Temporal trends in shade sensitive epiphytic cryptogams residing on old trees

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Abstract

Question: How does abandoned management affect species assemblages of shade sensitive bryophytes and lichens residing on old trees in traditionally light- open environments?

Method: I examined compositional change over 20 years in the epiphytic vegetation of old pollarded trees of *Fraxinus excelsior* in a cultural landscape of western Norway through re-sampling. The nature of changes in the epiphytic composition in relation to environment was identified through 1) Quantifying temporal turnover in species compositions along DCA axes; 2) Calculation of relative changes in Ellenberg indicator values for gradients of light and moisture through a weighted average technique and 3) Testing the effect of aspect, stem inclination/ height and the historical management regime on the rate of temporal turnover. This was done by mixed effect models with forward selection.

Results: Species composition of the epiphytic vegetation has changed significantly during the last 20 years. Species with lower indicator values for light (shade tolerant species) and higher indicator values for moisture (draught sensitive species) increased in relative abundance. An environmental trend towards more shady and moist conditions was detected. Among other shade sensitive species, shade and draught sensitive cyanolichens are negatively affected, whereas the shade and draught tolerant chlorolichens and liverworts residing throughout the stem within sheltered local environments, like *Lepraria spp, Phlyctis argena* and *Metzgeria conjugata* gain advantage.

Synthesis: The results imply a negative impact of abandoned management on temporal trends in assemblages of shade sensitive epiphyte bryophytes and lichens. The results demonstrated that the combination of approaches employed is operational and conceptually relevant for detecting temporal trends in cryptogam epiphytic communities in relation to environment at the scale of the landscape.

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Contents

Chapter 1. Introduction

The additive effects of agricultural change and silvicultural practices is expected to reduce the future viability of shade sensitive old- forest epiphytes throughout Europe (Ellis 2012; Johansson *et al*. 2013). Old pollarded trees are traditionally managed trees historically residing in different kinds of light- open wooded grasslands. High variation in ecological niches throughout the pollarded trunk provides habitats for many groups of organisms. Old pollards in open meadows are as such important to the survival of old growth, rare or endangered epiphytes adapted to light- open environments, like *Agonimia Allobata*, *Lobaria scrobiculata* and *Thelopsis rubella* (Rose 1992; Nilsson *et al*. 1994; Tønsberg *et al*. 1996, Gauslaa & Ohlson 1997; Moe & Botnen 1997, 2000; Bendiksen *et al*. 2008; Timdal *et al.* 2010).

Ceased pollarding and development of secondary woodland, followed by reduction in openness represent a main threat to many red- listed epiphytes (Jüriado *et al*. 2003; Johanson 2006). The degree of current openness is however conditioned by habitat history, and change in openness alters habitat conditions in terms of moisture, temperature and ventilation (Ranius *et al*. 2008). Humidity and shading is important to epiphytic composition (Leppik *et al*. 2011), and lichen assemblages are supposed to be more limited by light and less sensitive to desiccation than bryophytes (Kiraly *et al*. 2013). Low light availability limits lichen growth, but excessive light can however cause photoinhibition and quicken the dehydration of thalli (Green *et al*. 2008, Palmqvist *et al.* 2008). Studies on the photosynthetic activity of lichens claim that chlorolichens, as many other poikilohydric organisms like bryophytes, need nothing but humidity for initiation of their active period, as compared to cyanolichens who need liquid water (Lange *et al.* 1986; Büdel *et al.* 2013).

Several recent studies have addressed the impact of overgrowth to epiphytic diversity in European wooded grasslands (Leppik & Jüriado 2008; Juriado *et al.* 2009; Jönsson *et al.* 2011; Leppik *et al*. 2011; Jüriado *et al*. 2012; Johansson 2012; Marmor *et al*. 2012; Johanson *et al*. 2013; Ódor *et al.* 2013). In studies like these concerned with factors structuring epiphytic richness and composition, most often the spatial component of change in community structure from one sampling unit to another (turnover) and the levels of tree and stand are addressed (cf. Johansson 2006; Ellis 2012). To my knowledge, no study has ever measured temporal turnover in epiphytic communities of bryophytes and lichens at the fine scale and along environmental gradients, what might provide insights into the specific nature of epiphytic community development in relation to environment.

Old pollarded trees of *Fraxinus excelsior* and *Ulmus glabra* reside in the heterogeneous landscape of the cultural environment of Havrå. Moe & Botnen (1997) found that the species compositions of epiphytic bryophytes and lichens residing on the pollarded ash trees varied among trunks within local stands of variable openness across the landscape of Havrå. The high age (several hundred years) of the pollarded ash trees at Havrå, followed by slow vertical growth, provides high similarities in bark structure and consequently pH throughout the stem (even though fine- scale variations in bark chemistry may occur among discrete areas of the bole and along the height of the stem due to differences in stem- flow (Marmor *et al.* 2010)). High lateral and vertical heterogeneity in environments of light and moisture throughout the pollarded bole corresponds to a high within- tree variability in epiphytic composition along gradients of height/ stem inclination and aspect (Moe & Botnen 1997, 2000; Nordbakken & Austad 2010).

The combination of relatively high within- bole similarity in bark pH and high heterogeneity in environments of light and moisture throughout the pollarded stems provide favourable conditions for quantification of temporal turnover at the fine scale in relation to availability of light and moisture. Turnover requires one to define a specific gradient of interest with directionality (Andersson et al. 2011). In this study the community data on relative species abundances and associated environmental data of Moe & Botnen (1997) is re- sampled with the aim of answering the following questions: 1) Has there been any directional change in the species composition of the epiphytic communities on the pollarded trees at Havrå, with emphasis on the role of light and moisture availability? 2) Does the observed changes vary with the historical management regime of the pollards and surrounding meadows? 3) Is aspect and height important to within- tree variability in the observed changes? This approach may provide insight into the role of abandoned management to the future viability of assemblages of shade sensitive bryophytes and lichens residing on old trees in traditionally light- open landscapes.

Chapter 2. Materials and methods

Investigation area

The fieldwork of this study was performed at the southern side of the island Osterøy in western Norway, in the cultural landscape of the farm Havrå (Figure 1). Situated approximately 35 km from the coastline of Hordaland County, the area belongs to the boreonemoral vegetation zone (BN), within the markedly oceanic vegetation section, sub section humid (03h) (Moen *et al.* 1999). Mean temperature for the warmest month of July is 14 degrees, 0 degrees for the coldest month of January, and mean annual precipitation is approximately 2500 mm (Jordal & Gaarder 2009). A favourable local climate provides longer growth season as compared to other areas of the region (Austad & Skogen 1990). The bedrock of the area consists of a mica-schistzone in the major Bergen arc system and the soil in the area is fairly nutrient rich (Austad & Skogen 1988). The 31 farm buildings at Havrå, and the surrounding fields within which the pollards of investigation reside, are situated within an area of approximately 0.2 km2 rising from sea- level to 220 m. The steep south-facing slope of the area provide maximum insolation. During winter however, insolation is reduced due to shadow from the high mountains on the opposite side of Sørfjorden.

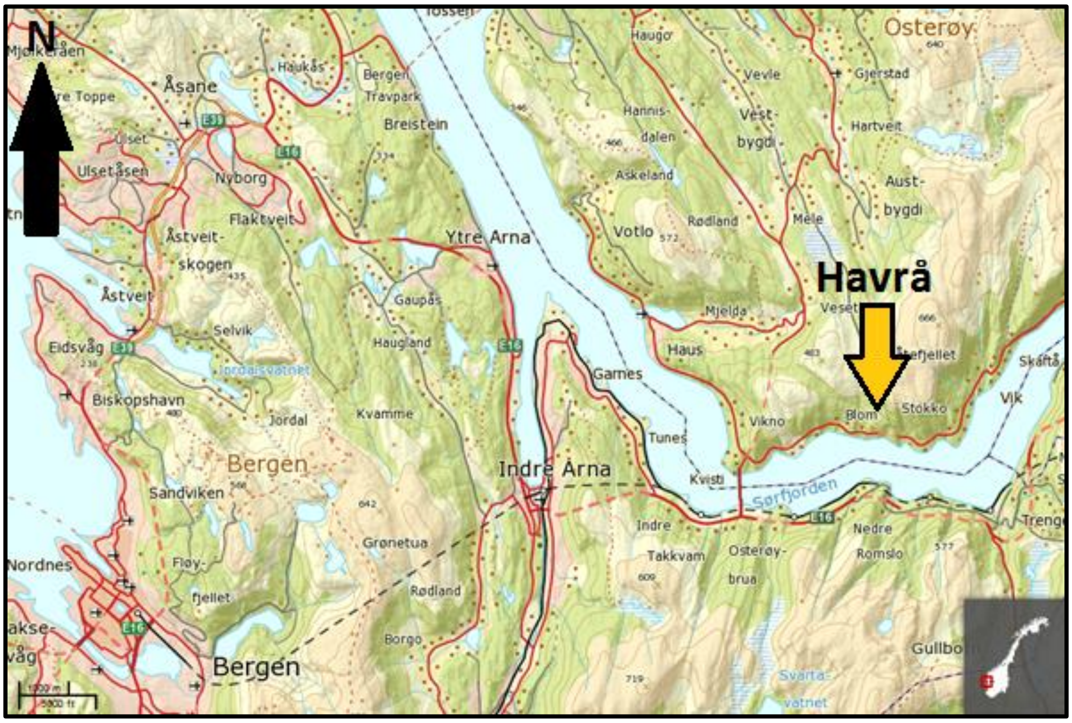


Figure 1: Map indicating the study area Havrå with a yellow arrow. The map is taken from norgeskart.no/ Norwegian national mapping authority.

Abandonment of the traditional management with pollarding, haymaking, grazing, and manuring at Havrå started in 1960, and overgrowth characterizes large parts of the outfield. Havrå was however the first cultural environment to be protected under section 20 of the Norwegian Cultural Heritage Act, and parts of the infield are still kept open through traditional management. In other areas, the secondary woodland developed during the last 50 years has recently been removed. This human- induced modification of canopy cover has created a gradient from open wooded meadows (tresatt slåttemark = lauveng) to semi-open wooded pastures (gjengrodd hagemark) to dense deciduous wood (gjengrodd slåttemark og høstingsskog) (Marit A. Jensen, personal communication 05.05.2012) across the landscape and through time.

Sampling

The most widespread pollarded tree species at Havrå is *Fraxinus excelsior*, whereas Ulmus glabra is more scattered. In order to eliminate floristic variations caused by different bark substrates, Moe & Botnen (1997) selected only one phorophyte species, *Fraxinus excelsior*, for investigation. The authors chose 19 pollarded ash trunks within grasslands varying in degree of canopy cover. This choice was also based in the structural characteristics of the tree, where easily distinguishable differences in stem inclination and aspect throughout the bole provides structural boundaries on which to base the selection of species compositions. The division of the within- tree epiphytic vegetation into 12 sampling units thus corresponds to the division of the tree into a basal zone (the lowest part nearest the ground), a middle zone (the central part of the trunk), and a top zone (the part just below the pollarded branches) to each of the four aspects (see fig. 2.1). The 3 heights on the tree thus correspond to differences in stem inclination among which the variation from 35 to 135 degrees makes it difficult to include stem inclination per se as a discrete environmental variable in the analysis. Consequently, the basal, middle and top zone of the trees correspond respectively to classes of < 90 degrees, 90 degrees and > 90 degrees (see fig. 2.1).

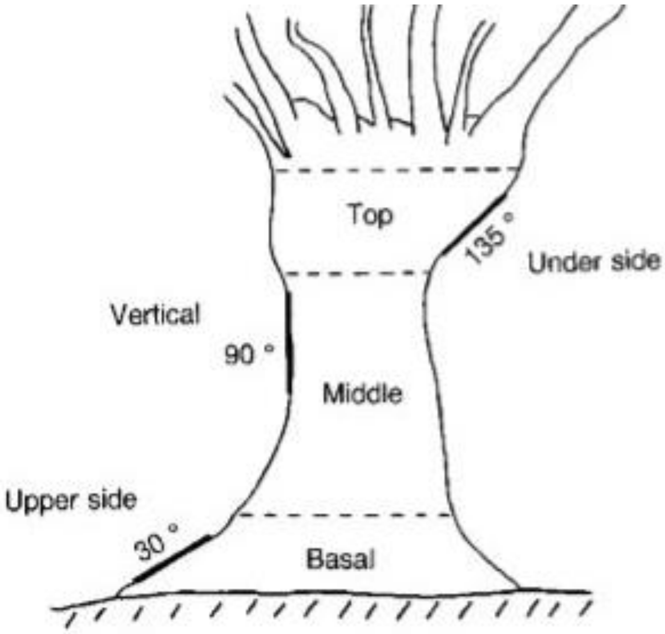


Figure 2: Stem inclination interacts with height on the trunk. The drawing is taken from Moe & Botnen (1997).

I detected the pollards primarily through interpretation of photos taken at the time of sampling of Moe & Botnen (1997) by the authors. Also conversations with the authors of the original study, locals and employees at Havrå, as well as MGRS coordinates, were useful in tracking the sites. Altitudes, locations and shapes of the analysed pollarded trunks can be found in Figure 1 in Moe & Botnen (1997), and see Appendix 2 in this present study for UTM positions of the trees, as well as values for h.a.s.l. (height above sea level) and DBH (diameter at breast height).

The trunks are pollarded at a level ranging from 1.5 and 3.0 m above the ground. Branches are chopped close to the main trunk. Some of the basal zones was left un- sampled by Moe & Botnen (1997) due to disturbances by stone walls or heaps of grass. Of the total 225 species compositions sampled by Moe & Botnen (1997), some were removed in this study due to high percentage of rotten wood and death of 2 of the 19 trunks. 17 detected trunks provided 187 species compositions. Detection of the 12 species compositions for each tree was achieved through employing the data on stem inclination/ height (degrees), aspect and area (cm^2) from Moe & Botnen (1997). An expected increase in area, more due to increase in stem diameter than to vertical growth, was calculated into the measures framing the species compositions. For each of the 12 species compositions per tree, the relative abundance of all bryophytes and lichen species were recorded along with area (cm^2) and percentage cover of total bryophytes; rotten openings as well as open bark substrate including or deprived of microlichens. Species covering less than 5 % of the area of the species composition were registered according to the number of individuals, with value classes from 1 to 4. Due to variability in shape and height of the trunks, the squares of the sampling units are irregular. The middle zone normally represents the narrowest part of the pollarded trunks, and the girth of the trees varied at the time of Moe & Botnen (1997) from 1.0 m to 3.8 m.

Identification of species was primarily performed in situ, but singular exemplars of which identification was problematic to execute in field were collected for determination ex situ. The nomenclature follows Santesson (1993) and Smith *et al.* (2009) for lichens, Frisvoll *et al.* (1995) for bryophytes and Lid & Lid (1994) for vascular plants. Species of the genera Agonimia, Arthonia, Arthopyrenia (with exeption of *Arthopyrenia punctiformis*), Cladonia, Lecanora, Lecidella (with exception of *Lecidella eleaeochroma*), Lepraria, Opegrapha (with exception of *Opegrapha rufescens*), Pertusaria, Placynthiella and Porina were identified only to generic level and hence registered as sp(p) in the species data sets of both sampling times. See appendix 1 for species list with Latin names and corresponding Ellenberg indicator values for light and moisture (Hill *et al.* 1999, Hill *et al.* 2004, Hill *et al.* 2007).

The species compositions was in this present study classified into two levels of a management factor according to the management history of the pollard and the site in which it reside: "Increase in canopy cover" and "Reduction in canopy cover". Information on the variable historical management regimes across the landscape ascribes from Moe & Botnen (unpublished data) as well as from conversations with employees and local inhabitants of the cultural environment Havrå. The category of "Reduction in canopy cover" comprises the trees exposed to reduction in canopy cover within the last 20 years due to management of the close surrounding fields and/ or pollarding of the tree. Trees no. 1, 2, 3 and 4 reside in sites where surrounding vegetation has changed from relative dense forest to semi- open meadow. Tree no. 4 was pollarded in 2009. The following trees of residence within continuously managed surrounding meadows until present time have also been pollarded within the last 10 years: tree no. 8 (pollarded 2007); no. 10 (pollarded 2001); no. 11 (pollarded 2003); no. 12 (pollarded 2007) and no. 16 (pollarded 2003).

The category of "Increase in canopy cover" comprises the trees exposed to increase in canopy cover within the last 20 years due both to lack of pollarding as well as to canopy closure at the stand scale: tree no. 5, 6, 7, 9 (pollarded 2012), 13, 17, 18 and 19. Pollards no. 17 and 18 are however surrounded with scattered openings followed by more light due to stochastic felling of old trees. Besides the variable historical management regimes, the management factor described above is likely to capture much of the variation in local climate, height above sea level and site quality. Trees classified into the level of “Reduction in canopy cover” correspond to trees located within close distance to the sea and to the farm buildings, where site quality is higher than in the uppermost area withstanding trees within the level of “Increase in canopy cover” (Appendix 3, DCA axis 1).

Figure 3: Pictures of pollards no. 13- west to the left and no. 10- south to the right.

Detrended Correspondence Analysis (DCA)

In order to reveal the structure of multivariate data sets, ordination methods seek to represent the data along a reduced number of orthogonal axes. In decreasing order these axes represent the main trends of the data. DCA ordination (Hill 1979, Hill & Gauch 1980) is a multivariate indirect ordination technique based on a unimodal relation between species and environment, i.e. based on the assumption of a unique set of optimal conditions for a species at which the species has maximal abundance. A DCA ordination was performed on the two species datasets from different sampling times employed in this study. Species situated close to each other along the DCA ordination axis are similar in species abilities towards particular environmental conditions. Environmental gradients in the species data are thereby revealed from interpretation of the arrangement of species scores along each of the axes.

Strength of relation between variables

DCA axes, the moisture gradient and the light gradient were regressed on various predictor variables (Table 2) and tested with Anova with F- test. The value of adjusted R- square from the summary output signifies the strength of the relations. The moisture gradient is termed “Moisture” and the light gradient is termed “Light”. “Height” and “Aspect” signifies respectively gradients in height/ stem inclination and aspect. “Management” signifies variation in historical management regime. “Sea” and “Moss Cover” means respectively height above sea level/ distance from sea and total percentage of moss cover. The plots from these regressions, indicating the correspondence between the environmental gradients in the species data and predictor variables, were used as a support in the interpretation of the quantified temporal trends in the species compositions as distributed along each axis and gradients of light and moisture values.

Temporal turnover

DCA axes

The site scores of the sampling of Moe and Botnen (1997) were extracted from the site scores of the sampling of this present study along each DCA axis. For each of the DCA axes, the procedure for calculation of the mean temporal turnover can be illustrated through the following expression: $\mathrm{DCA}_{\mathrm{change}} = \mathrm{Site\ Scores}_{T1} - \mathrm{SiteScores}_{T0}$

In order to evaluate whether the change is larger than what can be expected by random, the significance of difference in time to the 4 different $\mathrm{DCA}_{\mathrm{change}}$ was tested through paired t-tests.

Light and moisture gradients

The Null hypothesis of no difference in species optima values for light and moisture between the sampling time of the original study and the sampling time of this study was tested through applying a weighted average technique. Weighted averaging is a form of direct gradient analysis. It shows only one axis and is useful for situations where only one primary environmental gradient (at the time) is under consideration. The weighted average for light was calculated for each species composition by multiplying the abundance of each species times the Ellenberg light value for that species, whereby these values were summarized and subsequently divided by the sum of species abundances. The resulting light ranking for the species composition reflects its position along a light gradient. High light values correspond to shade sensitive species, whereas low light values correspond to shade tolerant species. Extracting the weighted light ranking of time 1 from that of time 2 for a species composition provides a value for the temporal change in its weighted light ranking, corresponding to a change in the position along the ordination gradient of light for that sample. The procedure was repeated for Ellenberg moisture values. High moisture values correspond to draught sensitive species, whereas low moisture values correspond to draught resistant species. Measurements for obtaining the mean temporal change in the weighted light and moisture ranking for all species compositions can be illustrated through the following expressions:

$$\mathrm{Light}_{\mathrm{change}} = \mathrm{wa}_{\mathrm{Ellenberg}}\mathrm{Light}_{\mathrm{T1}} - \mathrm{wa}_{\mathrm{Ellenberg}}\mathrm{Light}_{\mathrm{T0}}$$

$$\mathrm{Moisture}_{\mathrm{change}} = \mathrm{wa}_{\mathrm{EllenbergMoistureT1}} - \mathrm{wa}_{\mathrm{Ellenberg}}\mathrm{Moisture}_{\mathrm{T0}}$$

Subsequently the significance of difference in time to the $\mathrm{Light}_{\mathrm{change}}$ and $\mathrm{Moisture}_{\mathrm{change}}$ was tested through paired t- tests.

Direction of temporal turnover

Positive Average Change value from the t- tests of $\mathrm{DCA}_{\mathrm{change}}$ (Table 3) indicates a temporal compositional change towards increase in relative abundances of species with high positive score along the DCA axis in question, in turn revealing temporal environmental trends within the metacommunity at the scale of the landscape. Negative value signifies a temporal trend in the epiphytic vegetation of increase in relative abundances of species positioned at the negative end of the axis.

Positive Average Change value from the paired t- test of $\mathrm{Light}_{\mathrm{change}}$ indicates that the mean temporal change in weighted light ranking along the gradient of light is positive. Such a change would correspond to a temporal compositional change in direction of increase in relative abundances of shade sensitive species and hence indicate an environmental trend of increase in the availability of light. Negative value for Average Change corresponds to a temporal change along the gradient towards an increase in relative abundances of shade tolerant species and hence more shady conditions. Likewise, positive Average Change value for $\text{Moisture}_{\text{change}}$ indicates a temporal compositional change in direction of an increase in relative abundances of draught sensitive species and more moist conditions, whereas negative value implies a temporal increase in relative abundances of draught tolerant species and reduced availability of moisture.

Rate of temporal turnover

Beta diversity can be conceived of as a measure of the degree of dissimilarity among sample units as distributed along a gradient. Axes of DCA ordination are scaled in units of beta diversity. The significance of a variable to variation in temporal turnover rate along a DCA axis thus indicates the importance of that variable not only to the distribution of species compositions along the axis, but also in structuring community response to temporal environmental modification. The significance of the predictor variables of Aspect, Height and Management to temporal turnover rates along DCA axes and to temporal change in weighted light and moisture ranking was tested through mixed effect models with forward selection.

For all models fit to the data, AIC comparisons were performed in order to reveal whether or not models including the tree factor as random factor in mixed effect models performed better as compared to general linear models where the tree factor as random factor was omitted. Based on these AIC comparisons, the tree factor was treated as random effect factor in the linear mixed effect models employed, whereas Aspect, Height and Management were treated as fixed effect factors. Below follows the model expression employed, with x representing the predictor variables and “tree” representing the random factor:

$$\text{Fit.x.lme <-lme (DCA}_{\text{change}} \text{~x, random=~1|tree)}$$

$$\text{Fit.x.lme <-lme (Light}_{\text{change}} \text{~x, random=~1|tree)}$$

$$\text{Fit.x.lme <-lme (Moisture}_{\text{change}} \text{~x, random=~1|tree)}$$

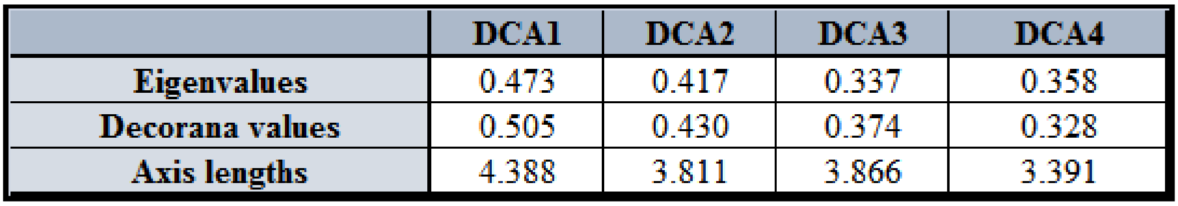
Testing of the null hypotheses of no variation in temporal turnover rates along the different variables was performed through Anova. I used forward selection to obtain the values for each step of inclusion of variables in the model building. Graphical explorations were carried out between response and predictor variables, and all predictors got into the selection procedure of regression models. Full models included interaction terms. Akaike's Information Criterion (AIC; Burnham and Anderson 1998) was employed to obtain the most parsimonious model (the minimal adequate linear mixed effect models; Zuur *et al.* 2009). Prior to modelling, preliminary data exploration were performed. Editing and transforming of data was performed in Microsoft Office Excel (Anonymous 2013). The data analyses were carried out by R 2.15.3 (The R Development Core Team 2013) and by the R package "nlme" (Pinheiro *et al.* 2011)

Chapter 3. Results

DCA

The seventeen trees detected (2 probably dead) provided 374 species compositions, comprising 159 species of which 80 bryophytes, 61 lichens and 18 vascular plants. DCA axes 1 to 4, based on 374 species compositions had eigenvalues of 0.47, 0.42, 0.34 and 0.36, respectively (Table 1). Even though the eigenvalues of the third and fourth DCA axes are quite similar (0.34 and 0.36 respectively), and much smaller than the second axis, all axes are considered in the interpretation. Figure 4 shows distribution of site scores along axis 1 and 2

Table 1: Summary of DCA ordination.



	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.473	0.417	0.337	0.358
Decorana values	0.505	0.430	0.374	0.328
Axis lengths	4.388	3.811	3.866	3.391

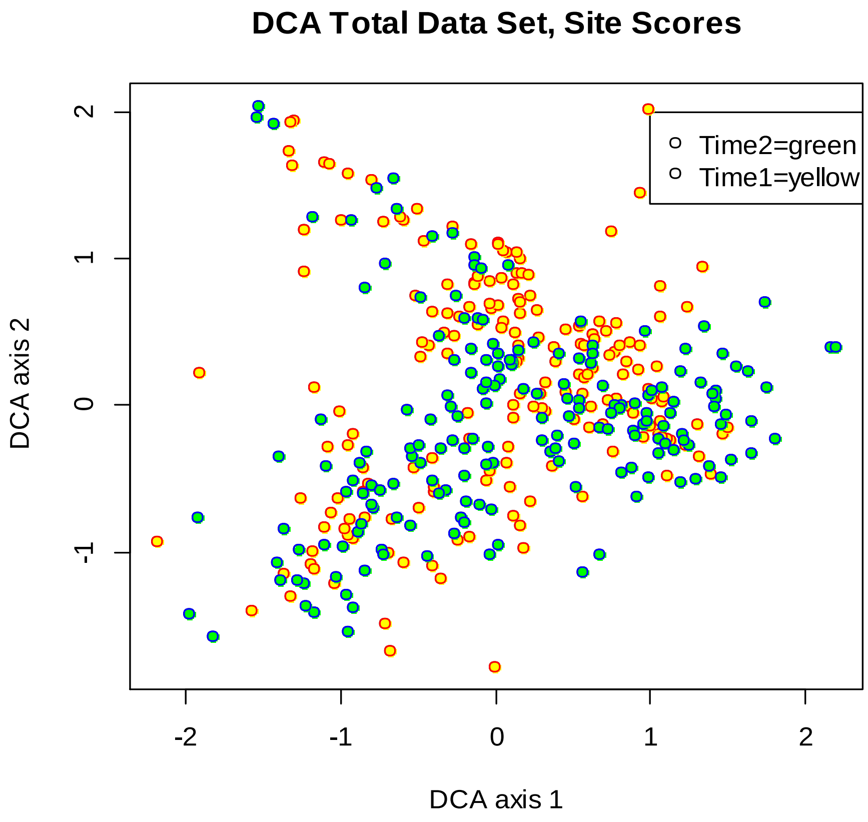


Figure 4: DCA ordination plot of site scores along axis 1 and 2.

Ecological interpretation of DCA axes

Four major gradients were revealed through interpretation of the species scores of the DCA ordination. A brief description of the revealed gradients is given in the discussion part of this study, whereas a more detailed ecological interpretation of the DCA axes can be found in Appendix 3. Figure 5 show the arrangement of species scores along axis 1 and 2, whereas Figure 6 show the arrangement of species scores along axis 3 and 4.

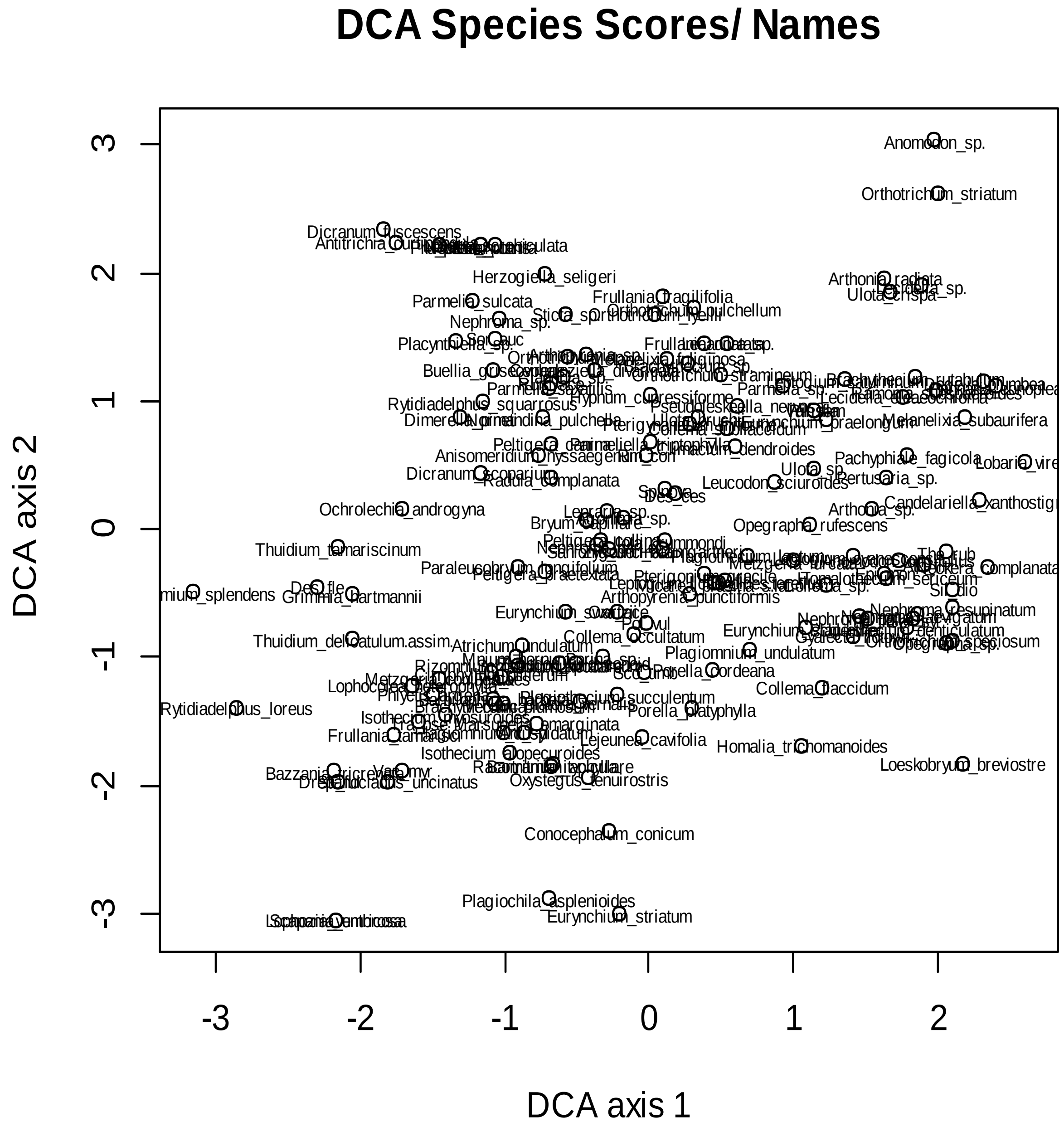


Figure 5: DCA ordination plot of species scores along axis 1 and 2.

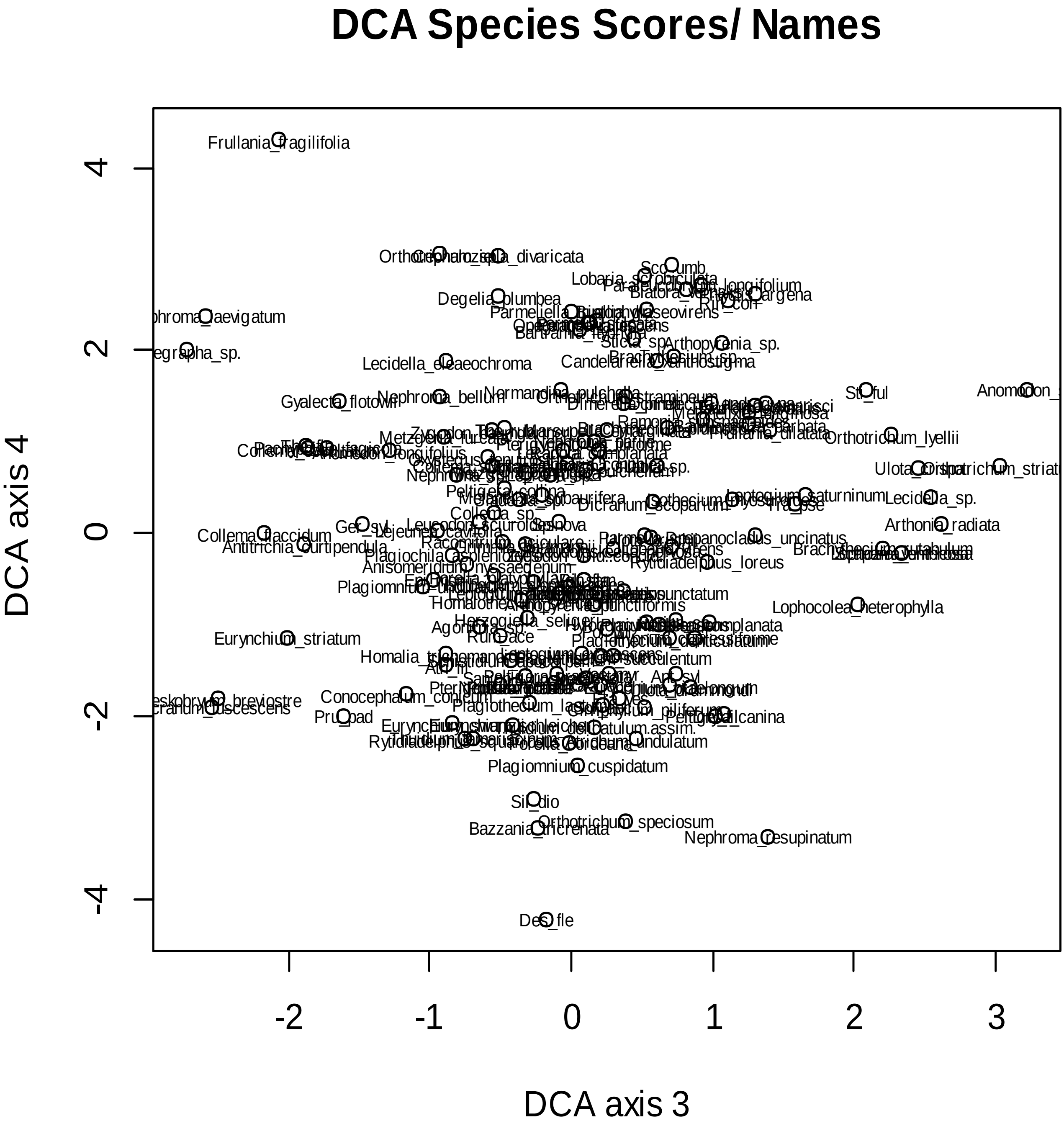
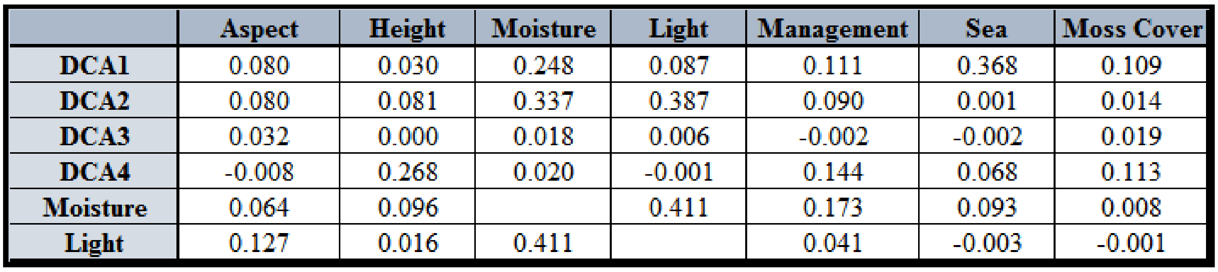


Figure 6: DCA ordination plot of species scores along axis 3 and 4.

Table 2 shows the adjusted R square values from the summaries of the regressions of response variables against predictor variables. High values indicate strong relation. The strength of the relation between DCA axis 1 and the explanatory variables was highest for Sea (0.368), followed by management history (0.111). For DCA axis 2, Management provides the highest adjusted R- square value (0.09), closely followed by Height (0.081) and Aspect (0.080). Aspect is the variable most strongly related to DCA axis 3, even though the strength of the relation is very low (0.032). Among the strength of the relations pertaining to DCA axis 4, the one to Management is the highest (0.144). Moisture is slightly correlated with Height (0.096) and more so with Management (0.173). Light corresponds relatively highly with Aspect (0.127). The strength of the relation between Moisture and Light is relatively high (0.411).

Table 2: Adjusted R square values from test of strength of relation between variables.

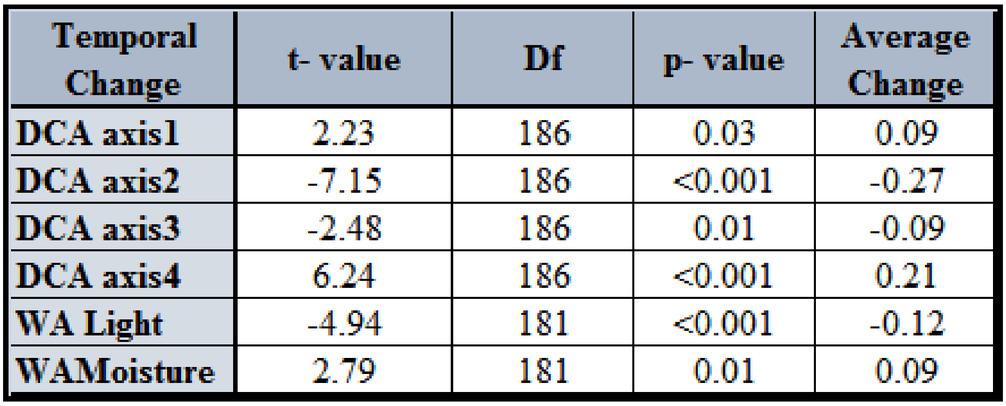


	Aspect	Height	Moisture	Light	Management	Sea	Moss Cover
DCA1	0.080	0.030	0.248	0.087	0.111	0.368	0.109
DCA2	0.080	0.081	0.337	0.387	0.090	0.001	0.014
DCA3	0.032	0.000	0.018	0.006	-0.002	-0.002	0.019
DCA4	-0.008	0.268	0.020	-0.001	0.144	0.068	0.113
Moisture	0.064	0.096		0.411	0.173	0.093	0.008
Light	0.127	0.016	0.411		0.041	-0.003	-0.001

Temporal turnover in species composition

The p- values from the t- tests of temporal change (Table 3) show that the difference in time is significant to the temporal turnover as distributed along each of the DCA axes as well as to the temporal change in weighted light and moisture ranking of the samples along the light and moisture gradients. A negative Average Change value in Table 3 signifies that the mean direction of the temporal turnover along the DCA axis or gradient of light and moisture is towards the negative end of the axis or gradient. A positive value signifies a temporal change towards the positive end. The significant temporal change in position of species compositions along DCA axes 2 and 3, as well as the significant temporal change in the weighted light ranking along the gradient of light, shows a negative direction. The compositions as arranged along DCA axis 1 and 4, as well as the weighted moisture ranking, changed significantly through time towards the positive end of respectively the DCA axes and the moisture gradient.

Table 3: Values from t- tests of significance of time to temporal change.



Temporal Change	t- value	Df	p- value	Average Change
DCA axis1	2.23	186	0.03	0.09
DCA axis2	-7.15	186	<0.001	-0.27
DCA axis3	-2.48	186	0.01	-0.09
DCA axis4	6.24	186	<0.001	0.21
WA Light	-4.94	181	<0.001	-0.12
WAMoisture	2.79	181	0.01	0.09

Importance of Aspect, Height and Management to temporal turnover rate

For all models fit to the data of variation in temporal turnover as well as to variation in temporal change in weighted average for light and moisture values, AIC comparison revealed that the models including the tree factor as random factor in mixed effect model perform better as compared to the general linear model where the tree factor as random factor is omitted. Both Aspect and Height was measured to be significant to rate of temporal turnover along axis 2 and axis 3, whereas these variables were found to be insignificant in relation to axis 1 and 4. Management was insignificant in relation to all axes. The model with Height as the only fixed effect factor represented however the most parsimonious model for axis 3, whereas the null model was found to be best for the axes 1, 2 and 4. The regressions showed that neither Aspect nor Height or Management was significant to the variation in temporal change in weighted light and moisture ranking along the gradients of light and moisture. The null model was thus the most parsimonious model in relation to both gradients of light and moisture. See Table 5 – 16 for values for anova tests and AIC comparisons for all models. Table 4 provides an overview of the most parsimonious models.

Table 4: Most parsimonious models.

Response variable	Best model
$\text{Moisture}_{\text{change}}$	Null
$\text{Light}_{\text{change}}$	Null
$\text{DCA}_{\text{change}}1$	Null
$\text{DCA}_{\text{change}}2$	Null
$\text{DCA}_{\text{change}}3$	Height
$\text{DCA}_{\text{change}}4$	Null

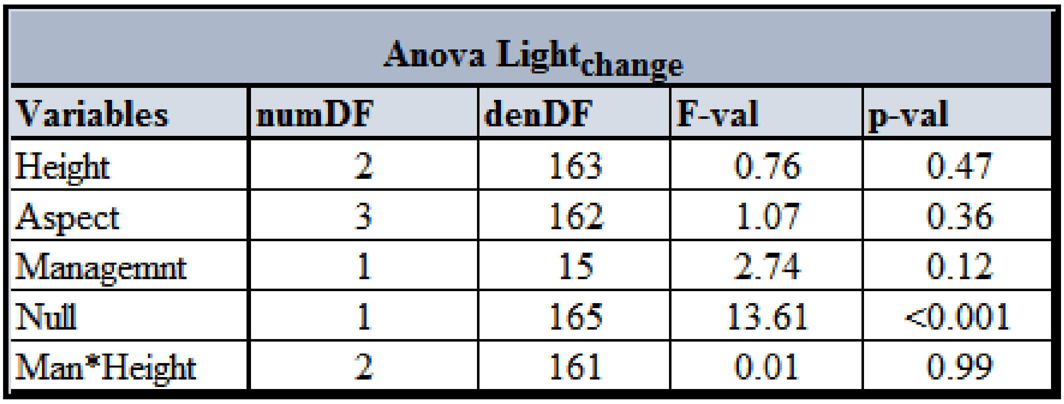
Table 5: Output from anova tests of models for temporal change in weighted moisture ranking.

Anova $\text{Moisture}_{\text{change}}$				
Variables	numDF	denDF	F-val	p-val
Height	2	163	0.26	0.77
Aspect	3	162	0.74	0.53
Management	1	15	2.07	0.17
Null	1	165	2.14	0.15
Height*man	2	161	0.20	0.82

Table 6: AIC test- models of temporal change in weighted moisture ranking.

AIC- $\text{Moisture}_{\text{change}}$		
Models/ Values	df	AIC
Null	3	214.25
Management	4	217.00
Height	5	224.77
Aspect	6	227.95
Management*Height	8	235.37

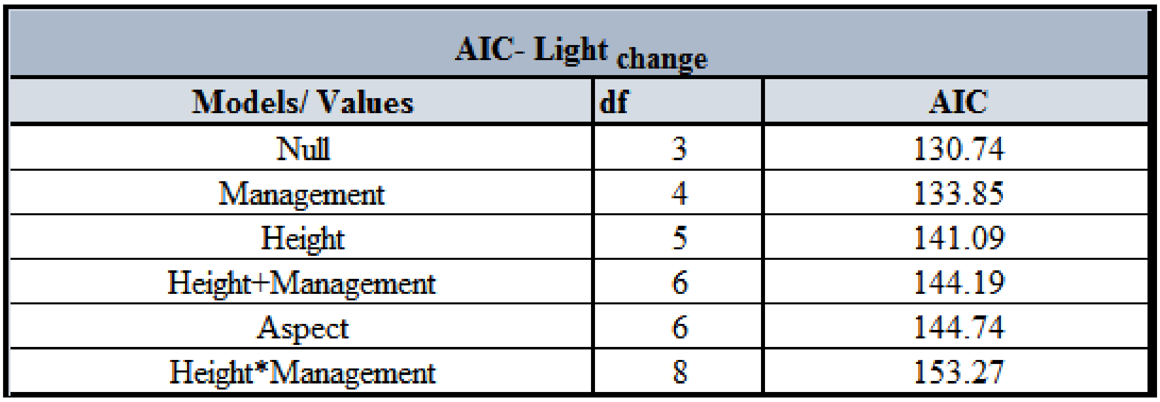
Table 7: Output from anova tests of models for temporal change in weighted light ranking.



Anova Light$_{change}$

Variables	numDF	denDF	F-val	p-val
Height	2	163	0.76	0.47
Aspect	3	162	1.07	0.36
Managemnt	1	15	2.74	0.12
Null	1	165	13.61	<0.001
Man*Height	2	161	0.01	0.99

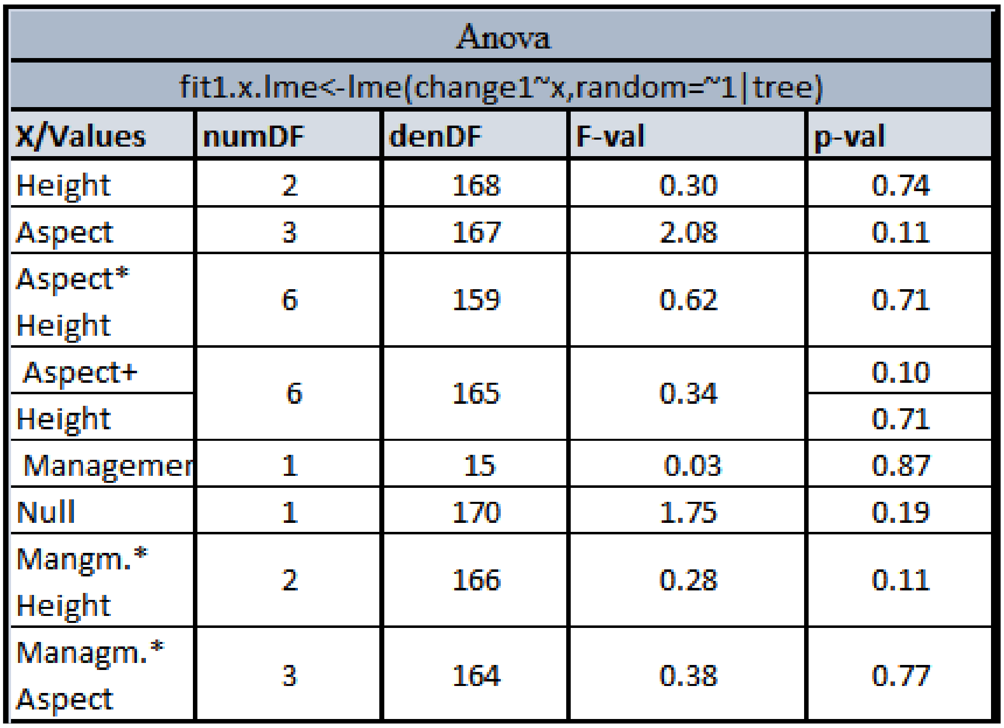
Table 8: AIC test- models of temporal change in weighted light ranking.



AIC- Light $_{change}$

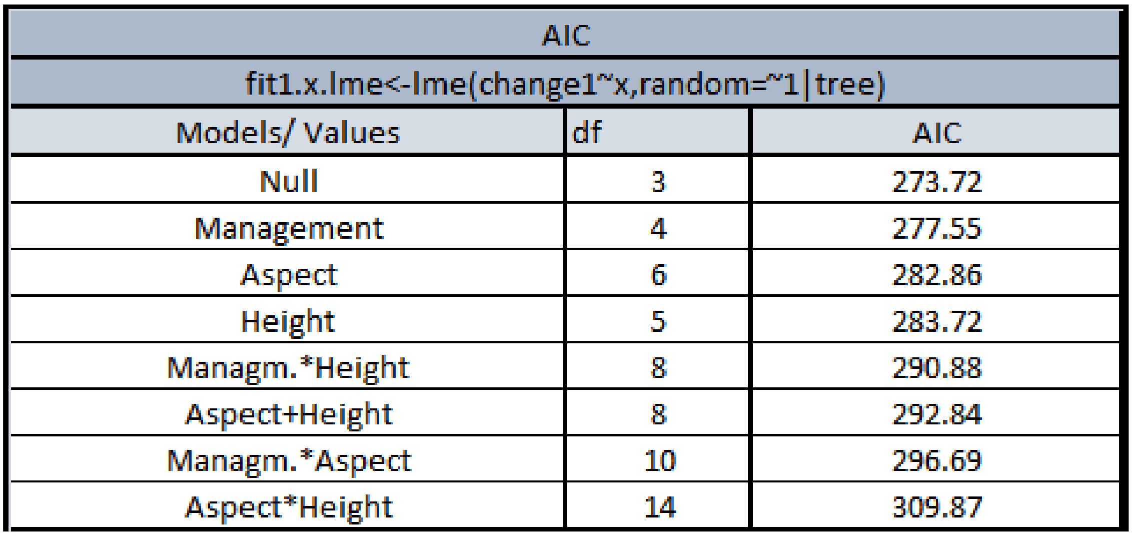
Models/ Values	df	AIC
Null	3	130.74
Management	4	133.85
Height	5	141.09
Height+Management	6	144.19
Aspect	6	144.74
Height*Management	8	153.27

Table 9. Output from anova tests of models for temporal turnover rates along DCA axis 1.



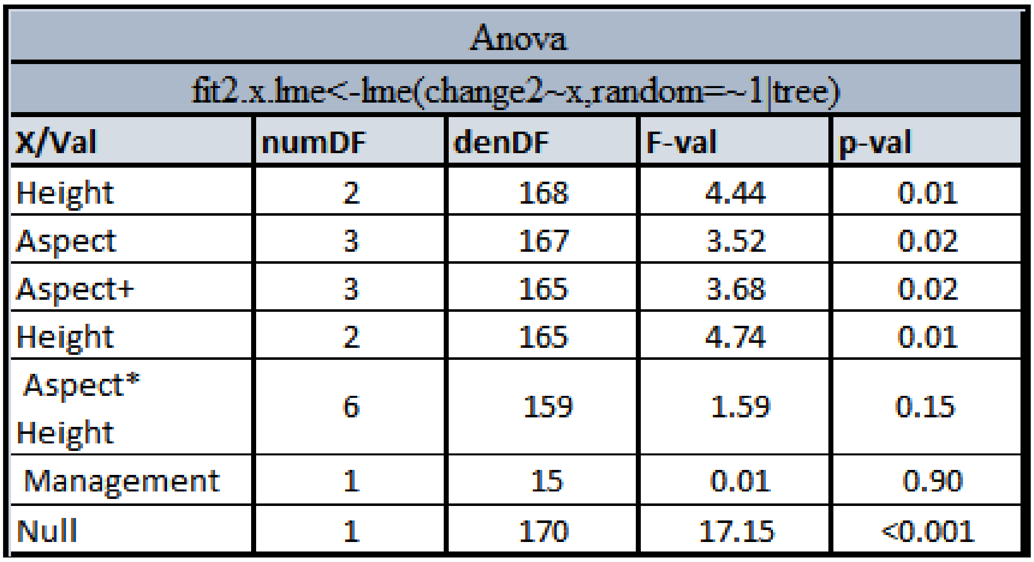
Anova				
fit1.x.lme<-lme(change1~x,random=~1|tree)				
X/Values	**numDF**	**denDF**	**F-val**	**p-val**
Height	2	168	0.30	0.74
Aspect	3	167	2.08	0.11
Aspect* Height	6	159	0.62	0.71
Aspect+	6	165	0.34	0.10
Height				0.71
Managemer	1	15	0.03	0.87
Null	1	170	1.75	0.19
Mangm.* Height	2	166	0.28	0.11
Managm.* Aspect	3	164	0.38	0.77

Table 10: Output from AIC test of most parsimonious model- DCA axis 1.



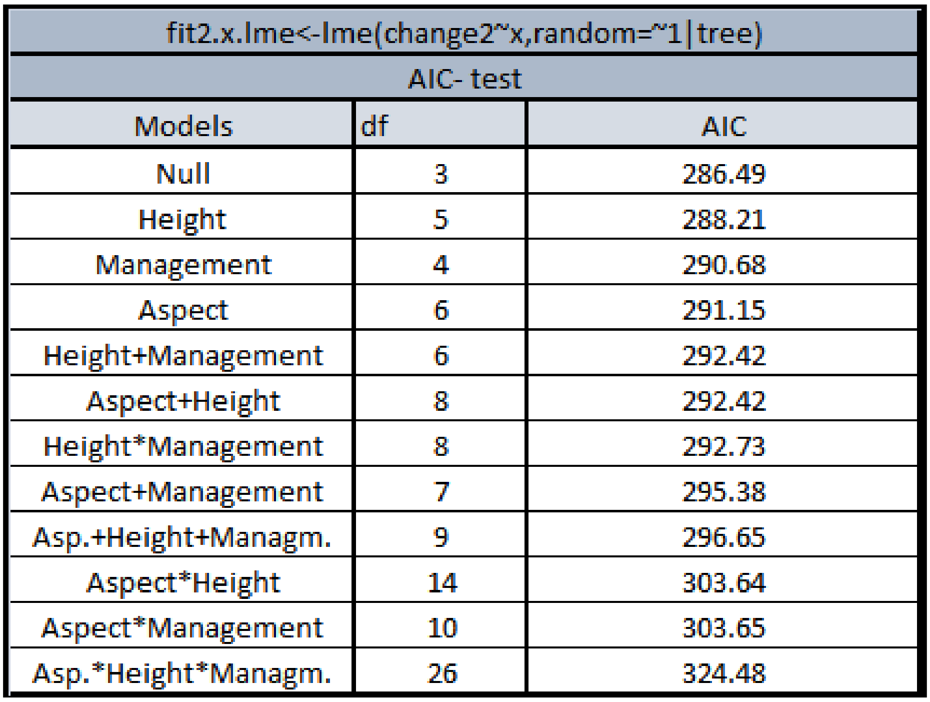
AIC		
fit1.x.lme<-lme(change1~x,random=~1|tree)		
Models/ Values	df	AIC
Null	3	273.72
Management	4	277.55
Aspect	6	282.86
Height	5	283.72
Managm.*Height	8	290.88
Aspect+Height	8	292.84
Managm.*Aspect	10	296.69
Aspect*Height	14	309.87

Table 11: Output from AIC test of most parsimonious model- DCA axis 2.



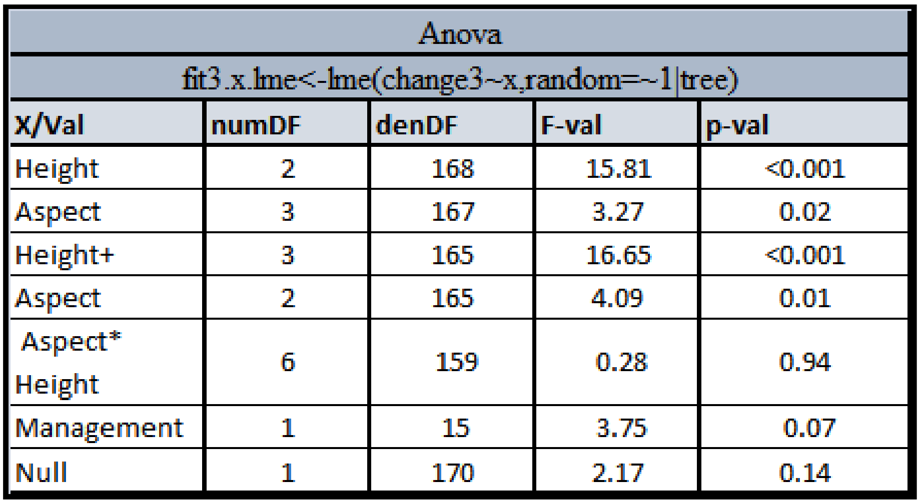
Anova				
fit2.x.lme<-lme(change2~x,random=~1|tree)				
X/Val	**numDF**	**denDF**	**F-val**	**p-val**
Height	2	168	4.44	0.01
Aspect	3	167	3.52	0.02
Aspect+	3	165	3.68	0.02
Height	2	165	4.74	0.01
Aspect* Height	6	159	1.59	0.15
Management	1	15	0.01	0.90
Null	1	170	17.15	<0.001

Table 12: Output from anova tests of models for temporal turnover rates along DCA axis 2.



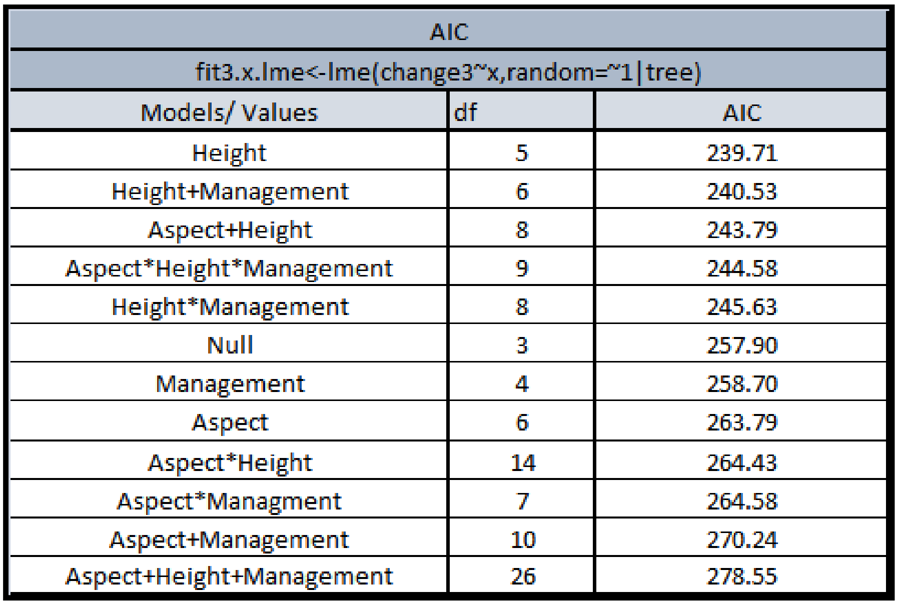
fit2.x.lme<-lme(change2~x,random=~1|tree)		
AIC- test		
Models	df	AIC
Null	3	286.49
Height	5	288.21
Management	4	290.68
Aspect	6	291.15
Height+Management	6	292.42
Aspect+Height	8	292.42
Height*Management	8	292.73
Aspect+Management	7	295.38
Asp.+Height+Managm.	9	296.65
Aspect*Height	14	303.64
Aspect*Management	10	303.65
Asp.*Height*Managm.	26	324.48

Table 13: Output from anova tests of models for temporal turnover rates along DCA axis 3.



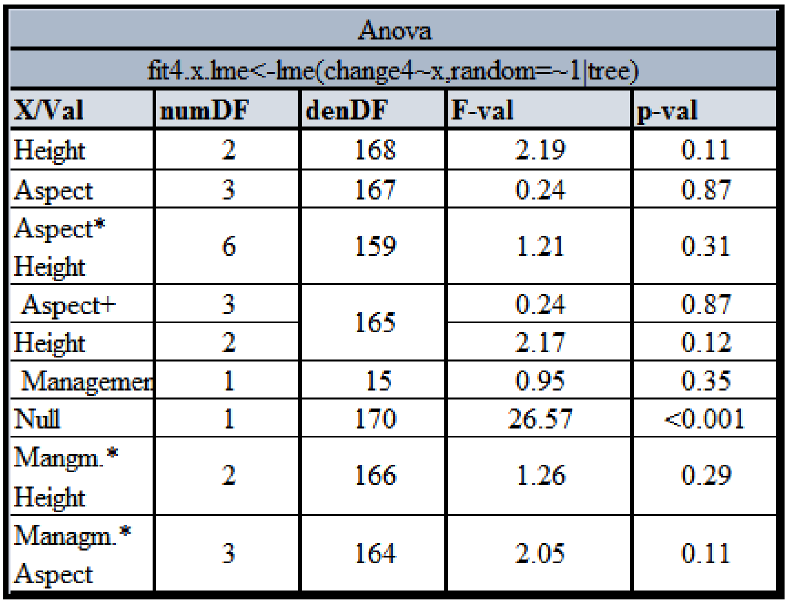
Anova				
fit3.x.lme<-lme(change3~x,random=~1|tree)				
X/Val	**numDF**	**denDF**	**F-val**	**p-val**
Height	2	168	15.81	<0.001
Aspect	3	167	3.27	0.02
Height+	3	165	16.65	<0.001
Aspect	2	165	4.09	0.01
Aspect* Height	6	159	0.28	0.94
Management	1	15	3.75	0.07
Null	1	170	2.17	0.14

Table 14: Output from AIC test of most parsimonious model- DCA axis 3.



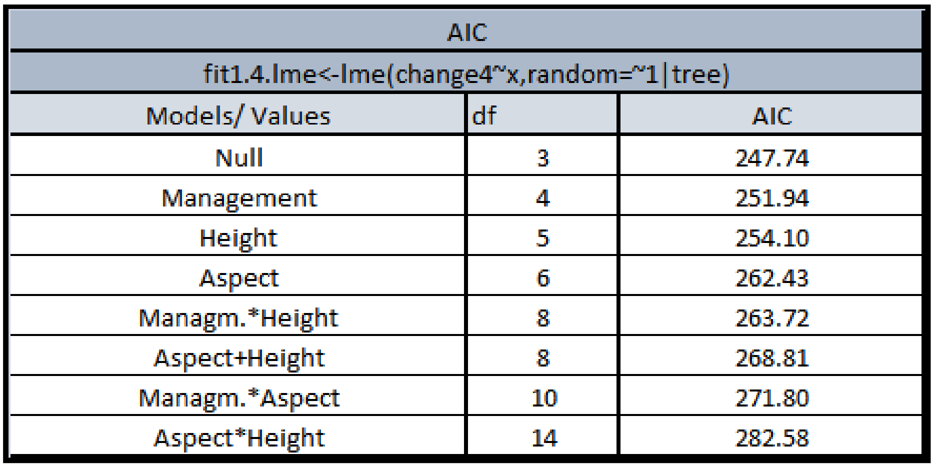
AIC		
fit3.x.lme<-lme(change3~x,random=~1|tree)		
Models/ Values	df	AIC
Height	5	239.71
Height+Management	6	240.53
Aspect+Height	8	243.79
Aspect*Height*Management	9	244.58
Height*Management	8	245.63
Null	3	257.90
Management	4	258.70
Aspect	6	263.79
Aspect*Height	14	264.43
Aspect*Managment	7	264.58
Aspect+Management	10	270.24
Aspect+Height+Management	26	278.55

Table 15: Output from anova tests of models for temporal turnover rates along DCA axis 4.



Anova				
fit4.x.lme<-lme(change4~x,random=~1|tree)				
X/Val	**numDF**	**denDF**	**F-val**	**p-val**
Height	2	168	2.19	0.11
Aspect	3	167	0.24	0.87
Aspect* Height	6	159	1.21	0.31
Aspect+	3	165	0.24	0.87
Height	2		2.17	0.12
Managemen	1	15	0.95	0.35
Null	1	170	26.57	<0.001
Mangm.* Height	2	166	1.26	0.29
Managm.* Aspect	3	164	2.05	0.11

Table 16: Output from AIC test of most parsimonious model- DCA axis 4.



AIC		
fit1.4.lme<-lme(change4~x,random=~1|tree)		
Models/ Values	df	AIC
Null	3	247.74
Management	4	251.94
Height	5	254.10
Aspect	6	262.43
Managm.*Height	8	263.72
Aspect+Height	8	268.81
Managm.*Aspect	10	271.80
Aspect*Height	14	282.58

Chapter 4. Discussion

Main results

The results from the paired t- tests (Table 3) demonstrate the significance of time to change in species composition from the sampling time of the original study to the sampling time of this present study along all DCA axes, as well as to change in the weighted light and moisture ranking. Consequently, during the last 20 years, the composition of the epiphytic communities on pollarded trunks of *Fraxinus excelsior* at Havrå has changed significantly in relation to availability of light and moisture.

Interpretation of species scores along DCA axis 2 and DCA axis 4 indicates that these axes explain much of the directional spatial change in community structure in the species data of this study. The direction of the temporal turnover as interpreted along these axes are therefore likely to indicate the overall direction of the change in composition of the epiphytic metacommunity of this study through time. Both DCA axis 2 and DCA axis 4 seems to represent a distribution trend along the stem. Species similar in abilities towards moisture as well as light correspond to a particular height and aspect along DCA axis 2, whereas DCA axis 4 separates species differing in their morphological adaptations towards retention of water. The direction of temporal turnover as distributed along DCA axis 2 and 4, as well as along the gradients in light and moisture, indicates a trend in the epiphytic vegetation towards homogenization of the within- tree variation in species composition at the expense of shade sensitive species. This trend in the epiphytic metacommunity corresponds to an environmental trend towards more shady and humid conditions at the scale of the landscape.

Historical management regime of the pollards and surrounding meadows has no significant effect on the rate of the compositional change through time, whereas temporal turnover rates along axis 2 vary significantly with Height and Aspect. The corresponding regression plots indicate a relatively higher rate of temporal turnover in the top zone and to the aspect of south where assemblages of shade sensitive species reside, as compared to the basal zone and the aspect of north. This result indicates that the temporal turnover in large is driven by a higher species response to change in availability of light and moisture within assemblages of shade sensitive species tolerant or sensitive to draught, as compared to assemblages of shade tolerant species more or less sensitive to draught.

The results from the testing of the effect of Aspect, Height and Management on the rates of temporal turnover thus support the indication from the measured direction of temporal turnover that abandoned management is a driver of compositional change through time in the epiphytic communities of this study, at the expense of shade sensitive species.

Before discussing the direction and nature of temporal turnover as distributed along DCA axes and gradients in light and moisture, in the following I describe the different DCA axes briefly (see Appendix 3 for a complete interpretation of species scores along each DCA axis).

Interpretation of DCA axes

DCA axis 1

At the positive end of axis 1 reside species found within the lowermost sites of the study area, e.g. *Gyalecta flotowii, Thelopsis rubella, Leucodon sciuroides, Homalothecium sericeum, Degelia plumbea* and *Lobaria virens. Ochrolechia androgyna, Scapania umbrosa and Lophozia ventricosa* have high negative score on axis 1 and are restricted to one or two trunks at 185 m altitude (Moe & Botnen 1997). The arrangement of species along axis 1 (Appendix 3) thus suggests a (non- directional) variance in community structure between sites within the lowermost situated areas of high site quality and short distance to the sea/ farm buildings, and sites within the uppermost areas of poorer site quality with longer distance to the sea. The kind of beta diversity along DCA axis 1 seems thus to reflect variation in the identities of species among species compositions within the study area, and not beta diversity as turnover in species composition (cf. Legendre *et al.* 2005; Anderson *et al.* 2011). The plots from the regression of DCA axis 1 on Sea and Management (highest R^2, see table 2) show that the negative end of the axis corresponds to the uppermost level of the study area and sites of increase in canopy cover. These results from the test of strength of relation between variables thus support the ecological interpretation of the species scores along axis 1.

DCA axis 2

At the positive end of DCA axis 2 reside shade sensitive and draught tolerant species like *Antitrichia curtipendula, Orthotrichum pulchellum, Orthotrichum lyelli, Orthotrichum striatum, Parmelia sulcata, Lobaria scrobiculata*, and *Pseudoleeskella nervosa* (Figure 5). Species typical of the lower, negative end of the axis are shade resistant/ draught sensitive species like *Loeskobryum breviostre, Plagiochila asplenioides, Plagiothecium denticulatum,* *Collema flaccidum* and *Eurynchium striatum.* DCA axis 2 seems thus to represent a distribution trend along the stem, with species similar in abilities towards moisture as well as light corresponding to a particular Height (Appendix 3). This arrangement of species might as well represent a gradient of aspect, with the positive end corresponding to the aspects of south and west were irradiation and evaporation is likely to be higher than to the north and east.

Plots of the regressions of DCA axis 2 on explanatory variables and gradients of light and moisture show that the basal part, the aspect of north, low light values (shade tolerant species) and high moisture values (draught sensitive species) correspond to the negative end of DCA axis 2. These plots also show that the top zone, south, high light values (shade sensitive species) and low moisture values (draught tolerant species) correspond to the positive end of axis 2. Results from tests of strength of relation between variables (Table 2) thus support the ecological interpretation of the arrangement of species scores along axis 2.

DCA axis 3

The arrangement of species along DCA axis 3 (Appendix 3) seems to reflect a non-directional gradient that may be explained by different substrate conditions on the trunk, what suggests that DCA axis 3 represent conditions related to the cyclical successive stages of the epiphytic vegetation. The difference in substrate conditions seem however to correspond to different heights along the trunk, what suggests differences in peeling- off rates along the gradient of height (Appendix 4). The strengths of all the relation between DCA axis 3 and predictor variables are low, and no clear trend of moisture or light availability was revealed along DCA axis 3.

Due to more windy environments in the upper parts of the trunk and to the aspect of south in open meadows (Appendix 3), re- colonization of the trunk after each peeling-off by the cryptogamic epiphytes at Havrå is likely to happen at a higher rate within the top zone and to the aspect of south (Appendix 4). Variation in cyclical successive stages may thus underlie the measured significance of Aspect and Height to temporal turnover rates along axis 3, as well as the result of the model with Height as predictor as the most parsimonious model related to axis 3. Differences in exposure may explain the higher turnover rates in the top zone and to the south relative to the other levels of height and aspect, as shown from regression plots. The results related to axis 3 illustrate the way structural properties of the habitat interacts with environment in producing spatial variation in stages in the cyclical succession in communities of sessile organisms residing in dynamic habitats, like epiphytes residing on old trunks in open environments.

DCA axis 4

Axis 4 seems to represent a gradient of height/ stem inclination followed by variation in the degree to which species adhere to their substrate, i.e. a gradient of morphological adaptations towards retention of water along the trunk (Appendix 3). The plot from the regression of DCA axis 4 on Height shows a correspondence between the top and middle zone and the positive end of axis 4 where species of the genera Orthotrichum, *Leidella elaeochroma, Parmelia sulcata, Opegrapha rufescens* and *Phlyctis argena* reside. These species adhere more or less strongly to their substrate as opposed to species positioned at the negative end of axis 4, which press loosely against their substrate, like *Nephroma resupinatum, Peltigera resupinatum, Bazzania tricrenata, Loeskobryum breviostre* and *Thuidium tamariscinum.* The negative end corresponds to the basal zone, and the results from the regression thus support the ecological interpretation of the arrangement of species along axis 4. The regression plot also indicates high similarity among top and middle zone with respect to environmental factors and floristic composition in relation to the basal zone (cf. Moe & Botnen 1997).

In the following interpretations of the direction and rate of the temporal turnover, focus is on the directional gradients identified along DCA axis 2 and DCA axis 4, as well as on the gradients of light and moisture.

Direction of temporal turnover.

Temporal trends revealed along gradients in light and moisture

The negative direction of the significant temporal change along the light gradient (Table 3) implies that the temporal change in composition of the epiphytic communities consist in an increase in relative abundances of shade tolerant species, corresponding to an increase in resemblance to the composition at the north side (highest R^2 with Aspect, Table 2). A positive direction of the significant temporal change along the moisture gradient implies that the temporal change in composition of the epiphytic communities consist in an increase in relative abundances of draught sensitive species. This temporal trend in the epiphytic vegetation correspond to an increase in resemblance to the composition of sites of increase in canopy cover as well as to the basal part of the trunk (highest R^2 with Management and Height, Table 2). A relatively strong relation ($R^2 = 0.411$) between Light and Moisture suggests that the gradients of light and moisture explain much of the same variation in the species compositions of this study, and the direction of temporal turnover as distributed along these gradients suggests a temporal environmental trend of more shady and moist conditions.

Temporal trends revealed along DCA axis 2

The direction of the significant temporal turnover as distributed along axis 2 towards the negative end of the axis (Table 3) indicates a change towards species compositions of the lower parts of the trunk and at the north side. This direction of the compositional change corresponds to an increase in relative abundances of draught sensitive and shade tolerant species, like *Plagiochila asplenioides, Eurynchium striatum and Conocephalum conicum*, as well as to a decrease in shade sensitive species like cyanolichens and old- growth indicators like *Antitrichia curtipendula.* This structural change in the metacommunity indicates a trend in the local environment of higher availability of moisture (from atmospheric humidity and/ or precipitation) and lower availability of light, and speak as such in favour of abandoned management as a driver of change in the epiphytic community.

Temporal trends revealed along DCA axis 4

The direction of the significant temporal change in community structure along DCA axis 4 towards the positive end (Table 3) indicates a trend in the species data towards resemblance to species compositions of the mid/ upper parts, towards sites of increase in canopy cover and finally towards decrease in moss cover. These trends may indicate an increase in species moderately pressed towards their substrate and which reside throughout the entire trunk and/ or thrive within environmental conditions provided by the middle zone/ overhanging upper zone of the trunk characterized by a low percentage of moss cover, like species of the genera Agonimia; Arthonia and Lepraria, *Radula complanata, Plagiomnium undulatum, Plagiothecium denticulatum, Metzgeria furcata, M. conjugata, Neckera complanata, Hypnum cupressiforme, Micarea prasina.s.lat.*, and *Nephroma parile.*

The trend revealed along axis 4 indicate more shady local environments with reduced moisture from precipitation, corresponding to the overhanging top zones and the middle part of the trunk. These results in turn suggest that the trend of increase in moist conditions found along DCA axis 2 and the gradient of moisture is likely to in large derive from increase in atmospheric humidity following canopy closure rather than increase in moisture from precipitation.

Variation in temporal turnover rates

DCA axis 4

The indication of the direction of temporal turnover as distributed along DCA axis 4 towards homogenization of species compositions along the gradient of stem inclination seems to be supported through the testing of Height on temporal turnover rates along the axis. Even though Height was not significant to temporal turnover rates along DCA axis 4, the plot from this regression shows that the highest response is found in the basal and top zones, where species respectively loosely and strongly pressed to their substrate reside. This pattern thus corresponds to a decrease both in large, draught sensitive pleurocarps residing in the basal part as well as in shade sensitive and draught sensitive species residing in the upper zones of 90 degrees (like cyanolichens, cf. DCA axis 2 in Appendix 3).

The process of homogenization in species compositions and environments of light and moisture at the fine scale along the stem illustrates the way the gradients of aspect and height becomes less important to the vertical distribution of epiphytes as canopy grow denser, corresponding to a lower variation in community responses to environments of light and moisture. Such a decrease in beta diversity throughout the stem following an extended period of dense canopy cover was indicated through regression plots showing a lower variation within unmanaged sites among rates of temporal turnover along axis 2 as function of Aspect and Height, as compared to a high variation within managed sites.

DCA axis 2

The overall significance of Aspect and Height, and insignificance of Management, to turnover rates along axis 2 indicates however that differences in access to light and moisture throughout the trunk are important to the vertical distribution of epiphytes despite increase in canopy cover. Limitation of light in this study seems therefore not to be sufficient to mask the effect of neither height nor aspect (cf. Barkman 1958; Kenkel & Bradfield 1981; Pirintsos *et al*. 1993; Moe & Botnen 1997, 2000; Marmor *et al.* 2012). The null model represented however the most parsimonious model for axis 2, implying that Height and Aspect does not have predictive power in relation to rates of temporal turnover in the epiphytic communities of this study (cf. Appendix 4).

Assemblages of shade sensitive species were interpreted through their arrangement along DCA axis 2 (Appendix 3) to reside within the upper parts of the trunk and to the aspect of south. Consequently, a larger effect of reduced availability of light and moisture is expected within these zones as compared to the north side and the basal zone. The plots from the regressions of temporal turnover rates along axis 2 on Aspect and Height, showing that the rate of compositional turnover is highest in the top zone and to the aspect of south, thus confirms this expectation.

In combination with the measured direction of temporal turnover along DCA axis 2, DCA axis 4 and the gradients in light and moisture, the results from the model testing thus supports the interpretation of an increase in canopy cover following abandoned management as driver of compositional change through time in the epiphytic communities of this study. This study thus demonstrate a decline in relative abundances of assemblages consisting of shade and draught sensitive cyanolichens, old- growth indicators like *Antitrichia curtipendula*, as well as other shade sensitive epiphytes like *Melanelixia fuliginosa, Orthotrichum striatum, O. lyelli, O. pulchellum, Pseudoleeskella nervosa, Pteridynandrum filiforme* and *Ulota crispa.* The results indicate that this temporal trend in shade sensitive species reflects a negative response to abandoned management during the last 20 years.

Uncertainties

Due to its use in this study for comparison among assemblages within the same vegetation type (cryptogam epiphytes), the employment of Ellenberg indicator values for assessment of temporal trends in the vegetation in relation to environment can be considered as reliable (cf. Wamelink *et al.* 2002). The reliability of the weighted average technique employed in this study is in addition supported through the equivalence of its results to the trends revealed along DCA axes 2 and 4 discussed in the following.

Relationships between current epiphyte occurrence patterns and the historical landscape structure have suggested more than century long time- lags (Ellis & Coppins 2007; Johansson *et al.* 2012). Ranius *et al.* (2008) claims that as old trees represent a long- lasting habitat, it might be likely that current epiphytic species distribution patterns may reflect the historical habitat quality. Johansson *et al*. (2013) demonstrated a great time lag in the response of shade sensitive species to environmental changes. A great time lag in the response of the epiphytic vegetation in this study to management would potentially overestimate the effect of abandoned management, with the consequence that the documented decline in shade sensitive species in this study would be exaggerated.

Management implications

In many European woodlands, negative impacts from cessation of pollarding on epiphytic and saproxylic biodiversity have recently been documented (Leppik *et al.* 2011; Jönsson *et al.* 2011; Marmor *et al.* 2012; Johanson *et al*. 2013; Sebek *et al.* 2013). There is as such mounting evidence for the need to mitigate the negative impact of overgrowth on the future viability of epiphytic cryptogams as well as micro- organisms residing on old trees and adapted to light open environments within the cultural landscape through pollarding and management of surrounding meadows. Jönsson & Thor (2012) showed that traditionally managed open wooded meadows had the highest incidence of ash dieback disease, followed by significantly higher risk of species extinction, compared with unmanaged closed forests and semi-open grazed sites. Ash dieback disease as such impose yet another factor to the assumed additive effects of agricultural change and silvicultural practices to the future viability of the shade sensitive old- forest epiphytes throughout Europe in general, and to the shade sensitive epiphytic vegetation of this study in particular.

Several of the pollards at Havrå are currently dying due to high age and/ or lack of pollarding. Increasing the viability of the host trees through pollarding, as well as recruitment of new trees, is thus in addition to management of surrounding vegetation a prerequisite to mitigate the temporal trend in relative abundances of shade sensitive epiphytes residing on the pollards at Havrå measured in this study to be negative.

Chapter 5. Concluding remarks

A negative impact of abandoned management on the temporal trend in an assemblage of shade sensitive cryptogam epiphytes residing on old trees in a traditionally light- open landscape was indicated through the results in this study. These results thus add to an amounting body of evidence for an ongoing and future decline within the cultural landscape in shade sensitive epiphytic bryophytes and lichens dependent on long continuity. In order to understand to what degree this trend represents an actual threat to the future viability of rare, obligate epiphytes within this group, further research is needed for assessing the way forestry and ash dieback disease add to the declining course of the successional trajectories of such species within the traditionally light- open cultural landscape.

Quantifying temporal turnover in species compositions along environmental gradients and measuring temporal change in species optimum values for light and moisture gradients at the fine scale revealed processes that is likely to be less detectable through addressing uniquely the spatial component of turnover and/ or courser spatial scales. The results of this study demonstrate that the combination of approaches employed is operational and conceptually relevant for detecting trends in old- growth epiphytic bryophytes and lichens dependent on light- open forested landscapes, in relation to environmental modifications at the scale of the landscape. The results also speak in favour of using communities of epiphytic bryophytes and lichens in detection of temporal environmental trends at the scale of the landscape.

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Figures

Tables

Appendix 1. Species list with Ellenberg indicator values

Table 17: Species list with Ellenberg indicator values.

Species	Light	Moisture
Anomodon longifolius	6	5
Anomodon sp.	6	5
Antitrichia curtipendula	6	4
Atrichum undulatum	4	6
Barbilophoza barbata	5	5
Bartramia ityphylla	4	6
Bazzania tricrenata	5	6
Brachythecium plumosum	5	8
Brachythecium rutabulum	6	6
Brachythecium sp.	5	6
Bryum capillare	6	4
Cephaloziella divaricata	7	5
Cirriphyllum piliferum	4	6
Climacium dendroides	7	7
Conocephalum conicum	3	7
Dicranum fuscescens	6	5
Dicranum scoparium	6	5
Drepanocladus uncinatus	8	9
Eurynchium praelongum	5	6
Eurynchium schleicheri	5	5
Eurynchium striatum	4	6
Eurynchium swartzii	NA	NA
Frullania dilatata	6	4
Frullania fragilifolia	5	5
Frullania tamarisci	6	5
Grimmia hartmannii	3	5
Herzogiella seligeri	4	6
Homalia trichomanoides	5	6
Homalothecium sericeum	7	3
Hylocomium splendens	6	5
Hypnum cupressiforme	6	4
Isothecium alopecuroides	4	6
Isothecium myosuroides	4	6
Lejeunea cavifolia	4	5
Leucodon sciuroides	6	4
Hylocomium breviostre	4	6
Lophocolea heterophylla	4	5
Lophozia ventricosa	5	6

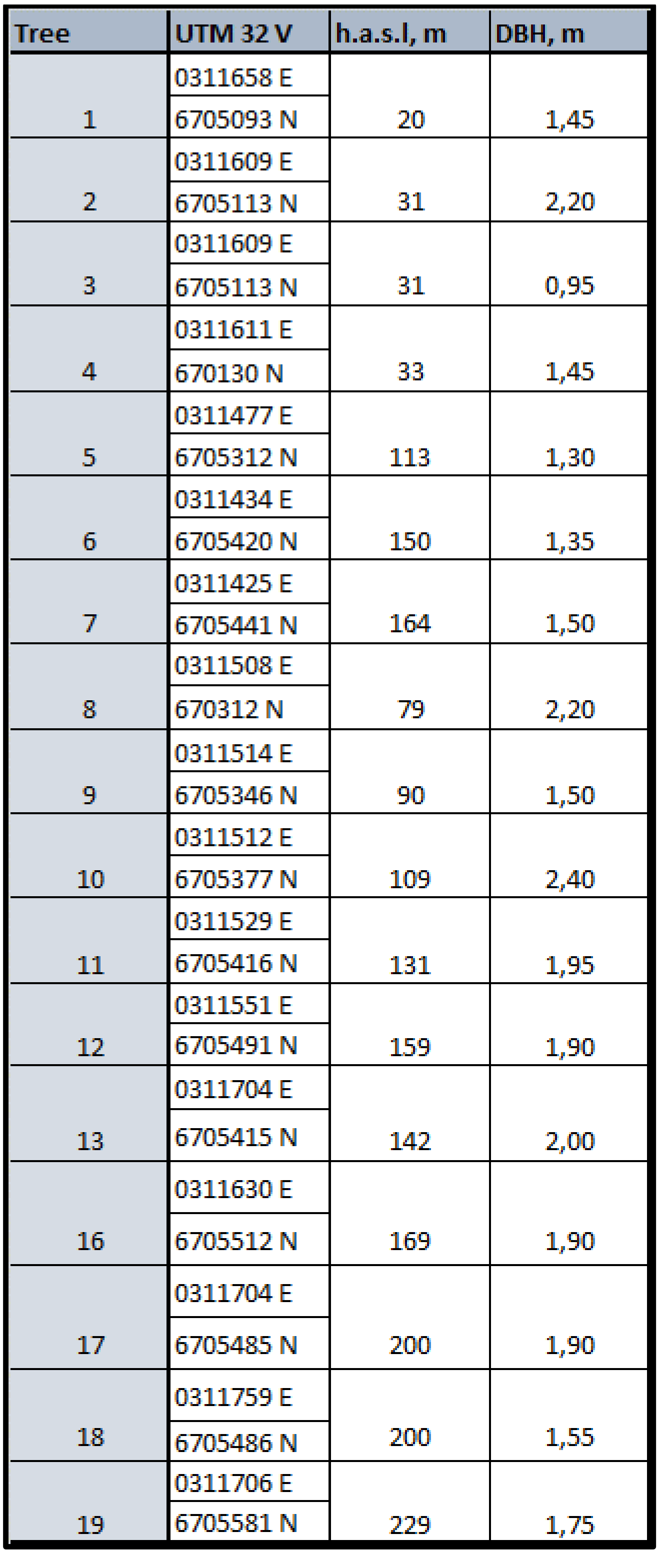
Marsupella emarginata	8	9
Metzgeria conjugata	4	5
Metzgeria furcata	5	4
Mnium hornum	4	5
Neckera complanata	5	4
Neckera pumila	5	5
Orthotrichum sp.	6	4
Orthotrichum lyellii	6	4
Orthotrichum pulchellum	6	4
Orthotrichum speciosum	6	4
Orthotrichum stramineum	6	4
Orthotrichum striatum	6	4
Trichostomium tenuirostre	4	7
Paraleucobryum longifolium	6	5
Plagiochila asplenioides	5	6
Plagiomnium cuspidatum	6	6
Plagiomnium undulatum	5	6
Plagiothecium denticulatum	4	6
Plagiothecium laetum	3	5
Plagiothecium succulentum	3	6
Pohlia nutans	5	5
Porella cordeana	5	6
Porella platyphylla	6	4
Pseudoleskeella nervosa	7	5
Pterigonium gracile	7	4
Pterigynandrum filiforme	6	5
Racomitrium aciculare	6	8
Radula complanata	5	4
Rizomnium pseudopunctatum	7	9
Rytidiadelphus loreus	5	6
Rytidiadelphus squarrosus	7	5
Sanionia uncinata	6	6
Scapania umbrosa	2	6
Schistidium apocarpum	7	2
Thuidium delicatulum/assim.	6	6
Thuidium tamariscinum	5	6
Ulota bruchii	5	5
Ulota crispa	6	4
Ulota drummondi	5	5
Ulota sp.	5	5
Zygodon baumgartneri	6	4
Zygodon virid./conoid.	6	4

Anisomeridium polypori	4	4
Agonimia sp.	4	4
Arthonia sp.	3	4
Arthonia radiata	3	4
Arthopyrenia punctiformis	NA	NA
Arthopyrenia sp.	NA	NA
Biatora vernalis	NA	NA
Buellia griseovirens	4	4
Candelariella xanthostigma	7	3
Cladonia sp.	6	6
Collema flaccidum	5	7
Collema occultatum	NA	NA
Collema subflaccidum	NA	NA
Collema sp.	NA	NA
Degelia plumbea	6	7
Dimerella pineti	NA	NA
Gyalecta flotowii	NA	NA
Lecanora sp.	7	5
Lecidella eleaeochroma	6	3
Lecidella sp.	6	3
Lepraria sp.	4	4
Leptogium cyanescens	NA	NA
Leptogium lichenoides/teretius.	4	4
Leptogium saturninum	6	7
Lobaria scrobiculata	7	7
Lobaria virens	NA	NA
Melanelixia fuliginosa	5	4
Melanelixia subaurifera	6	5
Micarea prasina s.lat.	3	4
Nephroma bellum	5	7
Nephroma laevigatum	5	7
Nephroma parile	5	7
Nephroma resupinatum	6	9
Nephroma sp.	5	7
Normandina pulchella	6	5
Ochrolechia androgyna	5	7
Opegrapha sp.	3	4
Opegrapha rufescens	3	4
Pachyphiale fagicola	5	7
Pannaria conoplea	6	9
Parmelia saxatilis	6	5
Parmelia sulcata	7	3
Parmelia sp.	6	5
Parmeliella triptophylla	6	9

Peltigera canina	6	5
Peltigera collina	6	9
Peltigera canina	6	5
Peltigera praetextata	5	5
Pertusaria sp.	4	5
Phlyctis argena	5	3
Placynthiella sp.	7	4
Porina sp.	3	4
Ramonia subspaeroides	NA	NA
Rinodina conradii	7	3
Rinodina flavosoralifera	7	3
Scoliciosporum umbrinum	8	NA
Sticta fuliginosa	5	7
Sticta sp.	5	9
Thelopsis flaveola	NA	NA
Thelopsis rubella	NA	NA
Trapeliopsis pseudogranulosa	5	NA
Anthrischus sylvestris	7	5
Athyrium filix- femina	3	7
Campanula rotundifolia	7	4
Deschampsia cespitosa	6	7
Deschampsia flexuosa	6	5
Dryopteris filix-mas	3	5
Epilobium montanum	4	5
Fragraria vesca	7	5
Geranium sylvaticum	6	6
Oxalis acetosella	1	5
Polypodium vulgare	2	4
Prunus padus	5	8
Rumex acetosa	7	5
Silene dioica	5	6
Sorbus aucuparia	6	6
Vaccinum myrtillus	6	6
Valeriana sambucifolia	NA	NA
Veronica chamaedrys	6	5

Appendix 2. UTM positions

Table 18: UTM positions, height above sea level and diameter at breast height..



Tree	UTM 32 V	h.a.s.l, m	DBH, m
1	0311658 E 6705093 N	20	1,45
2	0311609 E 6705113 N	31	2,20
3	0311609 E 6705113 N	31	0,95
4	0311611 E 670130 N	33	1,45
5	0311477 E 6705312 N	113	1,30
6	0311434 E 6705420 N	150	1,35
7	0311425 E 6705441 N	164	1,50
8	0311508 E 670312 N	79	2,20
9	0311514 E 6705346 N	90	1,50
10	0311512 E 6705377 N	109	2,40
11	0311529 E 6705416 N	131	1,95
12	0311551 E 6705491 N	159	1,90
13	0311704 E 6705415 N	142	2,00
16	0311630 E 6705512 N	169	1,90
17	0311704 E 6705485 N	200	1,90
18	0311759 E 6705486 N	200	1,55
19	0311706 E 6705581 N	229	1,75

Appendix 3. Ecological interpretation of DCA axes.

DCA Axis 1.

Species with high negative score on axis 1 reside mainly in the upper part of the investigated area, equivalent to the locations of longest distance to the sea. *Ochrolechia androgyna, Scapania umbrosa and Lophozia ventricosa* are restricted to one or two trunks at 185 m altitude (Moe & Botnen 1997). Other species with high negative scores are *Phlyctis argena, Grimmia hartmanni, Hylocomium splendens, Dicranum fuscescens, Antitrichia curtipendula, Rrytidiadelphus squarrosus, Isothecium alopecuroides, I. myosuroides, Thuidium tamariscinum and T. delicatulum.* These species with varying abilities towards moisture and light are all species most abundant at higher altitudes.

Species with high positive score reside mainly within the lower height levels of the area, corresponding to sites close to the sea: *Gyalecta flotowii, Thelopsis rubella, Leucodon sciuroides, Homalothecium sericeum, Degelia plumbea, Lobaria virens, Orthotrichum speciosum, Nephroma resupinatum, Ramonia subspheroides, Lecidella elaeochroma* and *Nephroma laevigatum.* Several of these species are sensitive to draught, and *Nephroma laevigatum* indicates humid communities in markedly oceanic habitats in relict woodlands (Smith *et al.* 2009). Moe & Botnen (1997) claimed that many of these species reside within the lower part of the investigated area (below 90 m). The red- list species *Thelopsis rubella* occurs mainly on old, porous bark with a high cover on the shadiest under-side of the top zones of the trunks (Moe & Botnen 1997).

In between these opposite ends of the axis are positioned species residing throughout the investigation area: *Radula complanata, Parmeliella triptophylla, Hypnum cupressiforme, Normandina pulchellum. Lobaria scrobiculata, Biatora vernalis* and *Buellia griseovirens.* These species reside in the mid part of DCA axis 1, of which some exist exclusively within the middle height level of the study area at trees residing at edges between dense wood and open meadow. *Lobaria scrobiculata* and *Biatora vernalis* are typical of old broad- leaved trees often residing at edges of old woodland in relatively well lit situations, and Biatora vernalis is typical of old woodlands on mossy tree trunks (Smith *et al*. 2009). Within the more central parts of the positive end reside the shade sensitive and draught tolerant pleurocarpous mosses *Homalothecium sericeum, Pterigonium gracile, Pterigynandrum filiforme, Pseudoleeskella nervosa and Leucodon sciuroides.*

Moe & Botnen (1997) found the age of pollarded branches to be lowest near the farm buildings (15 years for the youngest at that time), and the branches further away from the farm centre to be the oldest (60 years at the most). During the time between the sampling of Moe & Botnen (1997) and the sampling of this study, this pattern of level of pollarding was reinforced. The trees most close to the farm have been pollarded within the last 10 years (with exception of the pollarded tree nr. 16 situated at high altitude), whereas the trees situated in areas more distant from the farm have been left unpollarded. Even though there is higher site quality (the capacity of the field to produce wood) in the lower sites close to the sea (Kjetil Monstad, personal communication 05.05.2013), there is no clear trend of tree girth within the area. The higher site quality in the lowermost area may however interfere with the gradient revealed along axis 1 as effect of that bark pH/ nutrient status may be modified by an interaction with the soil environment.

DCA Axis 2

Examples of species which reside in the upper, positive part of axis 2 are *Antitrichia curtipendula, Orthotrichum pulchellum, Orthotrichum lyelli, Orthotrichum striatum, Ulota crispa, Parmelia sulcata, Lecidella eleaeochroma, Lobaria scrobiculata, Pseudoleeskella nervosa, Frullania fragilifolia, Orthotrichum stramineum, Dicranum fuscesence* and *Cephaloziella divaricata.* Within the upper mid part of the axis, among others, species sensitive to both shade and draught are found: *Nephroma resupinatum, Parmeliella triptophylla, Lobaria scrobiculata, Leptogium saturninum, Pannaria conoplea, Sanionia uncinata, Peltigera collina, Brachythecium rutabulum, Climacium dendroides and Degelia plumbea.* Example of species from the middle part of the axis with tolerance towards shade and draught are: *Metzgeria furcata, Radula complanata, Leptogium lichenoides/ terretius, Neckera complanata, Opegrapha rufescence.* Species typical of the lower, negative part of the axis are shade resistant/ draught sensitive species like *Loeskobryum breviostre, Oxystegus tenuirostris, Plagiochila asplenioides, Plagiothecium denticulatum, Plagiothecium succulentum, Rytidiadelphus loreus, Collema flaccidum, Eurynchium striatum* and *Conocephalum conicum.*

The arrangement of species along axis 2 suggests that species with low resistance towards shade and high resistance towards draught are situated at the positive end of DCA axis 2 and tend to reside in the upper parts of the trunk. Situated at the extreme positive end of axis 2 are shade sensitive species like *Orthotrichum lyelli, Parmelia sulcata* and *Lecidella elaeochroma,* separated from shade tolerant species with a more central position within the positive end, like *Thelopsis rubella, Ochrolechia androgyna* and Lepraria sp (p). This arrangement may reflect the variation in stem inclination within the height of the top zone. Species thriving in humid environments which are easily overgrown by mosses, reside within bark crevices in overhanging top zones where irradiation is low, like *T. rubella.* Species like *Parmelia sulcata,* adapted to dry environments/ high evaporation, reside in the top or middle zones of 90 degrees where evaporation is high and light is more abundant than within the top zones of high inclination.
Species tolerant both to desiccation as well as shade and/ or species residing throughout the entire tree are scattered within the mid part of axis 2. Species sensitive to shade as well as draught are found in the upper mid part. Species sensitive to draught and tolerant to shade reside at the negative end of the axis, and these species are restricted to the lowest part of the trunk, mainly representing species from the ground. DCA axis 2 seems thus to represent a distribution trend along the stem, with species similar in abilities towards moisture as well as light corresponding to a particular stem inclination/ height. This arrangement of species might as well represent a gradient of aspect, with the positive end corresponding to the aspects of south- west were irradiation and evaporation is likely to be higher than to the north- east.

The interpretations of species scores and plots from regression related to DCA axis 2 indicate that draught sensitive and shade tolerant species are confined to the lowest part of the trunk, i.e. the basal zone. This pattern indicates that near the base of the trunk the relative humidity is higher than within the upper parts of the trunk (cf. Kenkel &Bradfield 1986; Smith 1982). Some liverworts and mosses at the base that are sensitive towards draught are however also highly sensitive towards shade. Most of these species are facultative epiphytes or epigeous species deriving from the ground below the stem, like *Racomitrium aciculare, Drepanocladus uncinatus* and *Marsupella emarginata.* The domination of peurocarps and other bryophytes in the basal zone of the pollards in this study is also due to the high inclination that limits run-off of water from rainfall in summer and snowmelt in winter.

The positive end of this axis, corresponding to the upper parts of the trunk and the aspect of south, is in large dominated by lichens. Lichen assemblages are supposed to be more limited by light and less sensitive to desiccation than bryophytes (Ranius *et al.* 2008a; Kiraly *et al.* 2013). Within the upper part of the trunk and to the aspect of south, light availability and desiccation is higher than in the moister and darker, lower parts of the trunk, as well as to the aspect of north, where bryophytes dominates.

The relatively low light availability under forest canopies may limit photosynthesis and consequently the growth of lichen thalli (Green et al. 2008, Palmqvist et al. 2008). The epiphytic cyanolichens *Leptogium saturninum, Lobaria scrobiculata, Degelia plumbea, Pannaria conoplea* and *Parmeliella triptophylla* are species sensitive towards both shade and draught. From their position along DCA axis 2 these species were interpreted to reside in the upper part of the middle zone and to the aspect of south, what may represent a compromise between the need for good illumination and shelter from desiccating winds (cf. Rose 1993). This interpretation is supported by the observations that in temperate conifer forests of the Pacific North west of USA, cyanolichens take an intermediate position along the moisture gradient between the draught- resistant chlorolichens and the draught- intolerant bryophytes (Sillett & Antoine 2004).

DCA Axis 3

Several species (mainly crustose lichens) positioned on the positive end of axis 1, like *Arthonia radiata, Opegrapha rufescens* and species of the genera Pertusaria, are easily overgrown and prefer relatively smooth (not fissured) and bare bark. Also species from the genera Lecidella and acrocarps like *Ulota crispa, Orthotrichum lyelli and O. striatum* are situated at the positive end of the axis. In the mid part reside species that may thrive on various kinds of bark substrates or on mosses, but often common in old woodlands (Smith et al. 2009), like *Biatora vernalis, Rinodina conradii, Ochrolechia androgyna, Trapeliopsis pseudogranulosa, Phlyctis argena, Thelopsis rubella,* and *Ramonia subsheroides*. Members of the Lobarion community (foliose lichens with blue- green algal component) are also found scattered within this mid part of axis 3. These latter species grow on or among mosses in open patches at moderately fissured bark, like *Normandina pulchellum, Parmeliella triptophylla, Peltigera collina, Leptogium lichenoides, L. saturninum, Lobaria virens, L. scrobiculata, Nephroma resupinatum, Sticta fuliginosa* and *Degelia plumbea. Thelopsis rubella* and *Pachyphiale fagicola* are indicators of ancient woodland residing in moderately well- lit, mossy bark in open patches in the Lobarion (Smith *et al.* 2009). These indicators of ecological continuity reside at the lower end of the mid part of the axis among shade tolerant and draught sensitive species.

Examples of species residing at the negative end are; species from the genus Opegrapha, *Gyalecta flotowii, Pachyphiale fagicola, Collema flaccidum, Peltigera praetextata, P. canina, Lobaria scrobiculata, Loekobryum breviostre, Eurynchium striatum* and *Antitrichia curtipendula.* Species within this group are mostly slow colonizing pleurocarpous mosses and large foliose lichens thriving on mature or fissured old bark or on moss cover. Also some crustose lichens residing on bare patches among mosses appear within this group. The arrangement of species along DCA axis 3 seems to reflect a gradient that may be explained by different substrate conditions on the trunk, what suggests that DCA axis 3 represent conditions related to the cyclical successive stages of the epiphytic vegetation.

Pioneer species on smooth bark such as *Lecidella eleaeochroma* and *Ulota crispa,* were suggested by Moe & Botnen (1997) to be relicts from earlier succession stages of the bark related to the growth of the three, what may explain the residence within the mid part of axis 3 of the pioneer shade sensitive species *Lecidella elaeochroma* and *Buellia griseovirens*. Parts of a potential decline in relative abundances of such species might therefore be due to their affiliation to a passed succession stage related to three growth. The investigated trees are all probably close to the maximum age for *Fraxinus excelsior,* i.e. 300-400 years (Nedkvitne & Gjerdåker 1993). All the trunks under examination have as such passed the stage of extensive length growth, equivalent to a passed pioneer stage of smooth bark. Since the trunk have more or less reached the climax stage of rough bark, the arrangement of species along axis 3 suggests a gradient from species residing on more or less rough bark structure due to peeling-off to species thriving on more fissured bark structure.

The reached maximum age of the trees may be illustrated through the relation between axis 3 and Height ($R^2 = 0.000$). If maximum age would not have been obtained, length growth would have been more substantial and smooth bark species should as such correspond to the top zone of the tree where new bark substrate would develop. It is therefore likely that variation in bark substrate due to peeling- off followed by cyclical succession of the vegetation, rather than variation in bark substrate due to length growth, is underlying the ordination of species along axis 3, and the cryptogamic epiphytes at Havrå are likely to re- colonize the trunk after each peeling-off.

This pattern is likely to underlie the observations of Moe & Botnen (1997) who found thick mats of the pleurocarpous mosses (especially *Antitrichia curtipendula* and *Leucodon sciuroides*) as partly loosened with bare bark appearing underneath. *Antitrichia curtipendula* is a shade sensitive moss tolerant towards draught and associated with old-growth forests (Rosso *et al.* 2001). Rosso *et al.* (2001) suggested that dispersal and establishment limitations decrease the ability of A. curtipendula to establish in younger stands. Re- colonization of bare patches may result from remnants of the dislodged mat, growth of surrounding epiphytic vegetation, or diaspora establishment (Kenkel & Bradfield 1986, Sjögren 1995). Some of the pleurocarpous mosses at the negative end of the axis, like *Antitrichia curtipendula*, *Homalothecium sericeum* and *Leucodon sciuroides*, are shade sensitive and draught tolerant species. Other species at the negative end are shade tolerant and draught sensitive, like *Loeskobryum breviostre* and *Eurynchium striatum.* Also the opposite, positive end of the axis consist of contrasting species with respect to abilities towards light and moisture, what might explain the absence of clear gradients of light and moisture along axis 3.

In open habitats, higher wind speed increases evaporation and also has a stronger mechanical destroying effect (Barkman 1958). Along axis 2, the upper parts of the trunk was found to correspond to the south side and sites of reduction in canopy cover. Consequently, in addition to the relatively higher exposure of wind at the south side, the highest wind speeds are likely to be found in the upper parts of the trunk. Bryophytes in general are sensitive to desiccation (Ranius *et al*. 2008a; Kiraly *et al*. 2013), and large pleurocarps are likely to be more exposed to dessication and mechanical destroying effects from wind than acrocarps and lichens that are more apressed to the stem (cf. discussion of axis 4 in this study). The domination of large pleurocarps within the basal part of the trunks in this study, corresponding to the north side of the trunks, indicates that these parts of the trunk are relatively more sheltered and moist.

Like the interpretations of the species scores along axis 3 suggests, it is likely that the variation in substrate conditions related to the cyclic succession stages underlie the measured significance of Height and Aspect to the variation in turnover rates along axis 3. This suggestion is supported by the finding (from regression plots) of higher turnover rates in the upper parts of the trunk and to the south, relative to the lower parts and to the north. This pattern is likely to reflect relatively higher rates of peeling- off in the upper parts of the trunk and to the south due to relatively higher exfoliation from higher sun exposure (to the south) and stronger desiccating winds (in the top zone as well as to the south). At Havrå, such a pattern is highly plausible due to the position of the trunks in a south- facing slope at the south side of Sørfjorden, where the south side of the trunk therefore is relatively higher exposed than the north side both to irradiation as well as to winds.

DCA Axis 4

At the positive, upper end of axis 4 reside *Frullania fragilifolia,* species of the genera Orthotrichum, *Leidella elaeochroma,* and *Parmelia sulcata.* These species are sensitive towards shade and resistant towards draught. Also the shade tolerant and draught tolerant *Opegrapha rufescens* and *Phlyctis argena* are found in the upper part. The above mentioned species are more or less strongly pressed against the substrate, reside within the upper parts of the trunk in environments with little retention of water and exposed to more or less irradiation depending on the degree of stem inclination.

Species with different abilities towards light and moisture, and belonging to the groups of liverworts, small foliose lichens and small pleurocarps, are positioned within the mid part of the axis. The most abundant of these species are *Metzgeria furcata, Leucodon sciuroides, Homalothecium sericeum, Hypnum cupressiforme,* species of the genera Lepraria, *Isothecium myosuroides, Leptogium lichenoides* and *Melanelixia subaurifera.* These species are found either within the middle zone of the trunk or scattered throughout the entire trunk. Some variation in environments of light and moisture exist between the upper mid part and the lower mid part of the trunk (cf. discussion of DCA axis 2), but relative to the heterogeneity throughout the entire trunk, the environmental heterogeneity within the mid part can be characterized as low. Consequently, species residing in the mid part do not vary extensively with respect to their moderate to high resistance towards shade and draught. This homogeneity in species abilities towards light and moisture is reflected through the species' moderate adherence to substrate, corresponding to a lack of highly pendulate pleurocarps, most crustose lichens (except for the leprose) and large foliose lichens.

In the negative end of axis 4, *Nephroma resupinatum, Peltigera resupinatum, Bazzania tricrenata, Loeskobryum breviostre* and *Thuidium tamariscinum* reside. These latter species are all sensitive towards draught, more or less tolerant towards shade and found in the basal part of the trunk on the slanting upper side. The most striking common feature unifying these latter species is however the way they are loosely pressed to their substrate, indicating a residence within moist and shady environments. Evaporation is likely to vary both with height on the stem as well as with inclination within each height (cf. discussion of axis 2 in appendix 1). A gradient of stem inclination is consequently related to the way species are adapted to shade and moisture stress. Axis 4 seem therefore to reflect variation in the degree to which species adhere to their substrate.

Appendix 4. Importance of Height, Aspect and Management

The results from the model testing show that there are very small probabilities of that the variation in temporal turnover along DCA axis 2 as function of Height would have occurred by chance if the null hypothesis was true. The large F- value for axis 2 (F = 4.44) of the Anova- test of the regression of turnover rates along axis 2 as function of Height provide evidence to reject the null hypothesis of no variation in rates along this axis (no beta diversity). The significance of Height to turnover rates along axis 2 indicate an important role to gradients in light and moisture to the vertical distribution of the epiphytes along the stem.

The interaction term between Height and Aspect was not significant for axis 2, indicating that the change in temporal turnover rate by moving from one level to the next (e.g. from middle to top) of the predictor of Height does not depend on the predictor of Aspect, and vice versa. The null model (intercept-only model) represented the most parsimonious model for axis 2. These results indicate that the model with Height does not have predictive power to the variation in temporal turnover rates along axis 2. The fact that the null model is provided with the greatest support does only signify that it is the best model out of the ones included in the selection, and that the potential variation in temporal turnover rates cannot be predicted by the variables in the alternative hypotheses. There may be variation that is unrelated to the measured gradient, like indicated through the large F- value.

The results from the model testing show that there are very small probabilities of that the variation in temporal turnover along DCA axis 2 as function of Aspect would have occurred by chance if the null hypothesis was true. The large F- value for axis 2 (F = 3.52) of the Anova- test of the regression of turnover rates along axis 2 as function of Aspect provide evidence to reject the null hypothesis of no variation in rates along this axis.

Aspect and Height was significant to variation in temporal turnover along DCA axis 3. The results from the regressions show that it is unlikely that variation as function of these variables would have occurred by chance if the null hypothesis was true. The large F- values for axis 3 (F = 3.27 for Aspect and F = 15.8 for Height) from the Anova- tests of these regressions provide evidence to reject the null hypotheses of no variation in rates along this axis (no beta diversity).

The interaction term between Height and Aspect was not significant for axis 3, indicating that the change in temporal turnover rate by moving from one level to the next (e.g. from middle to top) of the predictor of Height does not depend on the predictor of Aspect, and vice versa. The model with Height as the only fixed effect factor represented the most parsimonious model for axis 3. These results indicate that Height has predictive power to the variation in temporal turnover rates along axis 3, whereas Aspect does not have predictive power. Other relevant factors that were not measured and included as potential predictive variables obviously might have had higher predictive power than Height to the variation along axis 3.