Relations between tree and habitat characteristics and the epiphytic lichen flora on oak

A case study from Lövön, Bohuslän

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Faculty of Landscape Architecture, Horticulture
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Relations between tree and habitat characteristics and the epiphytic lichen flora on oak. A case study from Lövön, Bohuslän.

Effekter av träd- och miljöfaktorer på eklevande lavar. En fallstudie från Lövön i Bohuslän

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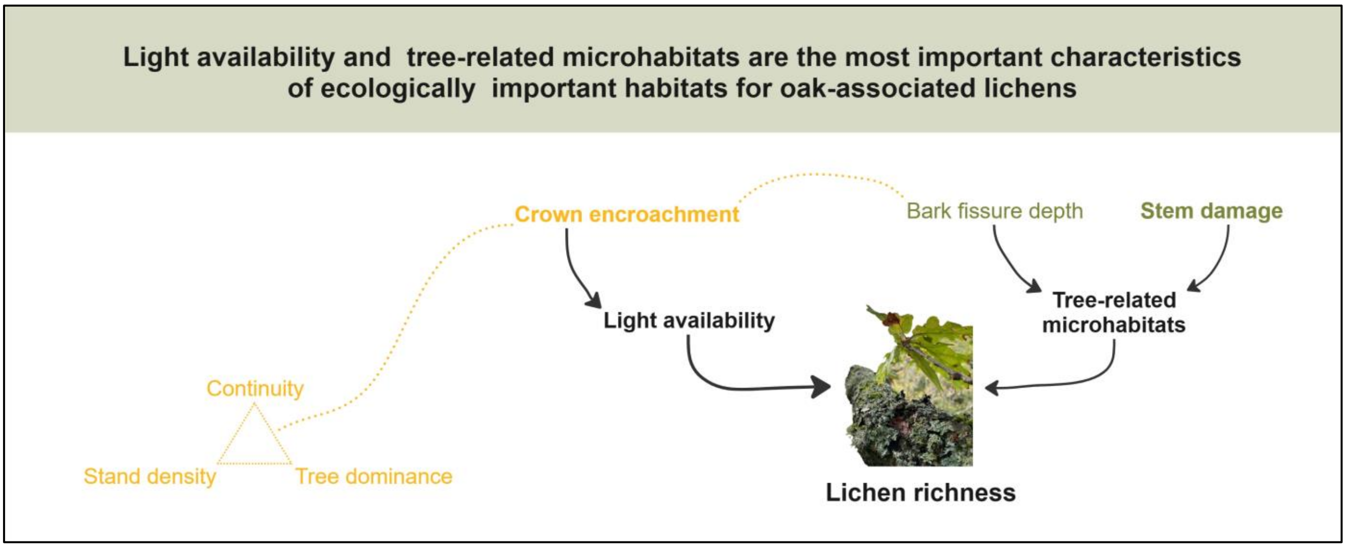
Abstract

Oak-rich forests and wooded pastures harbor diverse and distinct epiphytic lichen flora with many rare and threatened species. As these habitats have been subject to a substantial decline and degradation over the past centuries, oak woodlands have progressively come into focus for preservation. However, conservation-oriented measures require a thorough understanding of the characteristics of ecologically important host trees and habitats. Therefore, I investigated lichen diversity and characteristics of 50 trees on an island off the west coast of Sweden. Of the evaluated tree and habitat variables, crown encroachment had the highest explanatory value for lichen richness in a highly interrelated web of ecological influences. Combined with stem damage, crown encroachment showed the potential to capture biodiversity on a community level. These findings suggest that light availability, as an overarching primary factor, and microhabitat diversity are the most important characteristics for lichen diversity. Applied to management, this motivates measures to create more open forests with heterogeneous structures.

Keywords: *Epiphytic lichens, Tree characteristics, Habitat characteristics, Oak, Biodiversity, Lichen richness, Light availability, Tree-related microhabitats*

Graphical abstract



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1. Introduction

1.1 Background

No other tree in Sweden harbors as much biological diversity as old oak, and is as intertwined with the land use history and traditional agriculture (Nitare, 2019). Through centuries of establishment in the cultural landscape, oak woodlands have become highly valuable biological habitats with a long-term continuity. Scandinavian oak forests are especially exceptional as nowhere else in the world do they grow at such high latitudes (Lennarth Jonsson, 1997). Their northern limit of distribution is the ‘Limes Norrlandicus’ - the bio-geographical divide between the boreal forests in Norrland and the cold temperate forests in southern Sweden (Diekmann, 1994). Many cryptogams and species of conservation concern are closely related to those forests (Nordén et al., 2012; Ranius, Johansson et al., 2008). For example, in Sweden 260 epiphytic lichen species are associated with oak (Arup, 1997). However, forestry with its preponderance of coniferous trees and modern agriculture have severely reduced populations of oaks. Consequently, many of the oak-associated species are highly threatened due to their isolated and progressively degrading host trees. For example, about 40 % of all red listed lichen species occur on broadleaved deciduous trees, many of these on oak, while deciduous forests cover only 0.5 % of the total area of Sweden (Nitare, 2019). This makes the preservation of ancient oak woodlands important, as an ark for species of conservation concern associated to those habitats. Conversely, these species, which nowadays only occur in small and fragmented populations, have an important value in nature conservation as indicators of ancient trees and ancient semi-natural woods with high nature conservation value.

As many of the oak-rich mixed forests naturally developed from a more open, traditional agricultural landscape, active management methods to create more open forests are often motivated for conservation. However, for a deeper understanding of appropriate conservation measures, research on oaks with their associated cryptogam flora is required. While there has been research on this in the Baltic region such as Gotland and Östergötland (Henriksson, 2018; Jönsson et al., 2011; Nordén et al., 2012; Ranius, Eliasson, Johansson, 2008; Tibell and Hultengren, 2015), there is a lack of studies concerning the west-coast region of Sweden. With distinctively different climatic and soil conditions in this region, a different conservation approach might be required.

Therefore, this study is focused on the epiphytic lichen flora in oak habitats specific for the west-coast region. The study location, an island in southern Bohuslän, is of special interest, as it has a long-term continuity of oak, and no previous species reports in Artportalen or nature inventories had been made in the past 20 years. The study objective is to broaden the knowledge on characteristics of ecologically important host trees and habitats for epiphytic lichens associated with oak.

1.2 Conservation values and threats to oak forest habitats

Oak trees are of special value in the conservation of cryptogams and threatened species due to their varied wooden structures and longevity. The oldest oak in Sweden known as ‘Kvill oak’ located in Småland is estimated to be over 1000 years old and has a trunk circumference of approximately 13 meters (Pietrzak-Zawadka, 2016). The mosaic of different biological niches and microhabitats developing on old oaks (e.g., deeply furrowed bark, cavities and wood mould), provides a valuable habitat to many cryptogams and species of conservation concern (Bütler et al., 2020). Other elements of natural forest structures that contribute to a forest rich in biodiversity are dead wood in various stages of decomposition, dying and dead trees, age distribution and layering.

With the decrease of traditional agricultural methods and conifer-dominated forestry, the majority of oak forest habitats and their related species are threatened (Naturvardsverket, 2011). Thus, in many areas both oak and its associated species remain remnants from an ancient larger distribution. Many of the species have a relict-like behaviour due to their limited ability to spread and are dependent on the continuous availability of suitable habitats and substrates in immediate vicinity (Ranius, Eliasson, Johansson, 2008). Therefore, it is worth protecting old-growth oak forests in order to prevent further fragmentation and habitat degradation. The main threat to oaks, which are early to mid-successional and therefore light-demanding trees, is overgrowth and shading (Götmark and Kiffer, 2014). This is mostly due to abandoned traditional management methods and a general lack of management.

1.3 Oak forest habitats in the west coast region

Oak forests in Sweden are composed of two oak species, *Quercus robur* and *Quercus petraea*. These two species are distributed in the coastal regions of southern Sweden, which has a suboceanic climate (Rydin et al., 1999). Characteristically, they are oligotrophic, growing on nutrient-poor and acid sites, often situated on hills. Of the two species, *Q. petraea* prefers more oceanic conditions with high rainfall and less fertile soils, as typical for the west coast.

Heath-oak forests occur primarily in southwestern Sweden with a center of distribution in Bohuslän and Halland (Eriksson, 2008; Naturvardsverket, 2011). Historically used as wooded pastures and meadows, these forests form an important biological cultural heritage in the landscape, and are valuable habitats for many cryptogams and species of conservation concern. They are characterized by a sparse and semi-open tree layer, which was formed through centuries of traditional management practices like grazing, mowing, pollarding and coppicing. This favours a species-rich herb and shrub layer as well as epiphytic lichens. The shrub layer is dominated by species of the *Ericaceae* family, such as heather *(Calluna vulgaris)* and blueberry *(Vaccinium myrtillus)*. Birch *(Betula spp.)*, aspen (*Populus spp.)*, rowan *(Sorbus aucuparia)* and pine *(Pinus sylvestris)* are commonly found in the tree layer (Skogskunskap, 2023). Due to the sandy, lean and often shallow outcrop soils on which they are growing, the oaks exhibit a significantly slower growth and are often relatively small despite of their age. An additional feature in windswept coastal regions, are low-growing shrubby forests with crooked and slow-growing trees (‘krattskogar’).

2. Methods

2.1 Study site

The field work was conducted between 23rd January and 3rd February 2023 on the island Lövön in southern Bohuslän at the west coast of Sweden (Figure 1). The island was selected due to its long-term continuity of oak and the close connection of the tree species with the island's land-use history. Therefore, oak can be seen as the most important substrate for lichens on the island, especially for species associated with deciduous trees. Moreover, there are no recordings of nature inventories or species reports in Artportalen of Lövön from the past 20 years.

The island is approximately 2.2 km long and 1.3 km broad, with an area of 155 ha. It is characterized by a large number of hills and small plateaus, with the highest point being 67 m above sea level. The soils are mainly composed of crystalline rock ('urberg') with areas of postglacial sand and glacial clay ('glacial finlera') in the central valley (Lantmäteriet, 2022). This makes for relatively shallow and lean sandy soils. Lövön has a maritime climate (Cfb according to the Köppen climate classification) with fairly cool summers and mild winters, which allow for a long vegetation period (Kottek et al., 2006). The average annual temperature is 8.3 °C (Zepner et al., 2021). January is the coldest month with an average of 0.4 °C and July the warmest with 17.3°C. The total mean precipitation per year is 818 mm. The locally common wind direction is from northeast (Bergström and Söderberg, 2008). There are a number of summer houses but only two permanent residents on the island.

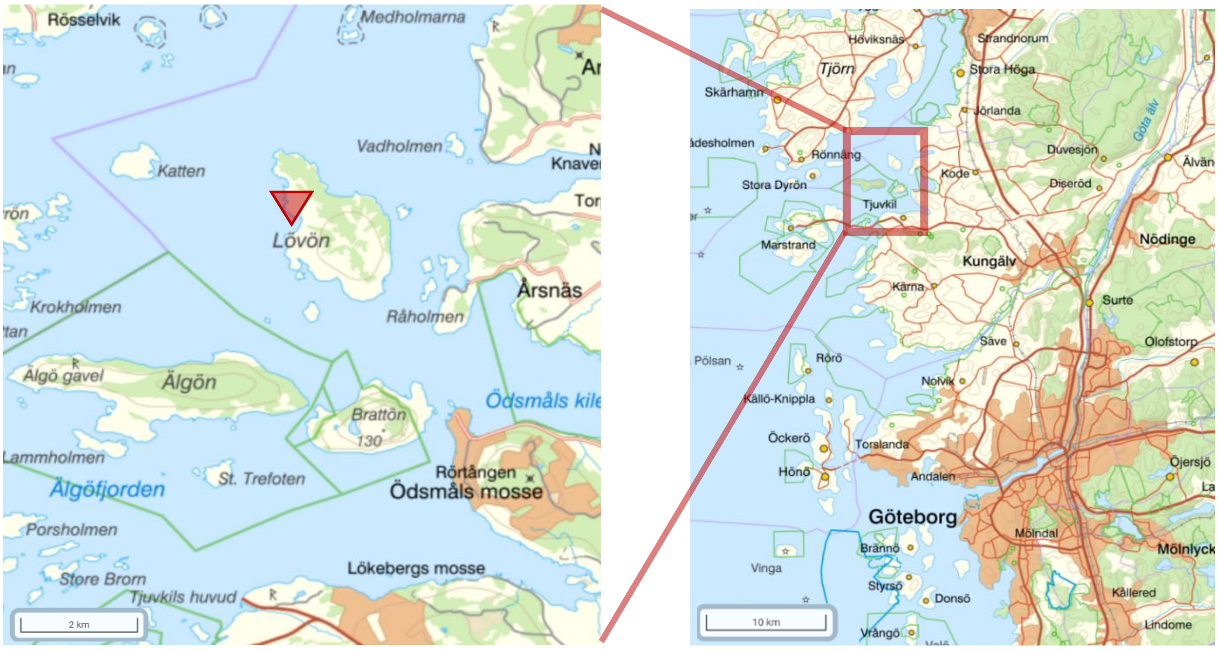

Figure 1. Map showing the location of Lövön close to the islands Älgön and Brattön (left) and the location of the area depicted on the left (red square) in relation to Gothenburg (right) (Swedish Land Survey, 2022).

2.1.1 Vegetation and land use history

The predominate vegetation type on the island are deciduous forests with a strong dominance of oak, due to its location in the nemoral zone (Skogskunskap, 2023). These forests remained mostly unaffected by early agriculture with grain cultivation and grazing (Westerström et al., 1998). In the 11th century, herring fishing increased resulting in a greater timber demand. This led to the devastation of forests, thickets and wooded pastures. Consequently, by the 18th century Lövön was mostly deforested. However, many oaks on the island remained as they were officially protected from being cut down without permission from the Swedish Crown until 1830. Additionally, the ability of oaks to grow coppice shoots allowed cut-down trees without grazing pressure to regenerate. This has led to a century long continuity and dominance of this tree species on Lövön.

From the 18th century, parts of the deciduous forest gradually reformed along the hillsides, especially on the central parts of the island. With the decline of agriculture since the mid-20th century, natural reforestation increased even further (Figure 2). The deciduous forests are dominated by oak *(Quercus spp.)* and birch *(Betula spp.)* with sparse admixture of lime *(Tilia cordata)* and elm *(Ulmus glabra)* (see Figure 3 for tree species distribution; Figure 4 A).

In the beginning of the 20th century, stands of pine (*Pinus sylvestris, P. nigra)*, and spruce *(Picea abies)* were planted in the northern and eastern parts of the island (Figure 3). These plantings are now mature and form rather dense forests that are characterised by a species-poor field layer and dead juniper trees, remnants of the previous open pasture (Figure 4 B).

Figure 2. Aerial photographs of Lövön from 1960 (left) and 2022 (right) showing the changes in the landscape from agricultural fields (1960) to pastures and forests (2022). Image scale is 1:50000 (Lantmäteriet, 2022).

The western parts of the island with many rocky outcrops remained without afforestation. Over time, a vegetation dominated by heather and juniper (*Juniperus communis*) developed in that area. In favourable locations, single groups of trees and shrubs have grown (Figure 4 C), including pine, birch, aspen, oak, rowan *(Sorbus aucuparia)*, wild rose *(Rosa canina)*, wild apple *(Malus sylvestris)*, hawthorn *(Crataegus rhipidophylla)* and alder backthorn *(Rhamnus frangula)*. The highest parts of the hills with ice-smoothed surfaces remained completely bare. Sometimes they are overgrown with lichens and mosses. Gradually downwards heather, juniper, birch and pine are added, meeting the deciduous forest climbing up from lower areas.

In the central valley, centuries of traditional livestock practice have formed Fennoscandian wooded pastures dominated by oak (Natura 2000 habitat 9070; (European Environment Agency, 2023)). Grazing is a key element in this habitat type, as it maintains an open forest structure and meadow-like herbaceous layer (Figure 4 D). Therefore, summer grazing with cattle has been reintroduced on the island in the 1980s.

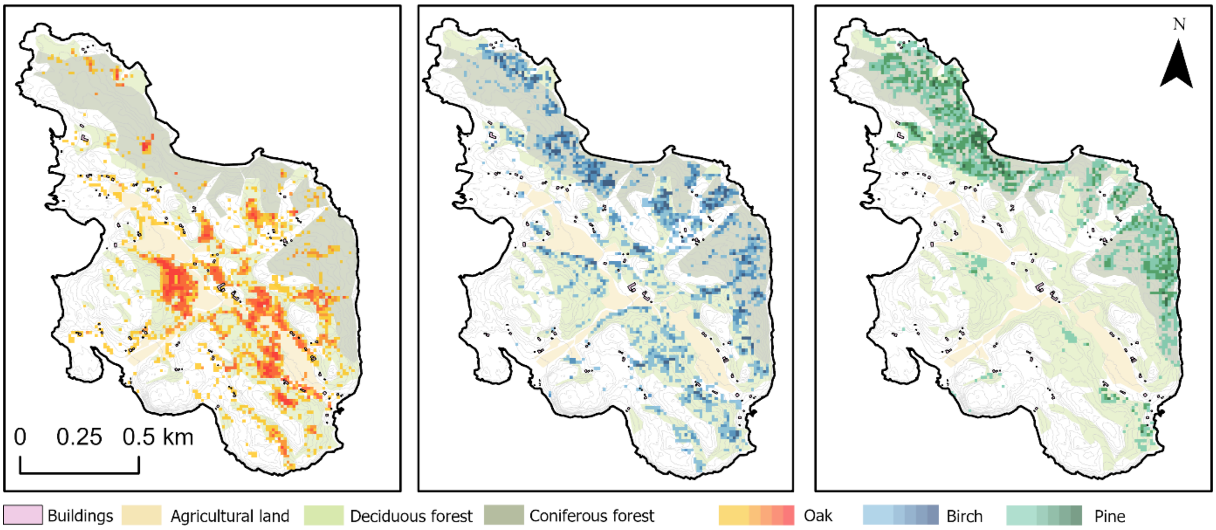

Figure 3. Maps showing the distribution of the dominant tree species oak, birch and pine based on volume on Lövön. Created from GSD-Fastighetskartan vektor © Lantmäteriet (2019), Ortofoto IRF 0.25 m 2009 - 2018 © Lantmäteriet (2021), SLU Skogskarta Tall Volym © The Swedish Forest Agency (2021), SLU Skogskarta Ek Volym © The Swedish Forest Agency (2021), SLU Skogskarta Björk Volym © The Swedish Forest Agency (2021), Nationell Höjdmodell © Lantmäteriet (2020).

Figure 4. Vegetation types on Lövön: oak-dominated deciduous forest (heath-oak forest; A), coniferous forest dominated by spruce and pine with sparse oak (B), Outcrop with shrub vegetation of heather, juniper, pine, birch and oak (C), wooded pasture with oak (picture taken outside vegetation period; D).

2.2 Study design

The aim of the study was to investigate the characteristics of ecologically important host trees and habitats. For this, an inventory of lichens and tree/habitat characteristics was carried out on 50 selected oak trees (*Q. robur* and *Q. petraea*) on Lövön. Oak was chosen as it is associated with a high diversity of lichen species of which many are relatively rare and of conservation concern (Nitare, 2019; Sundberg et al., 2019).

The tree selection was based on 100 stratified random points spread over the area of the island (156 ha), which were created in ArcGIS Pro (Tool 'Create Random Points (Data Management)') (Figure 5). The minimum distance between points was 50 m, to prevent growth interactions and overlapping radii of close points. Each point had a by default assigned objectID (1-100). For each of the points with the objectID 1-50, the closest tree fulfilling the following criteria was chosen: The trees needed to be within a 25 m radius from the associated points, alive and have a diameter at breast height (DBH) of at least 10 cm (when multi-stemmed at least one stem with DBH > 10 cm). If no suitable tree was within a points radius, the subsequent point was chosen (objectID 51 etcetera).

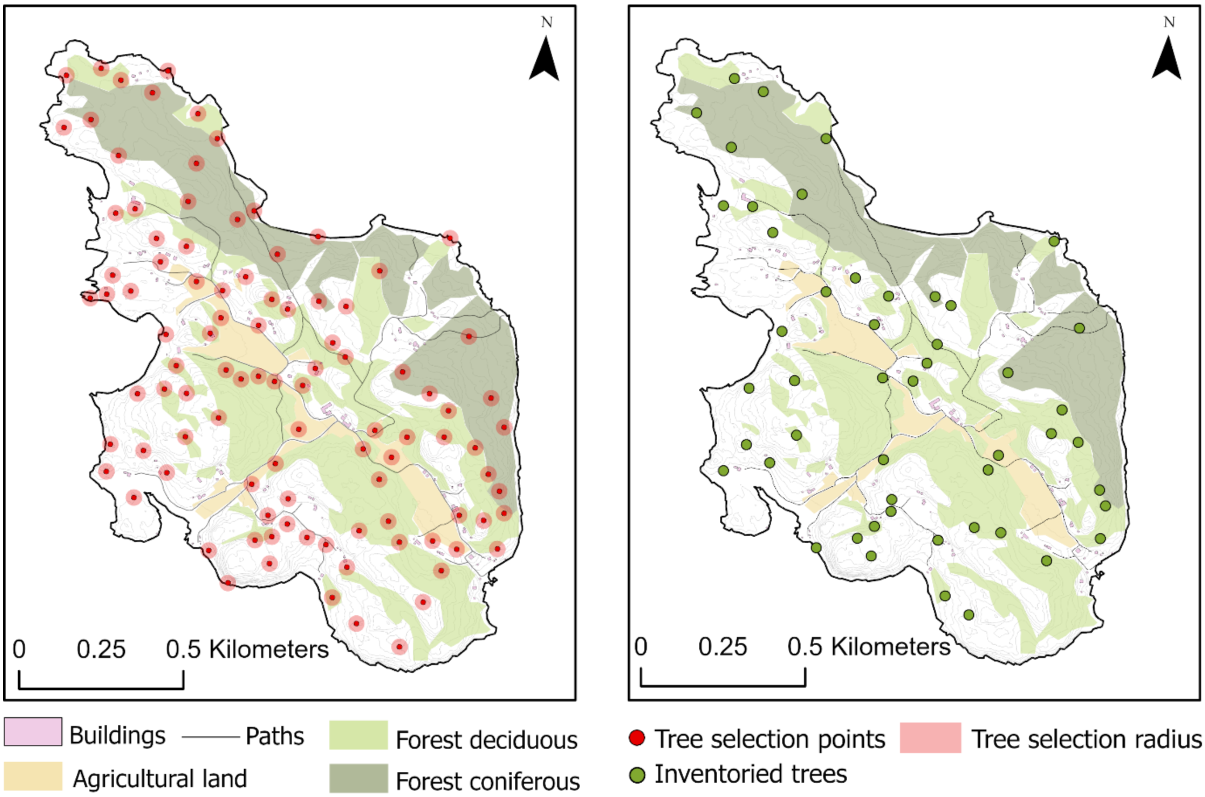

Figure 5. Maps showing the 100 stratified random tree selection points (left) and the position of the inventoried trees (right) on Lövön (Siegel 2023). Created from GSD-Fastighetskartan vektor © Lantmäteriet (2019), Ortofoto IRF 0.25 m 2009-2018 © Lantmäteriet (2021), Historiska ortofoton 1960 PAN © Lantmäteriet (2017), Nationell Höjdmodell © Lantmäteriet (2020).

For each tree, tree and habitat characteristics were evaluated through measurements and estimations (Table 1; see Table 1 of Appendix A for characteristics descriptions and mean values; see Table 1 and 2 of Appendix B for data records). Bark fissure depth was measured at breast height, with the depth gauge of a caliper perpendicular to the stem. Four measurements in each cardinal direction were done and the mean value calculated per tree. The distance to the coast was calculated through the coordinates of each inventoried tree in ArcGIS Pro. The radiation was also calculated through ArcGIS Pro as the direct incoming solar radiation each tree received as watt hours per square meter per year (Tool 'Points Solar Radiation (Spatial Analyst)').

I recorded presence of all epiphytic lichen species (crustose, foliose and fructose) growing above the bryophyte border, at the base of the stem, up to 2 m above ground on stem and branches (see Table 3 of Appendix B for data records). The time limit for the lichen inventory was ended after 5 minutes without a new species recording (J Brunet 2023, personal communication, 10 January). Lichens were identified in field and with photos through iNaturalist (California Academy of Sciences, 2023). Due to time constraints, identification through microscopy or chemical analyses could not be performed. However, as the primary focus of this study was on diversity patterns and ecological interrelations, the limitation in identification methods should not put major influential constraints on the outcomes. Additionally, through the involvement of the iNaturalist web community in the identification, the determination was improved through an openly accessible peer review. In case of uncertain taxonomy, lichenologists were consulted. Undeterminable specimen (too small or not identifiable from photo) were excluded. For each recording, the primary substrate the species was growing on and the abundance were recorded.

Table 1. Measured and evaluated characteristics for each tree, tree habitat, and inventoried lichen.

Tree characteristics	Habitat characteristics	Lichen characteristics
Species	Habitat type	Genus + Species
Height [m]	Tree dominance	Substrate
DBH [cm]	Continuity	Abundance
Crown diameter [m]	Connectivity	Growth form
Branching height [m]	Slope inclination [°]	
Tree damage	Cardinal direction	
Stem damage	South facing	
Crown encroachment	Radiation [WHm^{-2}]	
Stem encroachment	Wind exposure	
Bark fissure depth [mm]	Distance to coast [m]	
Stem inclination [°]	Accessibility	
Crookedness	Grazing	
	Stand density [m^2ha^{-1}]	
	Soil cover	

2.3 Data analyses

To investigate the characteristics of trees and habitats, the correlations between tree/habitat characteristics and lichen richness were assessed and evaluated. For this, data analyses were performed with Excel (Microsoft Corporation, 2022) and Minitab (Minitab Inc, 2021).

Lichen species richness was calculated through summarizing the recorded occurrences of different lichen species per specific tree. The distribution of these values was tested with a normality test (Anderson-Darling). Thus, a lichen richness value (predictor variable) could be linked to each tree/habitat characteristic (explanatory variable) per tree. Based on this, statistical models were used to investigate correlations between those variables. The models were linear regression for continuous explanatory variables, and analysis of variance (ANOVA) combined with Tukey's honestly significant difference (Tukey's HSD) *post hoc* test for categorical explanatory variables. Correlations between tree/habitat characteristics were calculated through Pearson correlation analysis. To investigate which variables can be combined to explain lichen richness, generalized linear models were created, based on the significant explanatory variables ($p < 0.05$). To avoid multicollinearity effects in models producing erratic relationships for individual predictors/explanatory variables, only less well-correlated variables (Spearman's correlation coefficient $< |0.5|$ and variance inflation factor < 5) were used. The model was tested through diagnostics of residual plots. The chord diagram of the correlating variables was visualized with R (R Core Team, 2022) using the function *chorddiag* of the package *chorddiag* (Flor, 2020) and the plot of the generalized linear model was visualized using the function *interact_plot* of the package *interactions* (Long JA, 2019).

3. Results

3.1 Lichen species diversity

In total 408 observations of 53 lichen species were recorded from 50 trees (on average 8 species/tree; see Table 3 of Appendix B for data record of inventoried lichens). Of the observed individuals 202 were crustose (50 %), 122 foliose (30 %) and 84 fruticose (20 %). An additional 41 observations which could not be identified to species level were excluded from the analysis (0 – 5 unidentifiable observations/tree with an average of 0.82 /tree).

The community consisted of a relatively small number of common species and a large number of relatively rare species. This low species evenness is reflected by the steep gradient of relative abundance (exponential decline) (Figure 6). The most common species which were recorded on more than 50 % of the trees were *Lepraria incana*, recorded on 38 trees (76 % of all trees), *Phlyctis argena* (70 %), *Evernia prunastri* (62 %), *Melanelixia glabratula* (58 %) and *Parmelia sulcata* (54 %) (see Figure 1 of Appendix C for entire species list with relative abundance).

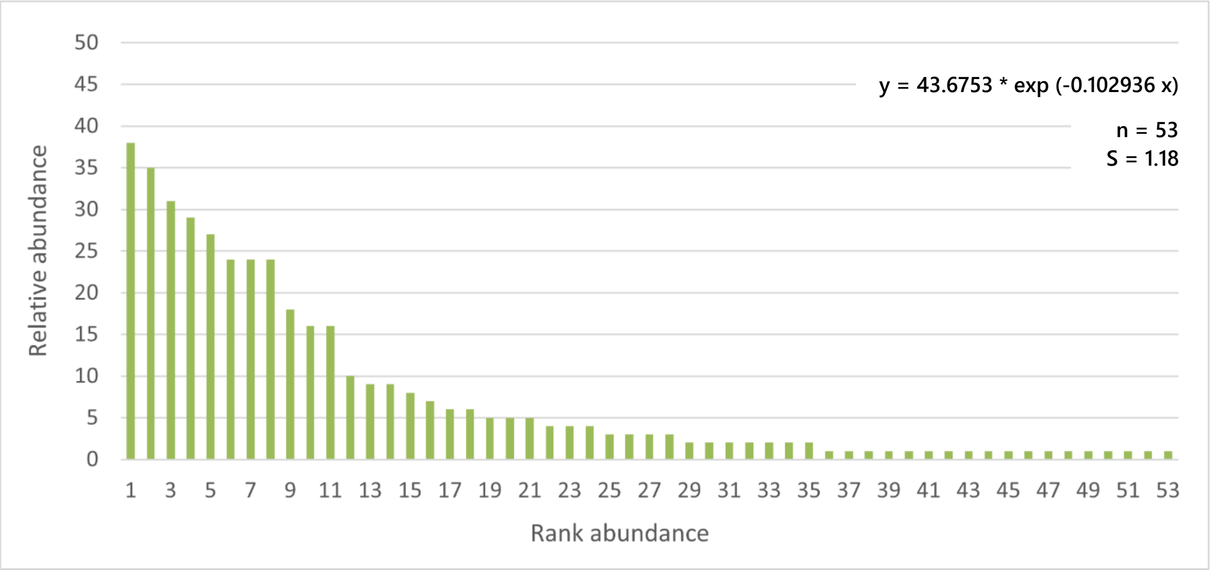

Figure 6. Rank-abundance diagram for the inventoried lichen community, illustrating the number of inventoried individuals in the community (relative abundance; y-axis) that are represented by the inventoried species (rank abundance; x-axis).

The high abundance of the above mentioned species and the relatively low evenness were also reflected in the relative frequency of genera (exponential decline with $y = 69.3287 * \exp(-0.149326 * x)$, $S = 3.02$) (Figure 7). The most common genera were *Lecanora* (54 observations), *Melanelixia* (53), *Lepraria* (42), *Cladonia* (40), *Parmelia* (35), *Phlyctis* (35) and *Evernia* (31). Over 70 % of all recorded individuals belong to these genera (which together make up for only a fourth of the total amount of recorded genera). This again illustrates the low evenness. Cladonia was the genus with the highest number of different recorded species (7 spp), followed by Lecanora (5) and Physcia (4).

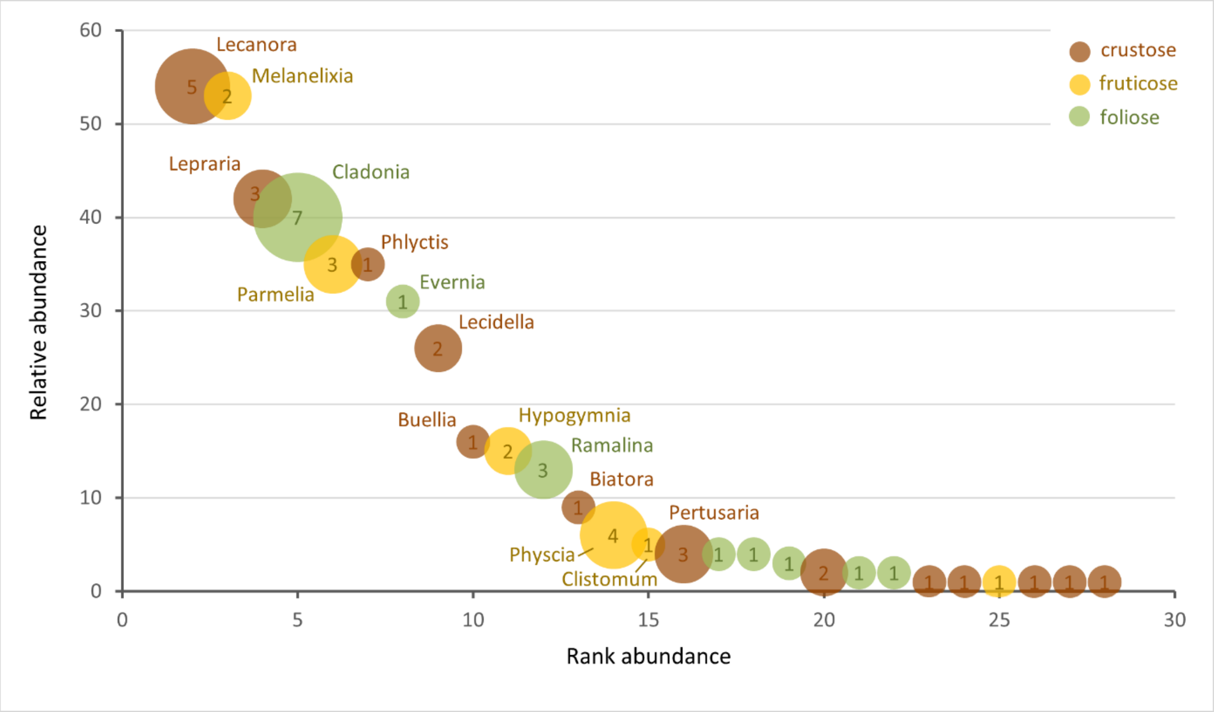

Figure 7. Patterns of relative genus abundance for the inventoried lichen community, illustrating the number of inventoried individuals in the community (relative abundance; y-axis) that are represented by the inventoried genera (rank abundance; x-axis) with the respective number of recorded species per genus (bubble size and number); genera with rank abundance 17 – 28 and only one recorded species are Platismatia, Xanthoria, Violella, Lepra (2 species), Ochrolechia, Pseudevernia, Coenogonium, Haematomma, Melanohalea, Parmeliopsis, Polycauliona, Pyrrhospora and Zwackhia in consecutive order.

3.2 Relations between tree characteristics and lichen richness

Three of the 11 examined tree characteristics (crown encroachment, stem damage and bark fissure depth) showed a significant correlation with lichen richness (see Table 1 of Appendix D). Between lichen richness and characteristics related to tree growth (height, DBH, branching height and crown diameter) or large-scale structural diversity (crookedness, stem inclination) no significant correlations could be found.

3.2.1 Crown encroachment

Crown encroachment, which negatively correlated with lichen richness, had the highest statistical significance and could explain about 40 % of the observed variation in lichen richness (Figure 8: $R^2 = 0.39$, $p < 0.001$). The model showed that trees which were free growing (crown encroachment class 1) or partially encroached on at least one side (2) had a significantly higher lichen richness than trees which were encroached on all sides (3) or overgrown (4) (Table 2).

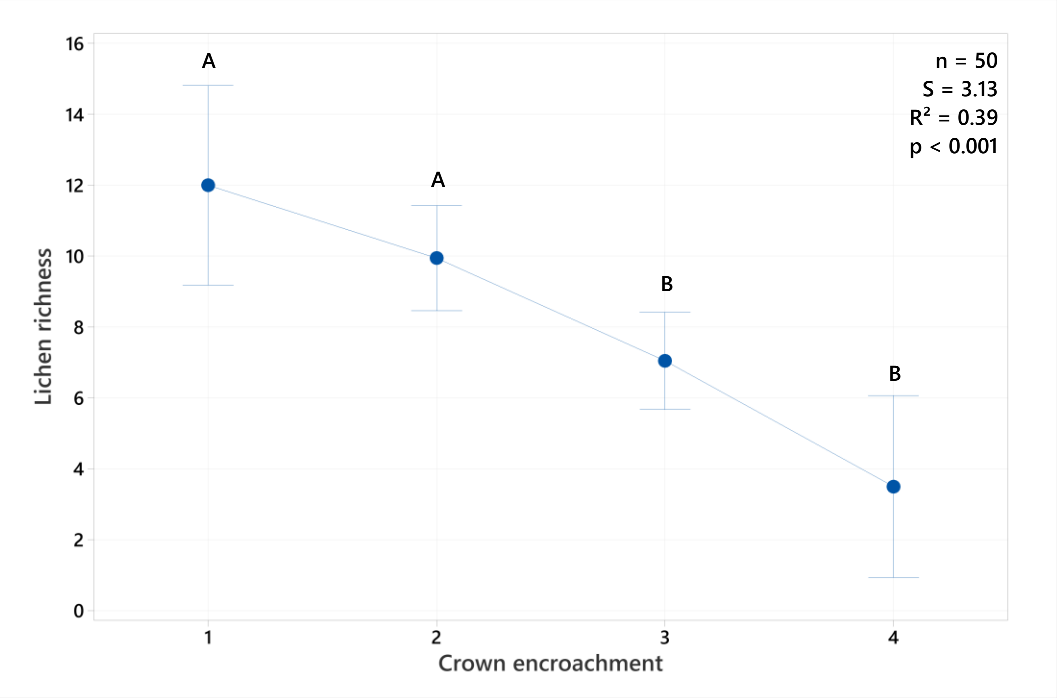

Figure 8. Relation between lichen richness (number of species observed per tree) and crown encroachment. Interval graph based on one-way ANOVA with 95 % CI for the mean. Differences between means that share a letter (A or B) are not statistically significant (p > 0.05, Tukey' HSD test). Crown encroachment classes: free growing (1), partial encroachment on at least one side (2), encroachment on all sides except from above (3) and overgrown (4).

Table 2. Lichen richness in different encroachment classes. Means that do not share a letter are significantly different (p < 0.05) according to Tukey' HSD test.

Crown encroachment class	n	Mean	95% CI	Grouping
1	5	12.00	(9.19; 14.81)	A
2	18	9.94	(8.46; 11.43)	A
3	21	7.05	(5.68; 8.42)	B
4	6	3.50	(0.93; 6.07)	B

3.2.2 Stem damage

Stem damage had a positive effect on lichen richness (Figure 9: $R^2 = 0.11$, $p = 0.018$), indicating that higher lichen richness could be found on stems with hollows or exposed dead wood (1) than without (0) (Table 3).

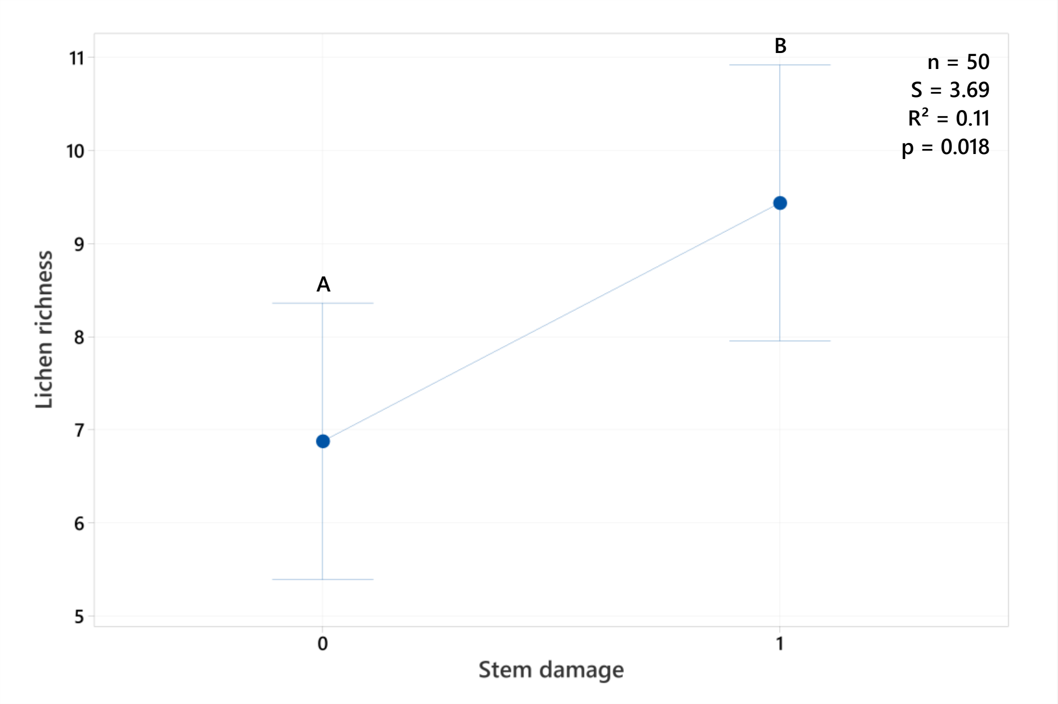

Figure 9. Relation between lichen richness (number of species observed per tree) and stem damage. Interval graph based on one-way ANOVA with 95 % CI for the mean. Differences between means (A and B) are significant ($p > 0.05$, Tukey' HSD test). Stem damage classes: hollows or exposed wood up to 2 m present (1) or absent (0).

Table 3. Lichen richness in different stem damage classes. Means that do not share a letter are significantly different ($p < 0.05$) according to Tukey' HSD test.

Stem damage class	**n**	**Mean**	**95% CI**	**Grouping**
1	25	9.44	(5.39; 8.37)	A
2	25	6.88	(7.96; 10.93)	B

3.2.3 Bark fissure depth

Bark fissure depth showed a positive correlation with lichen richness (Figure 10: $R^2 = 0.13$, $p = 0.011$), suggesting that higher lichen richness could be found on trees with deep bark fissures. 50 % of the variation in bark fissure depth could be explained through the positive correlation with DBH ($R^2 = 0.51$, $p < 0.001$), However, lichen richness was less strongly related to DBH ($R^2 = 0.07$, $p = 0.07$) than to bark fissure depth (see above).

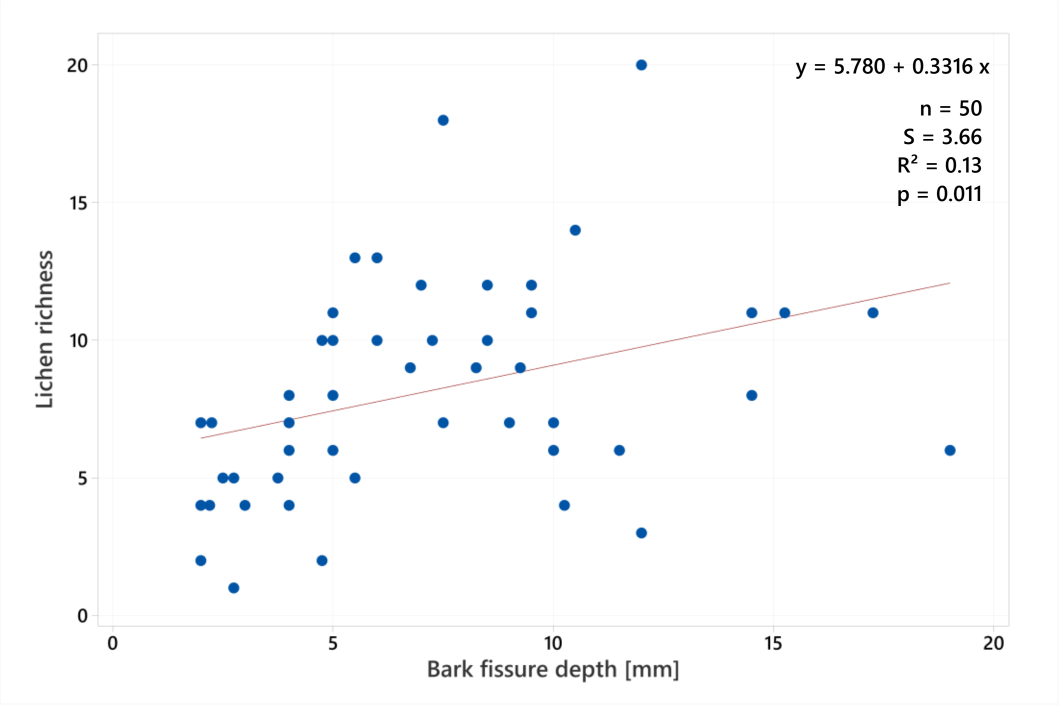

Figure 10. Relation between lichen richness (number of species observed per tree) and bark fissure depth.

3.3 Relations between habitat characteristics and lichen richness

Four of the 13 examined habitat characteristics (stand density, tree dominance, continuity, distance to coast) showed a statistically significant correlation with lichen richness (see Table 2 of Appendix D). Of those, stand density, tree dominance and continuity were variables directly related to the forest stand (small-scale biotic factors), while distance to coast was a physiographic factor. Larger-scale climatic/physiographic factors (radiation, wind exposure, slope inclination and south facing) and edaphic factors (soil cover) did not show significant correlations with lichen richness. Large-scale biotic factors like connectivity and variables of management/anthropogenic influence (accessibility, grazing) were also not significant in explaining lichen richness.

3.3.1 Stand density

Stand density (basal area) showed a highly significant negative correlation with lichen richness, explaining 27 % of the observed variation (Figure 8: $R^2 = 0.27$, $p < 0.001$). This suggests that lichen richness was favoured by more open forest stands compared to dense ones.

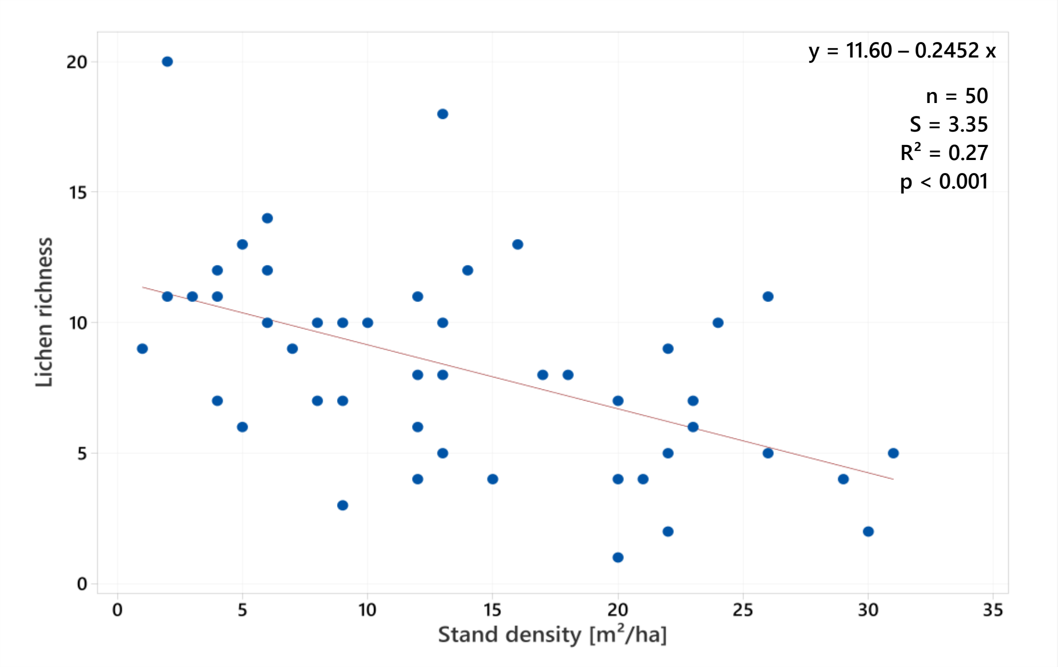

Figure 11. Relation between lichen richness (number of species observed per tree) and stand density.

3.3.2 Tree dominance

Lichen richness was significantly higher in forest stands dominated by oak trees compared to forest stands dominated by conifers (Figure 12: $R^2 = 0.22$, $p = 0.003$). In broadleaf stands, the mean value for lichen richness lay between conifer and oak stands, however, with no significant difference to either one of these (Table 4). Thus, it can be concluded that lichen richness on oaks was higher when they were surrounded by other oak trees compared to conifers.

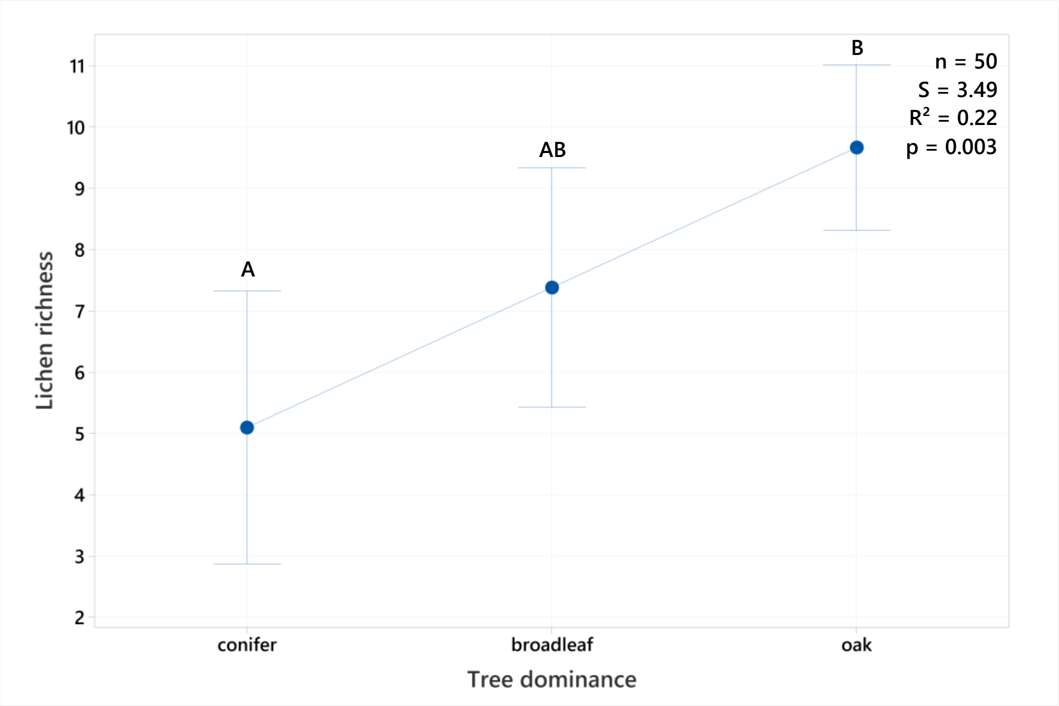

Figure 12. Relation between lichen richness (number of species observed per tree) and tree dominance. Interval graph based on one-way ANOVA with 95 % CI for the mean. Differences between means that share a letter (A or B) are not statistically significant ($p > 0.05$, Tukey' HSD test).

Table 4. Lichen richness in different tree dominance classes. Means that do not share a letter are significantly different ($p < 0.05$) according to Tukey' HSD test.

Tree dominance class	n	Mean	95% CI	Grouping
conifer	10	9.67	(2.88; 7.32)	A
broadleaf	13	7.38	(5.43; 9.33)	A B
oak	27	5.10	(8.31; 11.02)	B

3.3.3 Continuity

Lichen richness was significantly higher on trees growing in stands with mid-term to long-term continuity of oak (3; > 60 years) compared to stands with new establishment on oak (1) (Figure 13: $R^2 = 0.18$, $p = 0.01$), with a mean of lichen richness more than twice as high. In stands with short-term continuity of oak (2; 20-60 years), the mean value for lichen richness lay in between the other continuity classes, however, with no significant difference to either one of them (Table 5). This suggests that lichen richness was higher in stands with a long continuity of oak.

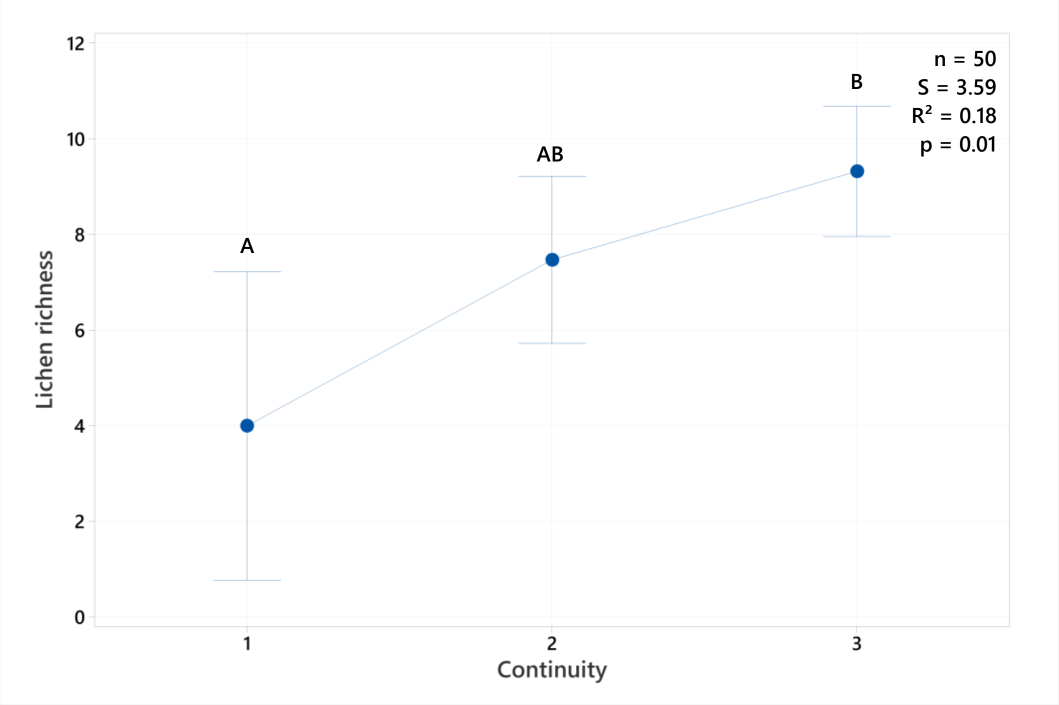

Figure 13. Relation between lichen richness (number of species observed per tree) and continuity. Interval graph based on one-way ANOVA with 95 % CI for the mean. Differences between means that share a letter (A or B) are not statistically significant (p > 0.05, Tukey' HSD test). Continuity classes: new establishment of oak (1), short-term continuity of oak (2; 20-60 years), mid-term to long-term continuity of oak (3; > 60 years).

Table 5. Lichen richness in different continuity classes. Means that do not share a letter are significantly different (p < 0.05) according to Tukey' HSD test.

Continuity class	n	Mean	95% CI	Grouping	
1	5	4.00	(0.77, 7.23)	A	
2	17	7.47	(5.72; 9.22)	A	B
3	28	9.32	(7.96; 10.69)		B

3.3.4 Distance to coast

Distance to coast showed a positive correlation with lichen richness (Figure 14: $R^2 = 0.08$, $p = 0.038$), indicating that lichen richness increased the further away from the coast. The model explained about 8 % of the observed variation in lichen richness.

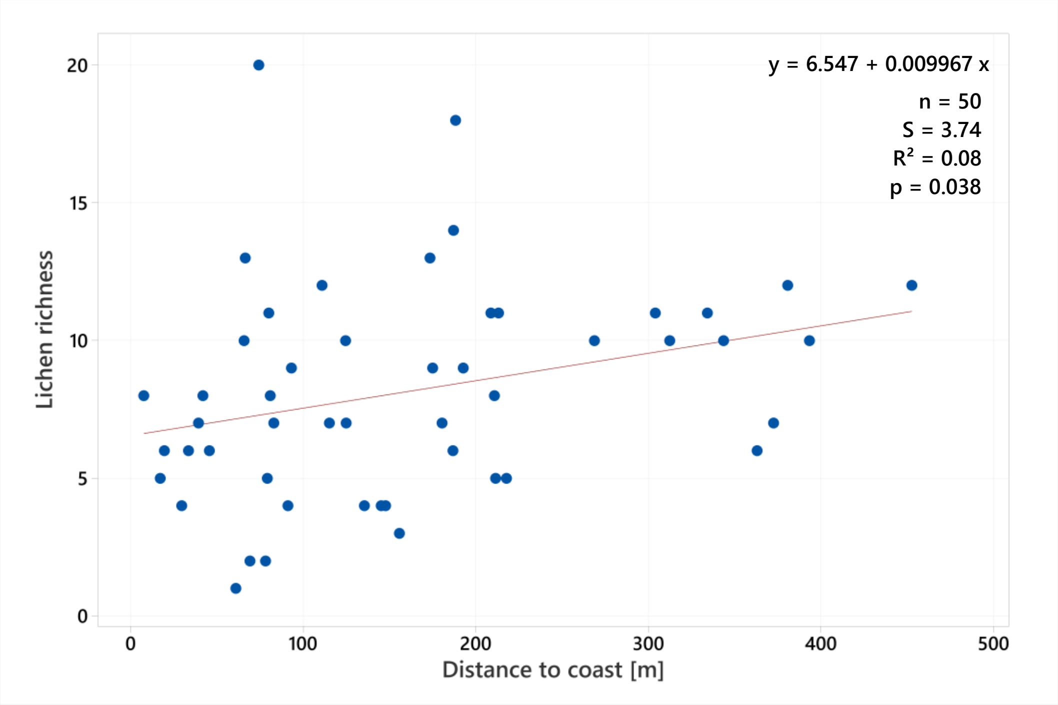

Figure 14. Relation between lichen richness (number of species observed per tree) and distance to coast.

3.4 Correlations between tree/habitat characteristics

Strong correlations (Spearman's correlation coefficient magnitude 0.3-0.7) could be found between the significant variables explaining lichen richness (Figure 15; see Table 3 of Appendix D for correlation coefficients and significance levels).

In the correlation model of all the significant variables, crown encroachment was the variable with the notably highest number of highly significant correlations ($p < 0.001$), correlating with all the small-scale biotic variables related to the forest stand (stand density, tree dominance and continuity) and bark fissure depth. Stand density was positively correlating with crown encroachment ($R^2 = 0.38$, $p < 0.001$), which indicates that the crowns in stands with higher density were more encroached. Both tree dominance and continuity negatively correlated with crown encroachment (respectively $R^2 =0.36$, $p < 0.001$ and $R^2 = 0.33$, $p < 0.001$). Which shows that the crown of trees in stands with a long continuity of oak and/or oak as the dominant tree species was less encroached. Bark fissure depth correlated positively with crown encroachment ($R^2 = 0.30$, $p < 0.001$), suggesting that trees under more open canopy conditions have a deeper furrowed bark.

The small-scale biotic variables also correlated between each other (stand density/tree dominance $R^2 = 0.30$, $p < 0.001$; stand density/continuity $R^2 = 0.12$, $p = 0.014$; tree dominance/continuity $R^2 = 0.10$, $p = 0.023$). Stem damage correlated positively with bark fissure depth and continuity (respectively $R^2 =0.13$, $p = 0.010$ and $R^2 = 0.14$, $p = 0.033$). Distance to coast was the most independent variable, with a marginally significant positive correlations to continuity ($R^2 = 0.53$, $p < 0.001$).

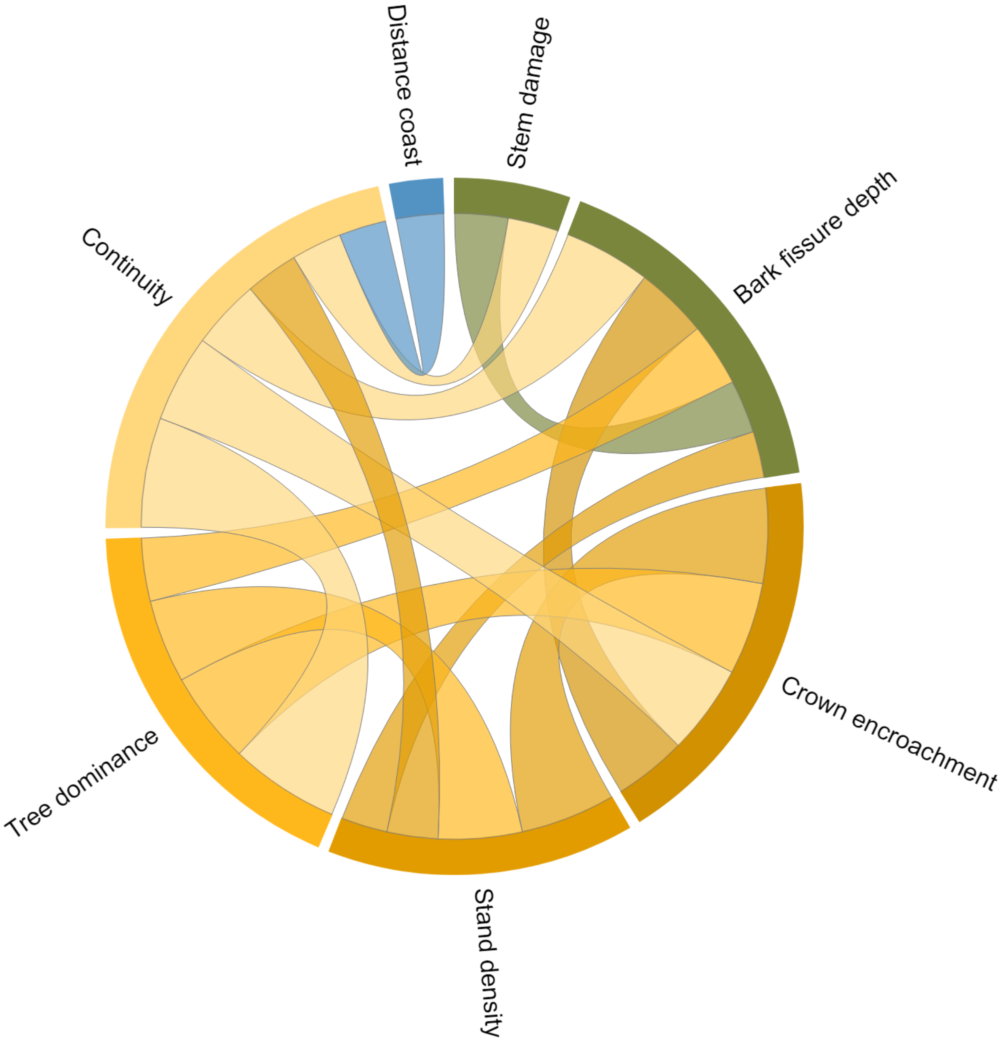

Figure 15. Chord diagram showing the significant interconnections between tree and habitat characteristics ($p < 0.05$, pairwise Spearman correlation) that are significantly correlated with lichen richness ($p < 0.05$, calculated through linear regression for continuous variables/ANOVA for categorical variables). The color of nodes and chords illustrates the type of variable: yellow for light availability related, green for microhabitat related and blue for physiographical variables. The breadth of nodes illustrates the interrelatedness of the variables. The breadth of chords illustrates the strength of correlation (Spearman's correlation coefficient).

3.5 Explanatory tree/habitat characteristics for lichen richness

The combination of independent variables with the highest explanatory value for lichen richness consisted of crown encroachment and stem damage. In a generalized linear model, these variables could explain 46 % of the variation in lichen richness (Figure 16: S = 2.97, $R^2 = 0.46$, $p < 0.001$; see Table 1-3 of Appendix E for coefficients, analysis of variance and fits and diagnostics for unusual observations; see Figure 1 of Appendix E for residual plots). The regression equation of the model is:

Lichen richness = 10.74 + 0.0 *Crown encroachment* (1) - 1.96 *Crown encroachment* (2) – 4.89 *Crown encroachment* (3) – 7.59 *Crown encroachment* (4) + 0.0 Stem damage (0) + 2.107 *Stem damage* (1).

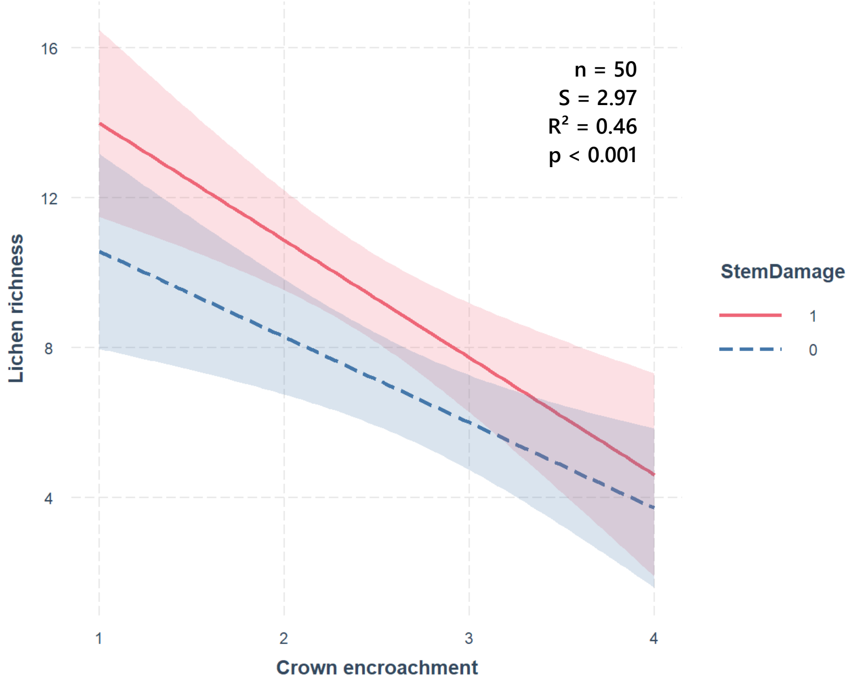

Figure 16. Generalized linear model explaining lichen richness through the independent variables crown encroachment and stem damage. Fitted line plot with 95 % confidence interval, with crown encroachment as predictor variable and stem damage as moderator variable.

Stand density, tree dominance and continuity were excluded from the model to prevent multicollinearity caused by the high correlation of these variables with crown encroachment (Spearman's correlation coefficient magnitude > 0.5). Bark fissure depth and distance to sea were excluded due to their high p value in the model (respectively 0.561 and 0.083), suggesting that changes in these predictors were not associated with major changes in lichen richness. Consequently, these variables did not add significant explanatory value to the model.

4. Discussion and Conclusion

4.1 Characteristics of ecologically important host trees and habitats

The most important tree and habitat characteristics for lichen diversity on a community level were light availability and microhabitats, with light availability being the overarching and most influential factor. Hence crown encroachment, as the most direct measure of light availability for epiphytic lichens, had the highest explanatory value for lichen richness in a highly interrelated web of ecological influences (Figure 17). In combination with stem damage, as an independent variable for the occurrence and diversity of microhabitats, 46 % of the observed variation in lichen richness could be explained (see 4.1.2 for light availability and 4.1.3 for habitats in detail). Which shows the potential of a few indicators to capture biodiversity better than the heterogeneity in structure itself.

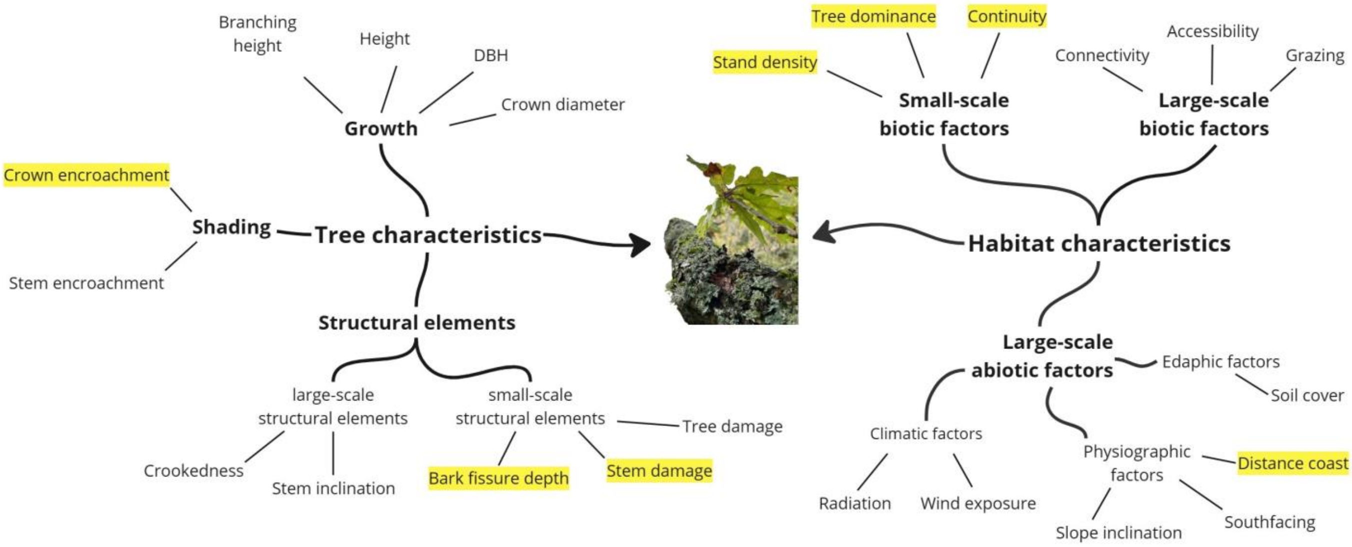

Figure 17. Schematic of the examined tree and habitat characteristics. Significant explanatory variables for lichen richness ($p < 0.05$, calculated through linear regression for continuous variables/ANOVA for categorical variables) are highlighted in yellow.

4.1.1 The age – size relationship. A glimpse into the complex relations between ecological variables

Various studies have observed these complex relationships between ecological characteristics, which govern host tree and habitat suitability and thus set the prerequisite for lichen diversity (e.g. Fritz et al., 2008; Johansson et al., 2009; Ranius, Johansson et al., 2008; Snäll et al., 2003; Thor et al., 2010). Especially the strong correlation between age and size has often been described as a limitation in pinpointing the primary drivers for lichen diversity (Johansson et al., 2009). Consequently, it cannot be clearly ascertained whether the commonly observed increase of lichen diversity with DBH (Johansson et al., 2007; Leppik and Jüriado, 2008; Löbel et al., 2006; Thor, 1998) is related to size or age. Both are important for colonization, which is relatively limited in lichens compared to e.g., vascular plants. As the establishment by spore dispersal requires the presence of a symbiotic photobiont (algae or cyanobacteria) and is spatially limited. This, in combination with the relatively slow growth and long time to reach maturity, can create a bottleneck for lichens in degrading habitats with no suitable host trees (Fritz et al., 2008). Tree size affects colonization through increasing spatial probability (higher colonization area), while age increases temporal probability (longer exposal to lichen dispersal) and the development of microhabitats.

For the studied trees, age was not necessarily related to size, due to limiting growth conditions, which might be a typical feature for oaks in the windswept west-coast region. This made it possible to distinguish the effects of size and age. Thus, the missing correlation between variables related to tree size (DBH, height, crown diameter) and lichen richness, points towards the assumption that age and the related changes in growth substrate are a more influential factor for total lichen richness than tree size. In fact, often small trees with structures suggesting a very slow and limited growth were observed to harbor a rich lichen flora (Figure 18). The aforementioned hypothesis is supported by other studies which did not find lichen diversity to be clearly affected by DBH (Hedenås and Ericson, 2000; Löbel et al., 2006; Thor et al., 2010). However, this conclusion may only be drawn for lichen richness and not assigned to composition or the occurrence of species of conservation concern. Indeed, red-listed and specialized species are generally attributed to large trees (Fritz et al., 2008; Jönsson et al., 2011; Thor, 1998; Thor et al., 2010). This can be explained by their high specialization and requirement for specific ecological niches, and the likelihood for the occurrence of those increases with area and thus tree size. While in comparison, common species are assumed to require primarily space and favorable photosynthetic conditions and not a specific microhabitat quality (Fritz et al., 2009).

Figure 18. The two trees with the highest richness of epiphytic lichens were characterized by a crooked growth and relatively small. With a DBH of 33 cm (left) and 15,5 cm (right), and a height of around 3 m. Harboring 20 (left) and 18 (right) different species.

4.1.2 Light availability

Light availability might be the most important factor for epiphytic lichen diversity on oak. This relationship has been shown in many other studies (Johansson et al., 2009; Jönsson et al., 2011; Leppik and Jüriado, 2008; Löbel et al., 2006; Nordén et al., 2012; Ranius, Johansson et al., 2008) and is attributable to the high light requirement of both oak and its associated lichen flora. Light availability is especially important for the algal photobiont of lichens – as foundation for photosynthesis and therefore growth and reproduction (Nash, 2008; Shrader, 2011). This makes light availability into a primary and superordinate factor for lichen diversity (Figure 19). Especially, as it affects and modulates many other ecological variables, such as microclimate and substrate quality (see 4.2.2 for the effect of shading on bark structures).

Figure 19. Observation illustrating the influence of light availability on lichen diversity. The two stems were growing only 1 meter from each other and are of similar DBH and size, with the only distinguishingly different variable being light availability, caused by a rock shading one of the stems. The shaded stem (left) hosts a poorer lichen flora of foliose species (Parmelia sulcata, P. saxatilis, Melanelixia subaurifera). The light-exposed stem (right) hosts a richer lichen flora of crustose, fruticose and foliose species (P. sulcata, P. saxatilis, Lecanora chlarotera, Lecidella elaeochroma, Ramalina farinacea, Evernia prunastri). This coincides with observations of south-facing sides of oak stems hosting the highest lichen richness (Hultengren et al., 1997; Ranius, Johansson et al., 2008).

Light availability is also a key factor for the survival and growth of oaks (Finnström, 2016). Therefore, oaks require an open to semi-open forest structure, such as can be found in wooded pastures or heath-oak forests. In late-successional forests dominated by shade-tolerant species, the regeneration of oak is relatively limited. Hence, for the long-term continuity of host trees which is required by many oak-associated lichens, a semi-open forest structure has to be maintained through large-scale disturbance regimes (Götmark and Kiffer, 2014; Naturvardsverket, 2011). Historically, this has been constituted by grazing and traditional agricultural methods like coppicing. The abandonment of these management practices over the past century in Sweden and all over Europe, has led to an increase in forest density and encroachment. The concomitant decrease in light availability for oak and associated cryptogams, has been shown to negatively affect lichen richness (Jönsson et al., 2011; Leppik and Jüriado, 2008; Nordén et al., 2012).

Due to the complex influences of light availability on other environmental factors, it can be difficult to associate the highly interconnected and ramified relationships. For instance, crown encroachment and stand density both correlated strongly with variables related to tree species composition (continuity and tree dominance). This suggests that oak forests, due to species-specific growth, have a more open structure and thus light availability compared to coniferous forests. Conversely, a more open structure favours light demanding species like oak. On a small-scale like in this study, crown encroachment was the strongest explanatory variable for lichen richness. As it is most directly related to the light reaching the stem and not species-dependent such as stand density (e.g., spruce stands are more shading than oak stands with the same basal area). Variables on a larger scale, like radiation and south facing did not show significant influences, which might be different in future studies investigating large-scale patterns of lichen diversity (e.g., on differently oriented mountainsides).

4.1.3 Tree-related microhabitats

The occurrence and diversity of tree-related microhabitats (TReM) might be another important factor for lichen diversity on oak. This showed in the positive relationship of both bark-fissure depth and stem damage with lichen richness. Bütler et al. (2020) defines TReMs as morphological features of trees which are characterized by specific conditions and often inhabited by highly specialised species. For epiphytic lichens, these are mostly related to growth structures or damages in the bark, such as bark fissures, cavities and rot holes. As those structures usually develop on a time-gradient, often a strong correlation with tree age and size can be found (MacFarlane and Luo, 2009). Which makes TReMs into one of the explanatory factors for studies observing increasing lichen diversity with tree age (Hultengren et al., 1997; Ranius, Johansson et al., 2008). This seems to be especially the case for species of conservation concern, which are often highly specialised and therefore require a specific microhabitat quality (Fritz and Brunet, 2010). Nonetheless, the requirements for structural and chemical diversity might also apply to common species, as suggested by the results of this study.

Bark fissures

As a tree ages the chemical and physical bark conditions change (Ranius, Johansson et al., 2008). The bark structure develops from smooth on young oaks to coarse with deep fissures on old trees (Figure 20). This not only increases the surface area for colonization and growth but also creates climate-related microhabitats. It also modifies the water-holding capacity of the bark, which many lichens as poikilohydric species depend on for water supply (Fritz et al., 2009; Hauck et al., 2000).

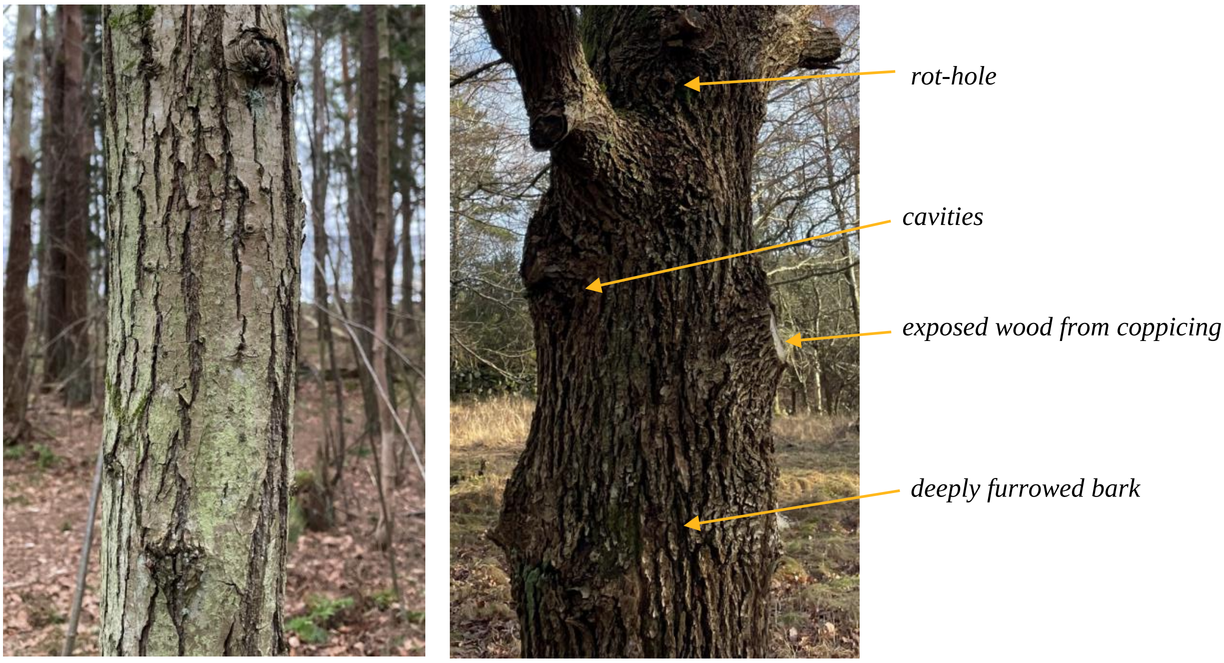

Figure 20. Comparison between bark structures of different development and age on two inventoried trees. Left: young relatively smooth bark (bark fissure depth = 2 mm). Right: old coarse bark with deep fissures (bark fissure depth = 20 mm) and elements of stem damage (rot-holes, cavities, exposed wood).

This development of bark structures might be negatively affected by shading, as suggested by the negative correlation between crown encroachment and bark fissure depth. Likely, concomitant changes in humidity lead to an increase in the decomposition of bark by epiphytic bryophytes and other microorganisms, which are favored by the more humid microclimate (Figure 21) (Ranius, Johansson et al., 2008). This assumption is based on the observations on inventoried trees under shaded conditions. Often, they were characterized by excessive moss traps and the outer bark structures peeling off.

Figure 21. Comparison between bark structures on two inventoried trees with different crown encroachment. Left: shaded bark with excessive moss traps and a structural loss through peeling off. Right: sun-exposed bark with very pronounced coarse structure and deep fissures.

Stem damage

Stem damages on old trees have been shown to positively affect lichen richness as they locally increases bark pH through mould and nutrient leakage (Fritz et al., 2009; Fritz and Brunet, 2010). Bark pH is important for epiphytic cryptogams as it regulates nutrient availability (Nash, 2008) and hydrogen concentration, which if too high (low pH) can damage the algal photobiont. Because lichen species show different preferences in bark pH, they are often associated with specific host tree species (for example oak with a relatively acidic bark). Conversely, the pH (and structural) heterogeneity created through stem damages can increase the habitat suitability for different species and thus increase lichen diversity. For example, some rare lichens only grow below rot-holes, where the bark pH is locally higher due to leakage from the cavity (Bütler et al., 2020). As stem damages increase with tree age, an age-related increase in bark pH can be observed (Fritz and Brunet, 2010). Unlike bark fissures, stem damage structures were not affected by shading. Which gives value to stem damage as an important independent variable for explaining lichen diversity in combination with light-related variables.

4.1.4 Physiographical factors

Interestingly, lichen richness increased with distance to coast. This correlation has been observed in previous studies, however, not yet investigated in detail. Jönsson et al. (2011) suspect maritime influences which impact climatic conditions, such as humidity and wind exposure, as well as saline air. These factors could impact the growth conditions for lichens and thus be restricting. Albeit also here correlations with other environmental factors might occur. For example, coastlines are often characterized by outcrops with a very low tree density, which can decrease connectivity and continuity of possible host trees and thus colonization probability for lichens. Such could be seen in the positive correlation between distance to coast and continuity. However, for a deeper understanding of the relationships between distance to coast and lichen richness, further studies are required.

4.2 Implications for research – a perspective on different indices and scales

Lichen richness vs. species composition and species of conservation concern

Both species richness and the presence of species of conservation concern are common indices in conservation ecology for assessing natural values (Nordén et al., 2007). Yet, for studies on lichen diversity, these approaches might lead to substantially different outcomes and should therefore be chosen in compliance with the study aim. A reason for this can be found in the succession of lichen species on aging oaks (Johansson et al., 2009) which is related to changes in bark chemistry and structure (see 4.1.3 for further explanation). On young trees, the community usually consist of common species of which many are generalists. Whereas specialists and species of conservation concern are usually associated with old trees. Thus, on ecologically valuable host trees and in woodland key habitats, lichen richness might be the same compared to trivial forests. While species composition might be completely different and enriched through species of conservation concern. For instance, it has also been shown that common species might not be as affected by changes in management in the same extend as red-listed lichens (Jönsson et al., 2011). Which again highlights the importance of distinguishing between lichen richness and composition, as well as the value of studies on species level. Because certain rare species, commonly referred to as signal species, can be valuable indicators for natural values such as long-term continuity. For the stated reasons, the applicability of this study may not be extended to species of conservation concern, as it was focused on richness of common species (though most of them specialists for hardwoods/oak).

Large-scale vs. small-scale patterns of diversity

The effects of different environmental factors on diversity patterns might change depending on the matter of scale. For instance, the effects of large-scale biotic and abiotic factors (such as climate, soil and connectivity) may be negligible on a community level, due to their marginal variance on such a small scale. Whereas on a larger scale, those factors might even govern lichen diversity. An example for this is connectivity, which failed to explain lichen richness in this study. The proximity of the inventoried trees (with a maximum distance of 2 km) might be sufficient for the dispersal of lichens within the study area. A similar observation was made by Fritz et al. (2008) who investigated cryptogams on 650 km^2 of beech stands in southern Sweden and could neither find a significant relationship with connectivity. On a larger scale however, which exceeds the dispersal range of lichens, connectivity has been shown to be highly important (Ranius, Eliasson, Johansson, 2008). Therefore, it would be interesting which impact the small-scale effects of crown encroachment and stem damage would have on a larger scale or whether they would be exceeded by large-scale factors.

The value of single vs. heterogeneity indices

In conservation, heterogeneity indices are a common tool for assessing biodiversity potential and predicting the richness of species of conservation concern (Hekkala et al., 2023; Nitare, 2019). This is because structural heterogeneity favors diversity through a mosaic of different niches and microhabitats and is therefore seen as a key component for the ecological value of habitats. However, in this study crown encroachment and stem damage by themselves, proved to capture biodiversity better than a combination of multiple variables. This can be explained by the high interconnectedness between the ecological factors, allowing for a single overarching variable to capture and represent the heterogeneity of the mosaic between numerous factors. On the practical side, the assessment of few categorical variables proves to be very easy and practical compared to the assessment of multiple complex factors. For instance, canopy openness (which equals crown encroachment on a large scale) and species composition could even be assessed on landscape level through remote sensing and thus provide valuable input for the identification of woodland key habitats. Data for such analyses is provided for example through the 2015 SLU Forest Map (2015), which is based on the co-processing of data from Sweden's National Forest Inventory, surface models from aerial photographs and satellite images, and illustrates volume and basal area per tree species for most of Sweden's forests. A glimpse into such possibilities is given in Figure 3 (see 2.1.1 Vegetation and land use history), which illustrates tree species volume based on the SLU Forest Map data.

4.3 Management and conservation objectives

Oak-rich forests and wooded pastures harbour a rich and distinct wood-associated cryptogam flora with many rare and threatened species (Nitare, 2019). For instance, 20 epiphytic lichens on the Swedish Red List are exclusively associated with oak (Ranius, Eliasson, Johansson, 2008; Thor et al., 2010). Due to changes of land-use and habitat degradation, these habitats with their associated cryptogam species are highly threatened and therefore in need of active management measures. Such are emphasized by studies showing that lichen richness and the occurrence of red-listed species are higher in managed open conditions compared to unmanaged meadows and secondary woodland (Jönsson et al., 2011; Paltto et al., 2011).

As light availability was the most important factor for lichen diversity, measures to create more open forests are motivated (Eriksson, 2008; Naturvardsverket, 2011). In habitats were traditional methods like grazing, pollarding and coppicing are insufficient or not applicable, partial cutting can be a valuable addition. This conservation-oriented measure referred to as conservation thinning by Nordén et al. (2012) has been shown to counteract succession and restores a semi-open canopy structure.

The availability of microhabitats can be addressed through enhancing structural heterogeneity by retaining and restoring structural elements. E.g., dead and dying wood in different decay stages and trees which are injured, crooked and old. A special focus should be laid on ancient trees, as they are key structures for biodiversity.

For long-term continuity and future persistence of inhabiting species, the establishment of new oak substrates is highly important. This is especially the case for lichens, due to their time lag response to environmental changes and the requirement of certain species for very old trees (Hanski and Ovaskainen, 2002; Nordén et al., 2012). Ranius et al. (2008) have found that the current occurrence patterns of lichens on oak might reflect higher historical habitat densities, because dynamics of habitat and colonisation-extinction-processes in lichens are relatively slow. This phenomenon could be observed with a few inventoried old and crooked trees, which had a rich lichen flora even though they were growing solitarily and outcompeted by surrounding vegetation (see Figure 18 for examples). These trees may be remnants of historically higher habitat densities.

The results of this study suggest that crown encroachment and stem damage have the potential to be predictors for lichen diversity on a small scale, which can practically be applied for nature value assessments and preservation measures, both on a small and large scale, e.g. through remote sensing as described in 4.2

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Appendix A.
Tree characteristics, habitat characteristics and lichen characteristics description and mean values

*Table 1. Tree characteristics (**a**) and habitat characteristics (**b**) evaluated for each inventoried tree and lichen characteristics (**c**) for each inventoried lichen. Including description and mean values.*

Characteristic	Unit	Description	Mean (Min – Max)
a. Tree			
Species		*Quercus robur* (QR) or *Quercus petraea* (QP)	16 QR, 34 QP
Height	m	total tree height, rounded off to closest half meter	6.3 (1.5 – 17)
DBH	cm	stem diameter 1.3 m above ground	26 (10 – 58)
Crown diameter	m	estimated diameter of the crown	7 (2.5 – 15)
Branching height	m	height of the lowest living branch	2 (0.2 – 9)
Tree damage		tree condition: healthy (1; < 5 dead branches), damaged (2; < 40 % of crown damaged) or dying (3; > 40 % of crown damaged)	1.7 (1 – 3)
Stem damage		hollows or exposed wood up to 2 m present (1) or absent (0)	0.5 (0 – 1)
Crown encroachment		encroachment from competing stems: free growing (1), partial encroachment on at least one side (2), encroachment on all sides except from above (3) and overgrown (4; encroached from above)	2.6 (1 – 4)
Stem encroachment		encroachment of the stem surface up to 2 m by vegetation close to stem: free growing (1), partial encroachment on at least one side (2) and encroachment on all sides (3)	1.9 (1 – 3)
Bark fissure depth	mm	Average depth of bark fissures along the circumference of the tree at 1.3 m (based on four measurements)	7 (1 – 19)
Stem inclination	°	Inclination of the center of the stem 0 to 2 m from the ground	6 (0 – 49)
Crookedness		stem curvature: straight (1), slightly crooked (2), strongly crooked (3)	2 (1 – 3)

b. Habitat

Habitat type		type of habitat: outcrop (O), pasture (P), cultural settlement (CS), coniferous forest (CF), mixed deciduous forest (DF) and oak forest (OF)	21 O, 4 P, 10 CS, 5 CF, 7 DF, 3 OF
Tree dominance		Dominant trees in the forest stand: conifer (1), broadleaf (2) and oak (3)	2.34 (1-3)
Continuity		continuity of oak in the habitat based on assessment of the stand structure and analysis of historic maps in ArcGIS Pro: new establishment of oak (1), short-term continuity of oak (2; 20-60 years), mid-term to long-term continuity of oak (3; > 60 years)	2.5 (1 – 3)
Connectivity		connectivity to other broadleaf habitats in close proximity (50 m): no other broadleaf habitats in close proximity (1), few broadleaf habitats in close proximity (2), surrounded by broadleaf habitats with a long-term continuity (3)	2 (1 – 3)
Slope inclination	°	inclination of the area the tree grows on	17 (0 – 51)
Southfacing		orientation of the slope towards the south: West – East (0), Southwest and Southeast (1), South (2)	0.3 (0 – 2)
Radiation	WH/m²	direct incoming solar radiation per year	518000 (350000 – 700000)
Wind exposure		wind exposure of stem to 2 m: wind-protected (1), slightly wind-exposed (2) and strongly wind-exposed (3)	1.8 (1 – 3)
Distance to coast	m	minimal distance to coast through coordinates in ArcGIS Pro	162 (8 – 453)
Accessibility		accessibility of the habitat: easily accessible (0; e.g. on open land) and secluded (1; e.g. in steep terrain)	0.6 (0 – 1)
Grazing		frequency of summer grazing: no grazing (1), partial grazing (2) and regular pasture like (3)	1.2 (1-3)
Stand density	m^2/ha	basal area 1.3 m above ground measured with a relascope	14 (1 – 31)

Soil cover	depth of soil cover: no soil cover (1; outcrop), shallow soil cover (2) and deep soil cover (3)	2 (1 – 3)
c. Lichen		
Substrate	Primary growth substrate of the inventoried specimen: stem (S), living branch, dying branch (DB) and dead branch (D)	327 S, 143 LB, 1 DB, 3 D
Abundance	Abundance of the inventoried specimen on the tree: single thallus (1), several thalli (2; 2-5) and many thalli (3; >5)	2.2 (1 – 3)
Growth form	Growth form of the species: crustose (cr), foliose (fo) and fruticose (fr)	202 cr, 122 fo, 84 fr

Appendix B.
Inventory data records for the analysis

Table 1. Data record of the 50 inventoried trees including tree characteristics.

Tree ID	**Tree Species**	**Height**	**DBH**	**Crown Diameter**	**Branching Height**	**Tree Damage**	**Stem Damage**	**Crown Encroach-ment**	**Stem Encroach-ment**	**Bark fissure depth**	**Stem Inclinat-ion**	**Crooked-ness**
1	QP	7.5	51.5	12	2.3	2	1	2	2	10.5	49	3
2	QP	3	11.7	4.5	0.2	1	1	3	3	2.25	0	3
3	QP	5	10	6	2	1	0	4	2	2.75	0	1
4	QR	7	12.9	6	4	1	0	4	2	2	0	1
5	QP	10.5	33.2	13	9	1	0	2	1	7.25	0	2
6	QP	5	28.1	5.5	2	1	0	3	3	6.75	14	3
7	QP	6	43.3	13	0.7	2	1	3	3	10.25	11	3
8	QP	11	36	6.5	3	2	1	2	2	9	3	2
9	QR	1.5	10.3	4.5	0.3	2	0	2	2	2	46	3
10	QP	8	27.9	9	2	2	1	2	2	10	8	2
11	QP	4.5	18.6	5	1.5	1	0	3	2	4.75	3	2
12	QR	13	58.3	15	1	1	1	1	1	14.5	0	2
13	QR	6.5	39.5	7.5	1.8	1	1	2	2	14.5	0	2
14	QR	3.5	15.5	4.5	0.2	2	1	2	3	7.5	10	3
15	QR	7	14.5	4.5	2	1	0	3	2	2.5	4	1
16	QR	17	33	10	3	1	0	2	1	10	0	1
17	QP	7	34.2	7	2.8	3	1	3	1	7	0	1
18	QR	8	39.9	11	1.6	2	0	2	1	8.5	0	2
19	QP	6	48.3	15	0.2	2	1	3	2	17.25	16	3
20	QP	8	43.5	7.5	1.9	1	0	2	1	8.5	0	2
21	QP	8	19.4	6	2	1	0	3	1	4	5	1
22	QP	6	20.2	4.5	1.4	2	1	3	2	4.75	0	2
23	QP	9	25.8	7	1.1	2	1	3	2	4	39	3
24	QR	4.5	18.9	7	1	2	0	3	2	3.75	0	2
25	QP	5.5	35.7	8	1.55	1	1	1	1	9.5	0	2
27	QP	5	20.8	5	1.2	1	0	3	2	4	7	2
26	QP	5.5	28.7	8.5	0.5	3	1	3	2	5	26	3
28	QP	3.5	13.2	6	0.7	2	0	3	3	2	7	3
29	QP	3	18.9	4.5	1.3	1	1	3	2	7.5	5	2
30	QP	3.5	19.2	5.5	1.8	2	1	3	2	9.25	0	3
31	QP	8	43.2	13	1.9	1	0	1	1	15.25	0	1
32	QP	5	20.2	4.5	1	3	0	2	2	8.25	0	2
33	QR	6.5	36.2	12	1.6	1	0	1	1	11.5	10	1
34	QP	2	13.2	4.5	1.5	2	0	3	2	5	0	3
35	QP	4.5	10	2.5	1	2	0	4	3	2.75	7	2
36	QR	8.5	20	5.5	1.5	2	1	2	1	5.5	12	1
37	QR	10	22.4	3.5	6	2	0	3	3	5.5	0	1
38	QP	11.5	50.3	11	3	2	1	3	1	2.2	7	1
39	QP	4	12.2	4.5	0.3	2	1	3	3	5	0	2
40	QP	11	52.9	9	1.6	1	1	2	1	19	0	1
41	QP	5.5	26.1	4	1.2	1	1	2	2	5	15	2
42	QP	3	33	5	1.2	2	1	1	2	12	0	3
43	QR	3	12.6	5	1.2	3	1	3	3	5	0	2
44	QR	3	18.8	4	1.6	2	1	4	3	12	0	3
45	QR	6	15.4	3.5	0.7	2	1	2	2	6	0	2
46	QP	3	18.1	4	2	2	1	2	2	9.5	0	3
47	QR	7.5	32.7	5	3	2	0	2	1	5	0	1
48	QP	4	14.1	6	1.5	2	0	2	1	6	0	2
49	QP	4.5	10.1	6	1	2	0	4	2	3	0	3
50	QP	5.5	14.8	5	1.6	2	0	4	2	4	9	1

Table 2. Data record of the 50 inventoried trees including habitat characteristics

Tree ID	**Habitat Type**	**Oak Broadleaf Coniferous Dominance**	**Continuity**	**Connectivity**	**Stand Density**	**Slope Inclination**	**South facing**	**Wind Exposure**	**Soil Cover**	**Grazing**	**Accessibility**	**Direct Radiation**	**Distance Coast**	**Lichen Richness**	**Lichen Crustose**	**Lichen Foliose**	**Lichen Fruticose**
1	P	3	3	2	6	0	0	3	3	3	0	556447	187	14	7	2	5
2	O	1	1	1	8	13	0	3	2	1	1	560300	181	7	3	2	2
3	CF	1	1	1	22	10	0	1	2	1	0	403281	17	5	5		
4	CF	1	1	1	30	9	0	1	3	1	0	527887	69	2	2		
5	CS	3	3	1	9	14	0	2	2	1	0	509580	66	10	4	4	2
6	O	2	2	1	22	14	0	1	2	1	1	390280	175	9	4	3	2
7	CF	1	2	1	29	15	2	1	3	1	1	607728	148	4	3	1	
8	O	3	3	2	9	27	0	2	2	1	1	435449	115	7	3	2	2
9	CS	3	2	2	4	4	0	3	2	1	0	588489	39	7	3	4	
10	DF	2	3	1	23	9	0	2	2	1	1	594783	83	7	1	3	3
11	O	1	2	1	22	10	0	2	2	1	1	594736	78	2	1		1
12	CS	3	3	2	4	13	1	2	3	1	0	601393	304	11	6	3	2
13	CS	3	3	2	17	15	0	1	2	1	0	629858	211	8	2	2	4
14	O	2	3	1	13	16	0	1	2	1	1	501074	188	18	7	7	4
15	O	2	1	2	13	27	0	1	1	1	1	545989	218	5	5		
16	OF	3	3	3	23	15	0	2	2	3	0	463296	363	6	2	3	1
17	CS	3	3	3	14	12	1	2	3	3	0	575794	453	12	6	3	3
18	CS	3	3	3	6	0	0	1	2	1	0	453484	393	10	3	4	3
19	O	3	3	3	12	24	1	2	1	1	1	699389	334	11	5	4	2
20	P	3	3	3	4	0	0	2	3	3	0	521158	381	12	5	4	3
21	P	3	3	3	20	15	0	1	2	3	0	533839	372	7	2	3	2
22	OF	3	3	3	24	40	0	2	2	1	1	389929	269	10	6	2	2
23	O	2	3	3	15	45	0	2	1	1	1	349926	145	4	2	2	
24	DF	2	2	3	31	18	0	1	2	1	1	511057	212	5	4	1	
25	CS	3	3	3	6	11	2	1	2	1	0	565913	111	12	6	4	2
27	O	3	2	2	13	7	0	2	2	1	1	447788	81	8	5	2	1
26	O	3	3	3	18	24	1	2	1	1	1	594729	42	8	6	2	
28	O	2	2	1	12	12	0	3	2	1	1	428776	30	4	3	1	
29	O	2	2	2	20	34	0	2	1	1	1	431620	125	7	5	1	1
30	DF	2	2	2	1	0	0	2	2	1	1	480232	193	9	6	1	2
31	CS	3	3	2	3	51	2	2	1	1	0	631344	80	11	4	5	2
32	O	3	3	1	7	5	1	1	1	1	1	575135	93	9	6	2	1
33	CS	3	3	2	5	32	1	2	1	1	0	564425	46	6	4	1	1
34	O	2	2	2	12	16	0	2	2	1	1	449224	34	6	6		
35	O	1	1	1	20	26	1	2	2	1	1	654869	61	1	1		
36	DF	2	3	3	16	5	0	2	2	1	1	497560	66	13	5	6	2
37	CF	1	2	2	26	27	0	1	2	1	1	402379	79	5	2	2	1
38	DF	3	3	3	20	10	0	1	2	2	0	481708	135	4	2		2
39	O	1	2	1	26	36	0	1	2	1	1	361534	213	11	3	4	4
40	P	3	3	3	12	8	0	2	3	2	0	550079	187	6	3	1	2
41	O	3	3	3	12	33	2	3	1	1	1	574942	8	8	5	2	1
42	O	3	2	1	2	12	0	3	1	1	1	692518	74	20	7	9	4
43	O	3	2	2	13	9	0	3	2	1	1	469843	125	10	4	5	1
44	O	2	3	2	9	16	0	2	1	1	1	432778	156	3	1	1	1
45	DF	3	3	2	5	20	0	2	2	1	1	603409	174	13	7	2	4
46	CS	3	3	2	2	20	0	2	1	1	0	466864	209	11	4	2	5
47	OF	3	3	3	8	26	0	2	2	1	0	509317	312	10	8	2	
48	O	1	2	2	10	38	0	2	2	1	1	501198	344	10	4	4	2
49	CF	1	2	2	21	0	0	1	2	1	1	527805	91	4	2	1	1
50	DF	2	2	2	23	9	0	2	2	1	1	479499	20	6	2	3	1

Table 3. Data record of the inventoried lichens accessible via: https://www.inaturalist.org/observations?created_d1=2023-01-01&created_d2=2023-02-11&place_id=any&user_id=juliasiegel&verifiable=any (Accessed: 25 February 2023)

iNaturalistID	Genus	LichenSpecies	Abundance	Substrate	Growth form	TreeID
147184659	Buellia	Buellia griseovirens	1	s	1	1
147184675	Lecanora	Lecanora argentata	2	s	1	1
147184773	Cladonia	Cladonia fimbriata	2	s	3	1
147184786	Phlyctis	Phlyctis argena	3	s	1	1
147185297	Melanelixia	Melanelixia subaurifera	2	s	2	1
147185355	Parmelia	Parmelia sulcata	3	s	2	1
147185654	Lepra	Lepra amara	2	s	1	1
147185677	Lepraria	Lepraria incana	2	s	1	1
147186533	Ramalina	Ramalina fraxinea	2	s	3	1
147186540	Ramalina	Ramalina farinacea	2	s	3	1
147186543	Cliostomum	Cliostomum griffithii	2	s	1	1
147186544	Lecanora	Lecanora chlarotera	2	s	1	1
147186550	Ramalina	Ramalina fastigiata	2	s	3	1
147186553	Evernia	Evernia prunastri	3	lb	3	1
147190089	Lecidella	Lecidella elaeochroma	3	s	1	2
147190123	Lecanora	Lecanora chlarotera	3	s	1	2
147190144	Evernia	Evernia prunastri	2	lb	3	2
147190160	Melanelixia	Melanelixia glabratula	2	lb	2	2
147190186	Ramalina	Ramalina farinacea	1	lb	3	2
147190255	Xanthoria	Xanthoria parietina	1	s	2	2
147190511	Lepraria	Lepraria incana	1	s	1	2
147192528	Lecanora	Lecanora chlarotera	3	s	1	3
147192574	Lecidella	Lecidella elaeochroma	2	s	1	3
147192604	Lecanora	Lecanora carpinea	2	s	1	3
147192628	Lepraria	Lepraria incana	2	s	1	3
147192850	Phlyctis	Phlyctis argena	2	s	1	3
147193827	Lepraria	Lepraria finkii	1	s	1	4
147193917	Lecanora	Lecanora expallens	2	s	1	4
147195119	Phlyctis	Phlyctis argena	2	s	1	5
147195166	Lecidella	Lecidella elaeochroma	1	s	1	5
147195188	Lecanora	Lecanora carpinea	1	s	1	5
147195224	Lepraria	Lepraria incana	2	s	1	5
147195230	Cladonia	Cladonia chlorophaea	3	s	3	5
147195388	Melanelixia	Melanelixia subaurifera	3	lb	2	5
147195402	Hypogymnia	Hypogymnia physodes	2	lb	2	5
147195442	Parmelia	Parmelia sulcata	2	lb	2	5
147195518	Evernia	Evernia prunastri	3	lb	3	5
147195541	Hypogymnia	Hypogymnia tubulosa	2	lb	2	5
147254004	Phlyctis	Phlyctis argena	3	s	1	6
147254071	Biatora	Biatora efflorescens	1	s	1	6
147254162	Lepraria	Lepraria incana	3	s	1	6
147254192	Parmelia	Parmelia saxatilis	2	s	2	6
147268864	Buellia	Buellia griseovirens	2	s	1	6
147268884	Cladonia	Cladonia chlorophaea	3	s	3	6
147268903	Evernia	Evernia prunastri	2	lb	3	6
147268908	Pseudevernia	Pseudevernia furfuracea	1	lb	2	6
147268915	Platismatia	Platismatia glauca	2	lb	2	6
147268963	Lepraria	Lepraria incana	3	s	1	7
147268997	Melanelixia	Melanelixia glabratula	2	s	2	7
147269013	Phlyctis	Phlyctis argena	2	s	1	7
147269019	Biatora	Biatora efflorescens	2	s	1	7
147269022	Parmelia	Parmelia sulcata	2	s	2	8
147269028	Ramalina	Ramalina farinacea	3	s	3	8

iNaturalistID	Genus	LichenSpecies	Abundance	Substrate	Growth form	TreeID
147269056	Parmelia	Parmelia saxatilis	2	s	2	8
147269121	Lecanora	Lecanora chlarotera	1	s	1	8
147269145	Lepraria	Lepraria incana	2	s	1	8
147269178	Evernia	Evernia prunastri	3	s	3	8
147269229	Lecidella	Lecidella elaeochroma	1	s	1	8
147269282	Lecidella	Lecidella elaeochroma	2	s	1	9
147269290	Lecanora	Lecanora carpinea	3	s	1	9
147269307	Melanelixia	Melanelixia subaurifera	2	s	2	9
147269317	Lecanora	Lecanora chlarotera	3	s	1	9
147269331	Xanthoria	Xanthoria parietina	3	lb	2	9
147269349	Physcia	Physcia aipolia	2	lb	2	9
147269383	Physcia	Physcia adscendens	2	lb	2	9
147269411	Cladonia	Cladonia fimbriata	2	s	3	10
147269431	Phlyctis	Phlyctis argena	3	s	1	10
147269449	Melanelixia	Melanelixia glabratula	1	s	2	10
147269465	Cladonia	Cladonia chlorophaea	2	s	3	10
147269485	Platismatia	Platismatia glauca	2	lb	2	10
147269496	Parmelia	Parmelia sulcata	2	lb	2	10
147269500	Evernia	Evernia prunastri	2	lb	3	10
147269515	Cladonia	Cladonia digitata	2	s	3	11
147269519	Phlyctis	Phlyctis argena	2	s	1	11
147330274	Melanelixia	Melanelixia subaurifera	3	s	2	12
147330310	Lepraria	Lepraria incana	3	s	1	12
147330321	Phlyctis	Phlyctis argena	3	s	1	12
147330331	Ramalina	Ramalina farinacea	3	s	3	12
147330381	Cliostomum	Cliostomum griffithii	2	lb	1	12
147330400	Lepraria	Lepraria finkii	1	lb	1	12
147330408	Parmelia	Parmelia sulcata	3	lb	2	12
147330414	Lecanora	Lecanora chlarotera	2	lb	1	12
147330418	Melanelixia	Melanelixia glabratula	3	lb	2	12
147330428	Lecidella	Lecidella elaeochroma	1	lb	1	12
147330430	Evernia	Evernia prunastri	3	lb	3	12
147330438	Cladonia	Cladonia chlorophaea	2	s	3	13
147330447	Cladonia	Cladonia fimbriata	2	s	3	13
147330456	Phlyctis	Phlyctis argena	2	s	1	13
147330463	Melanelixia	Melanelixia subaurifera	1	s	2	13
147330471	Lepraria	Lepraria incana	1	s	1	13
147330476	Ramalina	Ramalina fastigiata	1	lb	3	13
147330481	Evernia	Evernia prunastri	3	lb	3	13
147330492	Parmelia	Parmelia sulcata	3	lb	2	13
147330520	Lepraria	Lepraria incana	2	s	1	14
147330523	Buellia	Buellia griseovirens	3	lb	1	14
147330525	Cladonia	Cladonia chlorophaea	3	lb	3	14
147330552	Parmelia	Parmelia saxatilis	3	lb	2	14
147330566	Cladonia	Cladonia arbuscula	2	lb	3	14
147330579	Melanelixia	Melanelixia glabratula	3	lb	2	14
147330588	Lecanora	Lecanora chlarotera	3	lb	1	14
147330596	Hypogymnia	Hypogymnia physodes	3	lb	2	14
147330620	Biatora	Biatora efflorescens	1	lb	1	14
147330643	Lecanora	Lecanora carpinea	3	lb	1	14
147330645	Phlyctis	Phlyctis argena	2	s	1	14
147330711	Cladonia	Cladonia coniocraea	3	lb	3	14
147330722	Pseudevernia	Pseudevernia furfuracea	1	lb	2	14
147330774	Hypogymnia	Hypogymnia tubulosa	2	lb	2	14
147330824	Melanelixia	Melanelixia subaurifera	3	lb	2	14
147330851	Violella	Violella fucata	2	lb	1	14
147333828	Platismatia	Platismatia glauca	2	lb	2	14
147333836	Evernia	Evernia prunastri	3	lb	3	14
147330894	Phlyctis	Phlyctis argena	3	s	1	15

iNaturalistID	Genus	LichenSpecies	Abundance	Substrate	Growth form	TreeID
147330908	Biatora	Biatora efflorescens	1	s	1	15
147330917	Lepraria	Lepraria incana	1	s	1	15
147330923	Buellia	Buellia griseovirens	1	s	1	15
147330934	Pyrrhospora	Pyrrhospora quernea	1	s	1	15
147330941	Evernia	Evernia prunastri	3	s	3	16
147330946	Melanelixia	Melanelixia subaurifera	2	s	2	16
147330963	Phlyctis	Phlyctis argena	3	s	1	16
147330987	Melanelixia	Melanelixia glabratula	2	s	2	16
147331001	Lepraria	Lepraria incana	3	s	1	16
147331013	Parmelia	Parmelia sulcata	3	s	2	16
147331028	Parmelia	Parmelia sulcata	3	s	2	17
147331036	Ramalina	Ramalina farinacea	1	s	3	17
147331053	Phlyctis	Phlyctis argena	3	s	1	17
147331064	Melanelixia	Melanelixia glabratula	2	s	2	17
147331113	Biatora	Biatora efflorescens	2	s	1	17
147331146	Lecanora	Lecanora chlarotera	1	s	1	17
147331166	Evernia	Evernia prunastri	3	s	3	17
147331170	Lecanora	Lecanora carpinea	1	s	1	17
147331176	Polycauliona	Polycauliona polycarpa	1	s	2	17
147331188	Lecidella	Lecidella elaeochroma	1	s	1	17
147331191	Buellia	Buellia griseovirens	1	s	1	17
147331195	Cladonia	Cladonia fimbriata	2	s	3	17
147331217	Evernia	Evernia prunastri	3	s	3	18
147331223	Parmelia	Parmelia sulcata	3	s	2	18
147331247	Cladonia	Cladonia chlorophaea	2	s	3	18
147331266	Phlyctis	Phlyctis argena	3	s	1	18
147331286	Lepraria	Lepraria incana	2	s	1	18
147331293	Biatora	Biatora efflorescens	3	s	1	18
147331298	Melanelixia	Melanelixia subaurifera	3	s	2	18
147331306	Cladonia	Cladonia fimbriata	2	s	3	18
147331315	Hypogymnia	Hypogymnia physodes	2	lb	2	18
147331324	Hypogymnia	Hypogymnia tubulosa	2	lb	2	18
147331336	Cladonia	Cladonia chlorophaea	2	s	3	19
147331345	Phlyctis	Phlyctis argena	2	s	1	19
147331359	Lepraria	Lepraria incana	2	s	1	19
147331370	Melanelixia	Melanelixia subaurifera	2	lb	2	19
147331376	Melanelixia	Melanelixia glabratula	2	lb	2	19
147331387	Parmelia	Parmelia saxatilis	2	lb	2	19
147331390	Parmelia	Parmelia sulcata	2	lb	2	19
147331397	Buellia	Buellia griseovirens	1	lb	1	19
147331401	Evernia	Evernia prunastri	2	lb	3	19
147331413	Lecanora	Lecanora carpinea	1	lb	1	19
147331426	Lecidella	Lecidella elaeochroma	1	lb	1	19
147400720	Melanelixia	Melanelixia glabratula	3	s	2	20
147400730	Parmelia	Parmelia saxatilis	3	s	2	20
147400735	Parmelia	Parmelia sulcata	3	s	2	20
147400742	Evernia	Evernia prunastri	2	s	3	20
147400752	Lepraria	Lepraria incana	2	s	1	20
147400760	Phlyctis	Phlyctis argena	3	s	1	20
147400764	Buellia	Buellia griseovirens	2	s	1	20
147400767	Lecanora	Lecanora carpinea	2	s	1	20
147400772	Ochrolechia	Ochrolechia microstictoides	3	s	1	20
147400781	Parmelia	Parmelia ernstiae	2	s	2	20
147400790	Cladonia	Cladonia coniocraea	3	s	3	20
147400805	Cladonia	Cladonia chlorophaea	3	s	3	20
147400819	Phlyctis	Phlyctis argena	3	s	1	21
147400825	Melanelixia	Melanelixia glabratula	2	s	2	21
147400831	Evernia	Evernia prunastri	2	s	3	21
147400845	Parmelia	Parmelia sulcata	3	s	2	21

iNaturalistID	Genus	LichenSpecies	Abundance	Substrate	Growth form	TreeID
147400863	Cladonia	Cladonia fimbriata	2	s	3	21
147400873	Lepraria	Lepraria incana	2	s	1	21
147400877	Hypogymnia	Hypogymnia physodes	2	s	2	21
147400880	Evernia	Evernia prunastri	3	s	3	22
147400885	Cladonia	Cladonia coniocraea	3	s	3	22
147400899	Phlyctis	Phlyctis argena	2	s	1	22
147400904	Melanelixia	Melanelixia glabratula	2	s	2	22
147400936	Lepraria	Lepraria incana	1	s	1	22
147400941	Buellia	Buellia griseovirens	2	s	1	22
147400948	Lecanora	Lecanora carpinea	2	s	1	22
147400953	Ochrolechia	Ochrolechia microstictoides	3	s	1	22
147400960	Lecidella	Lecidella elaeochroma	1	db	1	22
147400965	Parmelia	Parmelia sulcata	3	lb	2	22
147400974	Melanelixia	Melanelixia subaurifera	2	s	2	23
147400978	Phlyctis	Phlyctis argena	3	s	1	23
147400984	Lepraria	Lepraria incana	2	s	1	23
147400987	Melanelixia	Melanelixia glabratula	2	s	2	23
147401009	Lepraria	Lepraria incana	1	s	1	24
147401016	Phlyctis	Phlyctis argena	2	s	1	24
147401039	Lecidella	Lecidella elaeochroma	1	s	1	24
147401059	Melanelixia	Melanelixia glabratula	2	s	2	24
147401069	Buellia	Buellia griseovirens	2	s	1	24
147401073	Melanelixia	Melanelixia glabratula	3	s	2	25
147401082	Phlyctis	Phlyctis argena	3	s	1	25
147401102	Evernia	Evernia prunastri	3	s	3	25
147401106	Lecidella	Lecidella elaeochroma	2	s	1	25
147401109	Lecanora	Lecanora carpinea	2	s	1	25
147401115	Parmelia	Parmelia sulcata	2	s	2	25
147401118	Lecanora	Lecanora chlarotera	2	s	1	25
147401128	Lecanora	Lecanora argentata	2	s	1	25
147401150	Melanelixia	Melanelixia subaurifera	3	lb	2	25
147401162	Lecidella	Lecidella euphorea	1	lb	1	25

Appendix C.
Lichen species diversity.

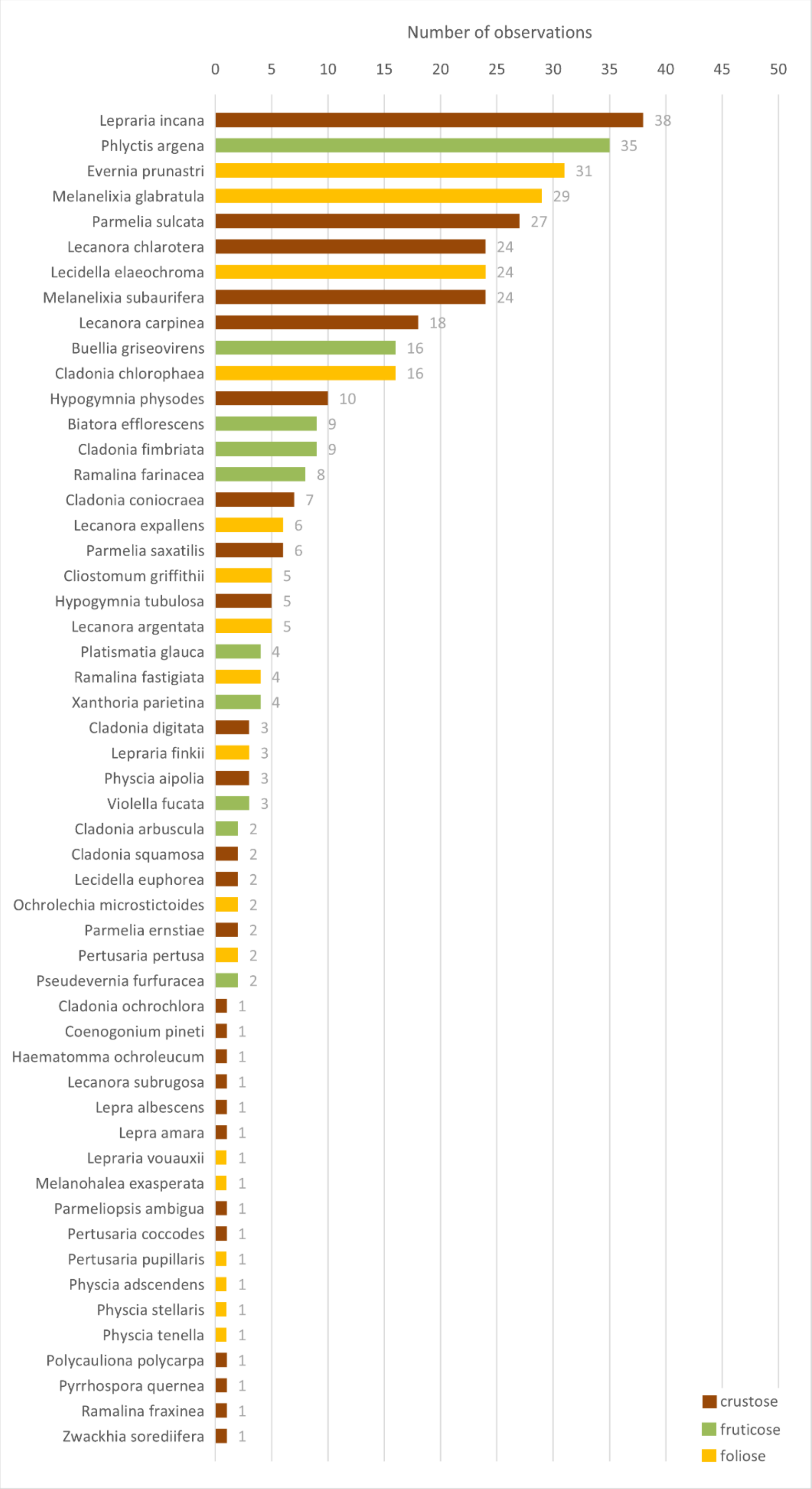

Figure 1. Relative species abundance of the recorded taxa including growth form

Appendix D.

Correlations between lichen richness and tree/habitat characteristics.

Table 1: Correlations between lichen richness and tree characteristics.

*Stated are the correlations between lichen richness and tree characteristics calculated with regression for continuous predictor variables and ANOVA for categorical predictor variables. Significant correlations are marked with * for p < 0.05, ** for p < 0.01 and *** for p < 0.001. Fields shaded in grey indicate negative correlations.*

Variable	**Method**	**R^2**	**P**	**Significance**
Height	Regression	0.00	0.653	
DBH	Regression	0.07	0.070	
Crown diameter	Regression	0.01	0.488	
Branching height	Regression	0.01	0.52	
Tree damage	ANOVA	0.03	0.512	
Stem damage	ANOVA	0.11	0.018	*
Crown encroachment	ANOVA	0.39	0.000	***
Stem encroachment	ANOVA	0.04	0.347	
Bark fissure depth	Regression	0.13	0.011	*
Stem inclination	Regression	0.00	0.934	
Crookedness	ANOVA	0.04	0.425	

Table 2: Correlations between lichen richness and habitat characteristics.

*Stated are the correlations between lichen richness and habitat characteristics calculated with regression for continuous predictor variables and ANOVA for categorical predictor variables. Significant correlations are marked with * for p < 0.05, ** for p < 0.01 and *** for p < 0.001. Fields shaded in grey indicate negative correlations.*

Variable	**Method**	**R^2**	**P**	**Significance**
Tree dominance	ANOVA	0.22	0.003	**
Continuity	ANOVA	0.18	0.010	**
Connectivity	ANOVA	0.01	0.834	
Slope inclination	Regression	0.00	0.716	
Southfacing	ANOVA	0.00	0.945	
Radiation	Regression	0.04	0.153	
Wind exposure	ANOVA	0.05	0.334	
Distance to coast	Regression	0.09	0.038	*
Accessibility	ANOVA	0.01	0.506	
Grazing	ANOVA	0.06	0.259	
Stand density	Regression	0.27	0.000	***
Soil cover	ANOVA	0.01	0.802	

Table 3: Correlations between tree/habitat characteristics

*Stated are the correlations between the significant tree/habitat characteristics calculated through pairwise Spearman method with 95 % CI for correlation coefficient. Magnitudes of correlation coefficient between 0.7 and 0.9 indicate high correlation of variables, between 0.5 and 0.7 indicate moderate correlation and 0.3 and 0.5 low correlation. Significant correlations are marked with * for p < 0.05, ** for p < 0.01 and *** for p < 0.001. Fields shaded in grey indicate negative correlations.*

	Crown encroachment	**Stem damage**	**Bark fissure depth**	**Stand density**	**Tree dominance**	**Continuity**
Stem damage	-0.158					
Bark fissure depth	*** -0.600	** 0.388				
Stand density	*** 0.629	-0.124	** -0.409			
Tree dominance	*** -0.606	0.177	** 0.412	*** -0.528		
Continuity	*** -0.586	* 0.368	* 0.566	* -0.333	*** 0.716	
Distance to coast	-0.145	0.183	0.307	-0.082	0.216	* 0.308

Appendix E.
Generalized linear model explaining lichen richness.

Table 1. Coefficients of the generalized linear model explaining lichen richness through the independent variables crown encroachment and stem damage.

Term	Coefficient	p-Value	VIF
Constant	10.74	0.000	
Crown encroachment			
2	-1.96	0.199	2.95
3	-4.89	0.002	3.02
4	-7.59	0.000	2.02
Stem damage			
1	2.107	0.020	1.07

Table 2. Analysis of variance for the generalized linear model explaining lichen richness through the independent variables crown encroachment and stem damage. The model's significance level α is 0.05. As the p-value of the lack-of-fit test is larger than the significance level (p = 0.402 > α = 0.05, there is no evidence that the model does not fit the data.

Source	DF	Adj SS	Adj MS	F-Value	p-Value
Regression	4	338.91	84.728	9.58	0.000
Crown encroachment	3	235.98	78.662	8.90	0.000
Stem damage	1	51.59	51.587	5.84	0.020
Error	45	397.81	8.840		
Lack-of-Fit	3	26.53	8.842	1.00	0.402
Pure Error	42	371.28	8.840		
Total	49	736.72			

Table 3. Fits and Diagnostics for unusual observations of the generalized linear model explaining lichen richness through the independent variables crown encroachment and stem damage. Showing two outliers (tree 14 and 42) with a significantly higher lichen richness than the model predicts. These outliers attributable to natural variation in the community and were therefore retained. R = large residual.

Tree	Lichen richness	Fit	Resid	Std Resid	
14	18.00	10.88	7.12	2.49	R
42	20.00	12.84	7.16	2.71	R

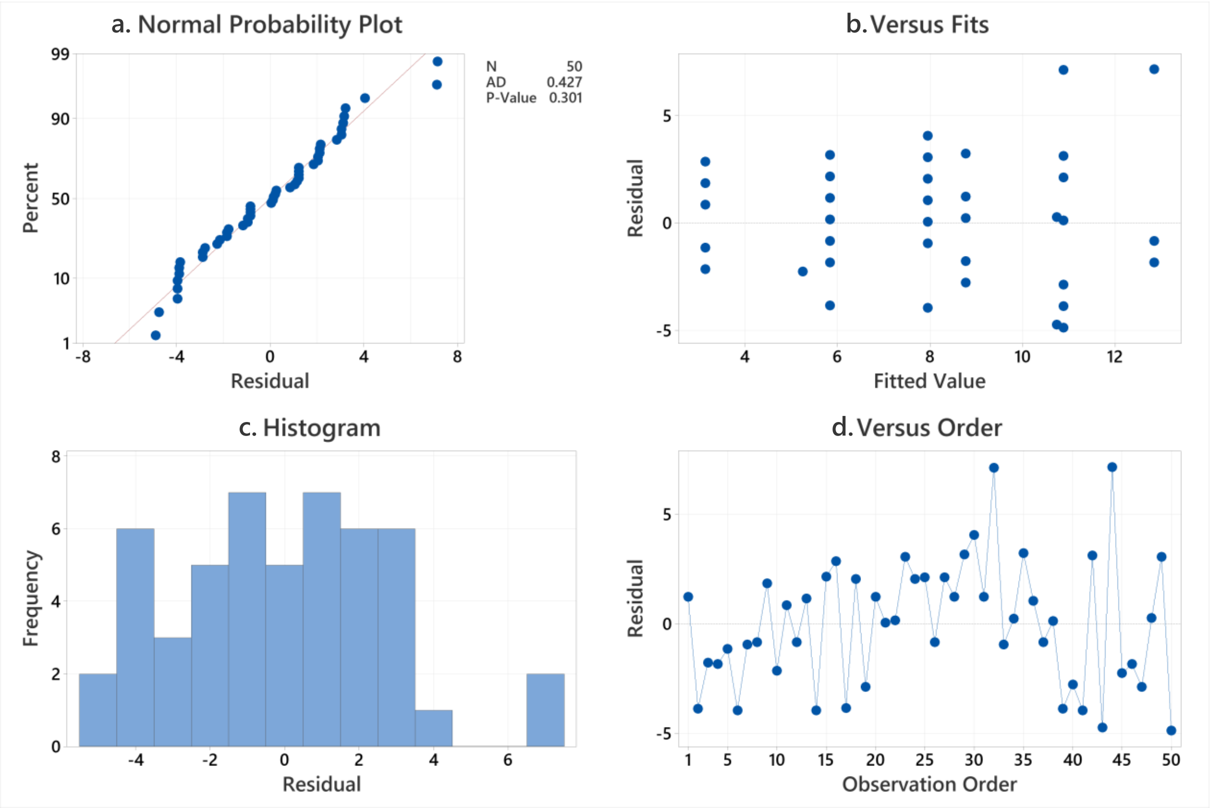

Figure 1: Residual plots of the generalized linear model explaining lichen richness through the independent variables crown encroachment and stem damage.

The normality probability plot (a) shows a normal distribution of the residuals following approximately a straight line (and two outliers) supporting the condition that the error terms are normally distributed. The residuals versus fits plot (b) shows a random distribution of residuals with constant variance. The histogram of residuals (c) shows an approximately normal distribution of residuals with two outliers* (uneven distribution can be caused by insufficient data points). The residuals versus order plot (d) shows a random distribution of residuals, which rules out systematic effects due to time or data collection order. * The two outliers attributable to natural variation in the community and are therefore retained.*

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