

Gastropod grazing may prevent reintroduction of declining N-fixing epiphytic lichens in broadleaved deciduous forests

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ABSTRACT

We studied the potential to use reintroduction of two declining N-fixing flagship lichens to identify factors affecting failure or success in SW Swedish sites that had experienced substantially reduced acidification. After transplanting the critically endangered *Lobaria amplissima* ± external cephalodia and its near-threatened associate *L. pulmonaria* onto tree trunks, seasonal growth rates were quantified. We added a phosphorus treatment, using site as a random factor. Growth was positive in winter, yet highest in *L. pulmonaria*, and negative in summer, particularly in *L. amplissima*. Reintroduction of *L. amplissima* was unsuccessful because gastropods, evidenced by grazing marks, caused significant loss. *Acer platanoides*, a high-pH host, had more grazing than the more acidic *Quercus petraea*. Gastropods preferred the cephalodia, resulting in substantial loss of cephalodiate *L. amplissima*. Phosphorus fertilization had no effects. The widespread *L. pulmonaria* grew faster than the rare *L. amplissima* that lost its local growth potential due to aggravated gastropod grazing.

Keywords:

biotic interactions; epiphytic lichens; herbivory; *Lobaria amplissima*; *Lobaria pulmonaria*; phosphorus; reintroduction; seasonal growth rate; terrestrial gastropods

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1. Introduction

Alongside with restoration of habitats, species reintroductions will increasingly be requested in future conservation of biodiversity (McDonald-Madden et al. 2011). Reintroduction, either into an intact habitat or as part of the restoration of degraded habitats, is the deliberate establishment of individuals of a species into sites or regions where it has become extinct. Well-designed reintroductions may allow conclusions on factors affecting successes and failures (Maunder 1992, Smith 2014, Taylor et al. 2017) when done as ecological experiments testing hypotheses on links between the species and specific ecological variables (Farmer et al. 1992, Flagmeier et al. 2016).

Many lichens experience declines due to habitat loss, climate change, and/or air pollution (Allen and Lendemer 2016, Nascimbene et al. 2016, Ruete et al. 2018). The conspicuous epiphytic old forest Lobarion community (Rose 1988, Nascimbene et al. 2016) hosts spectacular and declining epiphytic lichens such as *Lobaria* spp. considered as flagship species (e.g. Nascimbene et al. 2009, Grube and Spribille 2012). Hosting the majority of known N-fixing epiphytic lichens, the Lobarion significantly participates in N-cycling in the forests where it is as a major component (e.g. Forman 1975, Kobylinski and Fredeen 2015). Here, we studied the reintroduction potential for two lichens in the genus *Lobaria* s. lat.: *L. amplissima* (Scop.) Forssell (= *Ricasolia amplissima* (Scop.) De Not.) and *L. pulmonaria* (L.) Hoffm. *Lobaria amplissima* is primarily a western European species associated with temperate oceanic and suboceanic climate (Ellis 2016), but was recently recorded (by a new subspecies) from northwest America (Cornejo et al. 2017). By contrast, *L. pulmonaria* is considered a globally widespread forest lichen. Both species are red-listed in most European countries (e.g. Türk and Hafellner 1999, Scheidegger et al. 2002, Martínez et al. 2003, Gärdenfors 2005), but not in Norway where a local abundance in oceanic forests allows sampling without compromising future survival. *Lobaria amplissima* has strongly declined in Sweden where it has disappeared from 76% of former Swedish localities despite the fact that the forest structure had apparently not changed (Hallingbäck and Thor 1988, Hultengren et al. 1993), and no newly established populations have been found. It is listed as Critically Endangered on the Swedish red-list, while *L. pulmonaria* is classified

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as Near Threatened (ArtDatabanken 2015).

The Lobarion, *L. amplissima* in particular, grows on bark with high pH (Gauslaa 1985). Therefore, acidification and/or air pollution likely played a role for its former decline (Farmer et al. 1991a, b, Rikkinen 2015). Acidification peaked in northern Europe in 1970 (Lee 1998) after having caused major lichen die-back (Hawksworth and Rose 1970). After the subsequent decline in acidification, the chemical environment should again be favourable for epiphytic cyano- and cephalolichens. Yet, there is hardly any establishment in previous sites or other sites. Lobarion species disperse more slowly than many other forest lichens (Öckinger et al. 2005, Ellis and Coppins 2007, Nordén et al. 2014, Belinchón et al. 2017). Thus, poor dispersal may explain their low establishment rates during declining acidification in SW Sweden, although they disperse more efficiently in oceanic sites (Gjerde et al. 2015). A high success of reintroduced thalli would be consistent with such a dispersal-limitation hypothesis.

We aimed to study the potential to reintroduce *L. amplissima* by transplanting it to some forests within its previous core areas in SW Sweden using transplants from Norway, and thus tested whether a reintroduction could be an option for this species. We did not intend to reintroduce the species, and thus removed all lichen material of both species after the one-year trial period. Furthermore, we did not use the exact sites that previously hosted *L. amplissima*, but selected forests with structure and openness similar to forests that still support the species. Because lichen growth that integrates vital functions of all lichen biotopes is a good measure of lichen fitness, we used growth rate as a measure of reintroduction success for *L. amplissima* and its more common associate *L. pulmonaria* to trunks of Norway maple (*Acer platanoides*) and oak (*Quercus petraea*) on which they often grow. Our hypotheses were 1: Reintroduction of *L. amplissima* can be a conservation measure for this critically endangered species. 2: Lichen transplants on phorophytes with a high pH grow faster than those on phorophytes with a low pH. 3: Transplants of *L. amplissima* with large external cephalodia grow faster than those deficient in external cephalodia, because cephalodia in general add an extra supply of N to the thallus (Millbank and Kershaw 1969, 1970). Such knowledge may allow identification of the

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most successful type of thallus for future reintroductions. 4: Because a single phosphorus fertilization dose has been shown to boost growth of N-fixing lichens (McCune and Caldwell 2009), transplants with added phosphorus grow faster than those without in one or both tree hosts. There is e.g. a need to know whether phosphorus is a more limiting factor in *Quercus* than in *Acer*. 5: Transplants of a lichen species dependent on old forest continuity such as *L. amplissima*, grow more slowly than of a species that occurs in a wider range of forests.

2. Material and methods

2.1. Lichen material

Lobaria amplissima and *L. pulmonaria* share a green-algal *Dictyochloropsis* photobiont genotype as their main photobiont (Dal Grande et al. 2014). As a secondary photobiont, *L. pulmonaria* has localized *Nostoc* in internal cephalodia, whereas *L. amplissima* has *Nostoc* in large external, and according to Zalewska and Bohdan (2012), also in tiny internal cephalodia. We collected *L. amplissima* with and without external cephalodia, and *L. pulmonaria*, from large populations of the two species in Kvinnherad, Hordaland, Norway, 59° 58' 41.41202" N, 6° 3' 39.49946" E, 350 m a.s.l., October 2013. A portion from many separate thalli were cut from eight old pollarded ash trees (*Fraxinus excelsior*).

In the lab, we removed debris, tree bark and bryophytes. We cut each sample into pieces of 3-10 cm² for *L. amplissima* and 5-14 cm² for the more broad-lobed *L. pulmonaria*. For *L. amplissima*, we had 120 specimens with and 120 without external cephalodia, and we had 120 *L. pulmonaria*. All collected *L. amplissima* had abundant cephalodia, allowing the pieces of *L. amplissima* with and without cephalodia to be taken from the same individuals. All selected pieces, hereafter called thalli, had some actively growing lobes with intact apices, and a minimum of cut edges. Their area when hydrated (A_{wet}) was determined from photographs, using ImageJ 1.48 (Rasband 2014).

As a P-fertilization treatment, 60 of the 120 thalli in each lichen category were submerged while hydrated in a solution of 600 mg L⁻¹ K₂HPO₄*3H₂O dissolved in distilled water for 20 min (McCune

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and Caldwell 2009). The remaining 60 thalli stayed in de-ionized water for 20 min. Afterwards we dried the thalli at room temperature and weighed them. At each weighing session, five additional control thalli of each species were weighed air-dried, then oven-dried (24 h at 70°C) before measuring DM. We used the mean reduction factor in mass from the air-dry to the oven-dry state for each species to convert air DM to oven DM for all transplants. From collection to the transplantation, thalli had been air-dry for 2 weeks shielded from light at room temperature. Before assigning them to a treatment, all transplants were randomized for each species separately by random numbers.

2.2. Transplantation design and transplantation sites

Using linen thread, thalli were sewn in groups of six onto 60 pale, fiberglass-reinforced PVC nettings with a mesh size of 1.6 mm x 1.2 mm trimmed to 20 cm x 25 cm. Each group included: (1) *L. pulmonaria* with added P, (2) *L. pulmonaria* without P, (3) *L. amplissima* without cephalodia with P, (4) *L. amplissima* without cephalodia without P, (5) *L. amplissima* with cephalodia with P, and (6) *L. amplissima* with cephalodia without P. The sequence of thalli was randomized for each net. Only basal parts of *L. pulmonaria* were fastened by sewing, allowing younger tips to hang freely, permitting thalli to curl when dry; a response to desiccation providing photoprotection by self-shading (Barták et al. 2006). *Lobaria amplissima* does not curl in this way, hence was broadly fastened to the nets.

Prior to setting out our nets, we selected 30 tree pairs of *Acer platanoides* (with a high bark pH; Gauslaa 1995) and *Quercus petraea* (with more acidic bark; Gauslaa 1985) in the forests of Åby säteri, Nordens Ark, Bohuslän, Sweden. The mean annual rainfall was 1250 mm yr⁻¹ for the last 20 yrs (<http://luftweb.smhi.se/>; Fig. 1 shows rainfall and mean temperature for the entire periods). Each tree pair was selected sequentially during walk-about in four sites; each pair was chosen for proximity of the two trunks (<20 m distance), similar tree size, and an openness and forest structure similar to *L. amplissima* sites we have seen elsewhere. All sites, located 10-20 m a.s.l., had old and open mainly deciduous stands, but with a few *Picea abies* and *Pinus sylvestris*. Two sites were forested hills with slopes of varying aspects (site 1 - 58°26'57.63''N 11°25'58.73''E) site 2 -

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58°26'53.90''N 11°25'46.85''E. The two last sites were forested slopes, each facing one direction; site 3 facing east (58°26'44.78''N 11°25'41.23''E) and site 4 - facing south (58°26'39.70''N 11°25'23.38''E). On each of the 60 trunks in the 30 pairs, we stapled the net on the trunk at 1.9-2.4 m height. The nets were placed on the side of each trunk where rain hit or water trickled because *L. amplissima* requires much water (Longinotti et al. 2017). Percent cover of trunk epiphytes was estimated for the side of the trunk where the net was fastened. Both tree species had 40% bryophyte cover, 29-35% crustose lichens and 20% naked bark (Table 1). Only the cover of macrolichens significantly differed between the two hosts, with lowest cover on *Acer* (Table 1). Acidophytic lichens like *Parmelia sulcata*, *Evernia prunastri*, *Cladonia*, and *Hypogymnia physodes* were more common on *Quercus* than on *Acer*; *Melanelixia fuliginosa* was common on both hosts (Table 1). Among selected trees for transplantation, one *Acer* and one *Quercus* had natural *L. pulmonaria* thalli, as well as some surrounding trees.

We transplanted nets with lichen transplants to all sites 15 October 2013 and harvested them 29 April 2014 for assessment of DM and A_{wet} . Afterwards, we fastened the same lichens to their previous nets and re-transplanted them to the same trees 15 May 2014. They stayed in the field until the final harvest 13 October 2014 for a final DM and A_{wet} assessment. After the one-year trial period, all thalli of both species were permanently removed from the sites. In the following text, we refer to the two transplantation periods without and with canopy leaves as winter and summer, respectively.

We computed growth rates for winter and summer separately. Percent growth in dry mass = $(DM_{end} - DM_{start}) * 100 / DM_{start}$. Relative growth rate (RGR) = $(\ln(DM_{end}/DM_{start})) * 1000 / \Delta t$ ($mg\ g^{-1}\ d^{-1}$). Δt is the 196 d (winter) or 153 d (summer) between start and end at which DM (g) was measured (Evans 1972). Specific thallus mass (STM) = DM / A_{wet} .

2.3. Statistical analyses

Because phosphorus fertilization had no effects on measured variables in any category, thalli $\pm P$ were averaged for each category on each trunk before further statistical analyses. The averaging reduced n from 120 to 60. The few entirely lost thalli were not included in statistical analyses. When one thallus

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in a $\pm P$ pair was lost, the remaining thallus represented the mean for this pair. Generalized mixed linear models were run in Minitab 16 (Minitab Inc., State College, PA, USA) for percent change in dry mass in each season separately across the fixed factors 1: lichen category (*L. amplissima* with cephalodia, *L. amplissima* without cephalodia, *L. pulmonaria*) and 2: tree species (*Acer* and *Quercus*) with site ($n=4$) as a random factor. Thallus size (DM at start of each season) was used as a covariate if it contributed significantly. Percent DM change in summer (mainly negative values) were transformed by multiplying the values by -1 and then square-root transformed. For the DM change in winter, no transformation was needed. We checked all models using residual analysis.

3. Results

At start, *L. amplissima* with and without external cephalodia had similar size (A_{wet}), whereas *L. pulmonaria* thalli were larger. Specific thallus mass (STM), a proxy of thickness, differed for all categories (Table 2). *Lobaria amplissima* with cephalodia had 1.3x higher STM than those without, 6x higher STM than *L. pulmonaria*. Due to the contrasts in STM, DM differed between the *L. amplissima* categories (Table 2). One year after transplantation, differences in STM between *L. amplissima* with cephalodia and *L. pulmonaria* had diminished (Table 2) because cephalodiate *L. amplissima* had declined in STM, whereas *L. pulmonaria* had gained biomass per thallus area. Phosphorus fertilization had no effects on measured variables in any of the species and seasons (General mixed linear models; data not shown).

The growth variables RGR (Table 2) and percent DM change (Fig. 2) varied with season. For the winter, mean percent DM growth was positive for all categories, although growth was higher in *L. pulmonaria* than in *L. amplissima* (Fig. 2). Of the sixty trees, just four had *L. pulmonaria* transplants with slightly negative growth (Fig. 3A). By contrast, for *L. amplissima* with and without external cephalodia, 11 and 19 trees, respectively, had negative percent DM growth in winter (Fig. 3A). In summer, growth was negative in all categories, particularly in *L. amplissima* (Fig. 2) for which only three trees supported net growth for thalli without cephalodia and none for cephalodiate thalli (Fig. 3B). In summer, 50% of the trees supported DM loss more than 20% in cephalodiate *L. amplissima*.

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By contrast, $\approx 1/3$ of all trees had net growth for *L. pulmonaria* (Fig. 3B).

When growth rates for all categories (*L. pulmonaria*, *L. amplissima* with and without cephalodia) were run in correlation analyses ($n = 60$ trunks), there were no significant correlations for the DM change between any of the lichen categories in winter. Therefore, trunk-specific factors did hardly influence growth in the season with net growth. In summer when the loss of biomass exceeded growth, the DM change positively correlated between *L. amplissima* without cephalodia and *L. pulmonaria* ($P = 0.001$) as well as between the two *L. amplissima* categories ($P = 0.034$), suggesting a trunk-specific effect on the loss of lichen biomass.

The random factor site did not significantly influence growth in any season (Table 3), despite site-specific differences in aspect and topography. Two sites represented slopes, one facing east, the other south; two sites were small hilltops with a mix of aspects and slopes. By contrast, tree species influenced growth of lichen transplants in summer (Table 3) when the mass loss was significantly higher in *Acer* than in *Quercus* (Fig. 2).

Transplant size was a significant covariate for growth in winter (Table 3) when growth was positive and declined with increasing size across species categories (Fig. 3A; $P < 0.001$), as well as within *L. amplissima* with external cephalodia ($P < 0.001$) and *L. pulmonaria* ($P = 0.037$), but not in *L. amplissima* without cephalodia. In summer when net mass loss was substantial, the transplant size at start did not contribute significantly as a covariate in the generalized mixed linear models (Table 3).

Grazing marks were already present when transplants were inspected 29 April, but no loss of entire thalli occurred in winter. Many more grazing marks were seen at the final harvest 13. October 2014, particularly for *L. amplissima* in which grazing gastropods had almost terminated some thalli, and presumably entirely consumed lost ones (Fig. 2C). External cephalodia had many grazing marks, consistent with the significant reduction in STM for the cephalodiate *L. amplissima* (Table 2).

4. Discussion

Many species decline in suitable remnant habitats due to extinction debts (Hanski and Ovaskainen **Gauslaa, Yngvar; Johlander, Stina; Nordén, Björn.**

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2002, Snäll et al. 2005, Ellis 2017, Jönsson et al. 2017). For the critically endangered *L. amplissima*, most remaining Swedish populations are small and isolated, consisting of infertile thalli without external cephalodia (B. Nordén, personal observations). It likely experiences extinction debt, implying a need for an identification of main limiting factors through reintroduction experiments. Given the large DM loss in the transplants, our experiment was not successful as a reintroduction. The few and small earlier reintroduction studies with this lichen in UK were successful in early years (Gilbert 1991), although later damage and/or loss occurred in some thalli and habitats due to acidification (Farmer et al. 1992) or competition from bryophytes (Gilbert 2002).

The substantial mass loss of *L. amplissima* in summer when lichens in Scandinavia normally grow fast (Larsson et al. 2012), concurred with the formation of numerous grazing marks by gastropods. Therefore, recorded DM loss resulted from grazing. *Lobaria amplissima* was also attractive to gastropods in a Norwegian study (Asplund et al. 2010b). Grazing damage of palatable lichens is common during summer (Gauslaa 2008, Asplund et al. 2010b) particularly in broadleaved deciduous forests (Vatne et al. 2010, Cernajová and Svoboda 2014). Grazing often varies much between sites (e.g. Asplund and Gauslaa 2008), but not in our study. At a within-site level, positive correlations for DM-change in summer between lichen categories is consistent with trunk-specific factors influencing the grazing. Gastropod diversity and number of individuals increase with increasing pH of the local litter around a trunk (von Proschwitz 1994, Gärdenfors et al. 1995, Vatne et al. 2010). Some trees like *Acer* produce litter rich in soluble Ca, whereas Ca in *Quercus* litter mainly occurs as calcium oxalate supporting fewer snails (Wäreborn 1969, Nation 2007). Thus, the higher lichen loss on *Acer* trunks likely occurred because litter with soluble Ca-salts beneath *Acer* canopies attracts gastropods. An understanding of the spatial variation in gastropod grazing has been hindered by inefficient sampling techniques for populations of climbing gastropods. Traditional gastropod sampling using litter samples is not efficient for climbing gastropods (Vatne et al. 2010), and sampling of gastropods in epiphytic communities with *Lobaria* underestimates climbing lichen-feeding slugs like *Lehmannia marginata* and *Arion subfuscus* (Gauslaa et al. 2006). Nevertheless, artificial exclusion of gastropods

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from trunks reduced the grazing of *L. pulmonaria* in site-specific ways (Asplund and Gauslaa 2008). At a thallus level, the higher grazing in *L. amplissima* with external cephalodia is consistent with the documented preference by gastropods for cephalodia in other lichens (Asplund and Gauslaa 2010).

It seems that gastropod grazing threatens *L. amplissima* in parts of its former distribution area, and that grazing likely contributed to its former decline. Evidence for damage by gastropods has also accumulated from recent lichen transplantations (Gilbert 2002, Asplund and Gauslaa 2008, Gauslaa 2008, Asplund et al. 2010b). Gilbert (2002) emphasized that gastropod grazing became a problem during the last 5 years of a 20-years transplantation with *L. amplissima*. From such a perspective, important questions would be why grazing by indigenous gastropods was less serious in the past, and why some microsites and trees still experience low grazing. Such questions need considered before successful action plans for *L. amplissima* can be made.

Since 1990, the weather has become milder and wetter, and this trend is predicted to continue (IPCC 2014). A comparison of 1961-1990 with the following period 1991-2016, using data from <http://luftweb.smhi.se/>, shows that the annual rainfall in the study area increased from 1060 ± 28 to 1205 ± 40 mm ($P = 0.003$; ANOVA), and mean annual temperature increased from 6.87 ± 0.18 to 7.73 ± 0.15 °C ($P < 0.001$; ANOVA). Changed climate may not be the only trend facilitating climbing gastropods. High N deposition may also contribute. While acidification has strongly declined, N-depositions remain high (Grandin 2011, Karlsson et al. 2011). N-fixing lichens lose their competitive advantage under elevated N-deposition (Rai 1988) that represents a possible obstacle for recolonization. Despite the fact that N deposition reduces the palatability of lichens (Asplund et al. 2010a), N may yet boost gastropod populations at an ecosystem level because N content is a predictor of food quality for herbivores (Mattson 1980). Whereas lichens decline due to climate change *per se* (e.g. Rubio-Salcedo et al. 2017), our results suggest that global change also affect lichens by strengthening biotic interactions with climbing gastropods.

There was a trade-off between growth rates and thallus sizes in the season with net growth rates. This is partly caused by a trade-off between growth and size-dependent reproductive efforts (Gauslaa 2006, **Gauslaa, Yngvar; Johlander, Stina; Nordén, Björn.**

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Merinero et al. 2015). Yet, the trade-off is present also in juvenile phases (Larsson and Gauslaa 2011).

In summer when DM loss by grazing greatly exceeded growth, there was no significant contribution for thallus size in the model analyzing growth, likely because visiting gastropods grazed the lichens until they had consumed enough.

In winter, RGRs in *L. pulmonaria* were similar to rates reported elsewhere in Scandinavia (Larsson et al. 2012). By contrast, growth of *L. amplissima* in winter was remarkably low. We see three, not necessarily mutually exclusive explanations for recorded species-specific growth responses in winter. First, the higher growth in *L. pulmonaria* can be due to its more flexible hydration traits (Gauslaa et al. 2017, Longinotti et al. 2017). Second, higher growth in *L. pulmonaria* compared to *L. amplissima* is consistent with the more southern and low-elevation distribution of *L. amplissima* (latitude-altitude diagrams generated by the Norwegian Lichen Database <http://nhm2.uio.no/lav/web/index.html>). Finally, observed grazing marks suggest that gastropod grazing reduced growth of *L. amplissima* more than of *L. pulmonaria* even in winter.

Lack of phosphorus can limit lichen growth (Benner and Vitousek 2007, Hogan et al. 2010, Benner 2011, Johansson et al. 2011). Because P-fertilization increases N-fixation in symbiotic *Nostoc* (Weiss et al. 2005, Benner et al. 2007), it may increase N-fixation in external *L. amplissima* cephalodia with downstream benefits to thallus growth. P-fertilization facilitates growth of N-fixing lichens in some humid temperate and subtropical localities (Benner and Vitousek 2007, McCune and Caldwell 2009). The P-fertilization did not lead to changed growth rates in lichen transplants, suggesting that P was not a limiting factor in our sites, as seen in other temperate/boreal sites (Gauslaa and Goward 2012, Marks et al. 2015, Palmqvist et al. 2017).

5. Conclusions

Our study emphasizes the importance of biotic interactions between lichenivores and lichens. For each of our hypotheses, we make conclusions as follows: 1: Despite an efficient reduction of anthropogenic acidification, reintroduction of *L. amplissima* was not successful because lichen-

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feeding snails excessively grazed the transplants. 2: Among the two tree species used as stands for transplants, *A. platanoides*, a previous good host for *L. amplissima* with high bark pH, resulted in more grazing on transplants than did *Q. petraea*. 3: Because cephalodia were preferred by grazing gastropods, *L. amplissima* having cephalodia at start could not benefit much from N-fixation. 4: Neither growth of the lichens, nor grazing, was influenced by phosphorus fertilization, meaning that P was not a limiting factor in studied sites. 5: The widespread species *L. pulmonaria* grew much faster and was less grazed than the rare *L. amplissima*. Under present-day wetter and warmer climate with high N-deposition, biotic interactions exclude reintroduction as a useful conservation tool for *L. amplissima* in studied forests. Increasing gastropod grazing likely contributed to previous extinctions.

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Figure legends:

Fig. 1

Mean daily temperature (A) and daily rainfall (B) for all days during the two transplantation periods (marked by the two solid horizontal lines, one for winter: 15 Oct 2013 - 29 Apr 2014 and one for summer 15 May - 13 Oct 2014). The text on top gives the number of days for each period, number of rainy days, total precipitation and mean daily temperature. Data from <http://luftweb.smhi.se/>

Fig. 2

The change in dry matter during A: winter (15 October 2013 – 29 April 2014) and B: summer (15 May – 13 October 2014) in 1: *Lobaria amplissima* with cephalodia, 2: *L. amplissima* without cephalodia and 3: *L. pulmonaria* transplanted to pairs of two tree species (*Acer*, *Quercus*) co-occurring in four sites. Vertical bars show means \pm 1SE. Means sharing the same lowercase letter for one season did not differ significantly from each other ($P < 0.05$; Tukey multiple comparison test). C: Number of lost thalli (all in summer). Means were based on the pooled +P/-P pairs, the number of lost thalli refers to the total pool of 120 thalli in each category.

Fig 3

Specimen-specific growth rates as a function of thallus size in in *Lobaria amplissima* with cephalodia and without cephalodia as well as *Lobaria pulmonaria* in A: winter and B: summer. The hatched line is the zero growth line.

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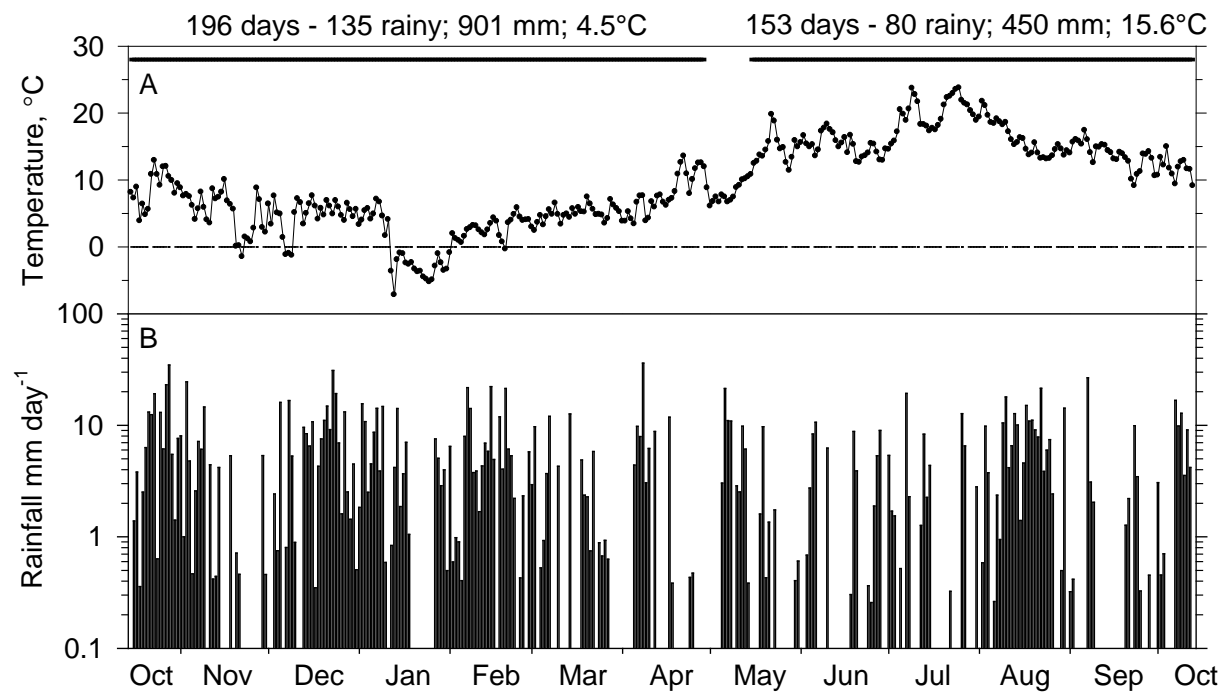


Fig. 1

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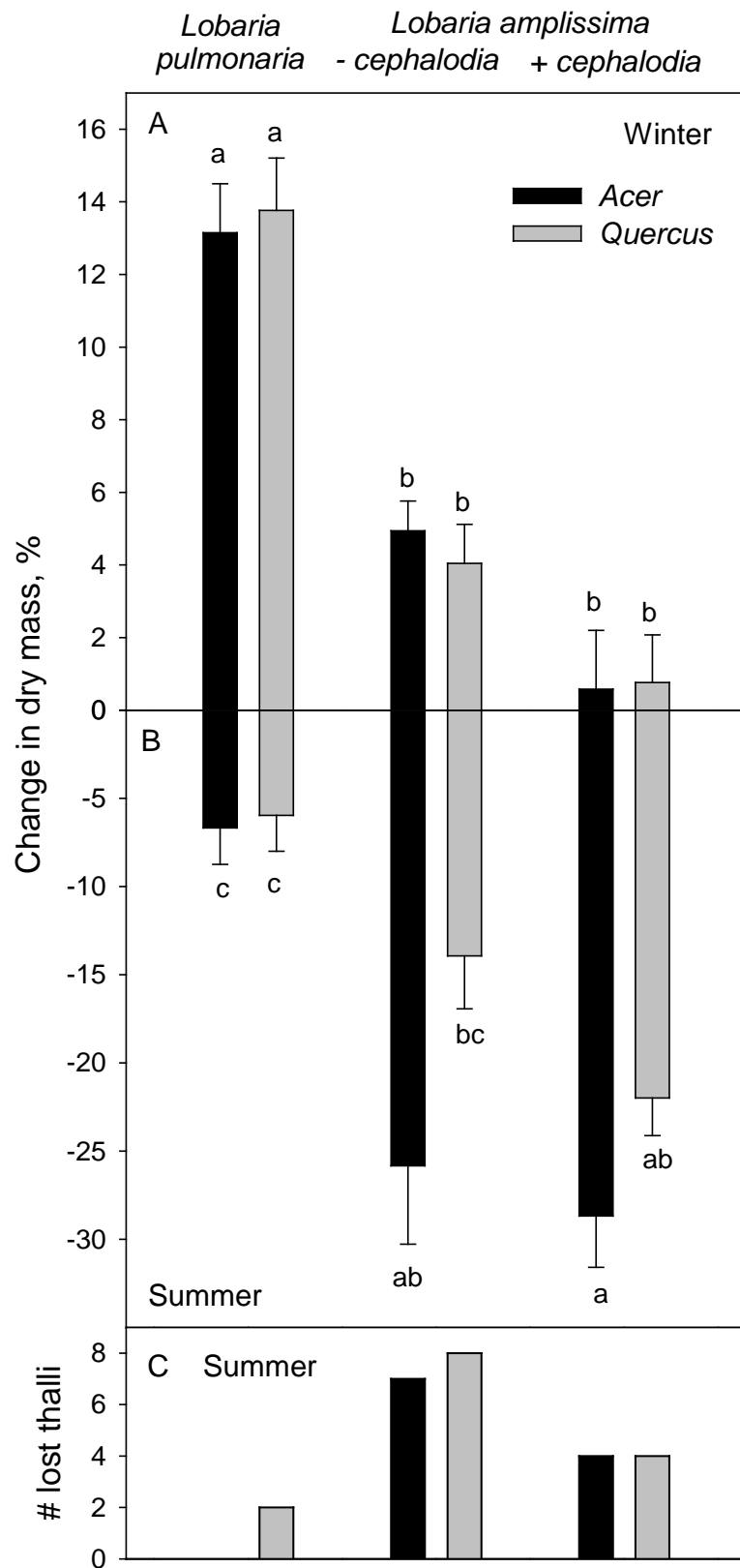


Fig. 2

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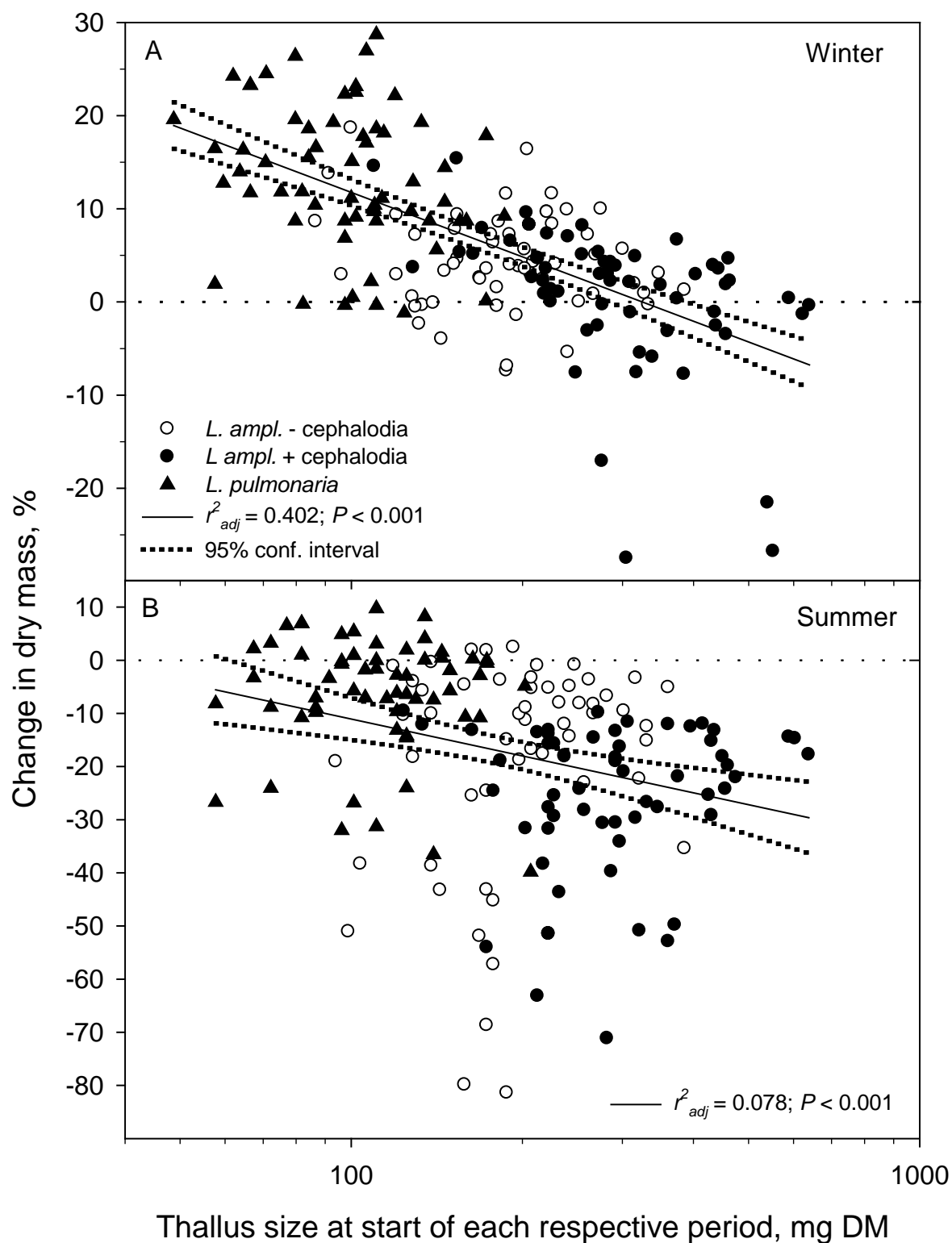


Fig 3.

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Table 1. Percent cover of major epiphytic vegetation groups and the frequency of macrolichens on paired trunks of *Acer platanoides* and *Quercus petraea* used for lichen transplantation.

	<i>Acer</i>	<i>Quercus</i>	<i>P</i> -value
Cover of macrolichens, %	3.7 ± 1.1	12.0 ± 3.1	0.004
Cover of bryophytes, %	40.7 ± 4.8	39.4 ± 5.2	0.837
Cover of crustose lichens %	35.0 ± 4.7	29.1 ± 4.5	0.275
Cover of naked bark, %	20.7 ± 3.0	19.3 ± 3.0	0.768
Number of macrolichen species	1.8 ± 0.2	2.6 ± 0.3	0.053
Occurrence of species (# trunks)			
<i>Melanelia fuliginosa</i>	18	16	
<i>Evernia prunastri</i>	13	20	
<i>Parmelia sulcata</i>	6	16	
<i>Cladonia spp.</i>	7	17	
<i>Ramalina farinacea</i>	7	5	
<i>Hypogymnia physodes</i>	0	5	
<i>Lobaria pulmonaria</i>	1	1	

P-values computed by pairwise t-tests. Means ± 1SE are given (*n*=30). Species occurring on only one tree: *Physcia tenella* on *Acer*, *Phaeophyscia orbicularis* on another *Acer*.

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Table 2. Transplant size (DM_{start} , A_{start}), relative growth rates (RGR) in winter and summer, and specific thallus mass (STM) at the start and at the end of a one-year transplantation period for *Lobaria amplissima* with and without cephalodia and for *L. pulmonaria*.

Species	<i>Lobaria amplissima</i>		<i>L. pulmonaria</i>
	With cephalodia	Without cephalodia	
DM_{start} (mg cm ⁻²)			
Mean \pm 1SE	312 \pm 16 ^a	196 \pm 8 ^b	102 \pm 4 ^c
Median	281	189	101
Min – max	110 – 640	86 – 385	49 – 186
$Area_{start}$ (cm ⁻²)			
Mean \pm 1SE	4.97 \pm 0.19 ^b	4.23 \pm 0.13 ^b	9.61 \pm 0.30 ^a
Median	4.55	4.00	9.30
Min – max	3.06 – 10.15	2.74 – 6.91	5.39 – 14.39
RGR_{winter} (mg g ⁻¹ d ⁻¹)			
Mean \pm 1SE	-0.016 \pm 0.070 ^b	0.211 \pm 0.033 ^b	0.622 \pm 0.045 ^a
Median	0.112	0.196	0.613
Min – max	-2.464 – 0.722	-0.422 – 0.872	-0.085 – 1.280
RGR_{summer} (mg g ⁻¹ d ⁻¹)			
Mean \pm 1SE	-2.178 \pm 0.224 ^a	-1.851 \pm 0.329 ^b	-0.510 \pm 0.121 ^c
Median	-1.601	-0.789	-0.249
Min – max	-8.120 – -0.657	-11.04 – 0.158	-4.535 – 0.607
STM_{start} (mg cm ⁻²)			
Mean \pm 1SE	62.5 \pm 1.7 ^a	46.7 \pm 1.4 ^b	10.5 \pm 0.2 ^c
Median	63.4	46.3	10.5
Min – max	34.2 – 93.7	25.8 – 70.7	8.6 – 14.5
STM_{end} (mg cm ⁻²)			
Mean \pm 1SE	55.6 \pm 1.7 ^a	44.5 \pm 1.2 ^b	13.7 \pm 0.2 ^c
Median	56.1	44.0	13.6
Min – max	32.7 – 99.9	28.3 – 62.8	10.3 – 18.8

Differences between specimens were analyzed by Kruskal-Wallis one-way ANOVA on ranks using an all pairwise multiple comparison procedure (Dunn's Method; means sharing the same superscript letter did not differ significantly from each other ($P < 0.05$). All variables differed among species ($P < 0.001$). All means, medians and min-max are based on the pooled +P/-P pairs ($n = 60$).

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Table 3. Generalized mixed linear models for change in dry matter during 1: winter and 2: summer across the fixed factors lichen category (*Lobaria amplissima* with cephalodia, *L. amplissima* without cephalodia, *L. pulmonaria*) and tree species (*Acer platanoides*, *Quercus petraea*) that co-occurred in four sites (random factor). Analysed data are shown in Fig. 2.

Source	% DM change in winter			% DM change in summer		
	DF	F	P	DF	F	P
Species	2	12.28	0.000	2	31.31	0.000
Tree	1	0.30	0.583	1	7.39	0.007
Species*Tree	2	0.21	0.809	2	1.42	0.246
Site (random factor)	3	2.09	0.103	3	0.71	0.546
DM _{start} (covariate)	1	17.02	0.000			
Error	169			167		
Total	178			175		
R^2_{adj}	0.425			0.276		

Percent DM change in summer (mainly negative values) were transformed by multiplying the values by -1 before they were square-rooted. Thallus size (DM_{start}) was only included as a covariate for the winter; it was not significant for the summer period.

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