



Lichen communities on understory rowans (*Sorbus aucuparia*) in managed, urban, and old-growth forests in southern Finland

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Abstract

Old-growth forests differ from even-aged managed forests, for example, in the age or size of canopy trees. In contrast, understory trees in managed and old-growth forests may appear superficially similar, but they may still differ in ways that would impact species communities associated with them, such as epiphytes. To address this, we surveyed epiphytic lichens on 270 rowans across managed, urban, and old-growth forests in southern Finland. The sampled trees were components of the understory and represented a size gradient, mostly in the range of 1–15 cm in diameter at breast height. Forest type and tree diameter affected both lichen species richness and composition significantly. A few species were associated with small rowans, but many more with larger ones. Thus, tree-level species richness increased with diameter. Tree-level diversity was higher in old-growth forests, independently of tree size, compared to managed and urban forests. Species composition was divergent in urban forests, which is apparently related to nitrogen pollution and the urban heat island effect, although these effects were relatively light. Ruderal species traits were more prevalent on small rowans and rowans in urban forests, and competitive traits on larger rowans and rowans in old-growth forests. Our results reflect differences in understory dynamics and structures between old-growth and managed (including urban) forests, which also affect associated species communities. The assumed main driver of our results was that, despite similar sizes, understory rowans may have been older in old-growth forests than in managed and urban forests. Understory trees can significantly contribute to epiphyte diversity, especially when their substrate properties differ from those of canopy trees. When that condition is met, as with rowans in spruce forests, understory trees should not be overlooked in epiphyte inventories, and retaining them during thinning and in clearcuts can support epiphyte diversity in managed forests.

Keywords Boreal forests · Forest management · Traits · Succession

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Introduction

Human activities frequently alter forest habitats, particularly in regions where forests managed for timber production comprise a large share of the forest area. Managed forests typically have altered tree species compositions and truncated tree age distributions (Kuuluvainen 2002). Consequently, managed forests often harbour depauperate species communities in comparison to unmanaged old-growth forests (Nirhamo et al. 2025). In Nordic countries, the management of urban forests — patches of natural-like vegetation within the urban matrix — emphasises supporting recreational use over timber production (Gundersen et al. 2005). As a result, management intensity is lower, and urban forests have the potential to provide habitat for species typically associated with old-growth forests (Korhonen et al. 2020, 2021). However, urban areas are characterized by altered conditions due to the urban heat island effect (Rizwan et al. 2008; Munzi et al. 2014) and pollution (Niepsch et al. 2021; Sebald et al. 2022; Wutz and Diekmann 2025).

When old-growth forests are compared to their younger counterparts, attention is typically directed to the evident differences, such as the size or age of canopy trees and the amount of deadwood (Siitonen 2001; Kuuluvainen 2002). In contrast, these forest types may superficially appear similar regarding smaller trees or saplings in the understory, but their understory dynamics are still different. Understory trees may remain stunted for several decades or even over a century, awaiting a canopy opening caused by disturbances (Antos et al. 2000). In boreal Europe, this strategy is utilized especially by rowan (*Sorbus aucuparia*) and spruce (*Picea abies*) (Hofgaard 1993; Żywiec and Ledwoń 2008). However, in managed forests, understory dynamics are dictated by thinning harvests. Thinnings from below target smaller and weaker trees, and in at least some cases, the understory is cleared alongside thinning (Kärhä and Bergström 2020). In the aftermath of thinning harvests, the regeneration of new saplings into the understory is amplified (Otto et al. 2012; Olson et al. 2014; Korhonen et al. 2023). Furthermore, herbivory can significantly impact understories, with rowan being especially vulnerable to browsing by mammals (e.g., moose) (Linder et al. 1997; Myking et al. 2013). Consequently, rowan saplings tend to be frequent in the understory, but full-grown individuals are only sporadic in mature or old-growth forests (Hofgaard 1993; Linder et al. 1997). In urban forests, however, large herbivores are absent, and rowan regeneration and growth may be abundant (Korhonen et al. 2023).

Lichens assemblages are more diverse in older, unmanaged forests, which is typically related to large and old trees or deadwood providing substrate types not found in managed forests (Lommi et al. 2010; Marmor et al. 2011; Ellis 2012). Epiphytes associated with understory trees have generally gained little attention, possibly because they have been overlooked since larger trees are thought to have overwhelming importance. Indeed, epiphyte diversity is typically higher on larger trees (Löbel et al. 2006; Johansson et al. 2007; Lie et al. 2009). When studying pine-dominated stands in boreal Europe, Lommi et al. (2010) found higher epiphytic lichen diversity in stands with a higher density of understory spruces, but considered this to be because of a correlation with management intensity rather than a contribution of the understory spruces. The different understory dynamics in managed and unmanaged forests may be reflected in the lichen assemblages hosted by understory trees. For example, understory trees in old-growth forests might support higher epiphyte diversity, since they may be much older than their size would suggest (Hofgaard 1993).

Lichens are famously sensitive to air pollution (Hawksworth and Rose 1970). Presently, nitrogen-based compounds are the main air pollutants in European cities (Vestrenge et al. 2007; Jonson et al. 2022). In contrast to sulphur pollution, which may eliminate all lichens (Hawksworth and Rose 1970), N pollution has an eutrophying effect on epiphyte communities and induces compositional changes (Sebald et al. 2022; Wutz and Diekmann 2025). Most studies on epiphytic lichens in urban conditions have been conducted in park-like habitats. Compared to parks, the effects of air pollution may be less obvious in urban forests, and the urban heat island effect may be more impactful instead (Munzi et al. 2014).

Lichen functional traits can provide insight and generalizable information on how species communities are affected by different environmental conditions (Ellis et al. 2021). A pattern conforming to the CSR plant strategies (Grime 1977) has been suggested for epiphytic lichen succession: ruderal traits are prevalent on small or young trees, and competitive traits become increasingly prevalent with increasing size or age (Ellis 2012). Specifically, species with smaller stature and propagules (such as spores) are replaced by species with larger thalli and propagules (such as asexual propagules) (Hedenås and Ericson 2000; Löbel et al. 2006; Ellis and Coppins 2006; Johansson et al. 2007). This pattern represents autogenic succession (Ellis 2012), but alternatively, epiphyte community dynamics may be driven by gradual changes in substrate properties (e.g. Nirhamo et al. 2026). In addition, the community consisting of species tolerant to aridity and eutrophication may be inferred as signals of nitrogen pollution and the urban heat island effect in urban habitats (Munzi et al. 2014). Lastly, different types of lichen photobionts are favored by different climatic conditions, with trentepohlioid species being more frequent in warmer climates (Marini et al. 2011; Phinney et al. 2022). Thus, the urban heat island effect may increase the frequency of trentepohlioid species.

In this study, we examined differences in tree-level species richness, species composition, and trait composition of epiphytic lichen communities on *Sorbus aucuparia* (hereafter, rowan) across old-growth, managed, and urban forests along a size gradient. Thus, we addressed the following questions:

1) How do lichen communities vary on rowans of different sizes? We expected to see an increase in species richness with tree size and that, with increasing tree size, communities shift from dominance of ruderal traits to that of competitive traits (Ellis 2012). More specifically, small rowans would be inhabited by small-sized species reproducing by spores, and larger trees would be inhabited by larger species reproducing by asexual propagules.

2) Are lichen communities different on the understory rowans of old-growth forests and younger managed forests? Since understory rowans are superficially similar in stands of different ages, small differences may be expected. On the other hand, rowans in the understory of old-growth forests may be much older than their size suggests (Hofgaard 1993), which may lead to higher epiphyte diversity.

3) Can urban forests provide valuable habitats to epiphytic lichens? Lower management intensity in urban forests potentially causes similarity with the epiphyte assemblages of old-growth forests (Korhonen et al. 2020, 2021), but unique abiotic conditions (N pollution and the urban heat island) may lead to divergent and/or depauperate assemblages. Rowan is a particularly interesting host tree to study in this context, given its abundant regeneration in urban forests, which may lead to unusual stand properties (Korhonen et al. 2023).

Methods

Sampling

This study was conducted in and near the city of Jyväskylä. The human population of the urban area of Jyväskylä is approximately 130,000. It is located in the southern boreal zone at an elevation of 140 m. The mean annual temperature is 4 °C, and the annual precipitation is 620 mm. The data were collected from three types of forests: old-growth, managed, and urban. Each forest type was represented by three sites, except that one managed forest site had few rowans, so we used a fourth site to complete the sampling (Online Resource 1). Old-growth forests were represented by three spruce-dominated sites, ranging in area from approximately 30 to 100 hectares, that were protected in the 1990s as part of an old-growth forest conservation program. These sites were located 9–13 km to the west of the city center of Jyväskylä. They have developed with minimal human intervention since the previous major disturbance in the mid-to-late 19th century, which would correspond with a stand age of about 120–170 years. Thus, succession in these stands is still ongoing, and they best represent the class “ageing forest” *sensu* Angelstam and Kuuluvainen (2004). Yet, they are clearly more natural in their structure, with the canopy consisting of significantly older trees, compared to managed forests of the region. In Central Finland, natural late-successional forests are virtually absent, and these stands are among the best representatives of old-growth forests. The sites representing managed forests were selected with the help of publicly available remote sensing data (Mäkisara et al. 2022) on estimates of forest age and tree species composition. We chose sites that were as close as possible to the old-growth forest sites, spruce-dominated, mature (i.e., stand age at least 50 years), state-owned, and located outside a protected area. The remote sensing data provides imprecise stand age estimates, but the selected managed forest sites were suggested to be about 50–80 years in stand age. Similar criteria for tree species composition and stand age were applied to select urban forests, except that one urban forest site had been protected for about 25 years. The sites representing urban forests were chosen based on the authors’ prior knowledge about fitting sites within the urban area of Jyväskylä.

In each study site, lichen surveys were conducted on 30 rowans (except that one set of 30 rowans was split between two managed forest sites; see previous paragraph), evenly distributed to three size classes: 1–2.4 cm, 2.5–7.4 cm, and ≥ 7.5 cm in diameter at breast height. Thus, we surveyed a total of 270 trees, with 90 per forest type and size class. These size classes were used to ensure a representative sample of rowan size variation, and these thresholds were judged to be the most effective after initial trials. At the study sites, we started from a haphazardly selected point and advanced along a route complying with the shape of the study sites, many of which were irregularly shaped and quite small. Every 25 m, we stopped and surveyed the nearest rowan belonging to each of the size classes, if present. The smallest size class (i.e., saplings) was present most of the time, while the larger size classes were much less frequent (except in urban forests). In study sites where this approach proved inefficient in finding rowans in the larger size classes, we began searching haphazardly and surveyed any tree we encountered. However, we did not survey multiple trees from tight clusters of rowans. Primarily, we surveyed trees at least 25 m from forest edges, but also surveyed some trees closer to the edges when they were not found elsewhere. Standing dead trees were accepted if the bark was still attached.

Epiphytic lichens were surveyed on the lowest two meters of the selected rowans. Some of the smallest selected rowans were shorter than two meters and were surveyed fully. The surveys covered all lichens with the exception of *Cladonia*, which were recorded merely as with or without cups in the podetia. When necessary, specimens were collected for identification with microscopy and chemical spot tests. Lichen nomenclature followed Pykälä et al. (2025).

Statistical analyses

We analyzed patterns in tree-level species richness using a generalized linear model (GLM) with a Poisson distribution, with forest type as a categorical predictor with three levels (old growth forest, managed forest, and urban forest), the log-transformed diameter at breast height (cm) of the trees as a continuous predictor, and an interaction term between site type and diameter. The diameter was log-transformed because the upper end of the diameter range in the data was represented by a low number of data points. To address patterns in species composition, we used nonmetric multidimensional scaling (NMDS) in three dimensions using the Jaccard dissimilarity index. Trees with 0–3 observed species ($n=28$) were excluded from the NMDS. The NMDS was performed using the vegan package in R (Oksanen et al. 2025).

To analyze the responses of individual species, we used a hierarchical modeling of species communities (HMSC; Ovaskainen and Abrego 2020), which is a joint species distribution model, with the R package Hmsc (Tikhonov et al. 2020). We fitted a probit model to a matrix of presence-absence of species with at least five observations. To evaluate whether the species' responses to the predictors were organized according to their phylogenetic relationship, we added a taxonomic tree of species constructed with the Linnaean rank taxonomy with an equal branch length among taxonomic levels, with the function *as.phylo* of the R package ape (Paradis and Schliep 2019).

The HMSC model had a similar structure to the GLM using the same explanatory variables. To account for the spatial structure of the data, we included site coordinates as a spatially structured random effect. The ID of each sampled tree was also included in the model as a random effect. We incorporated seven species traits as covariates in the model: reproduction mode, photobiont type, two ecological indices (tolerances for eutrophication and aridity), spore volume (log-transformed spore volume), and spore shape (log-transformed ratio of length and width). The trait data was taken from the ITALIC 8.0 database (Martellos et al. 2023), the Consortium of Lichen Herbaria (2025), and from papers when the traits were not available in those databases (Sheard et al. 2017). To calculate spore volume, we followed the procedure of Aguilar-Trigueros et al. (2019).

We fitted the model assuming the default prior distributions (Ovaskainen and Abrego 2020) and sampled the posterior distribution using four Markov Chain Monte Carlo (MCMC) chains, each of which ran for 375,000 iterations, with the first 125,000 iterations removed for burn-in. The chains were thinned by a factor of 1000 to yield 250 posterior samples per chain, resulting in a total of 1000 posterior samples. We examined the MCMC convergence by the potential scale reduction factors (Gelman and Rubin 1992) of the model parameters. We used variance partitioning to see the proportion of explained variance in species occurrences attributed to each covariate in the model. The posterior means of the beta (β) parameters were used to see the directionality (positive/increasing or negative/

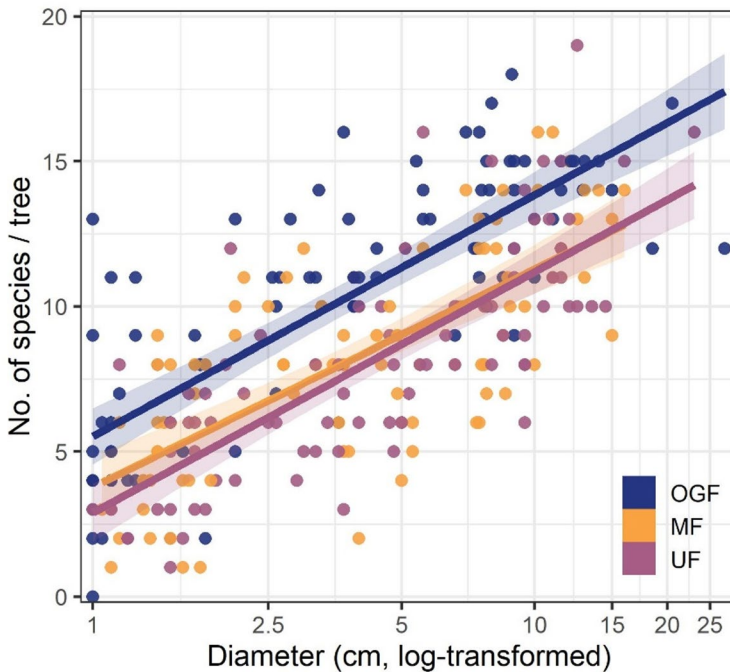


Fig. 1 Species richness of epiphytic lichens on rowan in response to log-transformed diameter at breast height

Table 1 Summary of a generalized linear model (Poisson distribution) with species richness as the response variable and log-transformed diameter at breast height, forest type and their interaction as explanatory variables. Parameter estimates have been transformed to the response scale

(Intercept)	Estimate	95% CI	<i>p</i> value
	6.054	5.28–6.91	<0.001
Diameter	1.434	1.33–1.54	<0.001
Forest type (MF)	0.738	0.59–0.91	0.006
Forest type (UF)	0.636	0.51–0.79	<0.001
Diameter: MF	1.050	0.93–1.18	0.424
Diameter: UF	1.110	0.99–1.25	0.083

decreasing) of the estimated responses of the predictors. Additionally, to determine whether related species exhibited similar responses to the covariates, the phylogenetic signal was assessed via the posterior distribution of the parameter ρ (p), where 1 indicates a strong signal and 0 indicates a weak signal.

Results

We observed 85 lichen species on the 270 surveyed rowans (Online Resource 2). Tree-level species richness (i.e., alpha diversity) was higher in old-growth forests than in managed and urban forests (Fig. 1; Table 1). The total number of observed species (i.e., gamma diversity) was similar in all forest types: 60, 62, and 62 in old-growth, managed, and urban for-

ests, respectively. Species richness increased with tree diameter at breast height (hereafter “diameter”), and no interaction was observed between tree diameter and forest type. When diameter was not log-transformed, species richness showed a non-linear response to diameter, particularly in old-growth forests (Online Resource 3). For the three size classes used in sampling, the total number of observed species was 45, 73, and 74 for classes 1–2.4 cm, 2.5–7.4 cm, and ≥ 7.5 cm, respectively. Lichen species composition was affected by both tree diameter and forest type (Fig. 2). Tree diameter was correlated with the first dimension of NMDS (Fig. 2a, c). The point clouds formed by trees of the three forest types showed separation in the three-dimensional ordination space, although the overlap was considerable (Fig. 2b).

In the HMSC model, forest type accounted for a greater proportion of the variation than tree diameter, with their interaction term also explaining a substantial portion of the variation (Online Resource 4). Among the 47 species included in the HMSC, occurrence probability increased with diameter for 22 species and decreased for 5 species (Fig. 3). There was no statistically significant effect of diameter on the probability of occurrence for 20 of the species included in the model, but most of these had a low number of observations (i.e., $n < 15$). The occurrence probability of 11 species was lower in managed forests, and of 22 species in urban forests, in comparison to old-growth forests (Fig. 3), with only one species (*Arthonia radiata*) having a higher occurrence probability in urban forests. However, occurrence probability increased more strongly with diameter for several species in urban forests and a few species in managed forests than in old-growth forests. There was no strong phylogenetic signal, meaning that phylogenetic relations among lichen species did not drive similarity in responses to the different covariates ($\rho = 0.47$; statistical support for posterior probability $p[\rho > 0] = 0.86$).

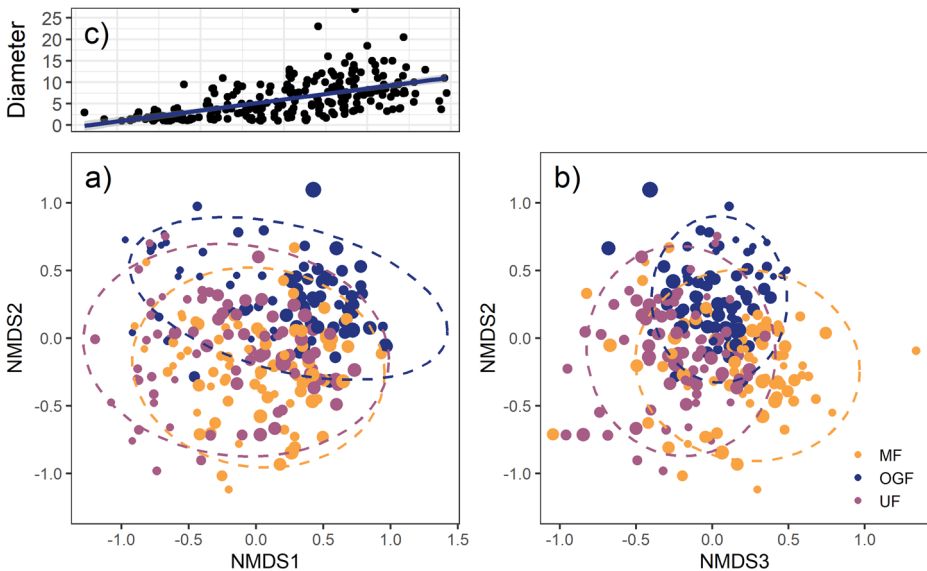


Fig. 2 Outcome of the three-dimensional NMDS ordination. (a) First and second dimensions, (b) second and third dimensions, (c) relationship between NMDS1 score and diameter. Stress=0.161. Ellipses for each forest type indicate regions where a new observation is expected to fall with 95% likelihood

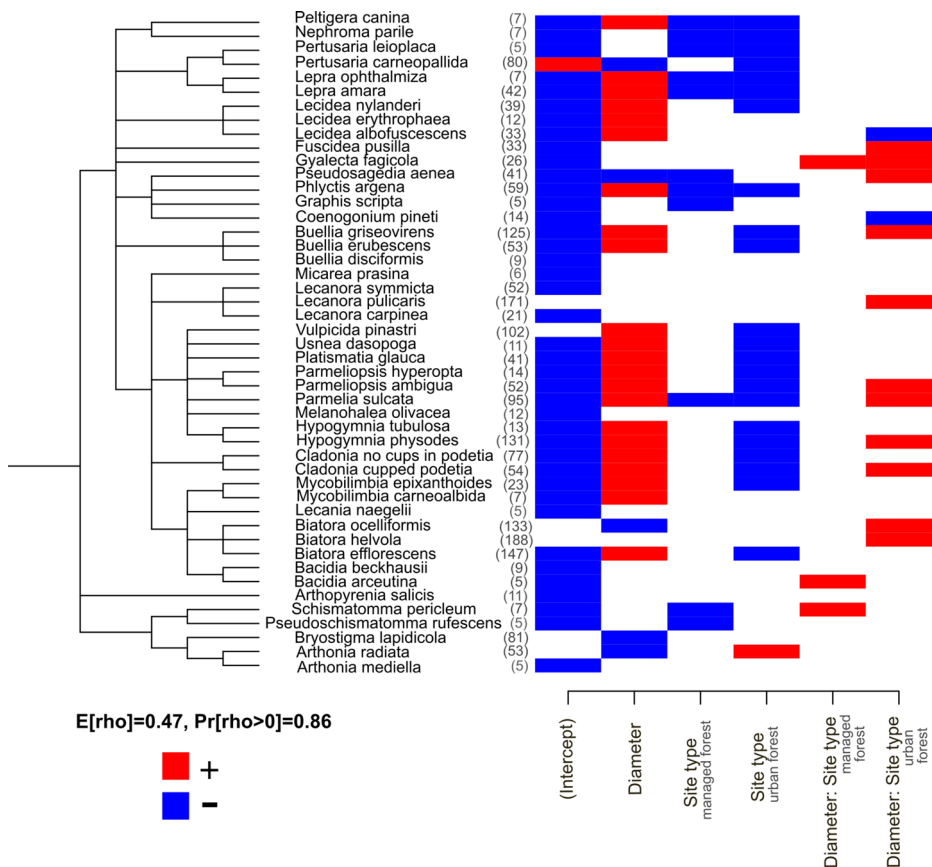


Fig. 3 Responses of the species to the predictor variables included in the presence-absence model. The plot shows those responses that were positive (red) or negative (blue) with a posterior probability of at least 0.95. Positive (negative) responses indicate that the species' probability of occurrence increases (decreases) with the increase of a given variable. Species are ordered based on their phylogenetic relationships shown in the taxonomic tree. The numbers in parentheses next to species names indicate the number of observations

The prevalence of sexual reproduction decreased with tree diameter (Fig. 4), and correspondingly, since reproductive mode was characterised as a binary trait, the prevalence of asexual reproduction increased with tree diameter. A similar but not statistically supported trend was observed for growth form: prevalence decreased for microlichens and increased for macrolichens with diameter (Online Resource 5). Microlichens and sexual reproduction were also more prevalent in urban forests compared to old-growth forests (Fig. 4). For these traits, managed forests were intermediate between the two other forest types (Online Resource 5), but the difference to old-growth forests was not statistically supported. Old-growth forests were inhabited by species with larger spores compared to both managed and urban forests (community weighted mean log spore volume: 6.67, 6.11 and 6.3 μm^3 in old-growth, managed and urban forests, respectively; Online Resource 6). In addition, species with a trentepohlioid photobiont tended to be more prevalent in urban forests (Online Resource 7), but the difference was not statistically supported, likely because having a tren-

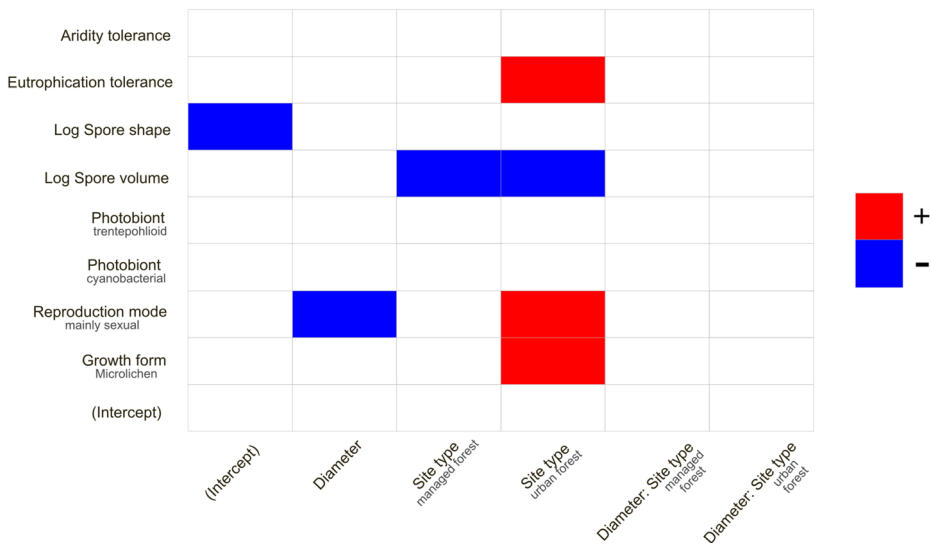


Fig. 4 Community-level results of trait responses in the presence-absence model are shown. The figure displays the average (intercept) and the influence of species traits (rows) on environmental responses (columns). Red and blue colours represent positive and negative effects, respectively, with a posterior probability of at least 0.95 for each trait's impact on each environmental response

tepohlioid photobiont was confounded with other traits, as all such species were sexually reproducing microlichens.

Discussion

A shift from ruderal to competitive traits with increasing tree diameter

Our findings aligned with a widely observed pattern in which a small number of epiphytic lichen species are associated with small (or young) trees, and much more with larger (or older) trees (e.g., (Johansson et al. 2007; Marmor et al. 2011; Nirhamo et al. 2026), which led to higher species richness on larger rowans. All species that were associated with small rowans were sexually reproducing microlichens. In contrast, most species associated with larger rowans were asexually reproducing ones, and many of them were macrolichens. Sexual reproduction and small thallus size are considered to be linked with more effective colonization in lichens, while larger size is thought to increase competitiveness via the ability to overgrow smaller species (Ellis 2012). Thus, the observed patterns suggest that species replacement with increasing tree size was driven by competition-colonization trade-offs among species, mirroring patterns observed in some previous studies (Hedenäs and Ericson 2000; Löbel et al. 2006; Ellis and Coppins 2006). Species replacement in epiphyte communities that occurs along increasing tree age or size has also been linked to changes in substrate properties (Nirhamo et al. 2026). In rowans, bark does not undergo major visually detectable changes with increasing tree size; thus, changes in substrate properties may have had minor importance as a driver of species replacement.

While both reproduction modes and growth forms changed as rowan size increased, only the former was statistically supported, indicating it to be the more important factor. There is likely to be a trade-off between the two reproduction modes such that sexual propagules (i.e., spores) can disperse over greater distances than asexual propagules, which have a more limited range, but in turn have a higher rate of successful establishment (Ronnås et al. 2017; Brunialti et al. 2021). Asexual propagules perform better at establishment assumably in part because they contain the photobiont whereas spores need to re-establish the symbiosis. Similarly, mean spore volume in lichen communities was higher in old-growth forests, although it was not related to diameter. This may also be due to a trade-off between dispersal range and establishment success in differently sized spores, where even small differences in spore size potentially have a meaningful effect (Norros et al. 2014), causing larger-spored species to occur more frequently in habitats with higher spatiotemporal continuity. However, it is important to note that some of the observed species mainly reproduce asexually and produce spores only rarely. In particular, a few species that had much higher occurrence on rowans in old-growth forests (e.g., *Lepra amara*, *Phlyctis argena*) have very large spores, but they mainly reproduce asexually. Therefore, the current data do not allow for strong conclusions regarding the role of spore size in the observed patterns.

Full-grown rowans are scarce in mature or old-growth boreal forests (Hofgaard 1993; Linder et al. 1997), which explains the limited coverage of large rowans (> 15 cm dbh) in our data. Still, with very limited data, it appears that lichen richness no longer increased with diameter when it reached about 15 cm. We are not aware of epiphyte studies that have addressed trees as small as those we examined, with the smallest being 1 cm in diameter. As expected, recently sprouted trees usually had very few epiphytes. Still, the epiphyte communities on the smallest rowans were quite variable, occasionally bearing epiphyte richness comparable to much larger trees.

Higher tree-level diversity in old-growth forests was presumably related to the older age of understory rowans

Tree-level species richness and the occurrence probability of several species were higher in old-growth forests compared to managed and urban forests. A very likely factor in these patterns was rowans in old-growth forests being older than rowans of the same size in the other forest types. In old-growth forests, rowan saplings may persist in the understory for several decades or even over a century (Hofgaard 1993). The periodic thinning of managed and urban forests stimulates tree regeneration (Otto et al. 2012; Olson et al. 2014), including that of rowan (Korhonen et al. 2023). Moreover, small understory trees may be removed prior to thinning harvests to facilitate machinery operations in managed forests in Finland (Kärhä and Bergström 2020), and larger rowans may be removed to reduce competitive pressure on trees with higher economic value. Thus, many of the surveyed rowans in managed and urban forests may have sprouted relatively recently (e.g., after the previous thinning). Two lines of evidence further suggest that rowans of the same size were older in old-growth forests compared to the other forest types. First, rowans in old-growth forests had a higher frequency of asexual species and macrolichens, independent of tree size, compared to other forest types, suggesting a more advanced lichen succession stage on rowans in old-growth forests. Second, tree-level species richness began to plateau at much smaller diameters in old-growth forests than in the other forest types. Another plausible explanation for these

patterns, which is not exclusive with the first one, is that lichens may have larger local populations in old-growth forests, and thus higher propagule production, leading to faster colonization compared to managed and urban forests.

Several epiphytic lichen species are considered old-growth specialists (Kuusinen 1996a; Marmor et al. 2011). A handful of species were more frequent in rowans in old-growth forests than either managed or urban forests, however, some of them (e.g., *Parmelia sulcata*) should certainly not be considered old-growth specialists given their occurrence patterns on other host species. There appear to be not many species occurring on rowan that are old-growth specialists, although our data is insufficient to confirm this for individual species, in part because of poor coverage of large rowans. For example, cyanolichens are considered old-growth specialists in boreal forests (Kuusinen 1996a), and they can also occur on rowans in old-growth forests, but we observed them infrequently. Moreover, it should be noted that the higher alpha (i.e., tree-level) diversity in old-growth forests did not translate to higher gamma diversity (i.e., total number of observed species), indicating that it was due to more frequent occurrence of common species rather than a higher variety of rare species. We sampled an equal number of rowans of different sizes in each of the forest types even though the forest types are sure to differ in overall availability of rowans, with urban forests having the highest rowan abundance (Korhonen et al. 2023). Thus, our data is reliable only for differences in tree-level diversity, and area-based (i.e., stand-level) inventories would also be necessary to fully understand differences between the forest types in rowan-associated lichen diversity.

The idiosyncratic abiotic conditions of urban forests led to distinct lichen assemblages

The lichen communities in urban forests were characterized by higher eutrophication tolerance, which may be considered a consequence of elevated nitrogen deposition in urban areas. While lichens in urban forests were statistically supported to have higher eutrophication tolerance, the frequency of nitrophilous species still was low compared to expectation based on their typical frequency in parks and other built-up areas of European cities (Sebald et al. 2022; Wutz and Diekmann 2025). Nitrophilous species are frequent also in non-forested areas in Jyväskylä, including in the immediate vicinity of the urban forests where our study was conducted (authors' observations). This suggests impactful levels of nitrogen deposition in the urban area of Jyväskylä, but which was dampened within urban forests. A potential explanation is that a significant portion of nitrogen deposition is uptaken by the forest canopy (Klopatek et al. 2006; Karlsson et al. 2019), and thus the deposition reaching the understory of urban forests has only a fairly light effect on lichen communities on rowans.

Although not statistically supported, trentepohlioid lichens appeared to be more common in urban forests. This may have been a signal of the urban heat island, since trentepohlioid species are favored by warmer temperatures (Marini et al. 2011; Phinney et al. 2022). In Portugal, an effect of the urban heat island on epiphytic lichens was inferred from a higher occurrence of species favoring xeric conditions (Munzi et al. 2014), which was not repeated in our results. It is worth noting that, in our study, the sites representing urban forests appeared to be more mesic than those representing rural forests. This could probably have been avoided if considered during study site selection, but on the other hand,

it may be representative of reality since urban forests are likely to be comparatively mesic because human settlements are typically established in fertile areas. Besides temperature, trentepohlioid species are also favored by humidity (Marini et al. 2011; Phinney et al. 2022). Thus, the more mesic conditions may have contributed to the higher occurrence of trentepohlioid species in urban forests.

Conclusions

We demonstrated that the community patterns of epiphytic lichens on rowans were affected significantly by a gradient of tree size. Analyses of lichen traits indicated a higher prevalence of ruderal traits on small trees, and of competitive traits on larger trees. There were marked differences in the lichen assemblages on understory rowans in old-growth forests compared to those in managed and urban forests. This is assumed to reflect differences in the understory dynamics of these forest types. Specifically, despite similar sizes, rowans in the understory of old-growth forests were likely to have been older, which may be attributed to the periodic thinning harvests in managed and urban forests. Tree-level lichen diversity was higher in old-growth forests, but it was predominantly caused by higher frequency of common species. While several species occurred much more frequently in old-growth forests, when accounting for the occurrence patterns of species on other host species, there appear to not be many species occurring on understory rowans that depend on old-growth stands. Thus, old-growth forests seem to have some special importance for the lichen flora addressed here, but still relatively little compared to differences often observed in the epiphyte communities on canopy trees of old-growth and managed forests (Lommi et al. 2010; Marmor et al. 2011; Nirhamo et al. 2025). Urban habitats are traditionally considered hostile to lichens due to air pollution (Hawksworth and Rose 1970). However, with the lower levels of pollution in the present, and the apparent buffering of nitrogen pollution in forested habitats (Klopatek et al. 2006; Karlsson et al. 2019), urban forests may be more favourable habitats for epiphytic lichens than expected. Therefore, further study of urban forests as habitats for epiphytic lichens is warranted.

It is well documented that conifers and broadleaved trees differ considerably as epiphyte hosts (Kuusinen 1996b). In addition, smooth-barked broadleaved trees such as rowan may differ from rough-barked broadleaved trees (Kuusinen 1996b; Gustafsson et al. 2023). Thus, as exemplified by rowans in spruce-dominated forests, even small understory trees may notably contribute to stand-level epiphyte diversity, particularly when they differ from canopy trees in substrate properties. When that condition is met, such as in the case of rowans in spruce forests, woody understory plants should not be overlooked in epiphyte inventories, and retaining understory trees during thinning and in clearcuts can be an easy and cost-effective way of supporting epiphyte diversity in managed forests. While even very small rowans appear to contribute to epiphyte diversity, their full potential is accessed only when the structural diversity of managed forests is not diminished by understory removal and rowans are allowed to reach larger sizes.

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Data availability Data used in the current study is available from the authors on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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