Ecology and Conservation of Bryophytes and Lichens on *Fagus sylvatica*

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Cover: Slow-growing and suppressed beech trees with rot holes are an important habitat for many rare bryophytes and lichens. Photo: Örjan Fritz.

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Abstract

Environmental factors related to the occurrence of epiphytic bryophytes and lichens were examined in beech (*Fagus sylvatica*) forests in the Province of Halland, Sweden. Patterns in species composition and species number at different temporal and spatial scales were analyzed with emphasis on species of conservation concern (i.e. red-listed and indicator species).

(I) At stand level, the availability of substrate, a high stand age and forest continuity were the most important factors explaining high species number of epiphytes of conservation concern. The difference in species number between stands with and without forest continuity was probably related to the presence of old trees and the time available for species colonization. **(II)** Within stands, plots containing old trees, at the base of slopes and with low recent forestry impact had the highest species number. At tree level, age, size and moss cover were primary factors in explaining both species number and species composition of all species. Red-listed lichens were associated with damaged beech trees older than 180 years, whereas the few red-listed bryophytes were also recorded on younger stems in dense stands. **(III)** The vertical distribution of epiphytes, recorded on newly fallen beech stems, could also be related to tree age. Some red-listed lichens were recorded only from above 2 m in height on trees older than 250 years. The presence of any species of conservation concern at 2-5 m height on standing living beech trees correlated positively to moss cover and bark structure, which in turn was dependent on tree age.

(IV) The effect of bark and tree characteristics on species occurrence was studied. It was found that the combination of high bark pH, high tree age and damaged stem best explained the number of species of conservation concern. The link between old beech trees and high bark pH was partly explained by a positive effect of tree age on stemflow pH. **(V)** At microhabitat level, the type of stem damage rot hole was found to positively influence bark pH and the occurrence of species of conservation concern. Old and slow-growing trees with rot holes are, however, often removed from managed beech forests. A spatial separation between managed and retention areas is therefore recommended in shelterwood forestry.

Keywords: bark pH, biodiversity, Biskopstorp, microhabitat, non-parametric multivariate analysis, red-listed species, rot hole, tree age

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Dedication

Hanna, Hampus and Karin
with love

Contents

List of Papers

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Fritz, Ö., Gustafsson, L. & Larsson K. (2008). Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation,* 141, 655-668.

II. Fritz, Ö., Niklasson, M. & Churski, M. (2009). Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science*, 12, 93-106.

III. Fritz, Ö. (2009). Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation. *Biodiversity and Conservation*, 18, 289-304.

IV. Fritz, Ö., Caldiz, M. & Brunet, J. Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. *The Bryologist*, accepted.

V. Fritz, Ö. & Heilmann-Clausen, J. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). Submitted manuscript.

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Preface

After moving to Halland in 1987, I soon realized that the growth form, extensive moss cover and the rough bark of the beech trees differed from those I was used to see in the neighboring Province of Scania. The humid climate was also new, where evaporating scattered clouds lifted slowly above the beech canopies following the plentiful rainfalls, creating the feeling of a cloud forest. The beech stems were also often covered by many lichens! These experiences made the beech forests incredibly inviting, and I was eager to learn more about the habitat and discover its epiphytes.

Inspired by an article about *Lobaria* species (Hallingbäck 1986), I began searching, in my free time, for these lichens which were thought to indicate valuable forests from a biodiversity point of view (Andersson & Appelqvist 1987). I recorded many local populations of *L. pulmonaria* (**Fig. 1**) but also a few other *Lobaria* species (Fritz 1992). From 1992 to 1997, I took part in the national woodland key habitat survey (Nitare & Norén 1992). I visited many beech forests and mapped hundreds of key habitats across the county. It was easy to spot particularly interesting beech trees for rare epiphytes even from a distance. But why were those trees so special for the rare epiphytes and not the neighbouring ones in the same stand?

Other patterns emerged; some stands and landscapes seemed to contain higher concentrations of key habitats and species than others. What could explain such differences? A study of forest history (Fritz & Larsson 1996) was followed by another with a scientific approach (= **paper I**). After having worked with surveillance and protection of the most valuable key habitats at the County Administration Board, I finally, in 2005, got the chance to study these issues via the Broadleaf Program in Alnarp. Now, I am happy to present the results of my scientific research in this thesis.

Figure 1. The large and easily identified foliose lichen *Lobaria pulmonaria* is frequently used to indicate woodland key habitats.

Introduction

Background

Beech (*Fagus sylvatica*) is an important tree species in forests across Europe. On calcareous soils vascular plants form a conspicuous herb layer. This is contrary to the beech forests growing on acid soils which are often very poor in vascular plants, but may contain species-rich communities connected with the trees. Epiphyte communities together with wood-inhabiting fungi and invertebrates may constitute the majority of the known biodiversity in such places. However, due to human activities, the area of temperate forests has decreased substantially, and it is considered to be one of the most altered forest biomes on the planet (Hannah et al. 1995). Natural beech forests have almost completely vanished from Europe (Peters 1997).

After the last glaciation beech was one of the last tree species to recolonize Sweden. Beech reached its maximum distribution in Sweden during early medieval times (Björkman 1997). In the study area of this thesis, the Province of Halland, forest cover had decreased substantially due to increased human exploitation by the second half of the 17th century, and this trend accelerated during the 18th and 19th centuries with large areas being transformed into heaths (Malmström 1939). Since the end of the 19th century, extensive plantations of norway spruce (*Picea abies*) have caused a shift in forest composition towards dominance of conifers in the study area. Rough estimates from maps suggest that less than 10% of the beech forest area in the mid 1600s remains today (cf **paper I**).

The decrease in the area of beech habitat has affected many species associated with beech trees. Pehr Osbeck, a pupil of Carl Linnaeus, recorded extensive lists of species of various organisms during the 18th century in southern Halland (Osbeck 1996, Fritz 2000). The species most sensitive to habitat

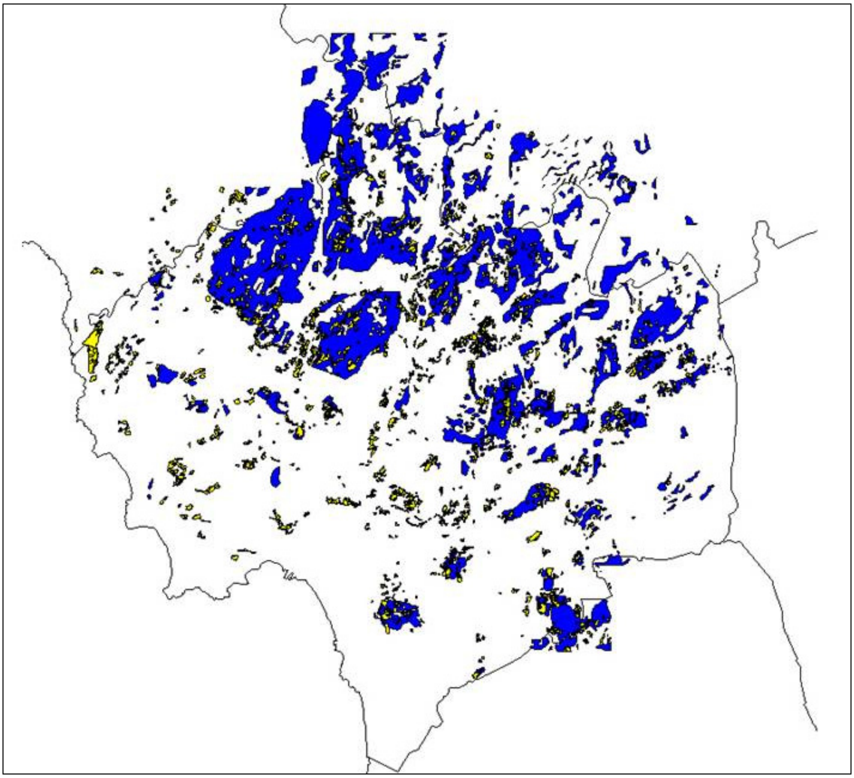

Figure 2. Temperate broadleaved forests in 1652 *as well as* 1841-42 (blue) compared with the distribution of beech and oak-dominated forest stands in 1995 (yellow) within the Municipality of Halmstad, Province of Halland (Malmström 1939; Forestry Board, survey 1995).

loss and landscape changes probably became extinct from the province already during the 19th century (Nilsson 1996, Larsson & Simonsson 2003). Lichens such as *Lobaria amplissima* and *L. virens* were recorded by Osbeck in the 1800s, but are no longer to be found anywhere in southern Halland. The area of beech habitat continued to decline during the 20th century, and the remaining forests exist as small fragments in the spruce matrix (**Fig. 2, 3**).

Habitat loss in combination with the negative effects of air pollution have contributed to a situation where many epiphytes are rare and their long-term survival is uncertain, i.e. they are red-listed (Gärdenfors 2000, 2005). In southern Sweden beech is the most important tree species (phorophyte) for red-listed lichens (Arup et al. 1997), with concentrations of records in the County of Halland (Brunet et al. 2005). In this county 62% of all records of red-listed lichens were recorded from beech (County Administration Halland, database 2005), despite the fact that beech forests now only cover

Figure 3. Beech forests of today often grow in a matrix of spruce plantations. Berg, Halland.

about 3% (9 000 ha) of the total forest area (Forestry Board Södra Götaland 2000).

With the above background information, knowledge of environmental factors influencing the occurrence of epiphyte species is crucial for adequate conservation planning. Such knowledge is also important for future restoration of habitats and management in reserves as well as in managed forests.

The habitat: Beech forest

Beech is a competitive broadleaved tree species. Being shade tolerant, beech seedlings can establish below other tree species and eventually grow higher, i.e. outcompeting them. Beech saplings can survive for decades under dominating trees, where other tree species would have perished. Such slow-growing suppressed beech trees are a common sight in unmanaged beech forests. If the dominant beech tree dies the suppressed trees can suddenly increase growth. This plasticity in growth is characteristic for beech (Peters 1997).

At young to mature ages beech has a smooth, thin but rather hard bark, superficially resembling hornbeam (*Carpinus betulus*). The buffer and water-holding capacity of the bark is low to moderate, whereas the nutrient availability and pH for beech bark are considered to be moderate (Barkman 1958).

Contrary to many other trees, such as oak (*Quercus* spp.), beech bark has no adaptations for withstanding heat and is susceptible to fire (Peters 1997). In sun-exposed conditions, the thin bark of beech may not be able to protect the cambium from overheating, resulting in cracks in the bark (Nicolai 1986) and a very dry microhabitat. Under these conditions beech bark does not support many substrate-demanding epiphytes.

In closed stands shaded beech bark is less affected by desiccation because of higher air humidity and a higher stemflow from the more erect branches (Falkengren-Grerup 1989, André et al. 2008). Stemflow can build up rather rapidly during rainfall and influence large parts of the beech trunk. Beech bark is also relatively sensitive to frost and other biotic damage (Braun 1976; Jönsson 1998, 2000). When old, beech bark can be rough and fissured, thus providing other microhabitats for epiphytes.

The maximum age recorded for a beech tree in the County of Halland is 400 years (Niklasson & Fritz 2003), but trees more than 300 years old in forest habitats are rare (Niklasson 2002). In most beech forests managed by shelterwood cutting, the rotation is between 100 and 140 years depending on site productivity. This means that very old beeches, between 200 and 300 years, are not present in heavily managed beech forests.

The existing beech forests are often relatively pure stands, probably due to the former and current economic importance of this tree species for, e.g. beech nut production for pig breeding and timber (Björkman & Karlsson 1999). In addition, the existing beech stands are often influenced by forestry management, resulting in one or sometimes two distinct cohorts, in contrast to a wide age distribution pattern in natural beech forests with gap phase dynamics (Niklasson et al. 2005).

Compared to the beech forests in the Provinces of Scania and Blekinge the average age of the dominating cohort in the beech forest stands in Halland is clearly higher (Forestry Board, Södra Götaland 2002). The age distribution of the present beech-dominated forests in the Municipality of Halmstad is skewed towards high ages (**Fig. 4**). Very few stands are younger than 60 years, and the estimates of stand ages from the Forestry board surveys are known to be an underestimate of the real age (cf **paper I**).

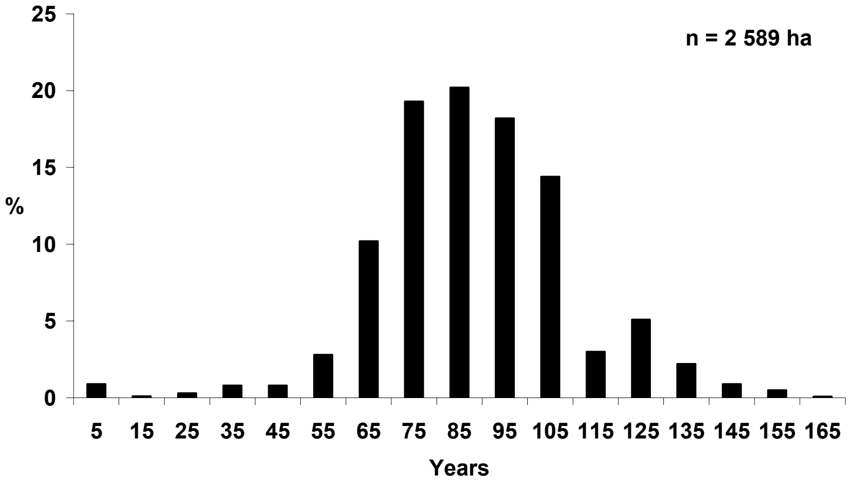

Figure 4. Beech-dominated (≥50% of basal area) forest stands in the study area distributed by ten-year classes of **estimated** ages in 1995 (Forestry Board, 1995).

The organisms: Epiphytic bryophytes and lichens

Epiphytes often grow on several phorophytes, and are rarely restricted to one particular tree species. However, the European beech is inhabited by a rather specialised set of lichens (Almborn 1948; Arup et al. 1997; Thor 1998; Berg et al. 2002), of which the crustose lichen *Pyrenula nitida* (**Fig. 5**) is one of the most common red-listed species. Of the bryophytes, the red-listed moss *Neckera pumila* (**Fig. 6**) was, in this study, not only recorded from old beech stands but also from rather young stands, perhaps recovering after recent decline in acid deposition (cf Hallingbäck 1992).

The highest number of lichens recorded in a beech forest in Sweden was 135 species, in the nature reserve Ödegärdet (20 ha) (Gustavsson 1995). The total number of epiphytic bryophytes and lichens growing on beech in the study area (**Fig. 7**) is not accurately known, but the minimum number of species growing in beech forests of southern Sweden has been estimated as 220 species (Hallingbäck 1995, 1996). The regional species pool included about 110 red-listed and indicator species of epiphytic lichens and bryophytes known to grow on beech in the study area, but not necessarily preferring beech over other tree species (County Administration Board, database 2005).

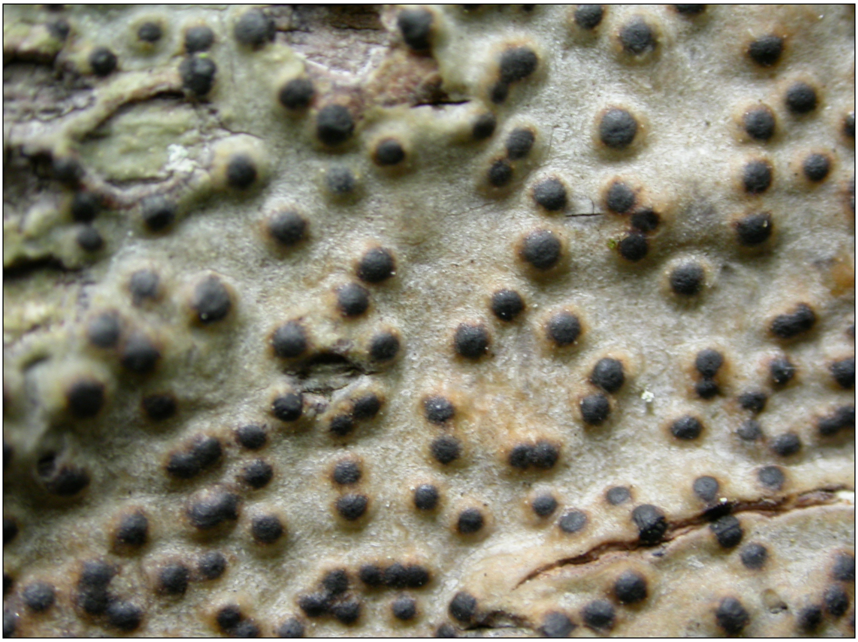

Figure 5. *Pyrenula nitida* is the most common red-listed lichen on beech in the study area.

Figure 6. *Neckera pumila* is the most common red-listed bryophyte on beech in the study area.

Crustose species are by far the dominating growth form of lichen in these forests, followed by some foliose and a few fruticose species. Many of the crustose species reproduce sexually and disperse primarily by means of spores from the mycobiont´s apothecia. However, some lichens disperse only a-sexually by the concomitant dispersal of the mycobiont and the algal component, in isidia and soralia, and only a few by thallus fragmentation.

Most bryophytes in the study are mosses, but some are liverworts. The bryophytes disperse sexually by many small spores or by vegetative means, such as gemmae.

Due to the different sizes, spores, soralia and gemmae may disperse further with the wind (Hutsemekers et al. 2008) than isidia and thallus fragments. Most of the propagules however, do not usually travel far from the source (e.g. Sundberg 2005).

The relationship between epiphytes and the environment

Light and humidity are often considered to be key factors for bryophytes and lichens since they regulate growth (Barkman 1958). Bryophytes and lichens are poikilohydric organisms and physiologically active only when they are wet. As a corollary, the distribution of lichens on a large scale is often considered to be primarily controlled by humidity (Peterson & McCune 2001, Giordani 2006, Ellis & Coppins 2006). For bryophytes wet conditions are also an important prerequisite for successful fertilization and spore germination (Goffinet & Shaw 2009).

There are many other abiotic and biotic factors affecting the distribution of epiphytic bryophytes and lichens, with their importance changing with spatial and temporal scales (Mikhailova et al. 2005). At a local scale tree characteristics, such as age, bark chemistry and structure, diameter and tree species are considered important for epiphytic species composition. At a regional scale forest continuity, forest management practices and fragmentation, humidity, soil properties and topography can influence epiphyte composition, whereas on a global scale air pollution and climate can be the main drivers (summarized in Aude & Poulsen 2000).

Objectives

The overall aim of this thesis was to identify limiting ecological factors for epiphytic bryophytes and lichens at different spatial and temporal scales in beech forest. The thesis work included conservation issues focusing on red-listed (Gärdenfors 2005) and indicator epiphytes (Nitare 2000).

The most important questions raised were:

I. How important is forest continuity for the occurrence of epiphytic lichens and bryophytes?

II. Is the succession of epiphytic lichens and bryophytes on beech age-structured?

III. Is the vertical distribution of epiphytes correlated to tree age?

IV. How important are differences in bark characteristics between individual stems for the occurrence of epiphytes?

V. Is there a relationship between different types of stem damage and the presence of epiphytic lichens and bryophytes?

The results from these five studies are likely to have significant implications for conservation in managed as well as in protected forests.

Material and methods

The study area: Halland, Sweden

All studies were conducted in the southern part of the Province of Halland, southern Sweden (**Fig. 7**). Altitudes in this area range from ca. 60 m to 200 m.a.s.l. Mean annual air temperature ranges from 6.5 to 8° C and mean annual precipitation is between 1 100- 1 500 mm with rainfall (of > 1 mm) on more than 140 days per year (Raab and Vedin 1995). The climatic conditions can be characterized as sub-oceanic. The bedrock is dominated by pre-cambric granites. Glacial moraine deposits dominate the soils, which are generally acid and oligotrophic (Fredén 1994). Almost all beech stands belong to the *Fagus sylvatica - Sorbus aucuparia - Deschampsia flexuosa* community (Diekmann et al. 1999). Phytogeographically the area is situated in the transition zone between the nemoral and hemiboreal regions (Jonsell 2004).

The province is exposed to predominantly southwesterly winds, bringing up air pollution from the European continent and the British Isles. Acid deposition has however, decreased markedly in recent years, from about 25 kg S/ha yr^{-1} in 1988 to about 5 kg S/ha yr^{-1} in 2007 in spruce forests. During the same period the pH of rainfall on open land has increased from about pH 4 to almost 5 (Karlsson et al. 2008).

The study sites: The Municipality of Halmstad and Biskopstorp

In paper **I** the study area covered the interior forest landscape of the Municipality of Halmstad (56° 46' N 13° 4' E) comprising 650 km^2 (**Fig. 7)**. This area was chosen primarily because it was the only region in the province with a digitized survey of the current distribution of broadleaved forests at the stand level. This survey was compared with the unique set of old forest

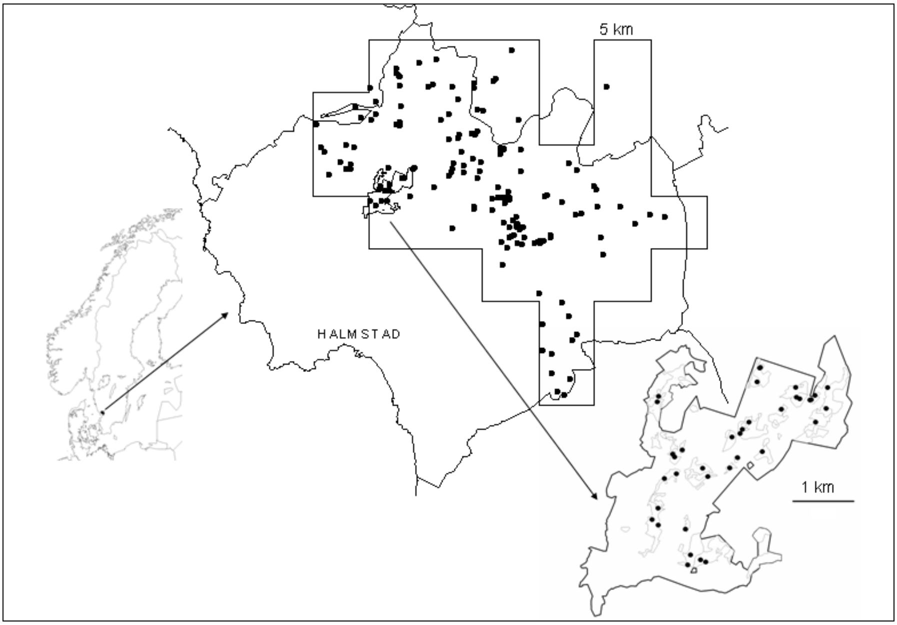

Figure 7. Study area in the Municipality of Halmstad situated in the Province of Halland, southern Sweden. Black dots mark the 150 beech stands surveyed (**paper I**). The position of Biskopstorp and the location of plots in beech-dominated stands are also given (**paper II-V**).

maps originating from 1652 and 1841-42 (Malmström 1939). Existing stands overlapping with the forest area from 1652 and 1841-42 were defined as having forest continuity (cf **Fig. 2**). Existing stands on open land in 1652 and/or 1841-42 were, in contrast, defined as lacking forest continuity.

The study area is also part of a core area for biodiversity associated with beech forests in Sweden (Brunet et al. 2005), with many hot spots for red-listed lichens in the region (**Fig. 8**).

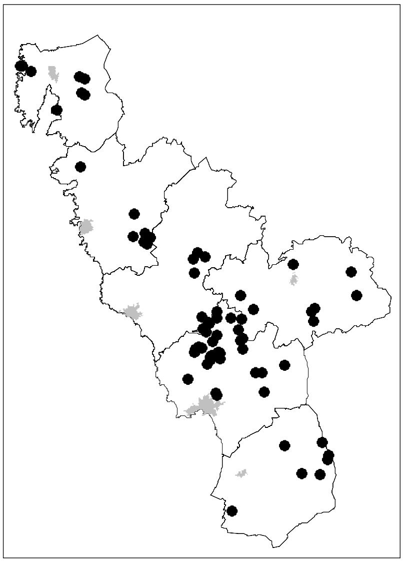

Figure 8. Hot spots for lichens in Halland, i.e. sites with > 10 red-listed lichens recorded (County Adm. Board, database 2003).

Forests covered 590 km^2 (91%) of this area in 1995 (Swedish Red Map, 1:250 000), mainly with norway spruce and scots pine (*Pinus sylvestris)*, together covering about 80%. Broadleaved forests with oaks and beech covered only 8-9% (Forestry Board, unpubl. data). All other studies **(II-V)** were conducted in the forthcoming nature reserve of Biskopstorp (56° 48' 5 N 12° 53' 47 E) (**Fig. 7**). Biskopstorp comprises about 900 ha, of which 190 ha are beech forests. The reasons for focusing on Biskopstorp were several; *first* the presence of a unique large number of beech trees which had been age-determined (Fahlvik 1999, Niklasson et al. 2005), *second* the occurrence of beech stands of various ages, topographical positions and human impact (Simonsson & Larsson 2007) and *third* the presence of many species-rich beech key habitats (Fritz 2006). In addition, selecting one area for the studies at this spatial scale restricted differences in for example macroecological conditions such as climate and forest history (cf Lindbladh et al. 2008), enabling focus on small-scale variations (Crites & Dale 1998).

Red Lists, indicator species and nomenclature

Habitat loss and air pollution are the most significant threats to epiphytic species in the temperate forests in southern Sweden (Arup et al. 1997). Estimating the extinction risk for species is the main purpose of Red Lists, which are also important tools for analysing habitat quality and setting conservation priorities (Gärdenfors 2005). Red Lists have been produced in Sweden since the 1980s and are revised every fifth year using criteria established by the International Union for Conservation of Nature (IUCN) (Gärdenfors 2000). After some initial changes the species and number of lichens and bryophytes associated with beech forest has remained rather constant. The most recent Red List (Gärdenfors 2005) has been used in all studies in this thesis.

Indicator species are frequently used to find woodland key habitats by indicating presence of red-listed species (Norén et al. 1995). After empirically testing proposed indicator species during the 1990s, a set of suitable indicator species was selected for each region in Sweden (Nitare 2000, Norén et al. 2002).

The species groups *red-listed* and *indicator species* have been selected in this thesis to represent epiphyte *species of conservation concern* (CC). All other species were considered as *species not of conservation concern* (NCC). The scientific names used for lichens follow Santesson et al. (2004) and for bryophytes Hallingbäck et al. (2006).

Methodological approaches

The methodology in the thesis followed two lines. *First* to step down in spatial scale from landscape to microhabitat **(Table 1)**. *Second* to base each new study on questions which emerged from preceding studies. The approaches were hypo-deductive (**I**) as well as inductive (**II**) but also a mixture of both approaches (**III-V**).

Table 1. Spatial scales and areas studied in different papers.

Spatial scale	Study area	Area	Paper
Landscape	Municipality of Halmstad	650 km^2	I
Stand	Municipality of Halmstad	0.5-5 ha	I
Plot	Biskopstorp	157-1 257 m^2	II
Tree	Biskopstorp	1-30 m^2	II-V
Microhabitat	Biskopstorp	< 1 m^2	V

Sampling methods

Surveys in the landscape study **(I)** were at a stand scale. Plots and trees from dendrochronological studies were used in the stands at Biskopstorp **(II-V)**.

Based on the literature and field experience from beech forests, different environmental variables were selected, from which a range of data were collected, depending on the scale studied (**Table 2**).

Epiphyte species were generally surveyed at the base of the beech trees, from 0 to 2 m in height. All species or only the species of conservation concern were surveyed around the entire stem at this height. The exceptions being in study **III** where the whole stem was surveyed, and study **V** where the survey of epiphytes was recorded within a frame placed in relation to particular microhabitats on the beech trees.

Statistical analyses

For analyses of species composition and species number in groups in response to environmental variables, the ordination method non-metric multidimensional scaling (NMS) was selected and performed in the programme PC-Ord (McCune & Mefford 1999). NMS was preferred for several reasons; assumptions of multivariate normality were not necessary, the robustness of the method to many zero values, and most importantly, NMS was used as it may provide a more accurate representation of the underlying data structure than other ordination techniques for ecological community data (McCune & Grace 2002).

For other statistical analyses the program MINITAB (Minitab inc. 1972-2008) was used.

Table 2. Sampled environmental variables depending on the scale studied. Descriptions of the variables can be found in the specific papers (**I–V**).

Variables	**Stand**	**Plot**	**Tree**	**Microhabitat**
Aspect	x			
Canopy cover	x			
Distance to closest key habitat	x			
Forest continuity	x			
Shape Index	x			
Site Index	x			
Spruce frequency	x			
Stand age	x			
Stand area	x			
Stand exposure	x			
Substrates	x			
Vegetation type	x			
Forest layering	x	x		
Geographical coordinates	x	x		
Recent forestry impact	x	x		
Basal area		x		
Elevation		x		
Location from forest edge		x		
Rocks and stones		x		
Slope inclination		x		
Stem density		x		
Topography		x		
Light		x	x	
Surveyed bark area		x	x	
Tree age		x	x	
Tree height		x	x	
Tree viability		x	x	
Bark diversity			x	
Bark fissure depth			x	
Bark recovery			x	
Bark thickness			x	
Bark water-holding capacity			x	
Crown projection			x	
Diameter at breast height			x	

Variables	Stand	Plot	Tree	Microhabitat
Moss cover			x	
Moss height			x	
Soil pH			x	
Stem inclination			x	
Stem growth rate			x	
Stemflow pH			x	
Tree exposure			x	
Tree type			x	
Bark structure (texture)			x	x
Bark pH			x	x
Stem damage type			x	x
Position in relation to stem damage				x

Results and discussion

Substrate, stand age and forest continuity explain species number (I)

Beech stands with forest continuity were consistently more species rich in epiphytes of conservation concern than beech stands on former open land in southern Halland. It was however in particular the quantity of suitable substrates in combination with high stand age and forest continuity that best explained the occurrence of rare epiphytic lichens and bryophytes. The continuity effect was probably due to a combination of higher substrate quality, i.e. old beech trees, and a longer period for colonization. The importance of high stand age for species number can be elucidated in a comparison between mature and old stands, both with forest continuity (**Fig. 9**). Consistently lower frequencies of species were recorded in the mature stands (roughly 125–145 years) compared to the old stands (roughly 160–250 years). In addition, many more species were recorded from the old stands despite the fact that a substantially smaller total area was surveyed compared with the mature stands. The effects of tree age and microhabitat were studied in greater detail in the following papers.

Due to the fact that old beech stands without continuity could not be identified in the study area, we were unable to separate effects of continuity *per se* from those of habitat quality (cf Ohlson et al. 1997). This problem was not foreseen at the start of the study, partly because the understanding of the association of rare epiphytes with old beech trees had not been studied in detail. The concept of continuity is notoriously difficult to fully comprehend and to discern from other environmental factors (Nordén & Appelquist 2001). The potential effect of continuity *per se*, i.e. the time required for colonization, needs further analysis. An alternative approach may be to study

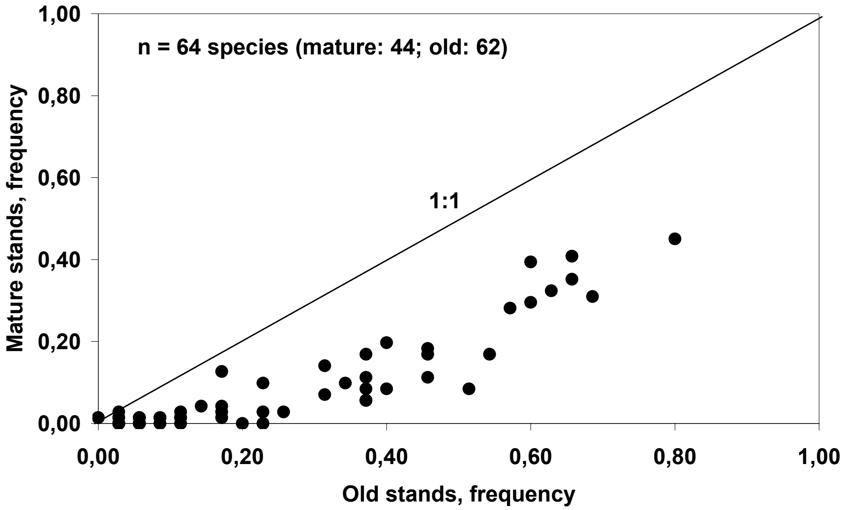

Figure 9. The relationship between the frequency of species (CC) in mature (ca 125-145 yrs, n = 71) and old (ca 160-250 yrs, n = 35) stands, both *with* forest continuity (**I**).

the effects of habitat connectivity at a landscape level at different periods on species distributions including genetical analysis (Gu et al. 2001, He et al. 2005, Snäll et al. 2005, Walser et al. 2005, Paltto et al. 2007, Hedenås & Ericsson 2008, Ranius et al. 2008).

In this study, the connectivity was analysed roughly by comparing the distance from each stand studied to the closest known source habitat for the epiphytes studied, with the number of epiphytes of conservation concern recorded from the stand. In stands with continuity, there was a trend for lower species number with increasing distance, even if no strong relationships could be discerned. In stands without continuity no trend was found.

The abundance of the species of conservation concern at a regional level however, was reflected in the local species assemblages in the studied stands (cf Mouquet et al. 2003): Species recorded in the stands lacking continuity were for the region the most common red-listed and indicator epiphytes. These represent a group of comparatively early colonizers, the crustose lichens *Lecanora glabrata, Pertusaria multipuncta* and *Pyrenula nitida,* associated with the relatively abundant substrate of mature beech trees which have smooth bark. Apparently these species have colonized matured new stands relatively recently from the surrounding landscape (**Fig. 10**). This suggests that at least these lichens, dispersed by ascospores, are not dispersal-limited *per se*, but are limited primarily by the availability of the substrate, i.e. they are substrate

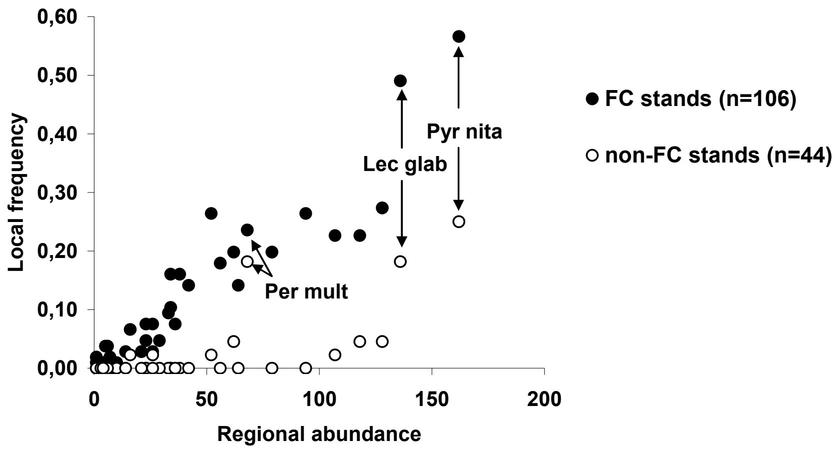

Figure 10. Correlation between regional abundance and local frequency, measured as the number of locations in the study area and the frequency of the same species in the surveyed stands with (FC) and without (non-FC) forest continuity **(I)**. 38 lichens of conservation concern mainly recorded on beech (County Adm. Board, database 2005). Lec glab = *Lecanora glabrata*, Per mult = *Pertusaria multipuncta* and Pyr nita = *Pyrenula nitida*.

-limited habitat specialists. In contrast however, the sterile populations in the study area of *Lobaria amplissima* and *L. virens*, which disperse only by thallus fragmentation, may truly be dispersal-limited (cf Öckinger et al. 2005). Between these extremes, there are many species in this study for which the dispersal and/or establishment capacity in the existing forest landscape is unknown (cf Johansson et al. 2007).

Strong positive correlations were found between the number of indicator and red-listed epiphyte species in the stands (**Fig. 11**). This result supports the use of the selected indicators in finding red-listed species and indirectly valuable beech habitats from a conservation point of view in this area. In addition, there were strong correlations between the number of bryophytes and lichens of conservation concern. Studies at plot and tree level **(II)** supported the strong correlations between the number of species in the subgroups red-listed lichens, indicator lichens and indicator bryophytes in particular, whereas red-listed bryophytes, lichen NCC and bryophyte NCC were uncorrelated or showed weak correlations to those subgroups.

The total number of species of red-listed and indicator species (CC) could be used as one important factor in prioritizing between conservation

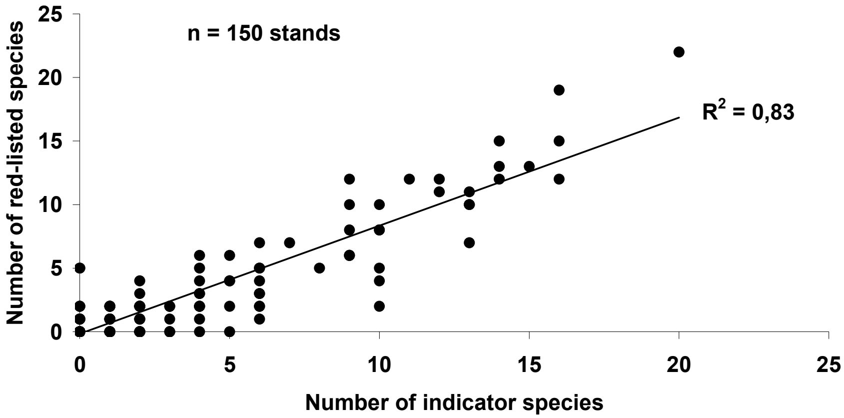

Figure 11. Correlation between the number of indicator species and the number of red-listed species of bryophytes and lichens in the 150 beech-dominated stands surveyed in the study area (**I**).

areas (Nordén et al. 2007). The use of the indicator species concept should however be practised with the awareness of its limitations, where differences in climatological conditions across larger regions may infer inconsistencies in frequency distribution and ecological behaviour of different species populations (Saetersdal et al. 2005, Will-Wolf et al. 2006).

The importance of tree age for beech epiphytes (II)

Within stands at Biskopstorp, the age of the oldest tree was the most important variable for species number and species composition. However, the effect of tree age differed among the species groups. The epiphyte species of conservation concern were strongly dependant upon old trees, whereas the species not of conservation concern were more related to the total area of bark surveyed, indicating that space was the limiting factor for these mostly generalist species. In addition, a low position on steep slopes favoured species numbers. Less exposure for air pollution and desiccation could explain this pattern (Gauslaa 1995). Another explanation could be that the impact from previous forestry is less on steep slopes compared to flat ground.

At tree level, the results also showed that tree age was the most important variable determining species number. Many species may require old beech trees because the suitable substrate develops only with high tree age, such as certain bark structures (Ranius et al. 2008).

Figure 12. Two beech trees, 232 and 249 years old, in the same plot but with different epiphyte composition. Twelve species of conservation concern were recorded on the damaged stem to the left, whereas only one such species (*Pyrenula nitida*) was found on the healthy beech tree to the right. The overgrown bark sample sites can be seen on the stems at breast height (**II**).

In total 104 lichens and 52 bryophytes were recorded (n = 571 beech trees), of which 22 were nationally red-listed and 25 indicator species (17 and 18, respectively, were lichens). Statistical estimations of species number (Colwell 2006) indicated that almost all bryophytes were recorded on the trees, but that about 20 lichens were still to be found. Of the recorded species only a few were common. As much as 86% of the lichens were found on less than 10% of the trees, whereas the corresponding frequency for bryophytes was 71%. Thirty species were only recorded once. Few common and many rare species are often a reported feature in ecosystems (Magurran 2004).

The species composition changed along the chronosequence of beech, suggesting niche separations. Most species were recorded from the oldest beech class (> 180 yrs), in particular species of conservation concern. The exception was several species of red-listed bryophytes, such as *Metzgeria fruticulosa*, *Neckera pumila* and *Orthotrichum pulchellum*, which were recorded on several occasions from rather young stands. However, all species occurring on old trees are not dependent on old-growth substrates. Some pioneer lichens, for example *Graphis scripta*, grow on smooth bark and are able to persist on such patches available on old beech stems. On old trees such bark diversity results in high total species number.

This study also showed that high tree age alone was not enough for the occurrence of many species of conservation concern. There were significantly more such species on damaged compared to healthy old beeches (**Fig. 12**). These results corresponded with studies which emphasize the importance of damaged trees for certain epiphytes (Barkman 1958; Bates 1992; Gauslaa 1995; Mikhailova et al. 2005). The effects of stem damage were further analysed in papers IV and V.

Vertical distribution of beech epiphytes emphasizes old trees (III)

A number of beech trees fell over following recent storms and this provided the opportunity to check whether the conclusions from standard surveys (0-2 m in height) were valid for entire trees. The results of this study confirmed the importance of tree age for epiphytic communities. A comparison between beech trees in three different age classes (young mature, ca 85 yrs; over mature, ca 155 yrs and old, ca 275 yrs), showed that the old beech trees hosted the highest number of epiphyte species, whereas the young mature trees hosted the lowest. Species of conservation concern were recorded high up the stem only from the old trees, and correlated to the microhabitat quality, i.e. presence of rough bark and moss cover, which concurs with other studies (e.g. McCune et al. 1997). When searching for species of conservation concern, a substantial number of epiphytes can occur high up on old beech trees (**Fig. 13**). If surveying only a few trees at the base in old stands, some species could be missed and species population sizes underestimated.

Figure 13. Old beech tree with moss cover, rough bark and stem damage. The stem is covered by species-rich epiphyte communities from the base to at least 20 metres in height (**III**).

The study could not establish any preference for particular stem heights, and the colonization height is probably due to chance, given the presence of a suitable microhabitat. However, all red-listed species recorded only from >2 m in height on stems surveyed and which had fallen over in the old stand, were also found at the base of other old, still standing trees in the same stand, the only exception being the crustose lichen *Candelariella reflexa*. In addition, when surveying trees for the presence of any species of conservation concern almost all such beech trees could be detected from the base.

Interaction of bark pH, tree vitality and tree age (IV)

Based on the results of paper II, the effects of bark and tree characteristics on species occurrence were examined in greater detail. Bark pH is frequently reported as an important factor at tree level for epiphytes (Farmer et al. 1991ab; Herk 2001, Purvis et al. 2008). In this study bark pH was confirmed to be a crucial factor in explaining species number and composition of epiphytes on beech stems. The effect of bark pH was stronger for lichen and bryophyte CC and for bryophyte NCC, than for lichen NCC.

However, the results also demonstrated that high bark pH alone was not enough. Interacting effects of high bark pH, high tree age and low tree vitality resulted in the best model for explaining the number of species of conservation concern on beech.

Large amounts of acidic stemflow in combination with a restricted buffering capacity of the beech bark could result in acidification of large areas of the stem. The long-term effects of air pollution may be one important reason why species of conservation concern are concentrated on old damaged beech trees with high bark pH in our study area. Bark pH was almost positively correlated with tree age. This may be an effect of the higher pH-values in the stemflow on older beech trees measured in this study. A higher stemflow pH on older trees may be due to increased nutrient leakage from areas of stem damage (Barkman 1958; Staxäng 1969; Gauslaa 1985, 1995, **paper V**) or possibly from frost related bark lesions (Jönsson 1998), which in turn will favour epiphytes associated with high bark pH on old trees. This is probably the reason for the positive interacting effect of stem damage and bark pH on species number in this study. The influence of stem damage was further analysed in the following study.

Soil pH did not correlate to bark pH nor to the epiphyte species. This result suggested that tree characteristics were more important than soil for bark pH, in contrary to other studies (Gustafsson & Eriksson 1995; Gauslaa & Holien 1998). However, this study was conducted on generally acid and nutrient-poor soils with low variation in pH, which probably increased the relative importance of stemflow in influencing bark pH. The data also suggest that the influence of soil pH on bark pH is weaker on acid soils than at higher soil pH. The relative importance of rainfall chemistry and leakage from stem damage for bark pH therefore increases on acid soils.

Rare epiphytes prefer damaged beech trees with rot holes (V)

In this study different types of stem damage at tree and at microhabitat level were related to bark pH, tree age, size, growth rate and the occurrence of epiphytes. For the first time, the possible effect of wood decaying fungi on epiphyte assemblages was analyzed. Three main types of damage on beech stems were identified: Canker, rot holes (**Fig. 14**) and surface rot.

At tree level, species number of epiphytes of conservation concern was strongly and positively related to the incidence and number of rot holes and bark pH. Slow-growing beech trees with rot holes were found to be an important habitat for the conservation of certain epiphytes (**Fig. 14**).

At microhabitat level, bark pH was significantly higher below than above rot holes, whereas no such relationship was found for canker and surface rot. Wood mould extracted from rot holes had a very high pH (median 8.2), which probably explains the higher bark pH below such damage types, and the preference of certain lichens and well as bryophytes of conservation concern for this microhabitat. Certain fungi were associated with particular types of damage, for example *Psathyrella cernua* with rot holes (**Fig. 14**), and *Fomes fomentarius* with surface rot.

Conclusions

Important factors at different scales

- **(I)** *Stand* age is a key factor regulating the availability of the tree substrates required for the many habitat specialists studied. Effects of habitat quality and forest continuity *per se* could not be separated because old stands were only found in areas having long forest continuity.

- **(II)** *Plots* confined to the base of slopes with old, unmanaged forest were particularly species rich in epiphytes of conservation concern. This pattern probably reflected the preference of many beech epiphytes for sheltered humid conditions, but it also indicates sensitivity to air pollution and forestry activities.

- **(II-IV)** At single *trees*, species succession was largely age-structured. Species number of epiphyte species of conservation concern was best explained by high tree age in combination with stem damage and a high bark pH.

- **(V)** At the *microhabitat* level rot holes created patches with high bark pH, conditions which hosted many species of conservation concern.

What is new?

- A unique data set of age-determined beech trees was used to demonstrate a close relationship between the occurrence of epiphytes and tree age.

Figure 14. Beech tree with a rot hole (top, left), with which most species of conservation concern were associated. *Psathyrella cernua* (top, right) could be one primary decay fungus creating the microhabitats suitable for epiphytes of conservation concern. Beech forest with old slow-growing trees on shallow soils (bottom). Biskopstorp (**V**).

- The results showed that beech trees have to be much older than previously assumed to host a rich epiphyte flora.

- The first systematic analysis of entire beech stems showed that the vertical distribution of epiphytes was greatly influenced by tree age. Species of conservation concern were recorded high up the stems only on the old trees emphasizing their importance in conservation.

- A previously unknown link between stem damage, stemflow and bark pH increased our understanding of the relationship between tree age, bark pH and the occurrence of epiphytes.

- For the first time, the relationship between stem damage and epiphyte composition on beech was analyzed with regard to rot fungi. The fungus *Psathyrella cernua* may be of particular importance for the formation of rot holes and the associated epiphytes of conservation concern.

Implications for conservation and management

Conservation and restoration of the beech forest landscape (I)

This thesis has shown that tree ages of at least some 150-200 years are required for the most demanding red-listed lichens. Forests that have survived the recent historical bottleneck period when broadleaved forest area was at a low level, and now contain such old trees, often harbour a large quantity of rare habitat specialists. In fact, these stands are the only areas remaining in the province for the rare and red-listed epiphytes. They serve as source areas from which species populations can expand to new suitable stands lacking continuity. They have therefore a very high conservation value.

Most of the remaining suitable beech habitats are fragmented however, in small patches embedded in a hostile matrix (**Fig. 2**). Small patches are susceptible to edge effects (Gignac & Dale 2005). This makes rare species in solitary woodland key habitats vulnerable to local species extinctions in the long term. Larger areas or concentrations of woodland key habitats offer better conditions to develop viable populations. These areas are also currently prioritised in conservation planning (SEPA & NBF 2005, County Administration Board & Forestry Board 2007).

The results also show that there is a potential for the restoration of beech forests. If habitat availability is increased the populations of at least some species will respond positively, in particular adjacent to source areas.

Conservation of epiphytes in shelterwood forestry is problematic (II)

The results in this thesis indicate that the combination of conventional shelterwood beech forestry and the conservation of epiphytes are not compatible at stand level. The relatively short rotation period in beech forestry reduces the survival of the species in the long term because of the long period between rotation age (100–140 yrs) and required age (≥180 yrs) for substrate demanding epiphytes. Comparisons between beech forests managed by shelterwood forestry and unmanaged – less managed forests also show a lower total number of species and/or fewer specialist species of epiphytes in the shelterwood forests (Aude & Poulsen 2000; Friedel et al. 2006; Nascimbene et al. 2007). It is the removal of most of the mature trees at regeneration felling (Bardat & Aubert 2007), and the regular cutting of slow-growing damaged trees during thinning that adversely affect epiphytes.

Retention of suitable trees for epiphyte species in the stand could in theory increase the possibility for demanding species to remain (Boudreault et al. 2000). The sensitive species on dispersed retention beech trees would, however, be vulnerable for rapid shifts in microclimate, reducing the probability of long term viability. There would also be practical problems during management in identifying the retention trees. To improve the success of the conservation of epiphytes in managed shelterwood forests, it is suggested that there is a spatial separation within the beech stands in production units and the areas set aside for sensitive and substrate demanding epiphytes. These set aside areas should ideally contain a mix of young, mature and old trees, preferably in sheltered humid conditions, in order to function in the long term (**Fig. 15**).

Survey methods and species capture (III)

Surveys normally only include a search of the base of trees for epiphytes. Using this methodology may result in species being missed. Results from this thesis showed that several species of conservation concern indeed also were growing high up on the trees, but only on the old trees. This means that the presence and population of species can be overlooked and underestimated in old stands. However, when only searching for trees valuable for conservation, red-listed or indicator species were almost always present at the base, implying that those trees can be readily identified from the ground.

Figure 15. Plot in Biskopstorp situated in a sheltered humid position low on a slope, a suitable location for a set aside area. The plot contains seven beech trees, of which five are healthy (mean age 210 yrs). Only *Pyrenula nitida* is recorded on these trees. On the thin suppressed beech (ca 150 yrs) behind the rucksack, at least seven rot holes and seven species of conservation concern were recorded.

Creation of substrate (IV-V)

Many protected old beech forests are currently developing suitable substrates. The decreasing deposition of acidifying substances may further improve substrate quality in protected beech forests. However, the existing beech forest in Halland has a skewed age distribution; with few young stands and many mature (**Fig. 4**). Few new beech forests are currently being created in the production forest landscape (Forestry Board, Södra Götaland 2002). Due to the long period of time required for suitable habitat to mature for the specialist species, there may be a gap in substrate availability, following the breakdown of the protected old stands. To link old forest substrates with formerly managed but currently homogenous and species-poor young-mature stands, active substrate creation might be required.

Figure 16. Example of substrate creation, aimed at facilitating fungal colonization; a cut piece by a chainsaw into an 85-year-old beech tree in a homogenous species-poor formerly managed stand. This is a study initiated by Mats Niklasson in Biskopstorp 2006.

Studies at the microhabitat level revealed that epiphytes of conservation concern were associated specifically with rot holes often found on slow-growing beech trees. Although more species were recorded from old beech trees, damaged young-mature stems with high bark pH had more species of conservation concern than vital stems of the same age. This result bears promise with respect to artificially reducing the time for substrate formation and increasing substrate quality in homogenous young-mature stands for the benefit of certain species of conservation concern. This could be tested by using chainsaws or axes to induce damage and stimulate colonisation by fungi that may eventually create attractive sites for establishment of, among others, epiphyte species of conservation concern (**Fig. 16**).

Inoculation of species thought to be primary rot agents, such as *Psathyrella cernua*, may speed up the formation of rot holes and could also be tested. The damage or inoculation should preferably be applied at height in order to have an impact on a larger area of the stem. Field experiments and surveillance of the effects are urgently needed in order to develop recommendations for active habitat restoration to favour epiphytes in beech forests.

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Lavar och mossor på bok – ekologiska studier och naturvårdstillämpningar

Potentiellt viktiga miljöfaktorer för epifytiska mossor och lavar i bokskog studerades i Halland. Fokus låg på naturvårdsintressanta arter, dvs rödlistade arter och sådana arter som bedöms vara indikatorer för nyckelbiotoper. Särskilt frågan om varför vissa skogsbestånd och trädstammar hyser fler naturvårdsintressanta arter än andra skulle belysas.

En rik tillgång på substrat, en hög beståndsålder och en lång kontinuitet av skogstäckt mark var utslagsgivande faktorer för ansamlingar av naturvårdsintressanta arter i jämförelser mellan bokbestånd. Inslag av gamla bokar och en längre tid för arter att kolonisera enskilda bokbestånd kan troligen förklara effekten av lång skogskontinuitet.

Bokbestånd med gamla träd, belägna vid basen av sluttningar och med en låg sentida påverkan från skogsbruk var särskilt artrika på naturvårdsintressanta arter. För enskilda träd var ålder, storlek och mosstäckning viktiga faktorer att förklara artrikedom och artsammansättning när alla lavar och mossor analyserades tillsammans. Däremot förekom rödlistade lavar främst på skadade bokar äldre än 180 år, medan de få funna rödlistade mossorna även noterades växa på yngre stammar i täta bestånd.

Studier av nyfallna bokstammar visade att utbredningen av lavar och mossor i höjdled också påverkades av trädålder och typ av substrat. Vissa rödlistade lavar hittades bara på över två meters höjd, men då enbart på mycket gamla bokar. Fynd av naturvårdsintressanta arter på två till fem meters höjd på levande bokar sammanföll med mosstäckt och/eller grov bark.

Vid detaljstudier av enskilda träd visade sig samverkan mellan högt bark pH, hög trädålder och stamskador bäst förklara antal av funna naturvårdsintressanta arter. Kopplingen mellan skadade bokar och högt bark pH kunde delvis förstås genom en positiv effekt av trädålder på pH i avrinnande stamflöde. Studier av olika stamskador visade att röthål var den enda skadetyp som genererade ett signifikant högre bark pH. Särskilt naturvårdsintressanta arter var överrepresenterade nedanför röthål, vilket tyder på en ekologisk koppling mellan rötsvampar och substratkrävande epifyter.

Gamla ofta klena senvuxna bokstammar med röthål, värdefulla för naturvårdsintressanta epifyter men inte för ekonomiskt skogsbruk, gallras normalt bort i skötta skogar. I bestånd med bokskogsbruk föreslås därför att partier med värdefulla träd för epifyter separeras från produktionsytor.