



Long-term dynamics of the iconic old-forest lichen *Usnea longissima* in a protected landscape

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ABSTRACT

Long-term data on spatial dynamics of epiphytic lichens associated with old-growth forests are fundamental for understanding how environmental factors drive their extinction and colonization in heterogeneous landscapes. This study focuses on *Usnea longissima*, a flagship species for biodiversity conservation. By using a long-term data set (37 yr.) of *U. longissima* in old *Picea abies* forests in Skuleskogen National Park, Sweden, we examined changes in the number of host trees, population size (sum of thallus length), extinction, colonization, dispersal, and distribution in a protected landscape. We surveyed the lichen in 1984–1985 by applying a line transect inventory and a total population inventory and tagged 355 occupied trees with an aluminium plate buried in the ground. We repeated the survey in 2021 using a metal detector and recorded GPS-position of host trees, tree and lichen population characteristics. We also measured the structure and age (tree-ring data) of the forest to understand how disturbance history influenced lichen populations. *Usnea longissima* occurred on 66 of the tagged trees and we recorded 141 new host trees. The number of host trees decreased with 41.7% and the population size with 41.9%. One third of the decline was caused by deterministic extinction (treefalls) and two thirds by stochastic extinction on standing trees. The probability of stochastic extinction on live trees decreased with population size in logistic regression. The decline in the sites with largest populations (35–87% loss) was more influenced by limited colonization than extinction. Colonization was highest in humid north-facing hillslopes with multi-layered forests driven by gap dynamics. The lichen was strongly dispersal-limited, with a median effective horizontal dispersal of only 3.8 m in 37 yr., explaining its strong dependence of long continuity of forest cover. The populations were clustered and had substantial local turnover, yet with stable distribution at landscape scale. The tree-ring index, growth releases and gap recruitments indicate extensive harvesting ~ 1860–1900, but without major disturbances during the last 70–80 yr. Instead, the decline of *U. longissima* was probably driven by air pollution, climate change (autumn/winter mortality and heatwaves) and denser forests. Our findings highlight that the long-term survival of this lichen may be at risk even in forests having a strong level of protection.

1. Introduction

Many epiphytic lichen species show strong associations with old forests. Such lichens have important ecosystem functions and significantly contribute to the biodiversity in forest canopies (Sillett and Antoine, 2004; Asplund and Wardle, 2017). Some lichens are also useful as indicators of long-term forest continuity and management and decline in managed forests, aggravated by air pollution and other land use (e.g., Pykälä, 2004; Ellis et al., 2009; Hauck, 2009; Scheidegger and Werth, 2009; Hauck et al., 2013; Cameron and Toms, 2016; Allen et al., 2019;

Ellis and Coppins, 2019; Giordani et al., 2020). For example, Esseen et al. (2022) documented a large-scale decline of the hair lichen *Alectoria sarmentosa* (Ach.) Ach. in managed Norway spruce (*Picea abies* (L.) H. Karst.) forests. However, lichens may also decline in unmanaged and protected forests (e.g., Esseen et al., 1981; Rolstad and Rolstad, 2008a; Fedrowitz et al., 2012; Jönsson et al., 2017).

Lichens' dependency of old forests is incompletely understood (Williams and Ellis, 2018). Ellis (2012) presented the hypotheses: (1) lichens are niche-specialized, requiring specific microhabitats (substrates) and/or microclimates, (2) they are dispersal-limited and need

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Fig. 1. A. Hydrated thalli of *Usnea longissima* on dead branches of a live *Picea abies*. B. Part of a north-facing hillslope in site 1, where we made a total population inventory of the lichen in 1984 and 2021. C. An aluminium plate placed under the moss carpet at the base of a *P. abies* hosting *U. longissima* in 1984 and located 2021.

long-term continuity of suitable habitat, or (3) a combination of both. For example, calicioid lichens (Goward and Arsenault, 2018; Ellis, 2022) and the globally threatened cyanolichen *Erioderma pedicellatum* (Hue) P. M. Jørg. (Power et al., 2018; Haughian et al., 2022; Nilsson et al., 2022) show a high degree of niche-specialism. Dispersal limitation has been documented in e.g., *Alectoria sarmentosa* (Esseen et al. 1996; Dettki et al. 2000), *Lobaria oregana* (Tuck.) Müll. Arg. (Sillett et al., 2000), *L. pulmonaria* (L.) Hoffm. (Öckinger et al., 2005; Scheidegger and Werth, 2009; Werth, 2010), and *Usnea longissima* Ach. (Gauslaa, 1997; Gauslaa et al., 2007; Strother et al., 2022; Esseen and Ekström, 2023). The development of epiphytic lichen communities is tightly linked to forest dynamics and many species can be characterized as ‘patch-tracking’ organisms that follow tree population dynamics. Changes in lichen biomass and species richness are driven by functional traits (morphology, reproduction, growth rate, water storage, defence compounds) modified by local microclimate, chemical and physical environments, as well as by larger-scale impact of forest disturbance. The standing crop of epiphytic lichens depends on the balance between growth and losses, as well as substrate availability. Lichens are poikilohydric organisms passively dependent on water from rain, dew, or humid air, and influenced by species-specific functional traits (Gauslaa, 2014; Ellis et al., 2021). Epiphytic lichens have spatially structured metapopulations that are linked to the spatiotemporal dynamics of their host trees (Snäll et al., 2003, 2005; Ellis, 2012). Colonization and extinction processes determine their metapopulation size (Hanski, 1999). Occurrence patterns of lichens in managed landscapes are often not in equilibrium due to their slow rates of colonization and high extinction risk. Some species are mainly regulated by deterministic extinction through tree mortality (Belinchón et al., 2017), whereas other species decline due to stochastic extinction on live trees (Fedrowitz et al., 2012). For understanding the spatial dynamics of old-forest lichens, the relative importance of deterministic versus stochastic extinction should be quantified. The foliose *L. pulmonaria* is a model species for studying population dynamics and dispersal in old-forest lichens (e.g., Öckinger et al., 2005; Scheidegger and Werth, 2009; Öckinger and Nilsson, 2010; Belinchón et al., 2017), but accurate long-term data of spatial dynamics in other rare and threatened lichens are also needed for their conservation in forests.

This study focuses on *U. longissima* (Fig. 1A), a large flagship species for conservation of biodiversity in forests. We surveyed the lichen 1984–1985 in Skuleskogen National Park, north-eastern Sweden and

tagged 355 host trees (mainly *Picea abies*) with an aluminium plate buried in the ground (Fig. 1BC). We repeated the survey in 2021 and searched for the tagged trees, in combination with a search for new host trees. This offered a unique opportunity to study long-term spatial dynamics of host tree and lichen populations in a protected, naturally heterogeneous landscape. We documented population size per tree (see 2.3 below), vertical range in the canopy, host tree characteristics as well as forest structure and disturbance history (tree-ring data) to assess their influence on lichen populations. The following questions were addressed: (1) How does the number of host trees and population size of *U. longissima* change over 37 years? (2) What is the relative importance of deterministic and stochastic extinction, and colonization to changes in lichen occurrence? (3) What is the effective dispersal distance (dispersal plus establishment; Scheidegger and Werth, 2009) of *U. longissima*? (4) Has the distribution changed at local and landscape scale? (5) Which environmental factors drive long-term spatial dynamics of *U. longissima*? Finally (6), we examine how the lichen responds to local habitat conditions as a guide for identifying optimal microrefugia.

2. Materials and methods

2.1. Study species

The world distribution of *U. longissima* includes western and eastern North America, Fennoscandia, Pyrenees, Alps, Carpathians, Ural area, Siberia, Himalaya, China, Taiwan, Philippines, Japan, and Papua New Guinea (Clerc, P., personal communication). The lichen grows on various tree species and is locally abundant in coastal areas and mountains with high rainfall and frequent fog. It is an important winter diet of the endangered snub-nosed monkey *Rhinopithecus bieti* in China (Grueter et al., 2009) and has wide ethnobotanical usage in Asia and North America (Prateeksha et al., 2016; Crawford, 2019; Yang et al., 2021). The lichen is extirpated from most of its historic range in Europe due to air pollution, forestry, and habitat loss (e.g., Ahlner 1948; Gams, 1961; Esseen et al., 1981; Rolstad and Rolstad, 2008a; Nascimbene and Tretiach, 2009; Litterski et al., 2019). The largest European populations outside Russia occur in Norway and Sweden (SLU, 2020, 2022; Haugan et al., 2021). *Usnea longissima* is red listed as vulnerable and protected by law in Sweden.

Short dispersal distances, causing a strong association with humid

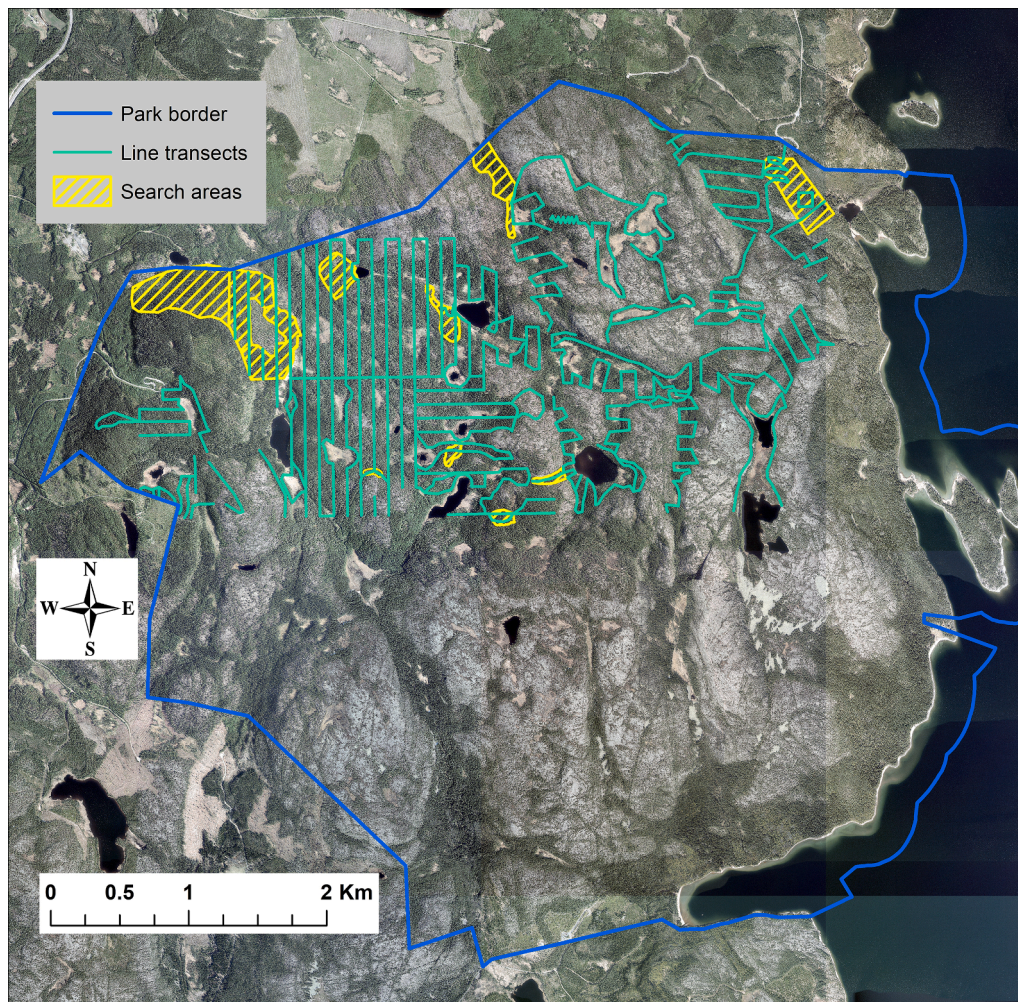


Fig. 2. Map of Skuleskogen National Park, north-eastern Sweden, with line transects and areas where we searched for *Usnea longissima* in 1984 and 2021. Orthophotograph from the Swedish Land Survey, 2020.

old-growth forests, and high habitat specialization contribute to the rarity of *U. longissima* (Gauslaa et al., 2007; Strother et al., 2022; Esseen and Ekström, 2023). This lichen has thin branches (Eriksson et al., 2018), which is an adaptation to rapid photosynthetic activation by fast uptake of water from humid air (Phinney et al., 2018). *Usnea longissima* has the pale yellow cortical pigment usnic acid that enhances transmission of light to the photobionts while hydrated (Gauslaa and Goward, 2023). This pigment facilitates photosynthesis and growth in the lower canopy with low-intermediate light. By contrast, *U. longissima* is sensitive to high light when desiccated (Färber et al., 2014), contributing to its absence from the upper canopy (Esseen and Ekström, 2023). The lichen has a high growth-potential (McCune et al., 1996; Keon and Muir, 2002; Gauslaa et al., 2007; Rolstad and Rolstad, 2008b; Jansson et al., 2009), but short dispersal distances (Esseen, 1985; Gauslaa, 1997; Esseen and Ekström, 2023). *Usnea longissima* disperses only by asexual propagules in Fennoscandia. In Europe, apothecia have only once been reported from France (Harmand, 1905), but they can occur in Asia and North America (Keon, 2002; Rolstad et al., 2013). Most dispersal occurs over only a few meters distance by thallus fragments, varying in size from ~ 1 cm to > 100 cm (Esseen, 1985). Long-distance dispersal may occur by small, asexual propagules (soredia, isidomorpha), but such propagules rarely establish as new specimens (Gauslaa, 1997). The population dynamics is driven by local dispersal from trees hosting large populations in the mid-canopy (Esseen and Ekström, 2023). Population size increases with tree size (Esseen and Ekström, 2023), but does not correlate with tree age (Esseen et al., 1981;

Rolstad and Rolstad, 1999).

2.2. Study area

Skuleskogen National Park (30.6 km²), north-eastern Sweden, Västernorrland county, is situated on the border between the southern and middle boreal zone (N 63° 6.63', E 18° 28.76'; Fig. 2). It is included in the High Coast UNESCO World Heritage Site and the European Natura 2000 network of protected areas. The park was established in 1984 and enlarged in 2009 to include the largest *U. longissima* sites. The bedrock is dominated by nutrient poor coarse-grained granite, with smaller areas of more lime-rich gabbro in the northwest and diabase in the northeast. The study area is in a fissure valley landscape characterized by steep hillslopes and narrow valleys. The hillslopes are often stair-shaped with 1–10 m high bedrock scarps. Elevation ranges from sea level up to 350 m.a.s.l. Skuleskogen is in the central part of the latest glaciation that ended here ~ 10 500 B.P. The quaternary deposits are strongly affected by postglacial isostatic land uplift, and because of the hilly terrain, also by wave-wash from the former sea. The highest postglacial shoreline (HS) is at 282 m.a.s.l. (Berglund, 2012).

The climate is cold temperate and slightly oceanic. Gridded climate data (4 km × 4 km) for the period 1961–2022 were obtained from the Swedish Meteorological and Hydrological Institute (SMHI, 2023; Fig. S1). Mean annual temperature 2001–2020 was +3.0 °C (range 0.8–4.6 °C), with monthly means of 14.7 °C in July and –7.0 °C in February (Fig. S2). Mean annual precipitation was 874 mm (range

614–1382 mm), of which about one third falls as snow. The mean number of days with temperature $> 0\text{ }^{\circ}\text{C}$ and $\geq 0.1\text{ mm}$ precipitation (when lichens are active) was 127 days (range 104–161 days). The area has received elevated dry and wet deposition of atmospheric sulphur (S) and nitrogen (N) due to both long-range transported pollutants and emissions from local industries along the coast (Engardt et al., 2017; Andersson et al., 2018). Deposition of S peaked in the 1970 s whereas N deposition peaked in the 1980 s (Ferm et al., 2019), with a faster decrease of S than of N deposition. The regional deposition of S decreased from $\sim 4\text{--}5\text{ kg ha}^{-1}\text{ yr.}^{-1}$ in 1998–2000 to $1\text{--}2\text{ kg ha}^{-1}\text{ yr.}^{-1}$ in 2015–2020, while N deposition decreased from $\sim 5\text{--}8\text{ kg ha}^{-1}\text{ yr.}^{-1}$ to $1\text{--}3\text{ kg ha}^{-1}\text{ yr.}^{-1}$ during the same period according to the MATCH model (Fig. S3; Andersson et al., 2018). Data on N deposition from modelling agree well with estimates based on measurements in spruce forests in this region (Karlsson et al., 2022). However, the wet deposition of N depends strongly on precipitation amounts which may vary considerably over short geographical distances.

The land cover is dominated by coniferous forest (57%), followed by open land with or without vegetation (37%), wetland (5%) and deciduous forest (1%; Naturvårdsverket, 2003). Spruce forests dominate mesic soils in hillslopes and mesic-moist soils in valleys, while open pine (*Pinus sylvestris* L.) forests grow on dry coarse-grained soils. Most of the forest was logged by high-grading of large-diameter trees in 1860–1900, followed by selective logging of smaller trees in the early 1900s (Kardell and Andersson, 1977). About 17% of the forest was also clearcut between 1922–1965, mainly near the sea. The present forests are old and naturally regenerated, and in transition from single-layered to multi-layered. The impact of fire is low or absent in spruce forests, but several local fires occurred in rocky pine forests until 1840 (Sandström et al., 2020). The epiphytic lichen flora is typical for mesic to moist boreal forests, but includes some oceanic species, e.g., *Platismatia norvegica* (Lynge) W.L.Culb. & C.F.Culb. The dominant pendent hair lichens are *Usnea dasopoga* (Ach.) Nyl., followed by *Bryoria capillaris* (Ach.) Brodo & D.Hawksw. and *B. fuscescens* (Gyeln.) Brodo & D.Hawksw., with locally abundant *Alectoria sarmentosa* and *B. nadvornikiana* (Hoffm.) Brodo & D.Hawksw.

2.3. The 1984 survey

We surveyed *U. longissima* in the whole park and north-west of the former park border in 1984–1985 by applying a line transect inventory and a total population inventory. Henceforth, we refer to 1984 as ‘the start year’ when $> 80\%$ of the observations were done. The transects were laid out in south-north or west-east directions but were adjusted to the topography (Fig. 2). The distance between transects was 100 m. We used a mirror compass for orientation and searched for the lichen in a $\sim 25\text{ m}$ wide belt along each transect. We also made a ‘free search’ in areas too steep for using transects and in suitable *U. longissima* habitat between transects. Hence, $\sim 25\%$ of the area was surveyed. Spruce forests rich in pendent lichens were searched more thoroughly, whereas less time was spent in other habitats. We searched for the lichen in the whole crown and on the stem by using naked eye and binoculars. The positions of host trees were marked on a map (scale 1:10 000; Fig. S4). We recorded tree species, vitality (live/dead), DBH, population size of the lichen, and the height of the highest positioned thallus (0.1–1 m accuracy). The ‘population size’ per tree (indicating abundance; Esseen and Ekström, 2023), was estimated as the summed length of all thalli along the main thallus branches by applying a semi-logarithmic scale with seven classes: 0.1–0.5, $>0.5\text{--}1$, $>1\text{--}5$, $>5\text{--}10$, $>10\text{--}50$, $>50\text{--}100$ and $>100\text{--}500\text{ m}$. A numbered aluminium plate (70 mm \times 70 mm \times 0.6 mm; Fig. 1C) was placed under the moss carpet or in the litter layer at 10–50 cm’s distance from the stem. Tree species composition, basal area and height were recorded in nine sites.

2.4. The 2021 survey

The 2021 survey covered only the northern half of the park ($\sim 14\text{ km}^2$) but included all *U. longissima* sites in the 1984 survey. The old maps had a different projected coordinate system (Swedish Grid RT90) than current maps (SWEREF99). Unfortunately, transformation between the coordinate systems using ArcGIS 10.3 led to substantial errors, due to the rugged topography. We therefore manually transferred the positions of transects and *U. longissima* sites to a new high-resolution map in ArcGIS. We then produced a detailed field-map using an infrared aerial photograph from 2018 as background (0.25 m pixel size). The map was transferred to smartphones (Apple iPhone, Samsung Galaxy) and tablets (Apple iPad Pro), by applying Avenza Maps and ArcGIS Collector, respectively. The transects and host trees were also transferred to four Garmin GPS. The orientation was mainly done with smartphones and iPads, while the positions were continuously logged in a Garmin GPS. The total length of the surveyed line transects was 83 km, including non-forest areas. Binoculars were used as in the first survey. For each tree hosting the lichen, we tied a yellow plastic band with an id-number to a lower branch and recorded the GPS position.

A total population inventory was then conducted in all areas hosting the lichen in both the 1984 and 2021 survey. Maps, field notes and GPS positions helped to locate the host trees. We used a Minelab Explorer II metal detector, Australia (<https://minelab.com.au>) to search for the aluminium plates around the base of all standing trees, stumps and treefalls within areas mapped in 1984. We also scanned trees up to $\sim 25\text{--}30\text{ m}$ outside these areas and around isolated host trees. After locating a plate, it was excavated from the humus layer (depth $\sim 10\text{--}40\text{ cm}$). If *U. longissima* was present on the tree, the plate was placed back at 5–10 cm’s depth. We located 290 (82%) of the 355 tagged trees. The remaining 65 trees were classified as treefalls based on the following points: (1) Several of these trees were dead or dying in 1984 and had likely fallen in the 1980–1990s. Many of the located treefalls were strongly decayed and barely visible. (2) It was difficult to locate the plates for uprooted trees as they were often buried deep in the soil. (3) We scanned the base of all standing trees in mapped areas at least twice. We also searched after newly colonized trees since 1984 within the same areas as described above. An aluminium plate was placed at the base of such trees. GPS coordinates and elevations of all host trees were recorded with a Garmin GPSMAP 66sr, with multiband capacity for improved accuracy. We measured the same variables as in the 1984 survey, but also included position of the stem (standing, treefall), and crown limit for live trees, defined as the height of the lowest live branch, using a 5-m pole. The population size was estimated as accurately as possible (0.1–1 m resolution; Esseen and Ekström, 2023).

2.5. Forest structure and history

The composition and age of the forest were studied in 2021 in one to four 50 m \times 10 m transects in the six sites with largest *U. longissima* populations in 1984. We recorded species, DBH, vitality, crown limit (see 2.4. above), distance along the transect, and occurrence of *U. longissima* for all trees with DBH $\geq 1\text{ cm}$. Species, DBH and decay stage were recorded for treefalls. We also counted all old stumps from logged trees. The height of the five tallest trees was measured with a Vertex IV ultrasound instrument (Haglöf, Sweden). We then cored all live trees with DBH $\geq 10\text{ cm}$ at breast height ($N = 403$), except those hosting *U. longissima*. The cores were glued to wooden core mounts and sanded to fine polish (Speer, 2010). Ring widths and number of rings were measured using a scanner and the image analysis software WinDendro (version 2014). In cases where the pith was missing, we used the curvature of innermost tree rings to estimate number of missing rings.

2.6. Data analysis

The data were analysed with R version 4.1.2 (R Core Team, 2021). Ten host trees with DBH < 5 cm were excluded, as the lichen was considered ephemeral on such trees. A ‘cluster’ of trees occupied by *U. longissima* was defined as one or several trees with ≥ 40 m horizontal distance to the nearest cluster. A ‘site’ consisted of one or more clusters, with > 103 m between sites. However, a new cluster located 44–120 m from site 7 was regarded as a new site (no. 16) because it was at 40–50 m higher elevation, and as upward dispersal is unlikely (Esseen and Ekström, 2023). The seven classes of population size in the 1984 survey were converted to thallus length (m) based on the mean population size for the corresponding classes in the 2021 survey. However, the 100–500 m class was not recorded 2021, and here we used the mid-point (300 m). We calculated mean and SE for DBH, crown limit, population size and highest occurrence of *U. longissima* for the host trees in both surveys.

We calculated a ‘change rate’ for *U. longissima* as the ratio between the total number of host trees present in 2021 and 1984 (Supplement 1; change rate > 1 = increase; 1 = no change; <1 = decrease; 0 = extinction). Similarly, a ‘colonization rate’ was calculated as the ratio between the number of newly colonized host trees and the number of host trees in 1984. We cannot evaluate the colonization rate for unoccupied trees, as these were not registered in 1984. The total extinction rate was calculated as the ratio of the number of trees where the lichen was extinct in 2021 to the number of host trees in 1984. We also calculated the deterministic extinction rate (by treefalls) and the stochastic extinction rate (on standing live or dead trees) following Belinchón et al. (2017). The average population longevity on standing trees was calculated as 37 yr. divided by the stochastic extinction rate. The above calculations were also done for each cluster and site.

We analysed the spatial distribution of the lichen in 1984 and 2021 by calculating the horizontal nearest neighbour distance between the host trees based on GPS-positions or positions in the 1984 map. Effective dispersal distances for the new host trees in 2021 were estimated as the distance to the nearest tree occupied by *U. longissima* in either 1984 or 2021. We examined the relationships between population size, highest occurrence and DBH for the host trees with correlation and regression. We then applied logistic regression (Hosmer et al., 2013) to identify the explanatory variables that best correlated with probability of stochastic extinction on live spruces. The following variables were included: DBH in 1984, increase in DBH between 1984 and 2021, population size in 1984, highest occurrence in 1984, and distance to nearest tree hosting *U. longissima* in 1984 or 2021. Fractional polynomials were applied to account for the possibility of non-linear relationships (Sauerbrei and Royston, 1999) using the library mfp in R. The final model selection was based on Akaike’s second-order corrected information criterion (AICc). The model was checked using the DHARMA library in R.

Each tree-ring series was standardized by dividing each tree-ring width by the average of all tree rings in the series, producing a unitless index for each year. The indexed series were then averaged to produce the standardized chronologies. Using the average growth rate, as opposed to a flexible spline, does not detrend the series, and thus maintains the stand-wide growth patterns resulting from major disturbances. Standardized chronologies were truncated when the no. of trees (sample depth) dropped below 10. To derive disturbance rates for the sites, we identified abrupt increases in radial growth, i.e., growth release, and early rapid growth at breast height, i.e., gap-recruited trees (Lorimer, 1985). As a threshold for gap-recruited trees, we used the mean width for the first 10 rings in the series exceeding 1.0 mm (Jönsson et al., 2009; in similar forests in the same region). To identify growth releases, we followed the absolute increase method by Fraver and White (2005). It is based on comparisons of consecutive 10-year periods of growth. As increase threshold we used 0.55 mm (equivalent to a 97% increase if averaged across all rates of prior growth), derived from Näslund’s (1942) data. This threshold was also used by Jönsson et al. (2009). To provide disturbance rates we tallied release and gap-

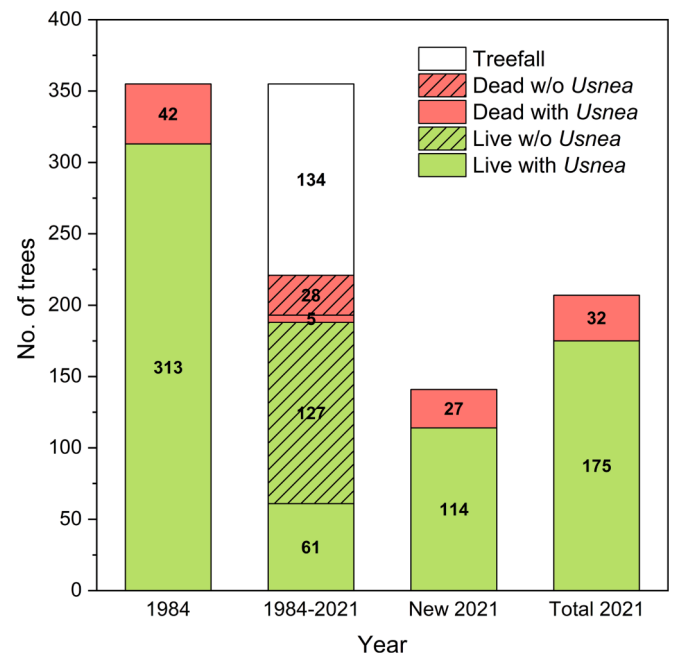


Fig. 3. Number of trees hosting *Usnea longissima* in 1984 by vitality, the status of these trees in 2021 (1984–2021), as well as new and total number of host trees in 2021. The labels denote the number of trees. The five dead trees hosting *U. longissima* 1984–2021 were alive in 1984.

Table 1

Number of host trees, DBH, crown limit (height of the lowest live branch; only 2021), population size per tree and highest occurrence of *Usnea longissima* in 1984 and 2021. The host trees in 2021 were divided into trees where the lichen occurred in 1984–2021, new trees and total number of trees.

	1984	1984–2021	2021 new	2021 total
No. of host trees				
Live	313	61	114	175
Dead	42	5	27	32
Total	355	66	141	207
DBH, cm, mean ± 1 SE				
Live	20.5 ± 0.4	25.8 ± 0.8	21.6 ± 0.8	23.0 ± 0.6
Dead	14.7 ± 1.1	22.7 ± 5.7	18.7 ± 1.4	19.5 ± 1.5
Total	19.8 ± 0.4	25.2 ± 0.9	21.0 ± 0.7	22.5 ± 0.6
Crown limit, m, mean ± 1 SE	–	5.5 ± 0.3	4.8 ± 0.2	5.0 ± 0.2
Population size, m, mean ± 1 SE				
Live	3.9 ± 1.0	4.7 ± 1.1	3.7 ± 0.7	4.1 ± 0.6
Dead	3.7 ± 1.4	2.7 ± 1.6	3.0 ± 0.8	3.0 ± 0.7
Total	3.9 ± 0.9	4.6 ± 1.1	3.6 ± 0.6	3.9 ± 0.5
Population size, m, total	1387	302	503	805
Highest occurrence, m, mean ± 1 SE				
Live	3.4 ± 0.1	4.6 ± 0.3	3.8 ± 0.2	4.1 ± 0.2
Dead	3.1 ± 0.2	4.4 ± 0.6	4.8 ± 0.5	4.7 ± 0.4
Total	3.4 ± 0.1	4.6 ± 0.3	3.9 ± 0.2	4.2 ± 0.2

recruitment events by decade. The number of releases and gap-recruited trees were expressed as percent of the total number of sampled trees alive during each decade. Disturbance chronologies were only constructed for a sample depth of at least 10 trees.

Table 2

Summary of *Usnea longissima* dynamics in the six largest sites, where we also collected data on forest structure and disturbance history (cf. Table 3). Sites are ranked after the level of decline (decreasing change rate; change rate > 1 = increase; 1 = no change; <1 = decrease; 0 = extinction).

Site	1	4	5	3	2	6
No. of host trees 1984	158	31	30	33	54	16
No. of host trees 2021	103	17	12	8	11	2
Change rate	0.65	0.55	0.40	0.24	0.20	0.13
Colonization rate	0.43	0.32	0.17	0.09	0.07	0.00
Total extinction rate	0.78	0.77	0.77	0.85	0.87	0.88
Deterministic extinction rate	0.39	0.68	0.40	0.33	0.20	0.19
Stochastic extinction rate	0.64	0.30	0.61	0.77	0.84	0.85
Average population longevity, yr.	58	123	61	48	44	44

3. Results

3.1. Host tree and *Usnea longissima* dynamics

Usnea longissima occurred on 355 trees (313 live and 42 dead) in 1984 (Fig. 3; Table 1), distributed over 15 sites and 26 clusters, with 69 trees in the largest cluster. Of these, 188 were live in 2021, 33 dead and 134 treefalls (69 observed and 65 classified; see 2.4. above). The lichen occurred on 207 trees in 2021: 66 old (=81.4% loss) and 141 new, distributed over 18 sites and 25 clusters. Ninety-eight of the colonized trees occurred in 11 old clusters, 13 in three new clusters close to old sites, and 30 in seven clusters in six new sites. The overall change rate was 0.583 (41.7% loss of host trees; Supplement 1). The lichen increased in only one site (Table S1). It decreased in all clusters (21–100% loss) and was extinct in 12 of the 15 smallest clusters. The total extinction rate was 0.814 (0.022 yr.⁻¹). Total extinction was rather similar among the

11 largest clusters (range 0.73–0.90) and did not correlate with the number of host trees in 1984 ($r^2 = 0.004$; Fig. S5). The deterministic extinction rate was 0.377 (0.010 yr.⁻¹), whereas the stochastic extinction rate was twice as high, 0.701 (0.019 yr.⁻¹), resulting in an estimated average population longevity of 52.8 yr. (range 37–123 yr.). Among the six largest sites (Table 2), those with steep decline (>50% loss; site 2–3 and 5–6) had high stochastic extinction, whereas deterministic extinction was highest in sites with moderate decline (<50% loss; site 1 and 4) and also in site 5. Notable is the low stochastic extinction in site 4, located in a gully and protected from high winds. The total colonization rate was 0.397, with large variation among sites and highest colonization in sites with moderate decline. The change ratio had a strong positive linear relationship with the colonisation rate in the 11 largest clusters ($R_{adj}^2 = 0.90$; $P < 0.001$; Fig. S5).

3.2. Population size and vertical range

The total population size decreased with 41.9%, whereas the mean population size per tree did not change (Table 1). The lichen increased on only a quarter of the 66 trees hosting the lichen in both surveys, with an overall decrease of 44%. The total and stochastic extinction rate decreased steeply with increasing population size, whereas the deterministic extinction rate showed no trend (Fig. 4A). The distribution of population size shifted over time (Fig. 4AB). Small populations (0.1–1 m) dominated over intermediate populations (1–5 m) in 1984 (47% vs 35%), whereas the pattern was reversed in 2021 (33% vs 50%). The proportion of large populations (>5 m) was stable over time. However, the number of such trees decreased from 63 to 36. The population size increased with the highest occurrence (Fig. 4CD). The lichen tended to occur at higher positions in 2021 than in 1984, with means of 4.2 and 3.4 m, respectively (Table 1; maximum 11 and 9 m). However, this was

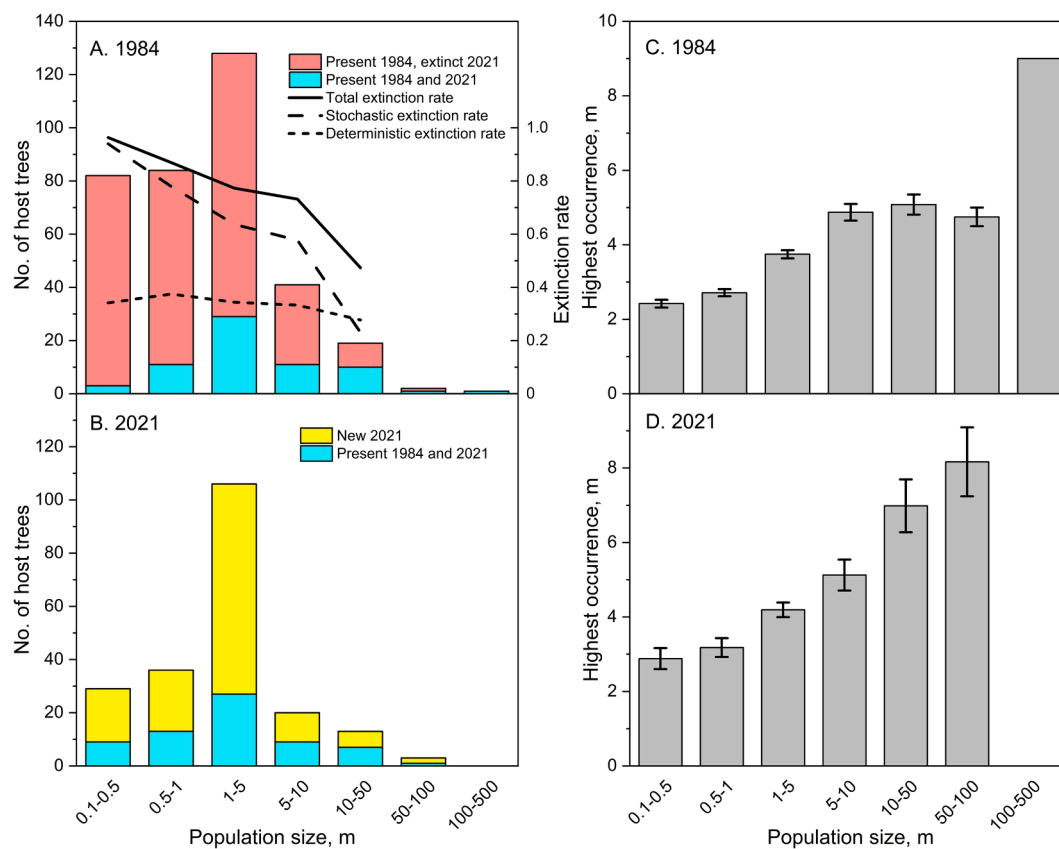


Fig. 4. Number of host trees (A, B), extinction rates (A) and mean height (± 1 SE) of the highest occurrence (C, D) of *Usnea longissima* per tree by population size class in 1984 and 2021. The trees in 1984 were divided into trees with *U. longissima* still present in 2021 and trees where *U. longissima* was extinct in 2021 (incl. treefalls). The trees in 2021 were divided into trees with *U. longissima* present in 1984–2021 and new host trees.

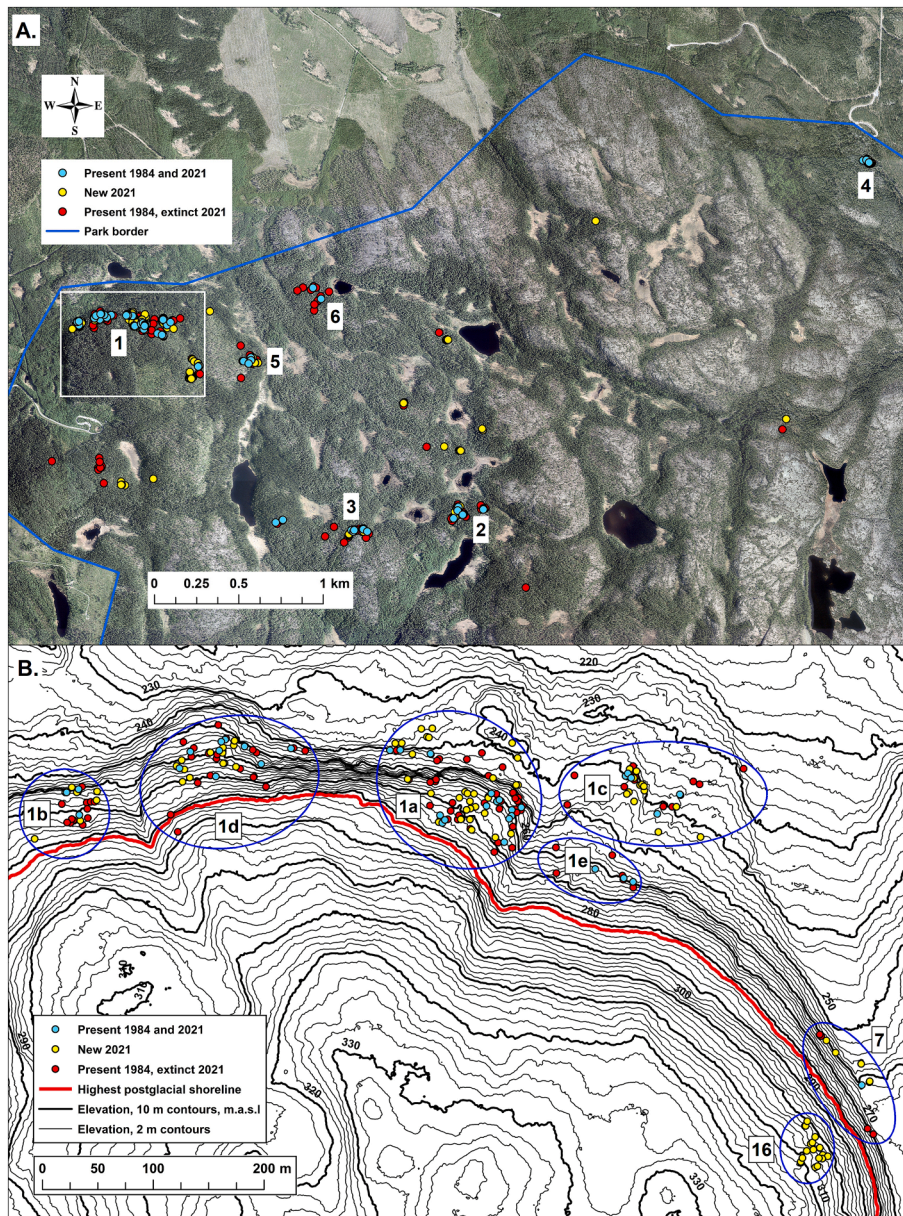


Fig. 5. A. Distribution of *Usnea longissima* in Skuleskogen National Park in 1984 and 2021. Each circle denotes a host tree, however, note that symbols overlap. The numbers refer to the six sites with largest *U. longissima* populations, where we collected forest data. B. Enlargement of (A) showing site 1 (five clusters), site 7 and site 16. The location of the highest postglacial shoreline is shown at 282 m.a.s.l. Elevations were extracted from a digital terrain model with 1 m resolution based on airborne laser scanning, produced by the Swedish Land Survey 2021.

mainly due to loss of lower canopy populations, and it is unclear if any vertical migration occurred.

3.3. Distribution and dispersal

Most sites were at higher elevations in the western, spruce-dominated part of the park (Fig. 5A), but below the HS. Elevations ranged from ~ 25 to 331 m.a.s.l. The lichen preferred semi-open forest in north and north-eastern hillslopes and was absent in depressions with closed forest (Fig. 5B). The large-scale distribution was stable over time. We observed only a few meters contraction or expansion of the old clusters. The nearest neighbour distance between the host trees ranged from 0.2 to 1654 m, with 78.1% and 77.8% <10 m in 1984 and 2021, respectively (Fig. 6AB). The median nearest neighbour distance increased from 4.0 m to 4.7 m over time. The new host trees had a median distance of 3.8 m (25th percentile = 1.6 m; 75th percentile = 6.5 m) to the nearest tree hosting the lichen in 1984 or 2021 (Fig. 6C), reflecting short dispersal distances. All but one of the new clusters were within 44–181 m from old clusters, indicating a few longer dispersal events over the 37 yr. period.

3.4. Host tree variables

Picea abies constituted > 97% of the host trees (Table S2). The proportion live host trees decreased from 88.2 to 84.5% over time. *Usnea longissima* was most common on trees of intermediate size (Table 1). Mean DBH increased with 13%, from 19.8 cm in 1984 to 22.5 cm in 2021 (Fig. S6). The 66 trees hosting the lichen 1984–2021 had 4.2 cm higher DBH and 0.8 m higher crown limit than new host trees. The population size in 2021 (log-transformed) had a weak positive relationship with DBH ($R^2_{adj.} = 0.013$; $P = 0.050$; $N = 207$), but a stronger positive relationship with highest occurrence (log-transformed; $R^2_{adj.} = 0.261$; $P < 0.001$). The probability of stochastic extinction on live spruces decreased significantly with population size in 1984 in the logistic regression model (Pseudo $R^2 = 0.153$; $P < 0.001$; $N = 188$; Table S3; cf. Fig. 4A), whereas DBH, increase in DBH, highest occurrence and distance to nearest host tree present in 1984 or 2021 were not significant.

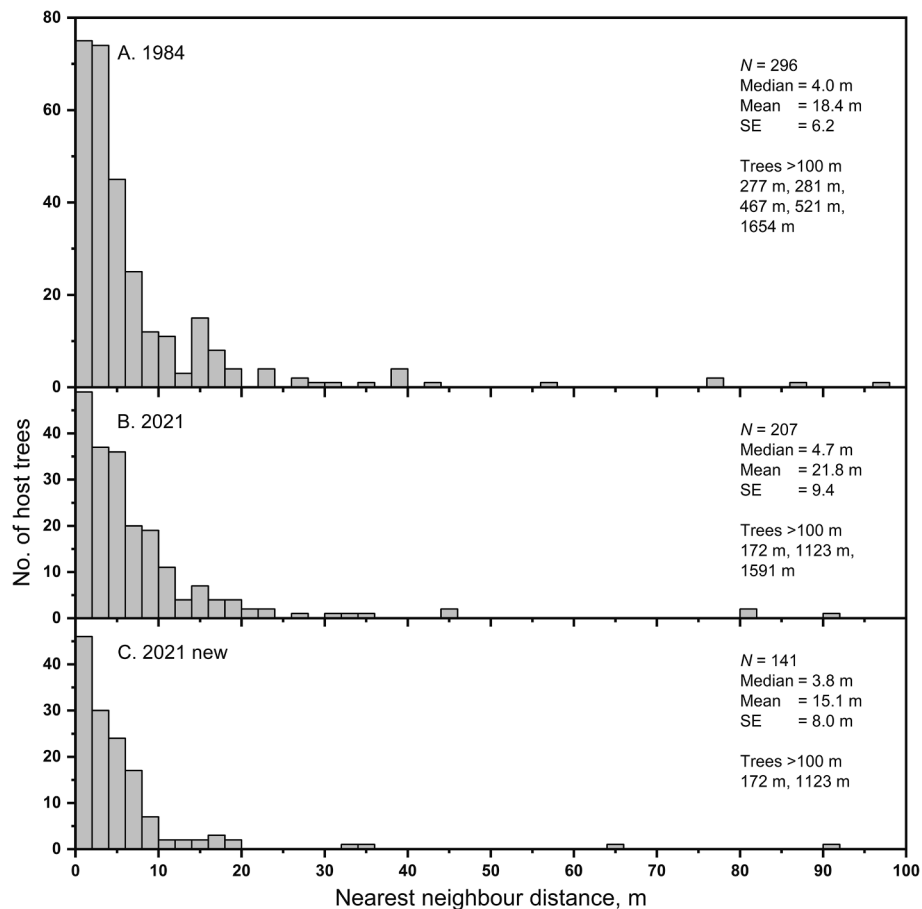


Fig. 6. Distribution of nearest neighbour distances between trees hosting *Usnea longissima* in 1984 (A), 2021 (B) and separately for the new host trees in 2021 (C; distance measured to the nearest host tree present in either 1984 or 2021, indicating dispersal distance).

3.5. Forest structure and history

Forest structure was typical for old-growth spruce forests in the region. Spruce basal area constituted 92.2%, followed by birch (*Betula* spp.) 3.8%, pine 2.4%, aspen (*Populus tremula* L.) 1.0% and goat willow (*Salix caprea* L.) 0.5%. The density of live stems varied between 940 and 1700 ha⁻¹ among the six sites (Table 3). Treefalls (170–335 ha⁻¹) were dominated by early to intermediate decay stages. Old stumps from logged trees occurred at all sites (80–230 ha⁻¹). Mean DBH of live trees varied between 11.6 and 18.4 cm but showed no trend with the decline of *U. longissima*. However, sites with steep decline were more single-layered than sites with moderate decline (Fig. 7AB). Live basal area varied between 25.2 and 33.5 m²/ha, with dead trees constituting ~10%. Basal area did not correlate with the *U. longissima* decline in the six sites but increased substantially from 1984 to 2021 in three sites with steep decline (site 2, 3 and 6; Table S4). Neither mean height (16.9–23.0 m) nor mean crown limit (3.5–5.3 m) showed any trend with the lichen decline. Mean stand age (range 104–144 yr.) was highest in sites with steep decline (Fig. 7CD). The radial growth of spruce did not correlate with the decline, but site 1 and 4, with moderate decline, had slightly higher growth 1984–2020 than sites with steep decline.

The tree-ring data indicate no major disturbances during the last 70–80 years (Fig. 8). The relatively few growth releases likely result from single trees dying naturally. The tree-ring index declined in five sites, representing the age-related decline in growth of old trees. The exception was site 4, where recent (1990–2020) growth releases indicate some natural mortality, maintaining higher growth among the remaining trees. Although no recent harvesting has taken place, there is strong indication that harvesting occurred in the past in most sites. The

gap-recruitment data suggest that site 1 and 6 were relative open during mid- to late 1800s. Moreover, site 3–5 had a marked increase in the tree-ring index during the first decades of the 1900s, connected to several gap-recruited trees and growth releases, indicating some small-scale harvesting. Only site 2 lacks clear indication of harvesting during the last 150 years, supported by the low radial growth (Table 3). A few gap-recruited trees and growth releases occurred, but these did not influence the tree-ring index.

4. Discussion

4.1. Population dynamics and dispersal

Our 37-year study provides key findings about the spatial dynamics and habitat ecology of *U. longissima* in boreal forests. Both deterministic and stochastic extinctions have occurred throughout 1984–2021, but the temporal pattern remains unknown due to only two inventories. Several undetected extinctions and colonizations have probably occurred, as observed in other sites (Esseen, P.-A., personal observation). Most populations were small in 1984, possibly due to declining trends in the 1970–1980s as documented by Esseen et al. (1981) in other sites in the region. Steep declines (54–95% loss of population size) were observed 1978–1993 in six of these sites (Esseen, P.-A., unpublished data). Substantial decline has also been documented in south-eastern Norway (Olsen and Gauslaa, 1991; Rolstad and Rolstad, 2008a). Our current population in Skuleskogen was smaller and had lower viability than that in Edsbodskogen nature reserve (Esseen and Ekström, 2023) as evidenced by the following points: (1) The total population (~800 m; 207 trees) constituted only 40% of the population in Edsbodskogen

Table 3

Summary of forest composition, age at breast height of live trees (DBH ≥ 10 cm) and radial growth of spruce in the six largest *Usnea longissima* sites. Sites are ranked after the level of decline (decreasing change rate). The forest data were recorded in 50 m \times 10 m transects.

Site	1	4	5	3	2	6
No. of transects	4	1	2	1	2	2
No. of stems, live/dead, ha ⁻¹	1090/ 220	1700/ 520	1070/ 180	940/ 200	1270/ 310	1310/ 310
No. of treefalls, ha ⁻¹	335	240	180	240	250	170
Decay stage ¹ , 1/2/3, %	50/25/ 25	50/25/ 25	39/56/ 6	50/25/ 25	52/32/ 16	59/12/ 29
DBH live trees, mean \pm 1 SE, cm	15.9 \pm 0.7	11.6 \pm 0.9	13.7 \pm 1.0	18.4 \pm 1.5	14.6 \pm 0.7	15.4 \pm 0.8
DBH dead trees, mean \pm 1 SE, cm	10.3 \pm 1.2	5.9 \pm 0.7	11.6 \pm 1.8	11.2 \pm 3.3	8.9 \pm 1.1	8.9 \pm 0.7
Basal area, live/dead, m ² /ha	30.5/ 2.9	27.6/ 2.0	25.2/ 2.7	32.9/ 3.5	26.8/ 2.8	33.5/ 2.3
Height, m	20.6 \pm 0.6	20.8 \pm 0.9	20.2 \pm 0.6	23.0 \pm 0.7	16.9 \pm 0.7	19.7 \pm 0.4
Crown limit, live trees, m	4.2 \pm 0.2	3.5 \pm 0.2	4.0 \pm 0.3	5.3 \pm 0.4	4.3 \pm 0.2	4.1 \pm 0.3
Age, maximum, yr.	233	213	233	189	312	177
Age, mean \pm 1 SE, yr.	122 \pm 2.5	104 \pm 5.0	131 \pm 4.3	144 \pm 4.7	130 \pm 3.8	140 \pm 1.7
Growth of spruce, mean \pm 1 SD, mm/yr.	0.674 \pm 0.239	0.597 \pm 0.204	0.704 \pm 0.237	0.658 \pm 0.237	0.546 \pm 0.154	0.642 \pm 0.184
Growth of spruce 1984–2020, mm/yr.	0.465	0.566	0.463	0.428	0.343	0.412

¹ Decay stages: 1) hard dead wood, >90% not decayed, 2) intermediate decay, 10–25% decayed wood, 3) decayed wood, 26–75% decayed.

(~2000 m; 189 trees in a 1 ha plot). (2) The mean population size per tree was about one-third (3.9 m vs 10.7 m). (3) The proportion of trees with populations ≥ 5 m was 2.7 times lower (17% vs 47%). (4) The highest occurrence was 1.5 m lower (4.2 m vs 5.7 m; means). (5) The median nearest neighbour distance between host trees was more than two times larger (4.7 m vs 2.2 m). Hence, there is strong support for that the decline was caused by both slow growth and high extinction.

Comparisons of extinction rates among empirical studies are confounded by differences in field sampling methods and length of study period. Our average annual deterministic extinction rate (0.010 yr.⁻¹) was slightly higher than in cyanolichens on aspen in a protected forest over 13 years (0.008 yr.⁻¹; Fedrowitz et al. (2012), but lower than in *L. pulmonaria* on aspen and goat willow in a managed landscape over 10 years (0.026 yr.⁻¹; Belinchón et al., 2017). Our stochastic extinction rate (0.019 yr.⁻¹) was lower than in *Usnea* spp. on live spruces in managed forests (0.027 yr.⁻¹; Esseen et al., 2022) and in *L. pulmonaria* (0.024–0.025 yr.⁻¹; Öckinger and Nilsson, 2010; Fedrowitz et al., 2012). In contrast, Belinchón et al. (2017) observed very low stochastic extinction (0.005 yr.⁻¹) in *L. pulmonaria*. Although deterministic extinction drives spatial dynamics of ‘patch-tracking’ epiphytic lichens, our study shows that stochastic extinction can be significant (cf., Öckinger and Nilsson, 2010; Fedrowitz et al., 2012). The high stochastic extinction in *U. longissima* can be explained by its lack of holdfast and long, brittle main axes hanging from branches and thus affected by wind, snow and ice.

The extinction rate was high in all sites and cannot explain differences in declines among sites. The magnitude of decline was instead linked to variability in colonisation, with no or low colonisation in sites with steep decline and intermediate colonisation in sites with moderate decline (Fig. S5). Successful colonisation involves production of

propagules, transport by wind, and establishment on a new host. We cannot separate these processes. However, the number of dispersed thallus fragments was probably substantially higher in sites 1 and 4 with moderate decline, having several trees with large populations, than in sites with steep declines. Site 1 and 4 were in north-facing hillslopes with a humid microclimate, enhancing lichen growth and establishment.

Our study provides empirical evidence for that *U. longissima* is strongly dispersal-limited, confirming indirect studies (Esseen, 1985; Gauslaa, 1997; Keon and Muir, 2002; Gauslaa et al., 2007; Strother et al., 2022; Esseen and Ekström, 2023). The estimated median effective dispersal distance over 37 yr. was only 3.8 m in old clusters (maximum 37 m). The distribution of nearest neighbour distance between host trees (Fig. 6) agreed well with the logistic regression model of Esseen and Ekström (2023). By comparison, the estimated effective dispersal distance in *L. pulmonaria* ranges from 15 to 35 m in field studies (Öckinger et al., 2005; Jüriado et al., 2011) to 97 m in modelling studies (Belinchón et al., 2017). Studies of direct dispersal in *L. pulmonaria* show that symbiotic clonal propagules disperse tens of metres and sexual propagules > 100–1000 m (Werth, 2010; Ronnås et al., 2017). Our data were less informative with respect to long-distance dispersal but suggest that *U. longissima* disperses ~ 40–200 m in 37 yr. However, we cannot exclude dispersal of thallus fragments from host trees present in areas not surveyed, or from unnoticed trees between surveys (‘stepping stones’).

4.2. Drivers of the decline

No stand-replacing disturbances occurred 1984–2021, implying that the decline resulted from changes in air quality, climate, and/or forest structure. Declines were observed throughout the study area, suggesting that one or more common drivers reduced growth conditions or number of microhabitats. Below we discuss the evidence for possible drivers, but their relative importance cannot be evaluated.

4.2.1. Air pollution

Lichens efficiently accumulate elements from atmospheric sources (Nash, 2008). *Usnea longissima* is pollution sensitive (Esseen et al., 1981; McCune and Geiser, 2009; Geiser et al., 2021) and its thin branches effectively filters elements from the air (Eriksson et al., 2018). Deposition of S and N has decreased substantially since the 1970–1980s, but N deposition is still higher than the background level (Karlsson et al., 2022). Wet deposition is high in the High Coast area due to elevated precipitation. N deposition exceeded the critical load for hair lichens (~2–5 kg ha⁻¹ yr.⁻¹; Esseen et al., 2016, 2022; Geiser et al., 2021) during most of the study period (Fig. S3). Consequently, air pollution has likely been important in driving the decline, by reducing growth, particularly in the 1980–1990s. This is also supported by the following points: (1) The concentration of pollutants in dew and fog, important water sources for *U. longissima*, is often higher than in precipitation (Nash, 2008). (2) Even at these far northern latitudes, episodes with highly polluted air masses may occur, such as for example high air concentrations of ammonium during the spring 2006 originating from biomass burning in eastern Europe (Karlsson et al., 2013) as well as high air concentrations of SO₂ originating from volcanic eruptions in Iceland during 2014 and 2015 (Hellsten et al., 2017). (3) N deposition contributed to decline of hair lichens in managed forests 1993–2012 (Esseen et al., 2022). (4) Lichen responses to N accumulate over time (Johansson et al., 2010; Johansson et al., 2012). (5) Lichens show strong recovery delays after N reductions (Hauck et al., 2013; Carter et al., 2017; Weldon and Grandin, 2021).

4.2.2. Climate

Growth of *Usnea* spp. is boosted by rainfall (Gauslaa et al., 2007; Phinney et al., 2021). However, the number of days with rain increased from 1964–1983 to 2001–2020 (Fig. S1) and shorter duration of hydration can hardly explain the decline. Other aspects of climate change

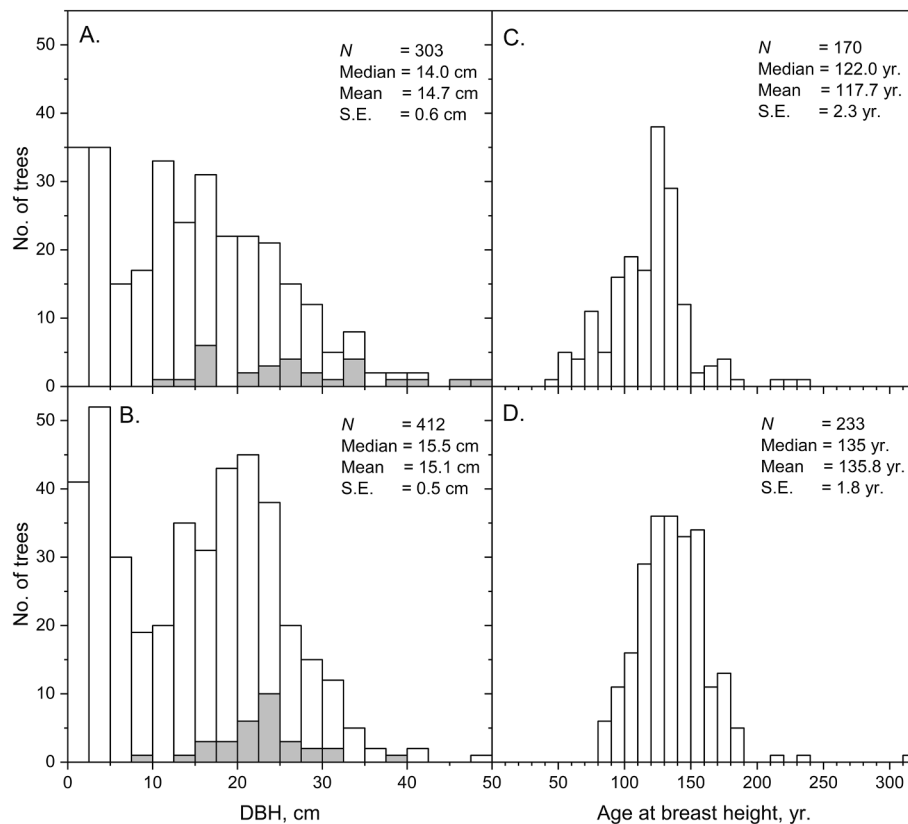


Fig. 7. Distribution of DBH and age at breast height (DBH ≥ 10 cm, live trees) in sites with moderate (A, C; Site 1 and 4) and steep (B, D; Site 2, 3, 5, 6) decline of *Usnea longissima*. The grey bars in A and B denote trees occupied by *U. longissima*.

are likely more important. The mean annual temperature has increased by 1.6 °C, with the highest warming in winter (Fig. S2). Warmer winters increases losses by dark respiration (when the temperature is > 0 °C) at these high latitudes with low light levels (Esseen et al., 2022). Most stochastic extinctions probably occur during storms in autumn and winter, with up to 10% annual losses by litterfall in other sites (Esseen, 1985). Skuleskogen is known for deep snowpacks (up to 1.8 m) and substantial losses can occur during winters with extreme snow-depth (Fig. S7). The current trend with more frequent thaw-freeze events increases damage to branches and lichens by snow, ice, and wind. Warming during the vegetation period increases evaporation and vapour pressure deficit, reducing the duration of lichen hydration and growth (Stanton et al., 2023). Skuleskogen is vulnerable to heatwaves, such as in 2018 (Esseen and Ekström, 2023), and storms due to its location near the sea, and rugged terrain with much exposed bedrock. Warming likely contributed to the decline in sites located close to open rocky pine forests, where heat stored in sun-exposed bedrocks raises temperature and accelerates evaporation after summer rainfall, in combination with enhanced wind.

4.2.3. Forest dynamics

The tree-ring index, disturbance rate and presence of old stumps confirm that most sites have been harvested to some extent. Our data indicate that the harvesting ceased after the Second World War. The few growth releases and gap recruitments probably results from natural death of single trees. Therefore, disturbance history cannot be a major driver of the decline during the study period. Sites with moderate and steep decline had similar disturbance history. However, the forests have become denser, as shown by the increase in basal area. Growth of *U. longissima* is substantially depressed in shaded lower canopy positions (Gauslaa et al., 2007; Colesie, C., and Esseen, P.-A., unpubl. data). Hence, less light in combination with fewer and smaller defoliated lower

canopy branches likely contributed to the decline, particularly in single-layered stands. Nonetheless, the basal area in most sites was lower than in other sites with large populations, where multi-layered stands with several gaps create optimal light levels (Esseen and Ericson, 1982; Esseen and Ekström, 2023). Finally, it is notable that an old-forest lichen like *U. longissima* showed steep declines in the sites with the oldest trees (Fig. 7). This is because the oldest spruces in the study area grow in sites with low-productive soils, close to open pine forests or in dense swamp forests. *Usnea longissima* thrives in forests with intermediate productivity on north-facing hillslopes, where mobile soil water improves nutrient availability that enhances element concentrations in canopy throughfall (Gauslaa et al., 2021). Variation in microtopography along moderate to steep hillslopes provides greater diversity of suitable microhabitats than in toe slope areas and on level ground.

4.3. Implications for monitoring

Our study highlights the urgent need of monitoring populations of old-forest lichens for understanding their extinction-colonization processes. *Usnea longissima* is not included in any systematic monitoring programmes using permanent plots, but the county administration records locations of host trees in some nature reserves. However, the occurrence of *Alectoria sarmentosa* (red-listed as near-threatened), *Bryoria* spp. and *Usnea* spp. have been monitored on *Picea abies* in permanent plots in the National Forest Inventory (NFI) in Sweden since 1993 (Esseen et al., 2016, 2022). Various conditions need to be considered when designing monitoring programmes for rare lichens, including sampling design, detection accuracy, and cost-efficiency (Yoccoz et al., 2001; Nimis et al., 2002; Britton et al., 2014; Brunialti et al., 2019). It is critical to balance monitoring of existing populations against sampling of additional areas to detect newly established populations, otherwise there is a risk to mainly detect declines. *Usnea*

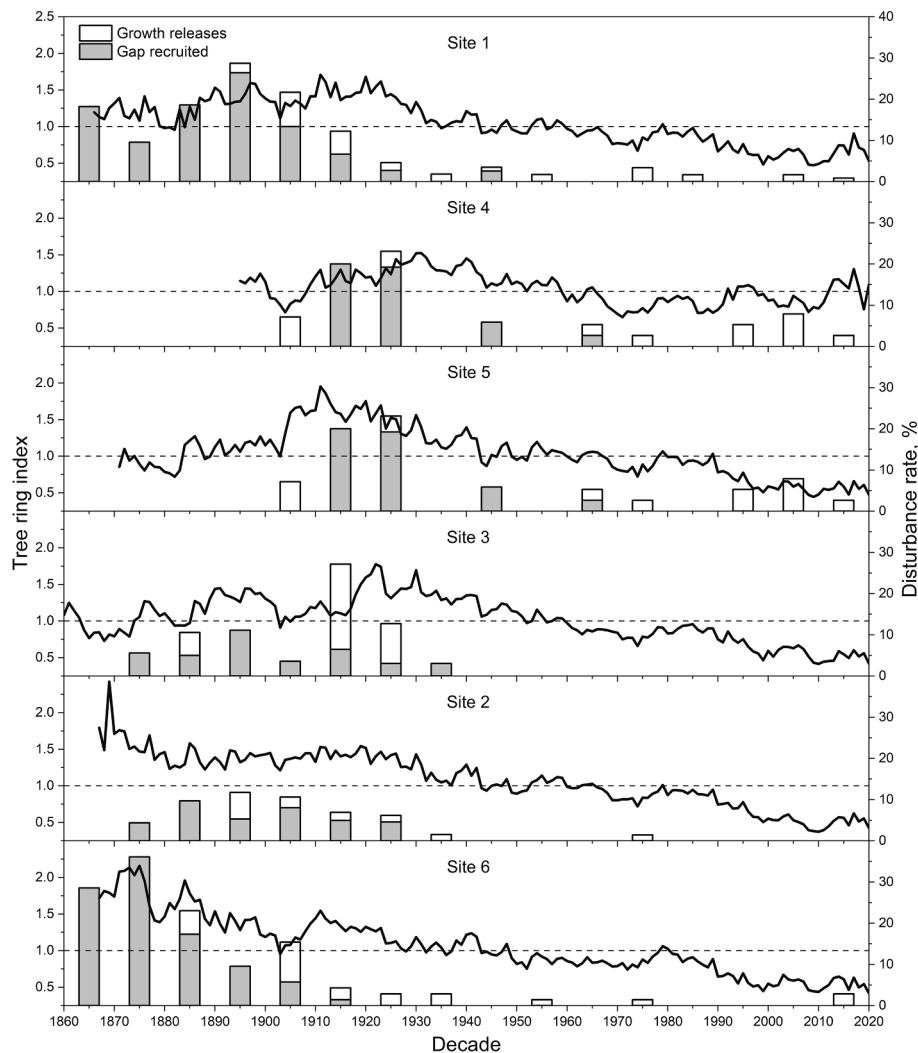


Fig. 8. Standard tree-ring chronologies for *Picea abies* and disturbance rate (percent trees recruited in gaps, percent trees showing growth releases) in the six sites with largest *Usnea longissima* populations. The sites are arranged after increasing level of *U. longissima* decline.

longissima and other old-forest lichens must be monitored throughout their distribution range, including both protected and managed forests. The observer error was likely small in our study. It was relatively easy to locate and identify a long, free-hanging thallus in the lower canopy. However, detectability varies with thallus morphology, branch height, branch density and weather conditions. Both GPS-positions and permanently tagged trees are needed for locating and identifying host trees. Current handheld GPS-units do not provide enough accuracy in dense forests and steep terrain. Tags on stems can be used as an alternative to plates in the soil, but such tags are sometimes detached from the bark. Our aluminium plates should persist for at least half a century and are preferred in case locations of host trees needs be hidden. We recommend a maximum survey interval of 5–10 years, as in the Swedish NFI (Fridman et al., 2014; Esseen et al., 2022).

4.4. Implications for conservation

Despite substantial turnover of host trees within local populations, the distribution of the lichen was remarkably stable over time, consistent with findings by Rolstad and Rolstad (2008a). The short dispersal distance explains *U. longissima*'s strong dependence of long continuity of forest cover and preference for fire-free refugia in boreal forests (Esseen et al., 1981; Josefsson et al., 2005). Most steeply declining populations lacked source trees and have high extinction risk. Hence, extinction is

time-lagged, with an extinction debt (Kuussaari et al., 2009; Hylander and Ehrlén, 2013). It remains to be seen whether some populations can shift to an increasing trajectory. At present extinction rates, such a shift requires more than a doubling of colonization rates. On the positive side, the clusters of host trees that had established in a few decades may provide a source of inoculum for further dispersal. *Usnea longissima* is vulnerable to climate change due to its morphology, highly specific habitat requirements and poor dispersal. Storms have caused devastating stand-replacing windthrow in several nature reserves hosting large populations, followed by large-scale outbreaks of spruce bark-beetle, eliminating many host trees. A topographically heterogenous landscape like Skuleskogen provide many microclimatic refugia (Ellis and Eaton, 2021), and populations are likely more resistant to large-scale disturbances than in small, protected areas embedded in a matrix of production forests. Storaunet et al. (2008, 2014) showed that selective logging in dense forests can improve growth conditions for *U. longissima* by increasing light availability. However, because various factors contributed to the decline, we do not recommend active management in Skuleskogen. The most important step is to continue monitoring host tree and lichen populations. Monitoring microclimate and individual lichen thalli in combination with growth experiments would help to better understand the spatial dynamics of this unique lichen. Although protected areas are essential for conservation of old-forest lichens, our study highlights that the long-term survival of *U. longissima*

may be at risk even in forests with a strong level of protection.

CRedit authorship contribution statement

P.-A. Esseen: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **J. Rytterstam:** Methodology, Investigation, Writing – review & editing, Funding acquisition. **A. Atrena:** Investigation, Writing – review & editing. **B.G. Jonsson:** Methodology, Investigation, 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 upon request to corresponding author.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121369>.

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