



Examensarbeten

Institutionen för skogens ekologi och skötsel

2012:3

Epiphytic lichen flora in a boreal forest chronosequence



Foto: Aron Sandling

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Epifytisk lavflora i en boreal kronosekvens

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Nyckelord / Keywords:

Island biogeography theory, gradient, succession, species richness, species composition,
bark structure, bark pH

ISSN 1654-1898

Umeå 2012

Sveriges Lantbruksuniversitet / *Swedish University of Agricultural Sciences*
Fakulteten för skogsvetenskap / *Faculty of Forest Sciences*
Examensarbete i biologi / *Master degree thesis in Biology*
EX0642, 30 hp, avancerad nivå/ *advanced level A2E*

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I denna rapport redovisas ett examensarbete utfört vid Institutionen för skogens ekologi och skötsel, Skogsvetenskapliga fakulteten, SLU. Arbetet har handledts och granskats av handledaren, och godkänts av examinator. För rapportens slutliga innehåll är dock författaren ensam ansvarig.

This report presents an MSc/BSc thesis at the Department of Forest Ecology and Management, Faculty of Forest Sciences, SLU. The work has been supervised and reviewed by the supervisor, and been approved by the examiner. However, the author is the sole responsible for the content.

Abstrakt

Epifytiska lavar utgör en viktig del av floran i den boreala zonen. Några miljövariabler är kända för att styra artrikedomen och artsammansättningen av epifytiska lavar på beståndsnivå, såsom träddiversitet, beståndsålder, fuktighet och trädens barkstruktur. Skogsbränder utgör den viktigaste störningen i boreala skogar men studier på brandeffekter på epifytiska lavar är mycket få. Detta arbete undersökte artrikedomen, diversiteten och artsammansättningen av epifytiska lavar på basala delar av björkar längs en gradient av 30 skogsbeklädda öar som skiljer sig i storlek och brandhistorik i den norra boreala zonen i Sverige. Målet med studien var att undersöka hur lavfloran påverkades av östorleken och miljövariablerna längs gradienten. Sammanlagt noterades totalt 21 lavararter av vilka majoriteten var habitatgeneralister. Med östorlek ökade täckningsgraden och antalet lavararter per stam, samt förändrade lavarnas artsammansättning. Diversiteten var i genomsnitt högre på större öar men inte signifikant. Öarnas brandfrekvens, vilket indirekt bestäms av öarnas storlek, påverkade många viktiga miljövariabler för de epifytiska lavarna. Oavsett östorlek hade skuggiga öar med hög barkstruktur på björkstammarna den mest diversa och artrika lavfloran. Lavfloran bestämdes i denna studie i största utsträckning av de brandförorsakade förändringarna i markvegetation, produktion och stamvariabler. Effekten av östorlek ansågs vara av mindre betydelse jämfört med miljövariablerna som påverkade både på ö- och stamnivå. Denna studie påvisar hur brandhistorik och miljövariabler i den boreala zonen kan strukturera epifytiska lavar.

Abstract

Epiphytic lichen species richness, diversity and composition was studied on basal trunks of *Betula pubescens* along a gradient of 30 forested islands differing in size and fire history in the northern boreal zone of Sweden. The goal of the study was to examine how the epiphytic lichen community changed with island size and environmental factors. The lichen community mainly consisted of habitat generalists and 21 species were recorded in total. Island size was found to increase species number per trunk and lichen coverage, and to change the species composition. Diversity was on average higher on larger islands, but not significantly. Fire history, which is indirectly determined by island size, was found to determine many of the important environmental factors for epiphytic lichens. Regardless of island size, islands with low incident light (i.e., shady) and trunks with high bark roughness were found to have the most diverse and species-rich lichen flora. The lichen flora was in this study mostly explained by the fire induced changes in vegetation, productivity and trunk variables. The effect of island area was considered of minor importance compared to the environmental variables operating at both the island and trunk levels. This study demonstrates how the most important natural disturbance in the boreal forest zone can structure the epiphytic lichen flora.

Introduction

Epiphytic lichens compose an important part of the boreal forest zone flora (Hauck, 2011), and contribute to biodiversity through having a large species pool (Nordin et al., 2011) and by serving as structural components that provide habitat, food and nesting material for other organisms (Galloway, 1992; Rhoades, 1995; Esseen et al., 1997). The species richness of epiphytic lichens is especially high in natural forests and other stands that have high biological and structural diversity (Esseen et al., 1992; Dettki & Esseen, 1998; Kuusinen & Siitonen, 1998). Other hot-spot sites for species-rich and distinct epiphytic floras include moist riparian zones particularly in ravines (Karström et al., 1993; Hallingbäck, 1995).

Despite the high diversity of epiphytic lichens in boreal forests, we have an incomplete knowledge about the factors that control their diversity. However, some factors known to influence epiphytic lichen species richness in the boreal zone include tree diversity (Esseen, 1981; Kuusinen, 1996), stand age (Dettki & Esseen, 1998; Kuusinen & Siitonen, 1998; Jonsson & Jonsell, 1999), moisture (Adams & Rissler, 1971; Eversman et al., 1987) and bark structure (Kuusinen, 1994; Gustafsson & Eriksson, 1995; Kermit & Gauslaa, 2001). Forest stand size and isolation are well recognized as important factors controlling species richness on larger spatial scales (MacArthur & Wilson, 1967). Island gradients are useful tools for aiding our understanding underlying mechanisms regulating patterns in diversity (Connor & McCoy, 1979; Wardle, 2002). Berglund & Jonsson (2001) studied the species richness of epiphytic lichens on forested patches or 'tree islands' of varying size in a mire mosaic landscape to determine the effects of stand size and isolation. They found that at the patch level, area was the most important factor for determining species richness of epiphytic lichens while patch isolation was unimportant.

Chronosequences represent important gradients of vegetation composition and soil fertility (Wardle, 2002; Wardle et al., 2008). Changes across chronosequences could potentially affect the epiphytic lichen community through alterations in tree species composition, light conditions and bark characteristics, but since there is a lack of studies concerning this, not much is known. Fire is the major driver of chronosequences in boreal forests and should affect factors known to influence epiphytic lichens, but since fire effects on epiphytic lichens remains largely unknown (Hauck, 2011) there is a need for studies exploring lichens across fire-driven chronosequences in natural boreal forests (Johansson, 2008).

In this study, I used a gradient of 30 islands comprising a chronosequence generated by increasing time since fire and spanning 5000 years. In this system, larger islands get struck by lightning more often than smaller ones, so as island size declines the mean time since the most recent fire increases (Wardle et al., 1997; 2003). With increasing time since fire the islands enter into a state of ecosystem 'retrogression' (Peltzer et al., 2010), accompanied by a decline in plant productivity, soil fertility and decomposition rates (Wardle et al., 1997; 2003). This retrogression is also characterized by a build up of organic matter and a shift in diversity of plants, insects, birds and some invertebrates (Wardle et al., 1997; 2003; 2012). On this island gradient I examined the epiphytic lichen flora on trunks of *Betula pubescens*, a tree that occurs commonly on all the islands. The goal of the study was to examine how the lichen species richness, diversity and composition changed with island size. Further I aimed to investigate how environmental variables that may have a role in controlling lichens changed across the island gradient, including trunk diameter, bark pH, bark structure and trunk inclination, and whether lichen community properties were related to these variables. I also determined whether variation in lichen community properties were related to other variables previously collected across these islands, such as island age, light conditions, island isolation, vascular plant species richness, productivity, humus pH and standing biomass (Wardle et al., 1997; 2003; 2008; Jonsson et al., 2009).



Fig. 1. An overview picture of the northern part of the study system in lake Hornavan corresponding to the map in fig 2C. The picture is taken from the nearby mountain Akkellis southwest of the motive in the picture. Photo: Aron Sandling

Materials and methods

Study area description

To conduct this study I used 30 forested islands located in the two neighboring lakes, Hornavan and Uddjaur, in the northern boreal zone of Sweden ($65^{\circ} 55' N$ to $66^{\circ} 09' N$; $17^{\circ} 43' E$ to $17^{\circ} 55' E$) (Fig. 1; Fig.2). All islands consist of moraine deposits created when the land ice retreated 9000 years ago (Wardle et al., 1997) and have relatively low influences of human activities (Bergman, 1995). These islands vary in size from 0.02 to 15 ha and are

equally divided into three size classes; 10 ‘large’ (>1.0 ha), 10 ‘medium’ (0.1 to 1.0 ha) and 10 ‘small’ (<0.1 ha) (Wardle et al., 2003; 2012). Island size determines fire regime; large islands burn more often than smaller ones because they are struck more frequently by lightning (Wardle et al., 1997). As such, the mean time since fire for the large, medium and small islands is 585, 2180 and 3250 years respectively. This variation in fire frequency has created a gradient in successional stage between the islands. The vegetation of the large islands is dominated by early successional species such as *Pinus sylvestris* and *Vaccinium myrtillus*, while small islands are dominated by late successional species such as *Picea abies* and *Empetrum hermaphroditum* (Wardle et al., 1997) (Fig. 4). Further, *Betula pubescens* occurs commonly across the gradient, although as succession progresses the plants become smaller and less productive, and their foliar tissues become more defended (Crutsinger et al., 2008; Wardle et al., 2012).



Fig. 2. A. A map of northern Europe with Sweden in gray and a rectangular showing the position of the study area. B. This map shows the two lakes Hornavan and Uddjaure, where the islands in this study are found. C. A part of the archipelago in Hornavan including some of the investigated islands.

Data collection and measurements

On all islands, four individual *Betula pubescens* trunks were surveyed for lichens and environmental variables (Table 1). The survey included living trees that ranged between 8 and 20 cm in diameter at breast height (DBH). Trees in the vicinity of plots used for previous work (Wardle et al., 2003; 2012) were chosen since most of the additional data used in this study derives from them (Table 1). To obtain cover estimates and species richness measures a vertically oriented 8 x 28 cm plot was placed at 4 locations on each trunk, two with the bottom edge 2 cm from the ground layer and two with the bottom edge 1.3m from the ground

layer. For the two plots at each height, one was placed on the south facing side of the trunk and the other on the north facing side. The plot consisted of a frame drawn on transparent plastic paper with a grid of 5 x 20 lines marked 1.3cm apart, yielding 100 points of intersection. Cover of each species was estimated through determining the number of times each species occurred at the points of intersection. All lichen species within the entire plot were also noted, to enable a measure of species richness. All species occurring below 2m on the trunk was also noted to get an estimate of species richness for the whole trunk. Because of a high number of underdeveloped individuals and identification difficulties, all the individuals belonging to the genus *Cladonia* were treated as *Cladonia* spp. in this study.

At each plot position the inclination of the stem was measured with an electronic clinometer (Haglöf). The inclination was measured in degrees from the vertical axis and given either a positive or negative value depending on if the stem was leaning from (positive) or towards (negative) the surveyor.

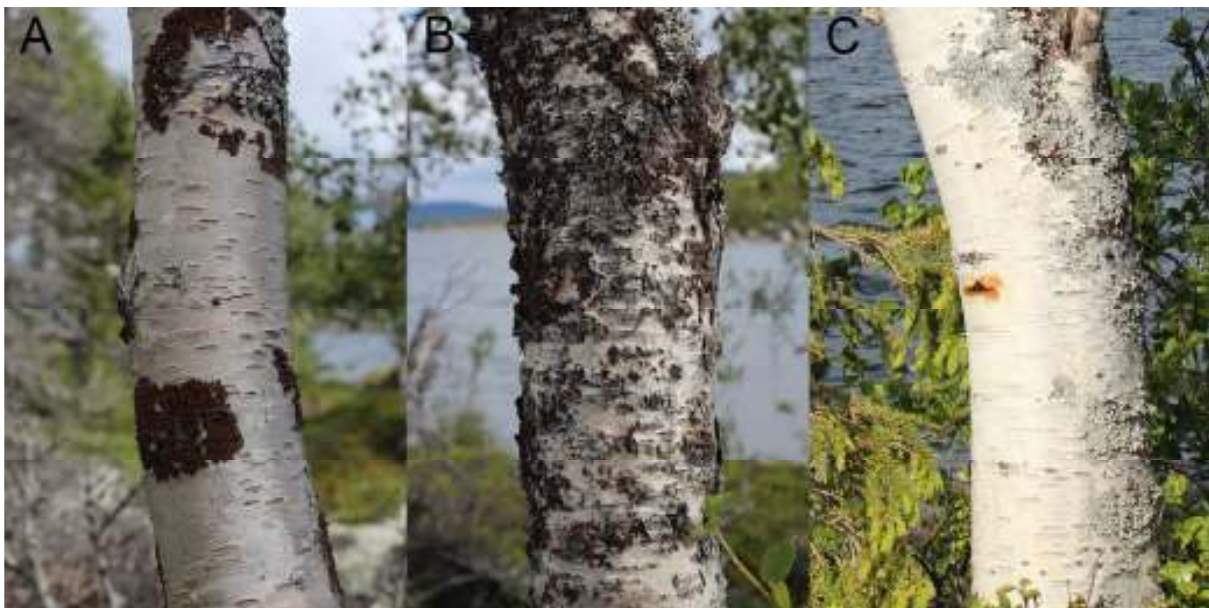


Fig. 3. Examples of different bark structures. **A.** Represents a smooth surface with no amount of cracks. **B.** A trunk with very rough surface structure. **C.** This trunk has a smooth surface with cracked bark (open wound with brown leakage). Photos: Aron Sandling

Two measures of bark structure were taken for each tree by examining epiphyte free surfaces of the trunks (Fig. 3). First, depending on the occurrence and size of cracks the trees were separated into three classes; (A) no cracks, (B) intermediate amount of cracks, and (C) high amounts of cracks. Second, the tree was placed in one of three classes based on surface structure: (A) smooth, (B) some roughness and (C) very rough surface structure. Since these are relative measures the delimitation between the categories was determined during a reconnaissance visit to the islands prior the study.

For each tree, a flat surface electrode pH meter (PH100: ExStick[®] pH meter) was used to measure the pH of the bark as described by Farmer et al. (1990). Measurements were taken at three epiphyte free bark surfaces on both the north and south side of the trunk. Before each measurement the bark surface was sprayed (3 spritzes) with a 0.1 M solution of KCl to enhance cation exchange. This approach has previously been shown to have high accuracy for measuring bark surface pH (Schmidt et al., 2001).

Statistical analysis

Four main response variables were used in this study, i.e., “trunk richness” which is defined as the total number of lichen species occurring from 0m to 2m height on the trunk; “plot richness” which is the total number of lichen species occurring inside the four plots on the trunk; “diversity” which is the Shannon diversity index (Shannon, 1948) calculated for each trunk using the cover estimates for each species from all the four plots on the trunks; and “coverage” which is the percentage cover by lichens on all the four plots on the trunks. Since individual islands serve as the units of replication in this study, the mean value of all four trunks was determined for each island, to yield a single value of each variable for all islands. One way ANOVA was used to test the effect of island size on the response variables.

To evaluate compositional responses, the species cover data was also subjected to Principal Components analysis (PCA) across the 30 islands; for each species the mean of all trunks on each island was used to provide a single data point for that island. The first and second principal component axis scores were analyzed by one way ANOVA to test for the effect of island size. Spearman rank correlation coefficients were calculated to evaluate relationships among pairs of environmental variables and between each of the lichen response and environmental variables.

Since all data for the study was analyzed by parametric tests the response variables were examined prior to analysis to check if they satisfied the assumptions of normality and homogeneity of variance. Some data was log transformed to fulfill the assumptions for parametric tests. The data for species composition was power transformed according to Yeo & Johnson (2000) since negative values were included. Analyses were made using the statistical program R ver. 2.14.0 for Windows (R Foundation for Statistical Computing, Vienna, Austria).

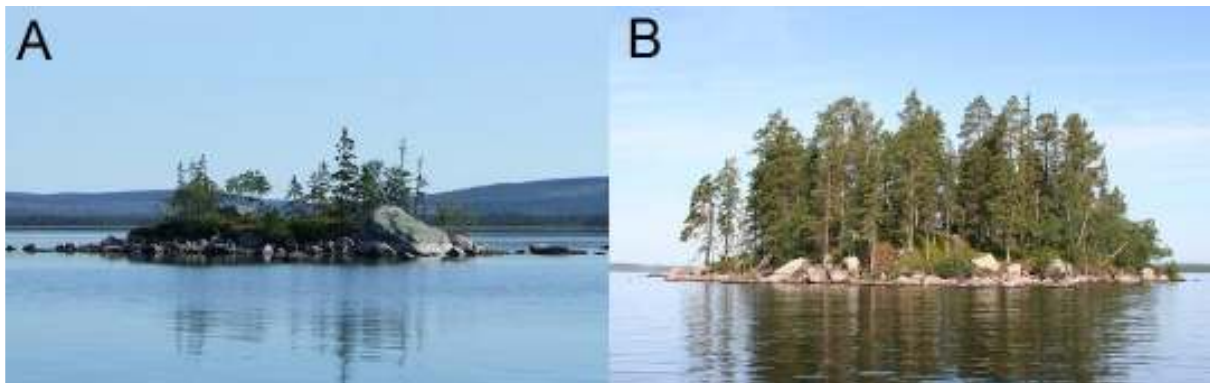


Fig. 4. Pictures of different sized islands. **A.** Small sized island. **B.** Medium sized island.
Photo: Micael Jonsson & Aron Sandling

Table 1. Description of the environmental variables used in analyses.

Variables	Scale	Description
Bark cracks	Categorical	(A) no amount, (B) intermediate amount and (C) high amounts of cracks.
Bark pH	Continuous	The averaged pH for both the north and south side of the trunks.
Bark roughness	Categorical	(A) smooth, (B) some roughness and (C) very rough surface.
Inclination	Continuous	Measured in degrees at each plot position with an electronic clinometer.
Island age	Continuous	Through ¹⁴ C dating of charcoal in the humus (Wardle et al., 1997; 2003).
Island size	Continuous	Island area in ha (Wardle et al., 1997).
Isolation	Interval	Proportion of land area of other land masses between the shoreline and 500 m from the shoreline (Jonsson et al., 2009).
Light	Interval	The proportion of incident light intercepted by the forest canopy (Wardle et al., 2003).
Production	Continuous	Carbon produced by trees and shrubs in kg/m ² /year (Wardle et al., 2003).
Plant richness	Continuous	Vascular plant species richness per unit area, in circular 10 m radius plots (Wardle et al., 2008).
Humus pH	Continuous	Averaged pH in the humus for each island (Wardle et al., 1997).
Plant diversity	Continuous	A shannon diversity index for the shrub and tree species calculated from data from Wardle et al. (1997).
Tree diversity	Continuous	A shannon diversity index for the tree species calculated from data from Wardle et al. (1997).
Trunk diameter	Continuous	Diameter at breast height of the <i>Betula pubescens</i> trunks measured in cm.

Results

In the study a total of 21 lichen species were found on the *B. pubescens* trunks (Appendix 1). The community was dominated by common habitat generalists, and *Hypogymnia physodes*, *Melanohalea olivacea*, *Parmelia sulcata* and *Parmeliopsis ambigua* collectively made up 88% of the total lichen coverage.

Species richness per trunk and total lichen coverage was significantly influenced by island size class, and was highest on medium and large islands (Fig. 5A, D). The species richness per plot and diversity of lichens was on average higher for medium and large islands but not significantly (Fig. 5B, C).

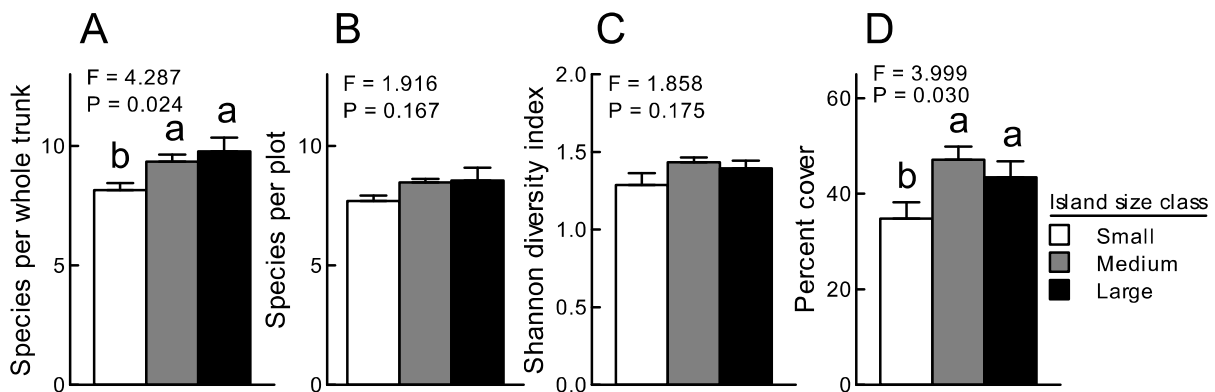


Fig. 5. **A.** Lichen species richness per trunk below 2m in height. **B.** Lichen species richness inside the four plots for each trunk. **C.** Shannon diversity index and **D.** Percent cover of all lichens depending on island size class. The F and P values are from one way analysis of variance, ANOVA. Vertical bars indicate +1 SE and bars topped with different letters differ significantly at P = 0.05 (Tukey's HSD test).

Species composition as assessed using ordination (PCA) scores was significantly different between island size classes for the first axis scores which explained most of the variation (Fig. 6), but was not different among island size classes for the second axis.

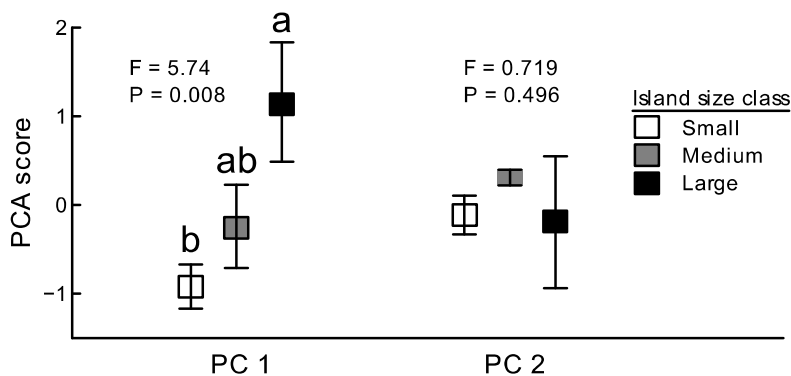


Fig 6. Mean PCA scores \pm 1 SE for species composition depending on island size class. The F and P values are from one way analysis of variance, ANOVA. Bars topped with different letters differ significantly at P = 0.05 (Tukey's HSD test). The first axis (PC 1) explained 23.6% and second axis (PC 2) explained 14.9% of the total variation in the species composition matrix.

The PCA scores for the first axis were primarily driven by the four most common species in the study, i.e., *H. physodes*, *M. olivacea*, *Parmelia sulcata* and *Parmeliopsis ambigua*, which were, with the exception of *M. olivacea*, all significantly affected by island size class (Fig 7). *H. physodes* and *P. ambigua* increased while *P. sulcata* decreased in coverage as island size increased (Fig 6). The frequency of two species known to be substrate and habitat specialists (Karström et al., 1993; Nitare, 2000), *Hypogymnia bitteri* and *Bryoria fremontii*, was relatively high on medium and large islands, but absent from small islands (Appendix 1).

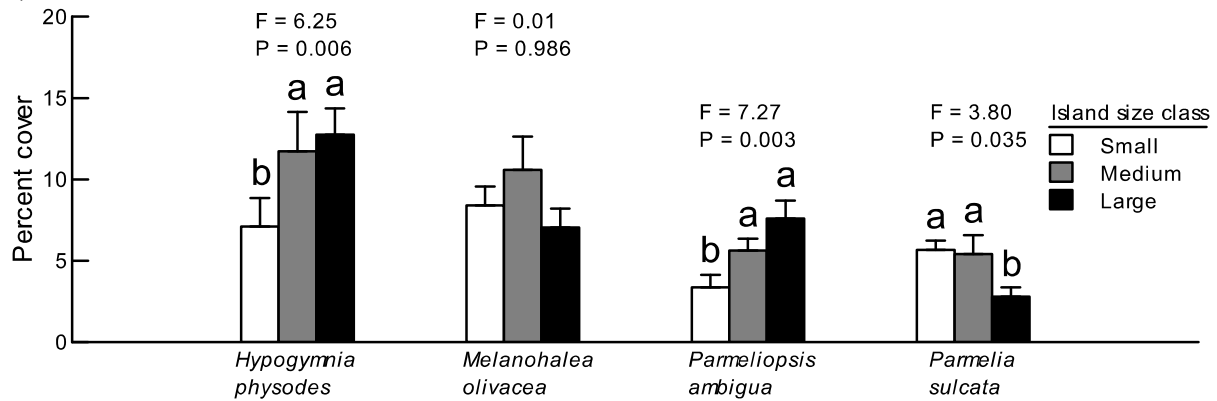


Fig. 7. Percent coverage of *Hypogymnia physodes*, *Melanohalea olivacea*, *Parmeliopsis ambigua* and *Parmelia sulcata*, depending on island size class. The F and P values are from one way analysis of variance, ANOVA. Vertical bars indicate +1 SE and bars topped with different letters differ significantly at P = 0.05 (Tukey's HSD test).

Table 2. Spearman correlations between the lichen response variables and the environmental variables (n = 30; * p < 0.05; ** p < 0.01; *** p < 0.001).

	Trunk richness	Plot richness	Diversity	Coverage
Inclination	-0.096	-0.095	-0.135	-0.133
Trunk diameter	0.438*	0.299	0.095	0.372
Bark pH	-0.489**	-0.469**	-0.318	-0.524**
Bark rough	0.484**	0.404*	0.387*	0.402*
Bark cracks	0.259	0.262	-0.088	0.185
Island size	0.435*	0.129	0.139	0.254
Humus depth	-0.569**	-0.344	-0.255	-0.327
Island age	-0.101	0.029	0.055	-0.123
Light	-0.519**	-0.461*	-0.474**	-0.429*
Isolation	-0.124	-0.023	0.064	0.055
Plant richness	-0.263	-0.069	-0.225	-0.154
Humus pH	0.286	0.034	-0.158	-0.125
Productivity	0.465**	0.346	0.212	0.271
Standing biomass	0.562**	0.301	0.154	0.564**
Plant diversity	0.099	0.405*	0.349	0.164
Tree diversity	0.270	0.523**	0.373*	0.281

Island size was significantly correlated with almost all other environmental variables in the study system (Appendix 2), and had a significant positive correlation with bark roughness and trunk diameter, and a negative correlation with bark pH (Appendix 2). Trunk inclination and the degree to which the bark was cracked were not significantly correlated with any other

environmental variable (Appendix 2). Lichen species richness (per trunk and per plot), diversity and coverage were all significantly negatively correlated with bark pH (though this was not significant for diversity) and light and positively correlated with bark roughness (Table 2). Productivity and standing biomass had a significant positive correlation with species richness per trunk, and standing biomass also had a significant relationship with lichen cover (Table 2). Tree diversity had a significant positive correlation with species richness per plot and diversity, and plant diversity was significantly correlated with species richness per plot (Table 2).

Discussion

The main goal of this study was to examine how epiphytic lichen species richness, diversity and composition changed with island size. Species richness per trunk was found to increase significantly with island size, which is consistent with results from other studies investigating island size effects on the plot or tree scale (Kruys & Jonsson, 1997; Berglund & Jonsson, 2001). Several mechanisms could explain the pattern in this study, however it is most likely explained by the fire induced changes in vegetation, productivity and trunk variables with island size. As such, the larger islands host *B. pubescens* trees that have higher bark roughness in more shaded environments. The increase of lichen species per trunk with island size is probably not a direct effect of the increase in land mass as predicted by island biogeography theory (MacArthur & Wilson, 1967) but is instead driven by the changes in stand and trunk factors across the island size gradient.

We found a significant effect of island size on lichen species richness only when whole trunks were considered as opposed to the plots on the trunks. Measurements on the whole trunks involved quantifying species richness over a larger area than on the plots, and this result can therefore be explained by the fact that the larger the examined area becomes, the higher the chance is of finding rare species on the trunks. This might also explain the non-significant relationship between diversity and island size, given that diversity was quantified at the scale of the plots on the trunks.

Species composition was significantly different between island size classes, and this was driven by a change in cover of the four most common species present. Lichen communities are formed through several inter-related processes at the tree and stand level (Ellis, 2011), and as such coexisting species respond differently to underlying environmental factors, to competition (Armstrong & Welch, 2007), and to lichenivory (Asplund, 2010). Identifying the specific variables responsible for driving changes in the most common species coverage across the gradient is therefore difficult. However, the higher bark roughness on medium and large islands could be partly responsible for the higher cover of *H. physodes*, since its soredia have been shown to have higher survival on rough bark (Armstrong, 1990). *Parmeliopsis ambigua* also responded positively to island size, but it should be less affected by bark roughness since it occurs mainly on the basal portion of the trunks, where bark roughness is generally high regardless of island size. Its cover may be better explained by the more shaded and protected conditions on the larger islands. *P. sulcata* responded differently to the other species to island size, and had on average half the coverage on large islands compared to medium and small ones. Compared to the other common species, *P. sulcata* is known to have preference for high bark pH (Hultengren et al., 1991) and the comparatively low bark pH on large islands could therefore be responsible for its response to island size. Regardless of the underlying mechanisms, the results clearly indicate that island size was an important driver of species composition. The higher frequency of substrate and habitat specialist lichen species on medium and large islands is probably mostly a result of these islands having more suitable micro-environmental and light conditions than small islands.

The study further aimed to investigate changes in environmental variables across the island gradient and link these to lichen community properties. Island size was clearly responsible for most of the changes in those environmental variables considered important for lichens. Light, bark pH and bark roughness stood out as the most important factors influencing lichen species richness, diversity and coverage in this study. The importance of bark roughness in structuring the lichen flora is well recognized (Brodo, 1973; Kuusinen, 1994; Gustafsson & Eriksson, 1995; Mistry & Berardi, 2005). As bark structure increases the lichen colonization rates probably increases as their diaspores more easily attach to the trunk. Increased bark structure also results in a higher micro-habitat heterogeneity and water holding capacity which may also allow higher lichen diversity. While an open forest structure can generally support a diverse lichen flora, the highest incident light values in this study are associated with a more open forest that will also allow greater weather and sun exposure. This could in turn serve to stress lichens through exposing them to higher variations in temperature, desiccation and mechanical damage by wind (Esseen, 1994). Similarly, intermediate and low values of incident light should be associated with more protected and shady conditions with higher humidity. This could explain the negative correlation between light and the response variables.

Bark pH responded in an unexpected manner to island size across the chronosequence. As such, while *B. pubescens* trees became smaller and less productive on smaller islands in conjunction with decreasing soil fertility and pH (Wardle et al., 2003; Crutsinger et al., 2008), the bark pH of *B. pubescens* increased (Table 3). This is in contrast to other studies which have shown positive correlations with soil and bark chemistry (Gustafsson & Eriksson, 1995; Gauslaa & Holien, 1998). Bark pH measurements was not done beneath obvious wounds and cracks in this study since these often leak nutrients and cations, and can therefore increase pH (Barkman, 1958; Staxäng, 1969; Gauslaa, 1995). Further, the relationship between cracked bark and bark pH was negligible (Appendix 2), meaning that the presence of visible cracks is not a likely explanation of the response of bark pH to island size in this study. However, the roughness of the bark was highly negatively correlated with bark pH (Appendix 2), and given that bark roughness was higher on the large islands, this may explain the decline in pH with island size. The bark on the small islands was thinner (personal observations) and more smooth compared to larger islands, and thinner bark is likely to be less rough (Fritz et al., 2009). As bark thickness increases, the pH has been shown to decrease (Hyvärinen et al., 1992; Legrand et al., 1996) probably as a result of an increase in the distance from the bark surface to the internal tissues of the trees which are rich in K⁺ ions which elevate pH. Considering this, the negative correlation between species richness and bark pH should be carefully interpreted.

In conclusion, this study demonstrates how fire history and island area can structure the epiphytic lichen flora. It also show how stand and tree scale factors, such as light conditions and bark roughness, can be regulated by fire history and how these factors subsequently influence epiphytic lichens. Whereas much work in the area of epiphytic lichen ecology has focused on landscape, stand or tree scale factors in relation to lichens, little interest have been addressed toward how natural disturbance can structure lichen communities. This study therefore provides an improved understanding in how epiphytic lichens can respond to succession following wildfire. The results from this study have some implications that could be applied to the boreal forest in general. The results suggests that even common lichen species becomes less frequent in small fragmented stands, this could imply that small stands not only inhibit rare species but could also have a negative effect on more common species. The small islands which have from the long term absence of wildfire gone into a state of retrogression, characterized by low plant productivity, soil fertility and decomposition rates, generally had poorer lichen flora compared to the medium and large islands. The results could

therefore also suggest that retrogressed areas have a poorer epiphytic lichen compared to areas that historically have been subjected to some kind of disturbance e.g. wildfire. It's important to point out the possibility that some variables in this system could be more or less inter correlated with each other. To further study the effects of ecosystem succession and fire history on the epiphytic lichen flora it's therefore important with additional studies in e.g. chronosequences on mainland.

Acknowledgements

I would like to thank my supervisors David Wardle and Johan Asplund for all support and feedback in all parts of this project. I would also like to thank all the people working on the islands this year for a pleasant field season. Big thanks to Bright Kumordzi and Benjamin Jackson for statistical help and lastly a special thanks to Micael Jonsson and Sara Rundqvist for all your support and help.

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Appendix 1. Lichen species noted on the *B. pubescens* trunks and their relative frequency (i.e., proportion of the trunks on which they occurred) and mean percent cover \pm 1 SE depending on island size class. Note that frequency is derived from the whole trunks and percent cover is from the plots.

Species	Frequency			Percent cover		
	Small	Medium	Large	Small	Medium	Large
<i>Bryoria cappillaris</i>	0.00	0.10	0.18	-	-	-
<i>Bryoria fremontii</i>	0.00	0.18	0.45	-	0.06 \pm 0.06	0.19 \pm 0.16
<i>Bryoria fuscescens</i>	0.00	0.03	0.13	-	-	0.30 \pm 0.30
<i>Bryoria simplicior</i>	0.81	0.93	0.88	0.14 \pm 0.04	0.52 \pm 0.14	0.61 \pm 0.30
<i>Cladonia spp</i>	0.24	0.25	0.45	0.05 \pm 0.05	0.06 \pm 0.06	0.02 \pm 0.02
<i>Hypocenomyce scalaris</i>	0.00	0.03	0.03	-	0.01 \pm 0.01	-
<i>Hypogymnia bitteri</i>	0.00	0.15	0.05	-	-	0.18 \pm 0.18
<i>Hypogymnia physodes</i>	1.00	1.00	1.00	7.11 \pm 1.75	11.7 \pm 2.42	12.8 \pm 1.62
<i>Hypogymnia tubulosa</i>	0.05	0.00	0.10	0.01 \pm 0.01	-	-
<i>Imshaugia aleurites</i>	0.00	0.05	0.05	-	-	-
<i>Lecanora circumborealis</i>	0.86	1.00	0.93	1.04 \pm 0.47	0.78 \pm 0.15	0.63 \pm 0.14
<i>Lecanora symmicta</i>	0.03	0.03	0.00	-	0.01 \pm 0.01	-
<i>Melanohalea olivacea</i>	1.00	1.00	0.98	8.40 \pm 1.15	10.6 \pm 2.04	7.04 \pm 1.17
<i>Mycoblastus sanguinarius</i>	0.03	0.13	0.10	0.01 \pm 0.01	-	0.04 \pm 0.03
<i>Ochrolechia androgyna</i>	0.30	0.33	0.35	0.21 \pm 0.11	0.09 \pm 0.06	0.53 \pm 0.32
<i>Parmelia sulcata</i>	1.00	1.00	1.00	5.68 \pm 0.56	5.41 \pm 1.15	2.79 \pm 0.58
<i>Parmeliopsis ambigua</i>	1.00	1.00	1.00	3.37 \pm 0.77	5.63 \pm 0.73	7.59 \pm 1.11
<i>Parmeliopsis hyperopta</i>	0.84	1.00	1.00	1.19 \pm 0.34	1.77 \pm 0.35	2.93 \pm 0.82
<i>Platismatia glauca</i>	0.00	0.05	0.05	-	-	0.01 \pm 0.01
<i>Tuckermannopsis chlorophylla</i>	0.08	0.15	0.13	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01
<i>Vulpicida pinastri</i>	1.00	1.00	0.95	0.23 \pm 0.08	0.41 \pm 0.10	0.23 \pm 0.10

Appendix 2. Spearman correlations between the environmental variables (n = 30, * p < 0.05; ** p < 0.01; * p < 0.001).**

	Inclination	Trunk diameter	Bark pH	Bark roughness	Bark cracks	Island size	Humus depth	Island age	Light	Isolation	Plant richness	Humus pH	Productivity	Standing biomass	Plant diversity	Tree diversity
Inclination	1															
Trunk diameter	0.315	1														
Bark pH	0.063	-0.420*	1													
Bark roughness	0.112	0.258	-0.678***	1												
Bark cracks	0.167	0.142	-0.015	0.094	1											
Island size	0.012	0.457*	-0.450*	0.422*	-0.223	1										
Humus depth	0.072	-0.360	0.218	-0.250	0.149	-0.769***	1									
Island age	-0.045	0.209	0.291	-0.333	0.213	-0.714***	0.554**	1								
Light	0.147	-0.357	0.339	-0.338	0.101	-0.391*	0.327	0.032	1							
Isolation	0.252	0.198	-0.097	0.185	0.175	-0.158	0.355	0.249	0.027	1						
Plant richness	-0.250	0.309	0.422*	-0.378*	0.284	-0.745***	0.455**	0.455*	0.226	0.154	1					
Humus pH	-0.048	0.218	0.081	-0.166	-0.156	0.411*	-0.573***	-0.241	-0.049	-0.281	0.345	1				
Productivity	-0.135	0.489**	-0.313	0.181	-0.299	0.636***	-0.509**	-0.280	-0.507**	-0.420*	0.179	0.630***	1			
Standing biomass	-0.049	0.552**	-0.544**	0.376*	0.035	0.782***	-0.637***	-0.468**	-0.558**	-0.498**	-0.014	-0.014	-0.342	1		
Plant diversity	-0.057	0.012	-0.187	0.214	-0.008	-0.386*	0.303*	0.340*	-0.132	0.375*	0.190	0.184	-0.080	0.930***	1	
Tree diversity	-0.011	0.074	-0.265	0.293	0.018	-0.192	0.146	0.186	-0.359	0.294	0.184	0.184	-0.080	0.930***	0.930***	1

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