonthier (2016) we therefore developed a permutation test of random labelling, where each label identifies whether a spruce is a host tree or not. In the permutation test, the locations of the spruces are held fixed, while the labels attached to the spruces are randomly permuted, with equal probability for each possible permutation. The null hypothesis of completely random labelling thus implies constant probability for the lichen to occur on a spruce and that the probability does not depend on spatial location. If the null hypothesis is true, then the spruces with the randomly permuted labels are statistically equivalent to the original set of labelled spruces. As test statistic we used the mean nearest neighbour distance between host trees, i.e., we first computed the distance from each host tree to its nearest neighbouring host tree, and then the statistic was defined as the mean of these distances. The value of the statistic was computed for each of *n* sets of randomly labelled spruces. If *m* of these values is smaller than or equal to the value of the test statistic for the original data, the *P*-value of the test is $(m + 1) / (n + 1)$. We used $n = 9999$. Note that the test is one-sided. The null hypothesis of random labelling was rejected if $P \leq 0.05$. Finally, we also visualized the distribution of the nearest neighbour distances between host trees in the observed data and the distribution of the corresponding distances from all randomly labelled sets as histograms.

Table 1
DBH (mean ± 1 SE) by tree species and vitality (VIT, live and dead) in the studied 1 ha plot. Spruce (*Picea abies*) was divided into trees without and with *Usnea longissima.*

	Live		Dead		Total	
	N	Mean ± 1 SE	*N*	Mean ± 1 SE	*N*	Mean ± 1 SE
Picea abies						
Without *U. longissima*	545	19.7 ± 0.4	124	17.6 ± 0.9	669	19.3 ± 0.4
With *U. longissima*	153	26.4 ± 0.9	36	25.1 ± 1.8	189	26.1 ± 0.8
Betula pubescens	32	18.2 ± 1.1	42	16.2 ± 0.9	74	17.0 ± 0.7
Salix caprea	2	17.0 ± 1.7	3	12.8 ± 3.2	5	14.4 ± 2.1
Sorbus aucuparia	2	12.7 ± 2.9	5	11.4 ± 2.4	7	11.8 ± 1.8
Total	734	21.0 ± 0.4	210	18.4 ± 0.7	944	20.4 ± 0.3

We examined the relationships between POP, BAS, DBH and UPPER for the host trees with regression and correlation. POP and UPPER were log-transformed to obtain approximately linear relationships. We then used logistic regression (Hosmer et al., 2013) to identify the variables that best correlated with occurrence of the lichen on spruce. We first ran a model with only distance to the nearest host tree (DIST) as explanatory variable. We only included spruces located ≥ 10 m from the edge of the plot to minimize bias in DIST. Thereafter we developed multiple models including BAS, DBH, DIST, POP, UPPER and VIT. Fractional polynomials of first and second degree were applied to account for the possibility of non-linear relationships (Sauerbrei and Royston, 1999) using the R library mfp. We developed two models, including either UPPER or POP, as these variables were highly correlated. We used Akaike's second-order corrected information criterion (AICc) for the final model selection. The models were checked using the DHARMa library in R. Model performance was evaluated with McFadden pseudo R^2, which is typically lower than R^2 in ordinary regression. Pseudo R^2 values of 0.2–0.4 have been shown to represent an excellent fit (McFadden, 1977; Petrucci, 2009). The multiple models were interpreted with odds ratios, which approximates how much more likely or unlikely (in terms of odds) it is for the lichen to occur on spruce with an increment of a variable with one-unit, while holding other variables constant (Hosmer et al., 2013; Esseen et al., 2022).

We calculated the mean of POP across all 1-m vertical sections for the subset of 48 trees where we had measured vertical light profiles. The mean PPFD fraction was calculated from 2 to 10 m height by live and dead trees, together with 95 % confidence intervals. The mean PPFD fraction for each 1-m section was then calculated from the values at the lower and upper height of each section. The relationship between POP and PPFD fraction for all 1-m sections where the lichen occurred was examined visually and with correlation. We calculated mean and range for PPFD, RH and TEMP from the logged microclimate data. The proportion of time with high light from April to September was calculated from the number of 10-min intervals with PPFD ≥ 400 μmol photons m^{-2} s^{-1}, based on Färber et al. (2014).

3. Results

3.1. Forest structure and host tree characteristics

A total of 944 trees occurred in the plot, 734 live and 210 dead

(Table 1). Spruce dominated, followed by *Betula pubescens* Ehrh. *Usnea longissima* occurred on 189 spruces. BAS was 38.9 m^2/ha with dead trees constituting 19 %. Spruce constituted 97 % of live BAS and *B. pubescens* 3 %. The distribution of DBH for all trees was multimodal and dominated by small and intermediate-sized trees, whereas DBH of host trees had an approximate normal distribution (Fig. 2). The host trees had larger DBH (26.1 cm) than trees without the lichen (19.0 cm), but the difference was not significant ($P > 0.05$). The height of the host trees ranged from 3.2 to 25.8 m, with tall trees dominating (Fig. S2). Live trees were taller (17.2 m) than dead trees (13.9 m; $P < 0.001$).

The forest had several small canopy gaps and some variability in stem density (Fig. 3). The empirical centred L-function ($\widehat{L}_{obs}(r) - r$) for all spruces stayed inside the simulated global envelope for CSR (Fig. 4A), except at ~ 0.5–1.0 m, indicating clustering. In contrast, the empirical centred L values for the host trees were above the envelope for CSR for all distances greater than ~ 1.3 m (Fig. 4B), indicating clustering. The mean nearest neighbour distance between the observed host trees was 0.57 m lower than the mean of the corresponding distances from the 9999 randomly labelled sets, 3.20 and 3.77 m, respectively. The permutation test was highly significant ($P = 0.0002$), showing that the lichen is not randomly allocated to trees independently of location and other trees. The distribution of nearest neighbour distance between host trees was dominated by short distances. The median nearest neighbour distance between the observed host trees was 1.36 m lower than the median of the corresponding distances from the 9999 randomly labelled sets, 2.22 and 3.58 m, respectively (Fig. 4C, 4D).

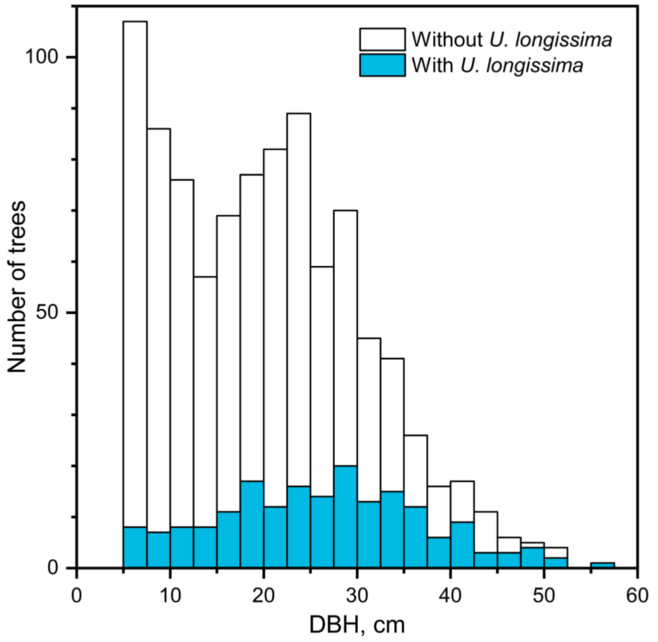

Fig. 2. Distribution of DBH for trees without ($N = 755$) and with *Usnea longissima* ($N = 189$) in the studied 1 ha plot.

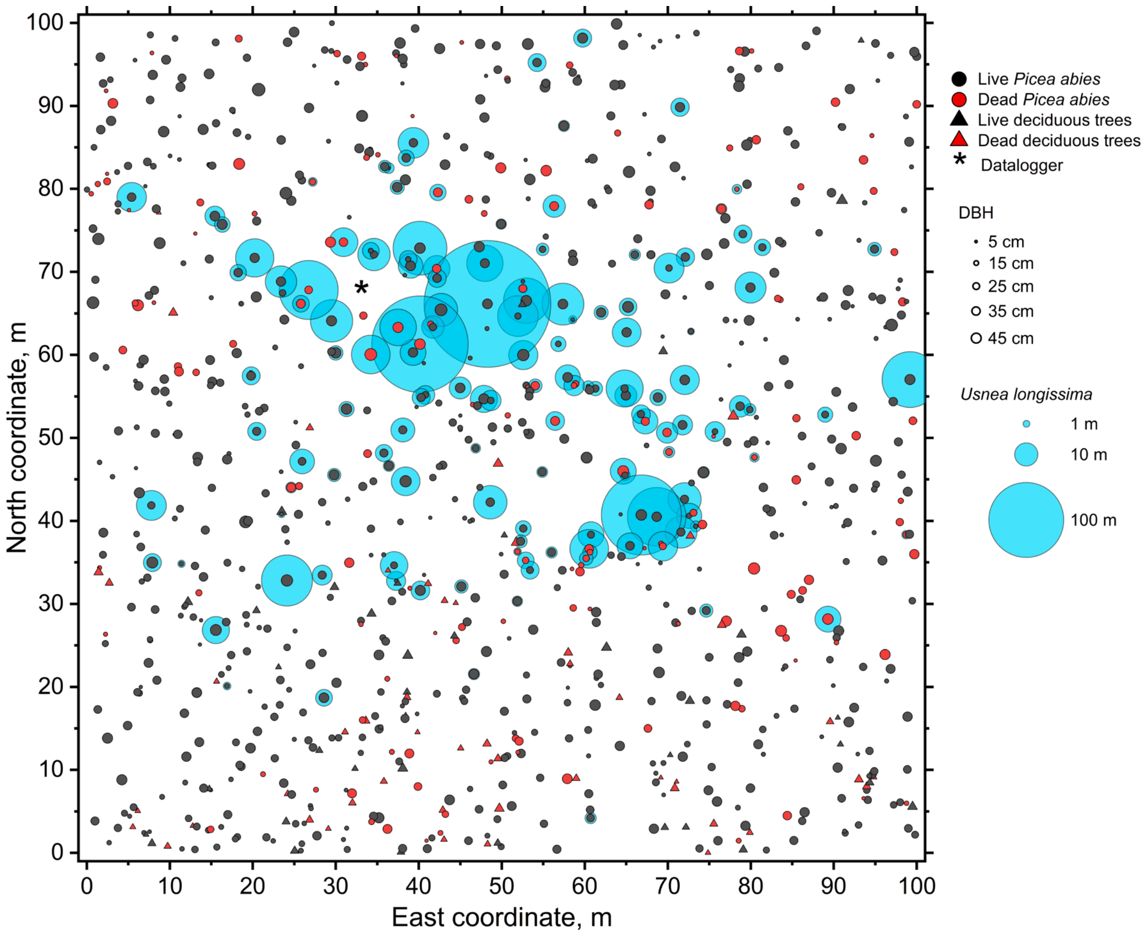

Fig. 3. Spatial distribution of live and dead trees and population size (POP, m thallus length) of *Usnea longissima* in the studied 1 ha plot. Area of symbols is proportional to DBH and population size of *U. longissima*, respectively. $N = 944$.

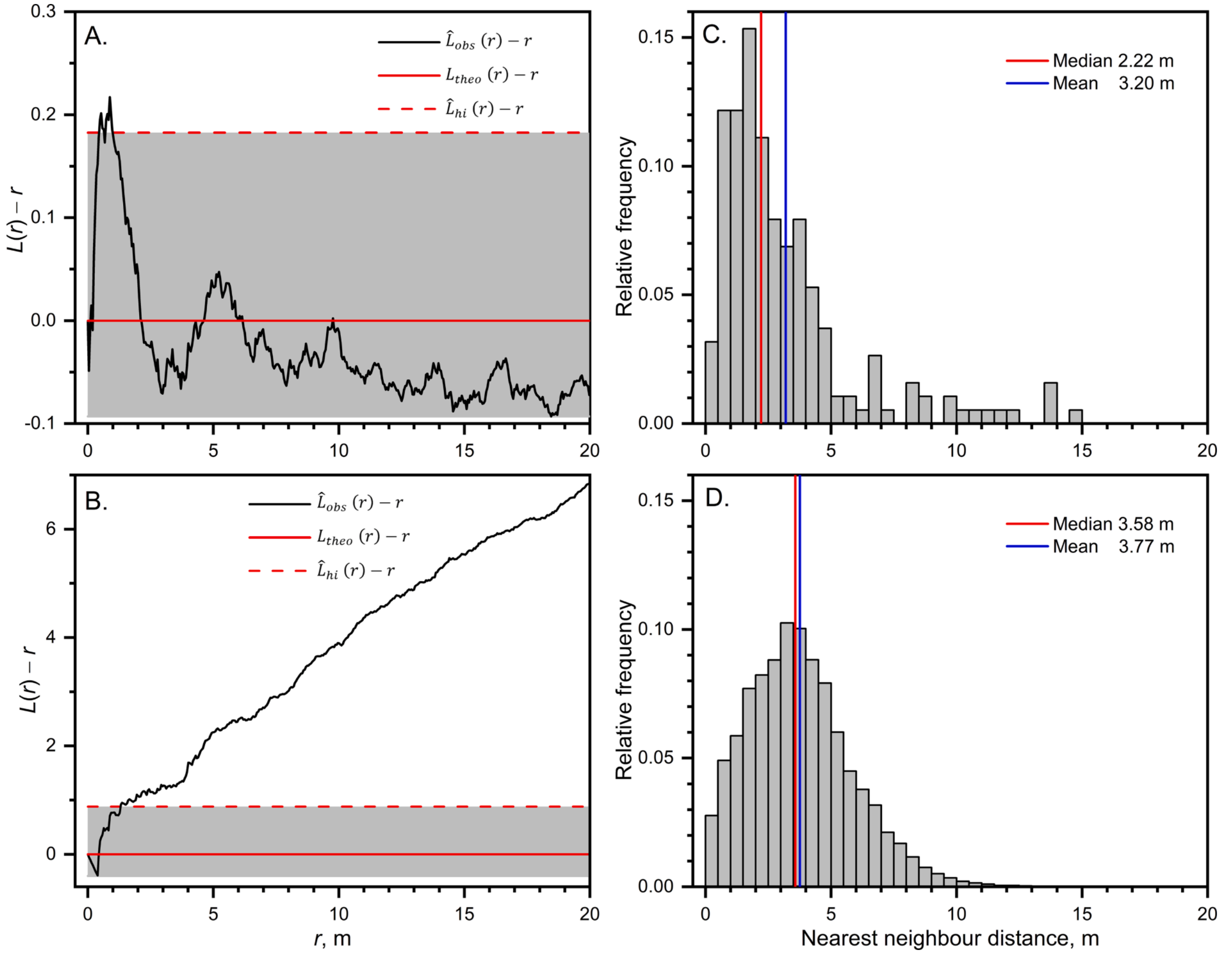

Fig. 4. A. Analysis of the spatial pattern of all spruces, and B, of spruces hosting *Usnea longissima*, using the empirical centred L-function ($\hat{L}_{obs}(r) - r$) plotted against distance (r) and a simulated upper global envelope. The hypothesis of CSR is rejected at the 5 % level if the empirical centred L-function ever wanders above the simulated upper global envelope. C. Distribution of nearest neighbour distances between observed host trees ($N = 189$). D. Distribution of nearest neighbour distances between host trees in the 9999 randomly labelled versions of the original data ($N = 189 \times 9999$).

Table 2
Population size (POP, m thallus length) as well as lower (LOWER) and upper vertical limit (UPPER) of *Usnea longissima* on live and dead spruces in the studied 1 ha plot. *P*-values refer to Students *t*-test on log-transformed data.

	Live ($N = 153$)	Dead ($N = 36$)	*P*
POP, m			
Range	0.1–279.2	0.1–162.8	–
Mean ± 1 SE	10.2 ± 2.1	12.9 ± 4.7	0.380
Total, m	1560	465	–
LOWER, m			
Range	0.4–10.4	1.0–6.3	–
Mean ± 1 SE	2.0 ± 0.09	2.2 ± 0.21	0.274
UPPER, m			
Range	1.0–12.5	1.4–11.5	–
Mean ± 1 SE	5.6 ± 0.23	6.0 ± 0.47	0.694

3.2. Population size

POP was highly variable (0.1–279 m), with a mean of 10.7 m (median = 4.3 m) and a total of 2025 m (Table 2). Most trees had small POP and the distribution was approximately log-normal (Fig. 5A). The 10 trees with largest POP hosted 44 % of total population. Dead trees had 27 % higher POP than live trees, but the difference was not significant ($P > 0.05$). The horizontal distribution was clustered, with trees hosting large POP often surrounded by trees with small POP (Fig. 3). The vertical range varied from 0.4 to 12.5 m (Fig. 5B). However, the mean of UPPER was only 5.6 and 6.0 m in live and dead trees, respectively (Table 2). Most trees had a continuous occurrence along the vertical range (Fig. S3). POP was rather stable (11.9–14.4 % of total) in the 1-m intervals between 2 and 8 m, but then decreased rapidly with height, with only 3 % occurring above 10 m. Isolated populations above a height of 5 m were only observed in five trees. Such thalli often formed loose clumps on branches close to the stem. In contrast, the thalli were mostly hanging freely on lower canopy branches (Fig. S1).

3.3. Predictors of population size and occurrence

POP (log-transformed) increased with DBH ($R^2_{adj.} = 0.21$; Fig. 6A), but the relationship with UPPER (log-transformed) was stronger ($R^2_{adj.} = 0.61$; Fig. 6B). However, POP did not correlate with BAS ($r = -0.052$; $P > 0.05$; Fig. S4). The probability of lichen occurrence decreased rapidly with DIST (square root transformed) in the logistic regression model with only this variable ($R^2 = 0.132$; $P < 0.001$; Fig. 7). The two multiple logistic regression models including UPPER or POP had R^2 of 0.232 and 0.251, respectively (Table 3), indicating very good fit. Both DIST and DBH were significant in these models, whereas BAS and VIT were not included. The models were interpreted with odds ratios (Fig. S5). Increasing DIST with 1 m in the model including UPPER decreased the odds for occurrence at small values of DIST but only slightly at larger values. Increasing UPPER with 1 m and DBH with 1 cm increased the odds with 1.13 and 1.08, respectively. The model including POP was

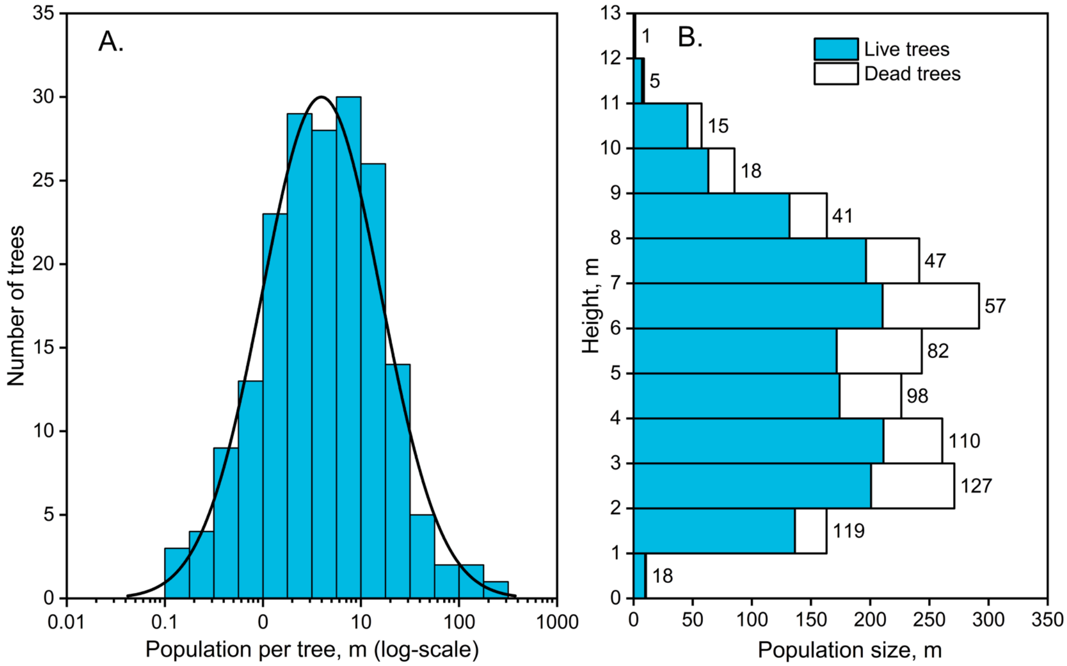

Fig. 5. Histogram of population size of *Usnea longissima* (POP, log-scale) on spruce, with fitted Normal distribution (A), and vertical profile of population size on live and dead trees. The labels in B indicate the number of trees with occurrence of the lichen at each height interval. $N = 189$.

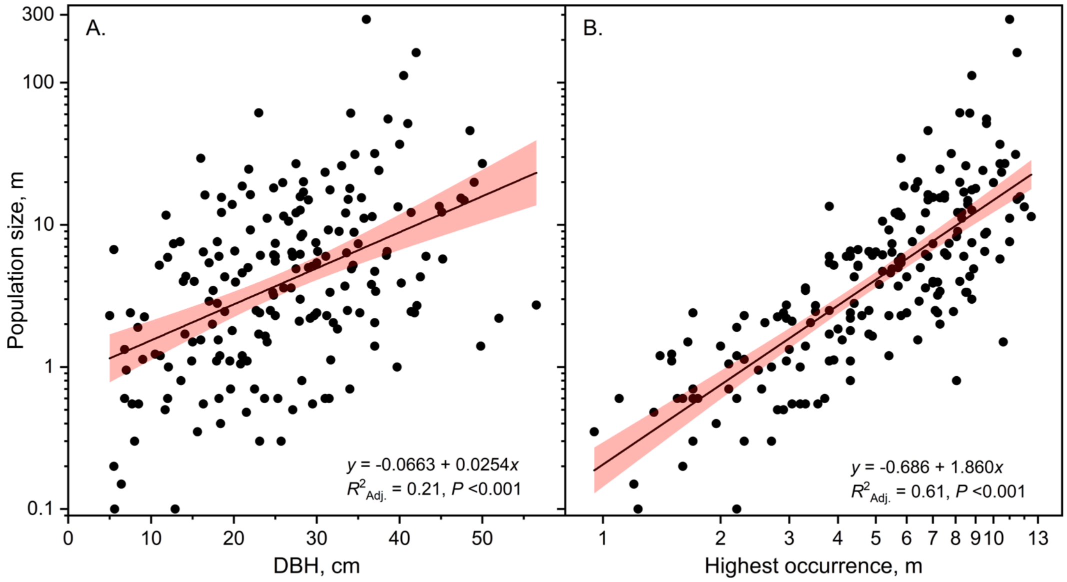

Fig. 6. Relationship between population size of *Usnea longissima* (POP, log-transformed) and DBH of host trees (A). Relationship between population size and highest occurrence of the lichen (UPPER, log-transformed) on each tree (B). Lines indicate linear regressions on transformed data and shaded areas 95 % denote confidence bands. $N = 189$.

more complicated as POP interacted with both DIST and DBH. Increasing DIST with 1 m decreased the odds for occurrence at observed combinations of POP and DIST. Increasing POP with 1 m increased the odds for occurrence at low values of DIST (~2.2–5.3 m), depending on DBH. Increasing DBH with 1 cm slightly increased the odds for occurrence at small values of POP, but these odds increased more at larger values.

3.4. Vertical light profiles

POP peaked at a height of 5–7 m for the 48 trees where we measured light profiles (Fig. 8A). The vertical profiles of PPFD fraction varied from no gradient to a moderately steep increase (Fig. S6). Low light occurred at all heights, whereas the highest PPFD fraction was 0.328 at 2 m and 0.607 at 10 m. Mean PPFD fraction increased non-linearly with height, from 0.196 at 2 m to 0.374 at 10 m (Fig. 8B). Dead trees had on average 40 % higher light than live trees, with significantly higher values above 5 m (Fig. 8C). The lichen occurred over a wide range of PPFD fraction (0.105–0.581; Fig. 9), but most occurrences were at low-intermediate light. The mean was 0.245 ± 0.006 (±1 SE; $N = 281$) for all 1-m sections and 0.297 ± 0.017 for sections with POP > 10 m ($N = 25$). POP (log transformed) did not correlate with PPFD fraction ($r = 0.094$; $P = 0.114$).

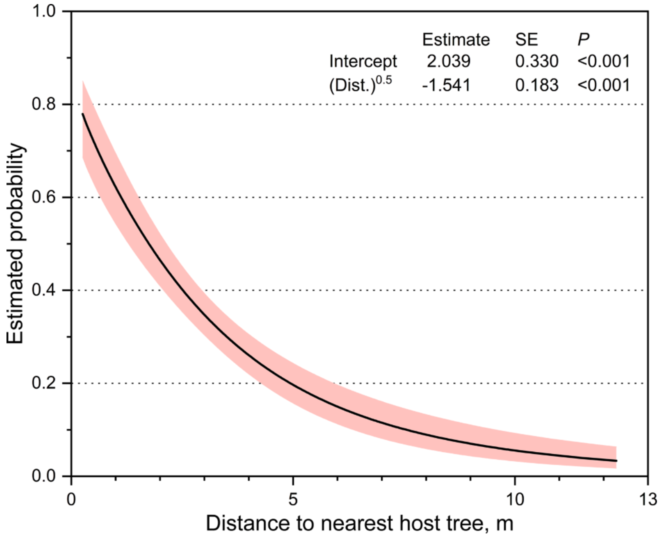

Fig. 7. Estimated probability of occurrence of *Usnea longissima* on spruce with distance to nearest host tree (DIST) from a logistic regression model with only this variable. The shaded area denotes the 95 % confidence band. Data from an 80 m × 80 m window in the 1 ha plot. $N = 534$, Pseudo $R^2 = 0.132$.

Table 3
Summary of two multiple logistic regression models predicting occurrence of *Usnea longissima* on spruce in an 80 m × 80 m window ($N = 534$). DBH = diameter at breast height of the focal tree, DIST = distance to the nearest host tree, UPPER = height of the uppermost *U. longissima* thallus on the nearest host tree, POP = population size of *U. longissima* on the nearest host tree.

Model, variable transformations	Estimate	SE	*P*
Model with UPPER (Pseudo $R^2 = 0.232$)			
Intercept	−0.047	0.460	0.919
(DBH/10)	0.746	0.106	<0.001
$(\text{DIST}/10)^{0.5}$	−5.222	0.631	<0.001
(UPPER/10)	1.201	0.415	0.004
Model with POP (Pseudo $R^2 = 0.251$)			
Intercept	−0.093	0.495	0.850
(DBH/10)	0.611	0.121	<0.001
$(\text{DIST}/10)^{0.5}$	−4.058	0.827	<0.001
(POP/10)	1.430	0.705	0.042
(DBH/10) × (POP/10)	0.334	0.130	0.010
$(\text{DIST}/10)^{0.5}$ × (POP/10)	−2.905	1.344	0.031

3.5. *Microclimate*

TEMP varied from –20.7 °C to 30.3 °C, with an overall mean of 3.2 °C (Fig. 10). RH was negatively correlated with TEMP ($r = –0.51$; $P < 0.001$). PPFD fraction was 0.312 for the sensor (3 m height), which was close to that at a height of 8 m in host trees (0.300; mean of 48 trees; Fig. 8B). PPFD exceeded 400 μmol photons m^{-2} s^{-1} during 4.2 % and 3.5 % of the time from April to September in 2018 and 2019, respectively. The periods with high PPFD were long during the warm summer of 2018 and experienced low RH during several days. In contrast, the lichens were more frequently rehydrated after being exposed to high irradiance in 2019.

4. Discussion

4.1. *Horizontal distribution*

The forest was regulated by gap dynamics driven by tree mortality at fine scales (gaps < 200 m^2; Kuuluvainen and Aakala, 2011). Such forests are characterized by lack of stand-replacing disturbances, long continuity of canopy cover, and a multimodal or all-aged structure. The old-growth character of the site resulted from autogenic disturbance by insects, wood-decay fungi and local windthrow. Although the lichen is associated strongly with old forests, neither Esseen et al. (1981) nor Rolstad and Rolstad (1999) observed any correlation between population size and age of host trees. Instead, we found that population size increased with DBH.

The horizontal distribution of the lichen was characterized by large variability in population size and strong clustering of host trees. The logistic regression model with distance to the nearest host tree shows that the probability of occurrence decreased to only ~ 0.20 at 5 m distance from host trees (Fig. 7), suggesting that the clustering was caused by limited local dispersal. The multiple logistic regression models show that distance to the nearest host tree was significantly negatively correlated with probability of occurrence also after controlling for other variables. Moreover, these models suggest that the horizontal distribution of the lichen is linked to its vertical distribution, because the probability of occurrence increased with upper limit and population size on the nearest host tree. All dispersal is asexual as apothecia have not been found in Fennoscandia. Local dispersal is mainly by thallus fragments (Esseen et al., 1981; Gauslaa, 1997). These fragments can be longer than 1 m, but most are shorter than 0.3 m (Esseen, 1985). They have low probability of being transported over longer distances than a few m's from the source trees, consistent with the clustering of host trees. Transplant studies suggest that dispersal limitations are important in determining the distribution of *U. longissima* (Keon and Muir, 2002; Strother et al., 2022) and other old-growth forest lichens (Sillett et al., 2000; Scheidegger and Werth, 2009).

4.2. *Vertical distribution*

Although the forest was tall, the multi-layered canopy and the ~ 20 % defoliated trees allowed enough light to reach the middle and lower canopy, where the humidity is higher and hydration periods therefore last longer (Coxson and Coyle, 2003; Sibley et al., 2022). The lichen extended up to mid-canopy (12.5 m), which is higher than in other Swedish sites (Esseen et al., 1981), but comparable to rich and wetter sites in Norway (Gauslaa et al., 1992; Gauslaa, 1997). It also grows in upper canopy in tall forests with high rainfall in the U.S. Pacific Northwest (Williams and Sillett, 2007), emphasizing that macroclimate is an important driver of vertical distribution. Here we suggest six additional functional mechanisms that likely influence the vertical distribution of the lichen. Similar mechanisms may also influence the horizontal distribution.

(1) Canopy architecture. Canopy structure, such as tree height, as well as the number, size, and arrangement of branches influence the distribution of lichens by providing substrates (Esseen et al., 1996; Ellis, 2012; Miller et al., 2017) and by modifying microclimates (De Frenne et al., 2021). The lower branches were often large and partially or totally defoliated and likely provide better conditions for lichen growth than foliated branches. This mechanism contributes to the lichen's preference for the lower canopy but cannot explain its relatively sharp upper limit.

(2) Sensitivity to high light. Low tolerance to high light likely contributes to the absence of the lichen from the upper canopy. *Usnea longissima* has a less efficient sunscreen and is more susceptible to high light when desiccated compared to other hair lichens (Färber et al., 2014). The recovery of its photosynthetic apparatus after light exposure and subsequent rehydration was delayed and less complete than in other studied hair lichens. Lichens in upper canopy experience both higher radiation intensity and longer duration of such periods than in lower canopy (Parker and Brown, 2000; Coxson and Coyle, 2003) causing substantial damage by photoinhibition of susceptible species during clear days. The PPFD fraction at ~ 8 m height was close to that at 3 m in the gap, indicating an exposure to high light (>400 μmol photons m^{-2} s^{-1}; Färber et al., 2014) during ~ 4 % of the time from April to September. Photoinhibition was probably more extensive during the warm and dry summer in 2018 than in 2019, when more frequent

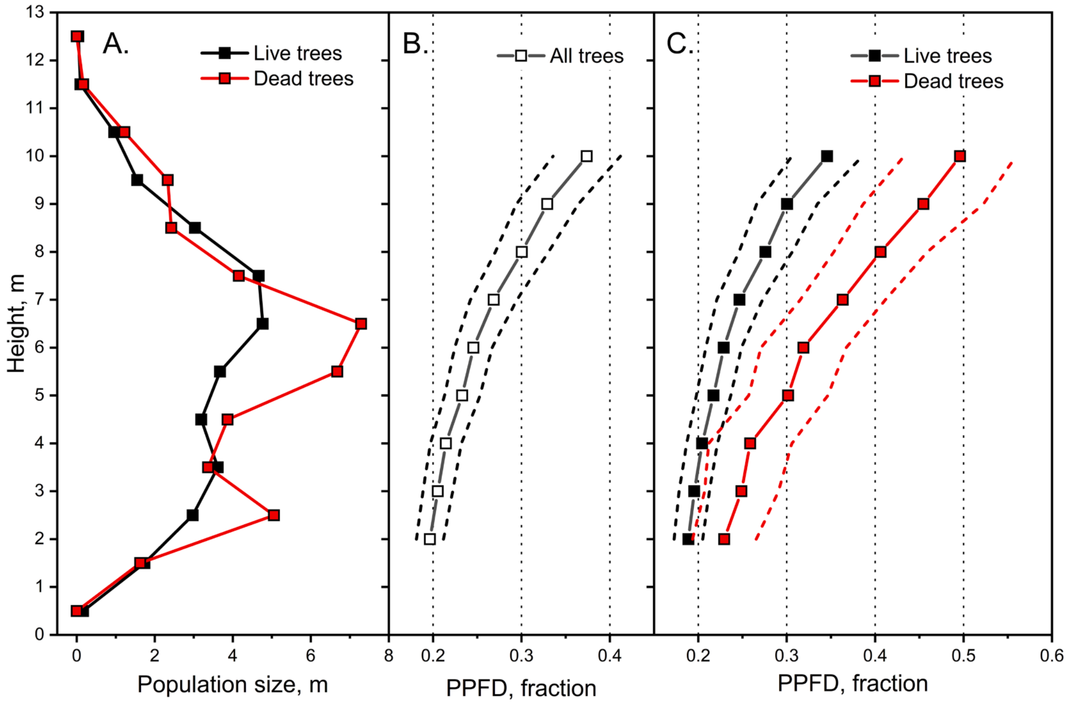

Fig. 8. Vertical profile of mean population size of *Usnea longissima* (POP) per tree for 39 live and nine dead spruces (A), mean PPFD fraction with 95% confidence bands on all trees (B), and separately for live and dead trees (C).

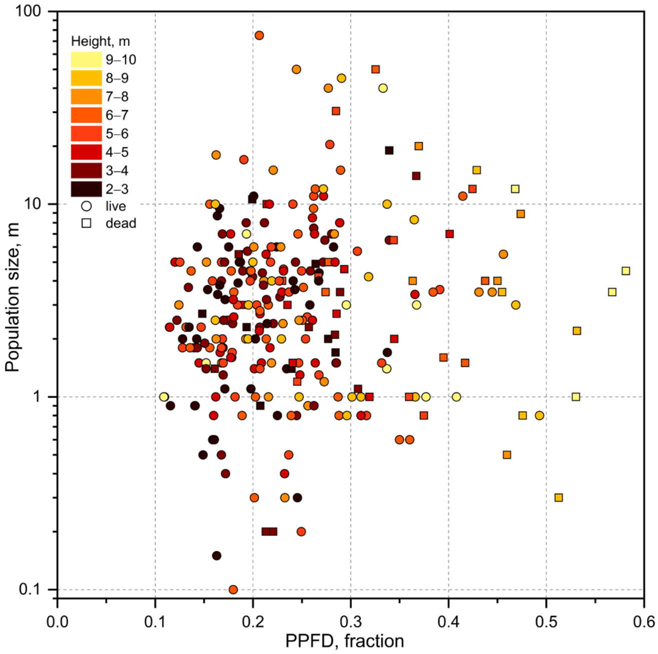

Fig. 9. Relationship between population size of *U. longissima* (POP, log-scale) and PPFD fraction in 1-m vertical sections on 39 live and nine dead spruces. Symbol colour indicates height of each section. $N = 281$.

rehydration events facilitated recovery. However, the impact of photoinhibition on lichen distributions operates over several years (Färber et al., 2014). Photoinhibition is less important in oceanic climates with high rainfall and shorter dry periods, where *U. longissima* and other usnic lichens extend into upper canopies (Gauslaa et al., 1992; McCune et al., 1997; Benson and Coxson, 2002; Antoine and McCune, 2004).

(3) Optimal light environment. This mechanism suggests that the lichen is most abundant in the vertical zone where the light environment is optimal for growth. The lichen has high growth-potential (Keon and Muir, 2002; Gauslaa et al., 2007; Jansson et al., 2009; Strother et al., 2022) including diffuse or intercalary growth along the main axis (Rolstad and Rolstad, 2008; Sanders and de los Ríos, 2012). The lichen occurred in the lower half of the partially shaded transition zone from dim light to bright light, which is characterized by high variability in light transmittance (Parker, 1997). Population size did not correlate with the PPFD fraction, suggesting that a large proportion of the thalli had fallen from upper branches and thus occurred at microhabitats with sub-optimal irradiance. The small population size in shaded lower canopy positions is explained by the low growth or mass loss at such low irradiance (Gauslaa et al. 2007; Colesie, C., and Esseen, P.-A., unpubl. data). More importantly, population size peaked at ~ 0.20–0.33 PPFD fraction, implying that growth was highest in this 'light window', supporting the existence of a zone with optimal growth. In addition, the ~ 40 % higher light on dead trees suggests a boost in growth after a tree dies. However, Gauslaa et al. (2007) found that growth from mid-June to early October was highest at an indirect site factor of 0.60–0.65, a variable correlated with PPFD fraction (Lhotka and Loewenstein, 2006). The high irradiance at peak growth in the model of Gauslaa et al. (2007) may be explained by: (1) that two sites were in Norway with higher rainfall and cloudier weather than in our site, and (2) that growth measured during one growing season do not reflect long-term lichen responses to microclimate (Ellis et al., 2017).

(4) Sensitivity to desiccation. *Usnea longissima* is also sensitive to desiccation without light stress, with substantial delayed recovery after rehydration (up to ~ 24 h; Lidén et al., 2010; Färber et al., 2014). This mechanism contributes to its absence from the upper canopy, where lichens experience shorter duration of hydration than in the lower canopy (Coxson and Coyle, 2003). *Usnea longissima* and *U. dasopoga* have similar hydration traits and are better adapted to frequent hydration than shrubby *Usnea* species (Eriksson et al., 2018). However, *U. longissima* may need to be hydrated over longer periods than *U. dasopoga* to achieve maximum growth rates because its main axis lacks photobionts (Nybakken and Gauslaa, 2007) and as the slender thalli dries out quickly in the air space between spruce branches.

(5) Dispersal limitation. Inefficient dispersal probably restricts the

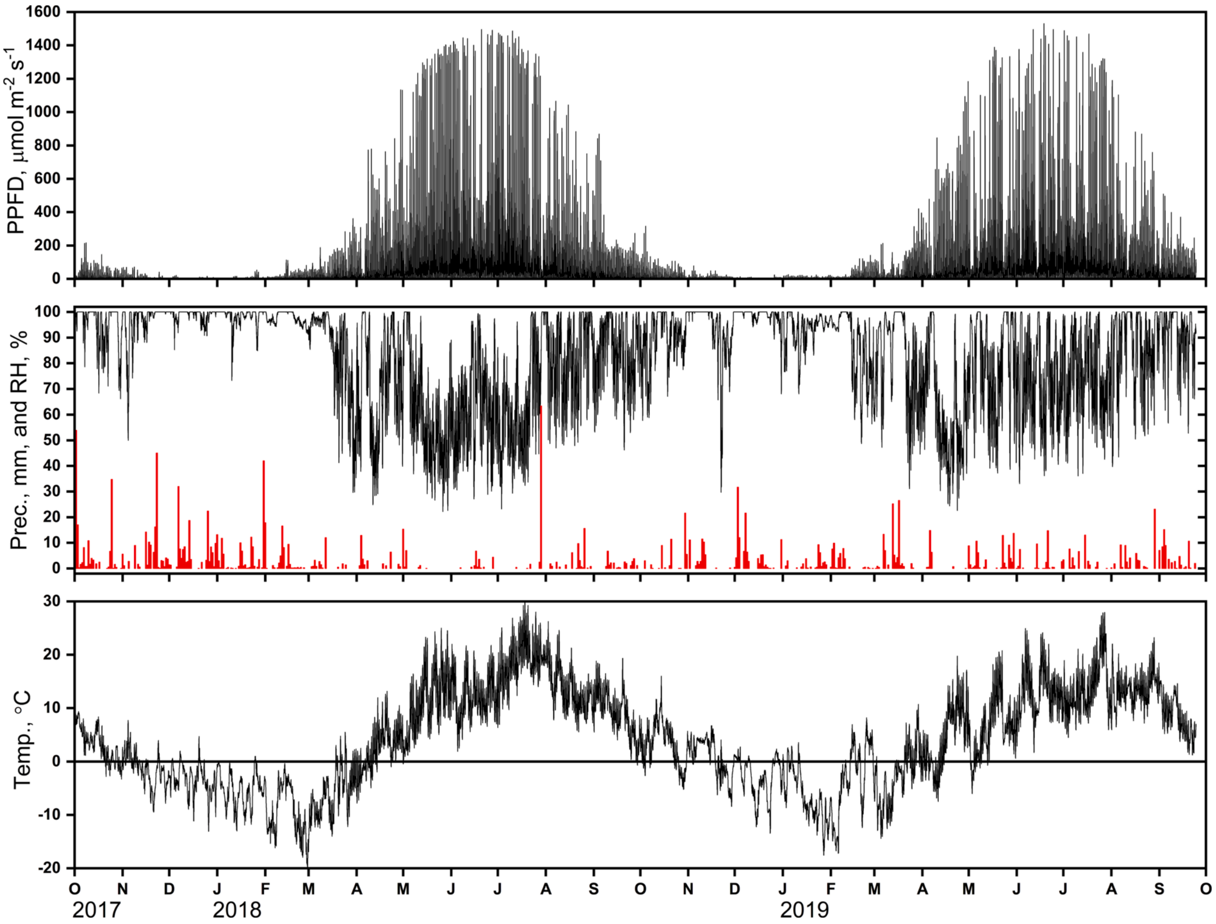

Fig 10. Photosynthetic photon flux density (PPFD), precipitation (Prec., red), relative humidity (RH) and air temperature (Temp.) from 1 October 2017 to 24 September 2019. PPFD, RH and temperature were logged at 3 m above ground in a gap surrounded by spruces hosting *Usnea longissima*. Precipitation data were from a meteorological station 8 km from the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lichen's migration to higher canopy positions. Dispersal by thallus fragments within a tree is mostly downwards as supported by the following points: (1) Dispersal by simple growth occurs from higher to lower branches (Gauslaa, 1997), (2) The lichen was often confined to only one side of a tree, and (3) Most trees had a continuous occurrence along the vertical range. Dispersal to higher canopy positions in neighbouring trees was likely favoured by the multi-layered canopy with several gaps, increasing turbulence and wind speed.

(6) Sensitivity to fragmentation. Pendulous lichens are susceptible to thallus fragmentation and mortality by strong winds at high-contrast forest edges (Esseen and Renhorn, 1998; Esseen, 2006; Jansson et al., 2009). By a similar mechanism, the increase in wind speed with height increases the probability of the thalli being fragmented, or detached, in the middle and upper canopy. This lichen is more sensitive to wind damage than other *Usnea* spp. because of its large size and because it lacks holdfast. Snow and ice in combination with high winds may aggravate the losses (Esseen, 1985).

4.3. Implications

Our study highlights that the 3D distribution of lichens in forest canopies is driven by forest dynamics, canopy structure, microclimate, and lichen functional traits. *Usnea longissima* has a set of functional traits that is unique among lichens: large size, high growth potential, poor local dispersal, as well as sensitivity to high light, desiccation, and strong winds. Both niche specialism and dispersal limitation (Williams and Ellis, 2018) contribute to its strong preference for humid old-growth boreal forests with long continuity of canopy cover. Despite high growth capacity (Gauslaa et al., 2007; Keon and Muir, 2002; Strother et al., 2022), the high degree of niche specialism and dispersal limitation suggest that the lichen has limited capacity to shift its vertical and horizontal distribution in response to changes in canopy structure and climate. The development of populations is driven by a small number of 'source trees' with large populations occurring at higher vertical positions, while 'sink trees' with small populations close to ground are less important. The build-up of large populations depends on rare colonization events at higher canopy positions, with subsequent downward dispersal. Loss of a few source trees may cause the whole population to decline and eventually become extinct. The number of source trees, with large populations, and high upper limit, are suitable indicators of the conservation status of the lichen.

Results also have implications for characterizing the light environment experienced by epiphytic lichens. We found no relationship between population size and basal area. Our site and other sites in Sweden had higher basal area (29–49 m^2/ha; Esseen and Ericson, 1982) than in Norway (15–26 m^2/ha; Liebe et al., 2017; Storaunet et al., 2014). Basal area over 100 m^2/ha has been reported from tall forests in the Pacific Northwest (Keon and Muir, 2002). Overall, basal area is a poor predictor of growth conditions for lichens as it cannot capture fine-scale variability in light. Our results and Phinney et al. (2021) show that an instantaneous measurement of PPFD fraction is an efficient method for assessing the light environment of epiphytic lichens.

The lichen cannot survive for longer periods of time in dense even-aged managed stands with short rotation cycles. Site protection is necessary to secure the long-term viability of the species. Protected sites must be large enough to avoid edge influence on microclimate from adjoining open habitats (Esseen and Renhorn, 1998; Jansson et al., 2009), and to secure sufficient local dispersal to replace host trees that are lost. Our data show that the studied population was large and viable, and hence no management is currently required. However, the population is at risk to become damaged by disturbances (windthrow, fire, pest insects, wood-decay fungi). This is evidenced by that one fifth of the trees were dead and that large patches of windthrown trees occurred west of the sample plot. Stand-replacing windthrow, followed by large-scale attacks of spruce bark beetle have caused extensive canopy damage in several nature reserves previously hosting abundant *U. longissima* in the region. Such disturbances are predicted to increase in future warmer climates (Seidl et al., 2017; Venäläinen et al., 2020).

Selective logging may be viable management option in dense single-layered forests, by increasing light and growth conditions for the lichen (Storaunet et al., 2014). Creation of small canopy gaps fill the same purpose but has the added benefit of increasing hydration through dew formed by nocturnal cooling (Bidussi and Gauslaa, 2015). However, all types of management in sites hosting this unique lichen must be based on detailed knowledge on population status, forest structure and microclimate. The success of conservation programmes for old-growth forest lichens depends on careful planning, implementation, and subsequent monitoring of lichen populations.

CRediT authorship contribution statement

P.-A. Esseen: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Funding acquisition. **M. Ekström:** Methodology, Software, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120667.

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