

Epiphytic bryophytes and lichens in Swedish beech forests – effects of forest history and habitat quality

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The occurrence of epiphytic bryophytes and lichens in beech forests in the County of Halland, Sweden, was related to environmental factors at different temporal and spatial scales. At stand level, the availability of substrates, a high stand age and forest continuity were the most important factors explaining high species number of epiphytes of conservation concern (i.e. red-listed and indicator species). Within stands, plots containing old trees, at the base of slopes and with low recent forestry impact had the highest number of species. 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 yr, whereas the few red-listed bryophytes were also recorded on younger stems in dense stands. The vertical distribution of epiphytes, recorded on newly fallen beech stems, could also be related to tree age. Species of conservation concern were recorded high up the stem only from the oldest trees, and their presence correlated positively to the presence of rough bark and moss cover. Studying the effect of bark and tree characteristics on species occurrence, the interaction of high bark pH, high tree age and stem damage 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. At microhabitat level, rot holes were found to positively influence bark pH and the occurrence of species of conservation concern. Old and slow-growing trees with rot holes are however, removed from managed beech forests. A spatial separation between managed and retention areas within stands is recommended in shelterwood forestry.

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The European beech *Fagus sylvatica* is inhabited by a rather specialised set of epiphytes, lichens in particular (Almborn 1948, Arup et al. 1997, Berg et al. 2002). Habitat loss however, in combination with the negative effects of air pollution has contributed to a situation where many epiphytes have declined and their long-term survival is not certain, i.e. they are red-listed (Gårdenfors 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 on beech (County Administration Halland, database 2005), although beech forests currently only cover ca 3% (9000 ha) of the total forest area (Forestry Board Södra Götaland 2000).

The decrease in the area of beech habitat has affected many species associated with beech trees. Pehr Osbeck, a pupil of Carl Linnaeus, recorded lichens such as *Lobaria amplissima* and *L. virens* in southern Halland around 1800 (Fritz 2000), and in 1756 *L. pulmonaria* was recorded in

great numbers in the beech forests of that area (Tidström 1891). The former two lichens are no longer to be found in southern Halland and the latter is rare. The area of beech habitat has continued to decline during the 20th century, and most of the remaining beech forests are surrounded by spruce forests.

In most beech forests managed by shelterwood cutting, the rotation is between 100 and 140 yr depending on site productivity. This means that old beech trees, between 200 and 300 yr of age, are not present in strictly managed beech forests. Shelterwood management has also resulted in one or sometimes two distinct cohorts, in contrast to a wide age range found in natural beech stands with gap phase dynamics (Niklasson et al. 2005).

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

This paper summarizes the most important findings from a project on the ecology and conservation of epiphytic lichens and bryophytes in beech forests (Fritz et al. 2008, 2009a, b, Fritz 2009a, b, Fritz and Heilmann-Clausen 2010). The overall aim was to identify limiting factors at different spatial and temporal scales for the occurrence of epiphytes, providing knowledge for conservation and management. Thus, the project focused on red-listed (Gärdenfors 2005) and indicator epiphytes (Norén et al. 2002), together called species of conservation concern.

The central questions were: 1) how important is forest continuity for the occurrence of epiphytic lichens and bryophytes? 2) Is the succession of epiphytic lichens and bryophytes on beech age-structured? 3) Is the vertical distribution of epiphytes on stems correlated to tree age? 4) How important are differences in bark characteristics between individual stems for the occurrence of epiphytes? 5) Is there a relationship between different types of stem damage and the presence of epiphytic lichens and bryophytes?

Material and methods

The study area

All studies were conducted in the 650 km² large interior forest landscape of the Municipality of Halmstad in the southern part of the County of Halland (Fig. 1). This area was chosen primarily because it was the only region in the county with a digitized survey of the current distribution of broadleaved forests at stand level. The digitized survey was compared with a unique set of old forest maps originating from 1652 and 1841–1842 (Malmström 1939). Present stands overlapping with the forest area in 1652 and 1841–1842 were defined as having forest continuity. On the contrary, current stands on open land in 1652 and/or 1841–1842 were defined as lacking forest continuity. The maximum age recorded for a beech tree in the County of Halland is 400 yr (Niklasson and Fritz 2003), but ages above 300 yr in nature reserves are rare (Niklasson 2002). This means that the definition of forest conti-

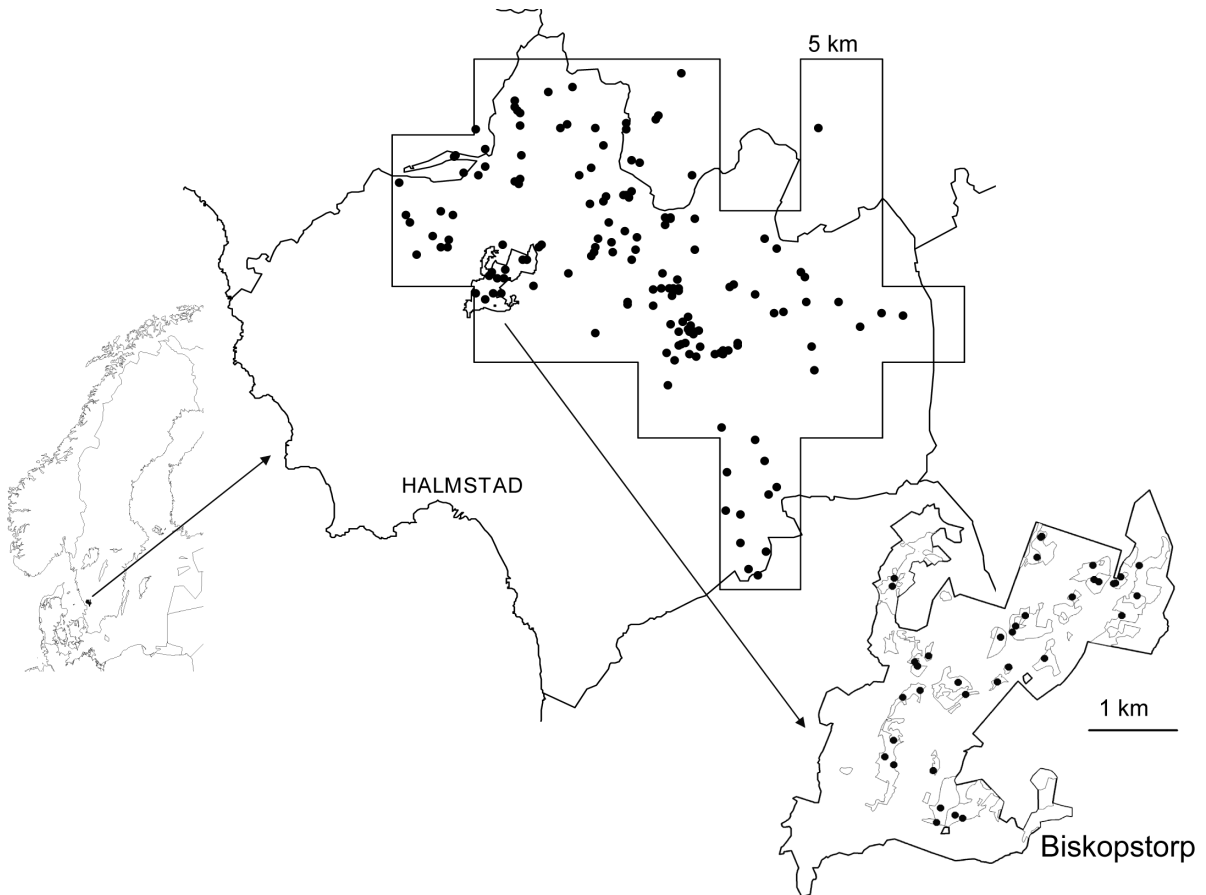


Figure 1. Study area in the Municipality of Halmstad located in the County of Halland, southern Sweden. Black dots mark the 150 beech stands surveyed (Fritz et al. 2008). The position of Biskopstorp and the location of plots in beech-dominated stands are also given (Fritz et al. 2009a).

nity, in this study, covers at least two or three generations of beech, from the present time back to the late medieval period.

Altitudes in the study area range from ca 60 to 200 m a.s.l. Mean annual air temperature ranges from 6.5 to 8°C and mean annual precipitation is between 1100 and 1500 mm with rainfall (of >1 mm) on >140 d yr⁻¹. The climatic conditions can be characterized as sub-oceanic. The bedrock is dominated by pre-cambrian granites. Glacial moraine deposits dominate the soils, which are generally acid and oligotrophic. 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 boreo-nemoral regions.

The study area 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 ca 25 kg S ha⁻¹ yr⁻¹ in 1988 to ca 5 kg S ha⁻¹ yr⁻¹ in 2007 in spruce forests. During the same period the pH of rainfall in open areas has increased from around pH 4 to almost 5 (Karls-son et al. 2008).

In Halland, broadleaved forest cover decreased substantially between the 17th and 19th centuries due to increased human exploitation with large areas being transformed into heaths (Malmström 1939). Extensive plantations of Norway spruce *Picea abies*, created since the end of the 19th century, have caused a shift in forest composition towards the dominance of conifers. Rough estimates from maps suggest that <10% of the beech forest area in the mid 1600s remains today (Fritz et al. 2008).

In the 1990s, forests covered ca 59 000 ha of the study area, of which 80% were dominated by Norway spruce and Scots pine *Pinus sylvestris*. The proportion of broadleaved forests with oaks *Quercus* spp. and beech was only 8–9% (Forestry Board unpubl.); nevertheless these forests form a national core area for the biodiversity of epiphytic species (Brunet et al. 2005).

Within the study area, the 900 ha forest landscape at Biskopstorp (56°48'5"N, 12°53'47"E), of which 190 ha are beech forests, was chosen for studies at plot, tree and microhabitat level (Fig. 1). The reasons for focusing on Biskopstorp were several; firstly the occurrence of beech stands of various ages and topographical positions, secondly the unique presence of a large number of age-determined beech trees (Niklasson et al. 2005) and thirdly the presence of many species-rich beech key habitats (Fritz 2006).

Sampling methods

Within the study area of Halmstad Municipality surveys were carried out at stand scale (Fritz et al. 2008). Plots and trees from dendrochronological studies were used in the stands at Biskopstorp (Fritz et al. 2008, 2009a, b, Fritz

2009b, Fritz and Heilmann-Clausen 2010). The circular sample plots (radius 7 or 20 m) were placed either in a typical part or were randomly distributed in the stands (cf. Fritz et al. 2009a).

Epiphyte species were mainly 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 stem (Fritz et al. 2008, 2009a, b). The exceptions include one study where the entire stem was surveyed (Fritz 2009b), and another where the survey of epiphytes was recorded within a frame directed at specific microhabitats on the beech trees (Fritz and Heilmann-Clausen 2010).

Based on the literature and field experience from beech forests, different environmental variables were selected, depending on the scale studied (Table 1, 2).

Red-Lists, indicator species and nomenclature

Estimating the extinction risk for species is the main purpose of Red-Lists, which also are important tools for analysing habitat quality and setting conservation priorities. In this project, species were classified as red-listed according to Gärdenfors (2005).

Indicator species are frequently used to find woodland key habitats by the fact that they often indicate the presence of red-listed species. After empirical testing of proposed indicator species during the 1990s, a set of suitable indicator species was selected for each region in Sweden (Norén et al. 2002).

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

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 and Mefford 1999). All NMS ordinations were carried out in autopilot mode comparing one- to six-dimensional solutions. The ordinations explained 70–92% of the variation in the original distance matrix (Sørensen index), resulting in two or three dimensional solutions, in which the final stress varied between 11.8 and 19.4 (cf. Fritz et al. 2009a). In addition, in study 2 an indicator species analysis was computed in PC-Ord. For analyses of correlation, regression (linear/logistic, single/multiple), variance and non-parametric methods, the program MINITAB (Minitab 1972–2008) was used.

Table 1. Environmental variables studied at four different spatial scales in the project. Significant variables for CC species number are in bold. The direction (corr. +/-) of the relationship is indicated as well as the study in which a variable is analysed and defined.

Variables	Corr	Stand	Plot	Tree	Microhabitat	Study
Canopy cover		x				1
Distance to closest woodland key habitat		x				1
Forest continuity	+	x				1
Shape Index		x				1
Site Index	-	x				1
Spruce frequency		x				1
Stand age	+	x				1
Stand area		x				1
Substrates	+	x				1
Vegetation type		x				1
Exposure (aspect)		x	x			1, 2
Forest layering		x	x			1, 2
Geographical coordinates	+	x	x			1, 2
Recent forestry impact	-	x	x			1, 2
Basal area			x			2
Elevation			x			2
Location from forest edge			x			2
Low position in slope	+		x			2
Rocks and stones			x			2
Slope inclination	+		x			2
Stem density			x			2
Light	+		x	x		2, 4
Surveyed bark area			x	x		2, 3
Tree age	+		x	x		2-5
Tree height	-		x	x		2, 4
Tree viability	-		x	x		2, 4, 5
Bark diversity				x		2, 4
Bark fissure depth				x		3, 4
Bark recovery	-			x		4
Bark thickness	+			x		4
Bark water-holding capacity				x		4
Crown projection				x		4
Diameter at breast height				x		2-5
Moss cover	+			x		2-4
Moss height	+			x		3
Soil pH				x		4
Stem growth rate				x		5
Stem inclination	+			x		2, 4
Stemflow pH	+			x		4
Tree exposure				x		4
Tree type				x		3
Bark structure (texture)				x	x	2-4
Bark pH	+			x	x	4, 5
Rot hole				x	x	5

Table 2. An overview of the main issue, spatial scale and sample size (number/area) in each study.

Study	Main issue	Spatial scale	Number of samples	Area per sample (range)
1	Forest continuity	Stand	150 stands	5000–50 000 m ²
2	Age	Plot/tree	37 plots/571 trees	157–1257 m ² /0.1–6.5 m ²
3	Vertical distribution	Tree	16/140 trees	1–30 m ²
4	Bark characteristics	Tree	101 trees	0.3–6.5 m ²
5	Type of stem damage	Tree/microhabitat	145 trees/61 microhabitats	0.3–6.5 m ² /0.04 m ²

Results and discussion

Study 1: substrate, stand age and forest continuity explain species number

Beech stands with forest continuity were consistently more species rich in CC epiphytes than beech stands on former open land in the Municipality of Halmstad. 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 (Fig. 2). The continuity effect was probably due to a combination of higher substrate quality, more of older beech trees, and a longer period for colonization. The importance of high stand age on species number can be elucidated in a comparison between mature and old stands, both with forest continuity (Fig. 3). Consistently lower frequencies of species were recorded in the mature stands (roughly 125–145 yr) compared to the old stands (roughly 160–250 yr). In addition, many more species were recorded from the old stands (Fig. 3) despite the fact that a substantially smaller total area was surveyed compared with the mature stands. The effects of tree age and microhabitat were analysed in greater detail in the following studies.

Due to the fact that beech stands older than 200 yr without continuity could not be identified in the study area, we were not able to separate the effects of continuity per se from those of habitat quality (Ohlson et al. 1997, Nordén and Appelquist 2001). This problem was not expected at the start of the study, partly because the knowledge of the association of rare epiphytes with old beeches had not yet been studied in detail.

The abundance of the CC species at a regional level (i.e. the Municipality of Halmstad) was reflected however, in the local species assemblages in the studied stands (cf. Mouquet et al. 2003). Species recorded from the stands lacking continuity were the most common red-listed and indicator epiphytes for the region. They represented a group of comparatively early colonizers, the crustose lichens *Lecanora glabrata*, *Pertusaria multipuncta* and *Pyrenula nitida*, associated with the relatively abundant substrate smooth bark on mature beech trees. Apparently these species have colonized recently matured new stands from the surrounding

landscape (Fig. 4). This suggests that at least these lichens, dispersed by ascospores, are not dispersal-limited, but are limited primarily by the availability of the bark substrate, i.e. they are substrate-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 be dispersal-limited. Between these extremes, there are many species in the study area 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 ($r^2 = 0.83$, $p < 0.001$, $n = 150$ stands, linear regression). This result supports the use of the selected indicators (cf. Material and methods) in finding red-listed species and indirectly valuable beech habitats from a conservation point of view. In addition, there was a strong correlation between the number of CC bryophytes and lichens (Fritz et al. 2008). Studies at plot and tree level (Fritz et al. 2009a) supported the strong correlation between the number of species in the subgroups red-listed lichens, indicator lichens and indicator bryophytes in particular. The total numbers of CC species could thereby be used as one important factor in prioritizing between conservation areas (Nordén et al. 2007).

The use of the indicator species concept should however be practiced with an awareness of its limitations. Differences in climatological conditions across larger regions may infer inconsistencies in frequency distribution and ecological behaviour of different species populations (Sætersdal et al. 2005, Will-Wolf et al. 2006).

Study 2: the importance of tree age for beech epiphytes

In plots at Biskopstorp, the age of the oldest tree was the most important variable for species number and species composition (Fritz et al. 2009a). The effects of tree age however, differed among the species groups. The CC epiphyte species depended on old trees, whereas the NCC species were more related to the total area of surveyed bark, indicating that space was the limiting factor for these

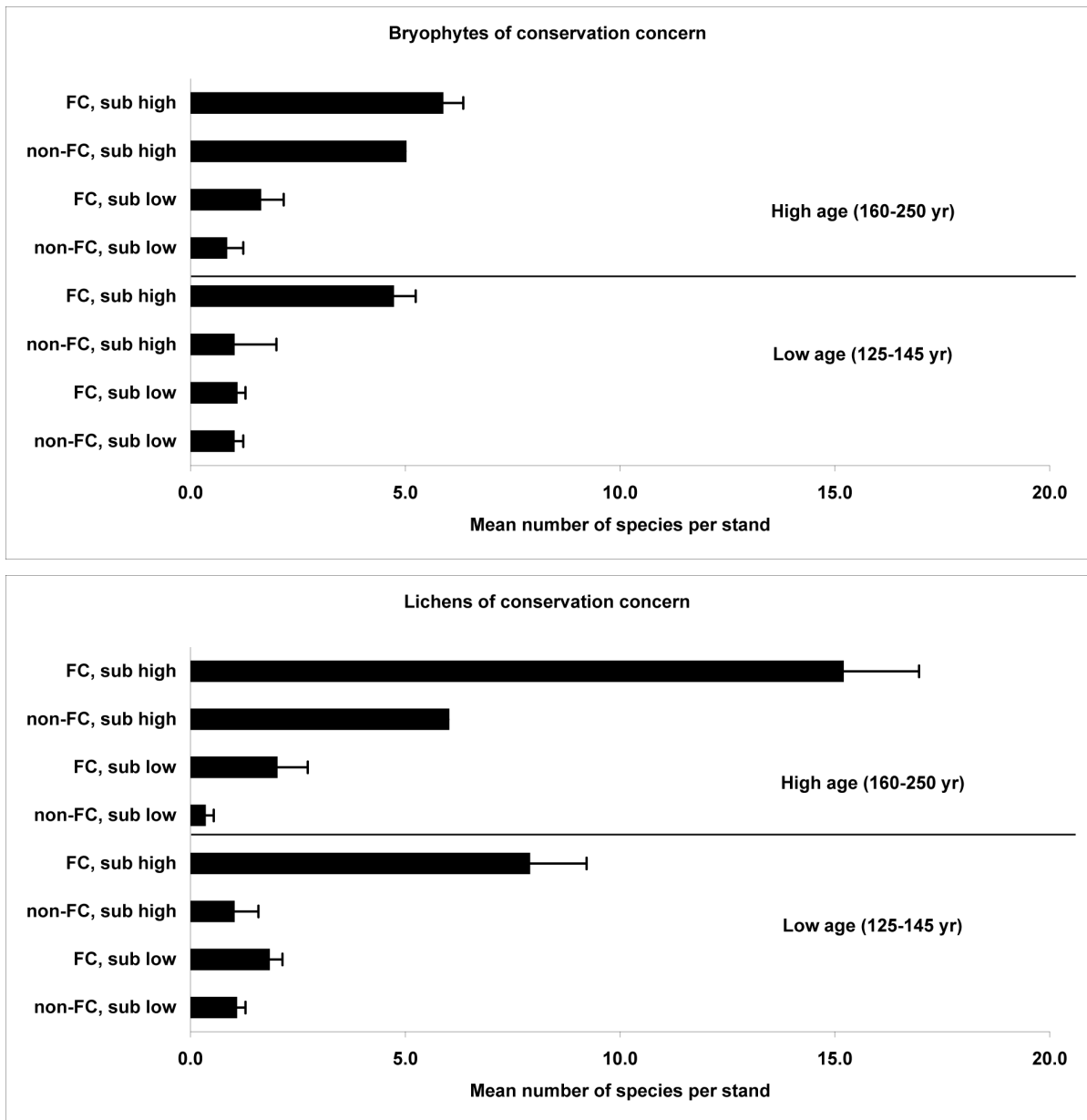


Figure 2. Mean number (\pm SE) of CC species, bryophytes and lichens respectively, in surveyed beech-dominated stands ($n = 150$, Municipality of Halmstad) for combinations of stand age (low 125–145 yr, high 160–250 yr), forest continuity (non-FC, FC) and substrate quantity (low 0–9, high 10–18).

mostly generalist species. In addition, a low position on steep slopes favored species number in plots (Fritz et al. 2009a). Less exposure to 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 with flat ground.

At tree level, the results showed that tree age was also the most important variable determining species number, in particular for CC lichens (Fig. 5). Many species may

require old beech trees because the suitable substrate, such as certain bark structures, develops only when the trees become old (Ranius et al. 2008).

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).

The species composition changed along the chronosequence of beech, suggesting niche separations. Most CC

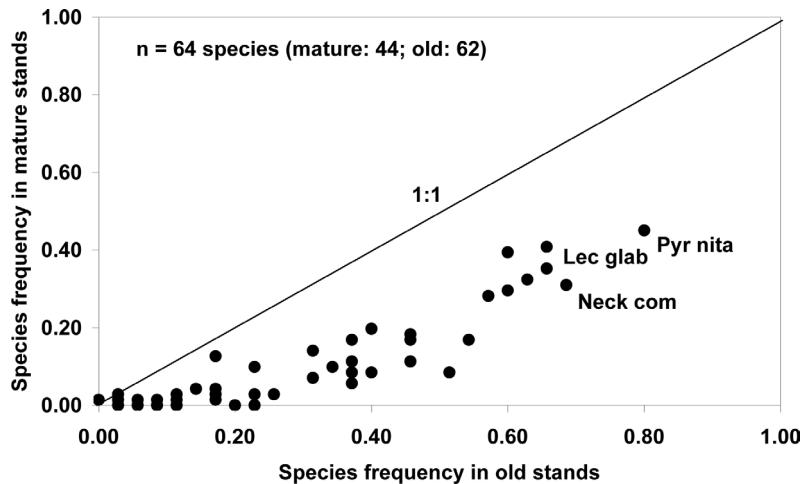


Figure 3. The relationship between the frequency of 64 CC species (•), exemplified by the most frequent species *Pyrenula nitida* (Pyr nita), *Neckera complanata* (Neck com) and *Lecanora glabrata* (Lec glab), in mature (ca 125–145 yr, n = 71) and old (ca 160–250 yr, n = 35) stands, all with forest continuity, in the Municipality of Halmstad.

epiphytic species were recorded in the oldest beech age class (>180 yr) (Fritz et al. 2009a). The exceptions were 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 (Fig. 5). Species occurring on old trees are not all however, dependent on old-growth substrates. Some pioneer lichens, for example *Graphis scripta*, grow on smooth bark and are able to persist on similar patches available also on old beech stems. On old trees such bark diversity results in a high total species number.

The study also showed that high tree age alone was not enough for the occurrence of many CC species. There were

significantly more such species on damaged compared to healthy old beech trees (Fritz et al. 2009a). These results correspond 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 studies 4 and 5.

Study 3: vertical distribution of beech epiphytes emphasizes old trees in conservation

A number of beech trees which had fallen in recent storms at Biskopstorp provided the opportunity to check wheth-

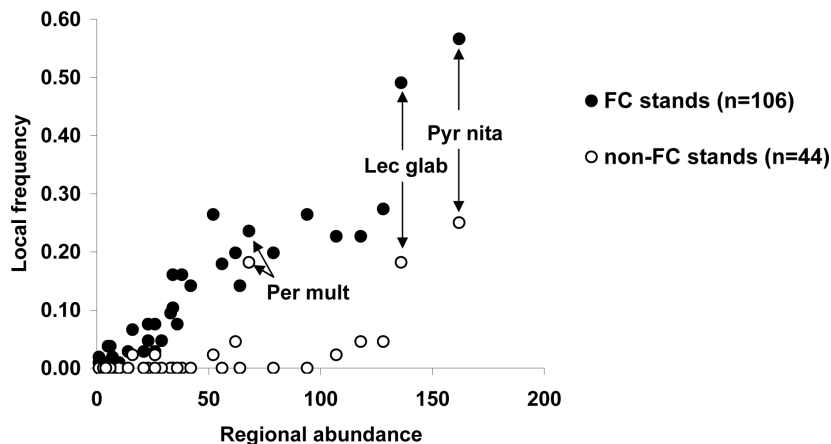


Figure 4. Correlation between regional abundance, measured as the number of locations in the whole study area (Municipality of Halmstad), and local frequency, measured as the frequency of the same species in the surveyed stands with (FC) and without (non-FC) forest continuity. The data include 38 lichens of conservation concern mainly recorded on beech (County Administration Board, database 2005). Some species are specified: Lec glab = *Lecanora glabrata*, Per mult = *Pertusaria multipunctata* and Pyr nita = *Pyrenula nitida*.

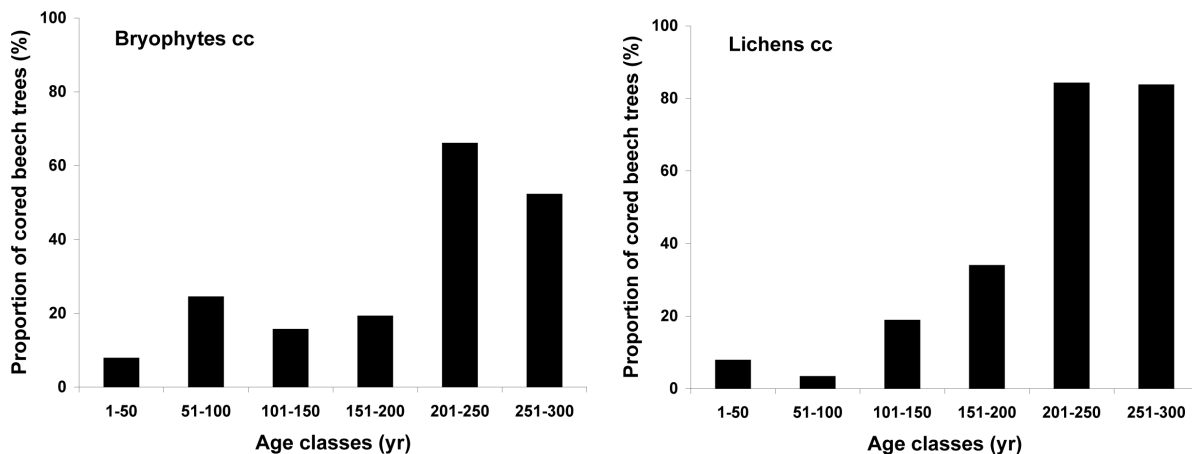


Figure 5. The frequency of occurrence of any CC species, bryophytes cc (n = 155 trees) and lichens cc (n = 163 trees) respectively, on age determined beech trees (n = 571) at Biskopstorp across the age gradient in fifty-year intervals.

er the conclusions from surveys carried out at 0–2 m in height were valid for entire trees. The results of this study confirmed the importance of tree age for epiphytic communities (Fritz 2009b). A comparison between beech trees in three different age classes (young mature, ca 85 yr; over mature, ca 155 yr and old, ca 275 yr), showed that the oldest trees hosted the highest number of epiphyte species, whereas the young mature trees hosted the lowest. CC species were recorded high up the stem only from the oldest trees, and correlated to the microhabitat quality, i.e. presence of rough bark and moss cover, which concurs with other studies (McCune et al. 1997).

When searching for CC species, a substantial number of epiphytes can occur high up on old beech trees. If surveying only a few trees at the base in old stands, some species could be missed and species population sizes underestimated. The study could not establish any preference for particular stem heights, and colonization height is probably due to chance, given the presence of a suitable microhabitat. All red-listed species recorded only from >2 m in height on stems surveyed and which had fallen over in the old stand, were however, 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 CC species almost all such beech trees could be detected from the base (Fritz 2009b).

Study 4: interaction of bark pH, tree vitality and tree age explains the occurrence of species of conservation concern

Based on the results of study 2, the effects of bark and tree characteristics on species occurrence were examined in greater detail at Biskopstorp. Bark pH is frequently report-

ed as an important factor at tree level for epiphytes (Farmer et al. 1991a, b, van Herk 2001, Purvis et al. 2008). In this study bark pH (H₂O) was confirmed to be a crucial factor in explaining species number and composition of epiphytes on beech stems. The effect of bark pH was strong for all species groups except for the NCC lichens (Fritz et al. 2009b).

The results however, also demonstrated that high bark pH alone was not enough to explain the number of CC species on beech. The interacting effects of high bark pH, high tree age and low tree vitality resulted in the best model for explaining species number (Fig. 6).

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 CC species are concentrated on old damaged beech trees with high bark pH in our study area. Bark pH was almost positively correlated to 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 an area of stem damage (Barkman 1958, Gauslaa 1985, 1995, Fritz and Heilmann-Clausen 2010) or possibly from frost related bark lesions (Jönsson 1998). The influence of stem damage was further analysed in the following study.

Soil pH (H₂O) 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 contrast to some other studies (Gustafsson and Eriksson 1995, Gauslaa and Holien 1998). This study was however, 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

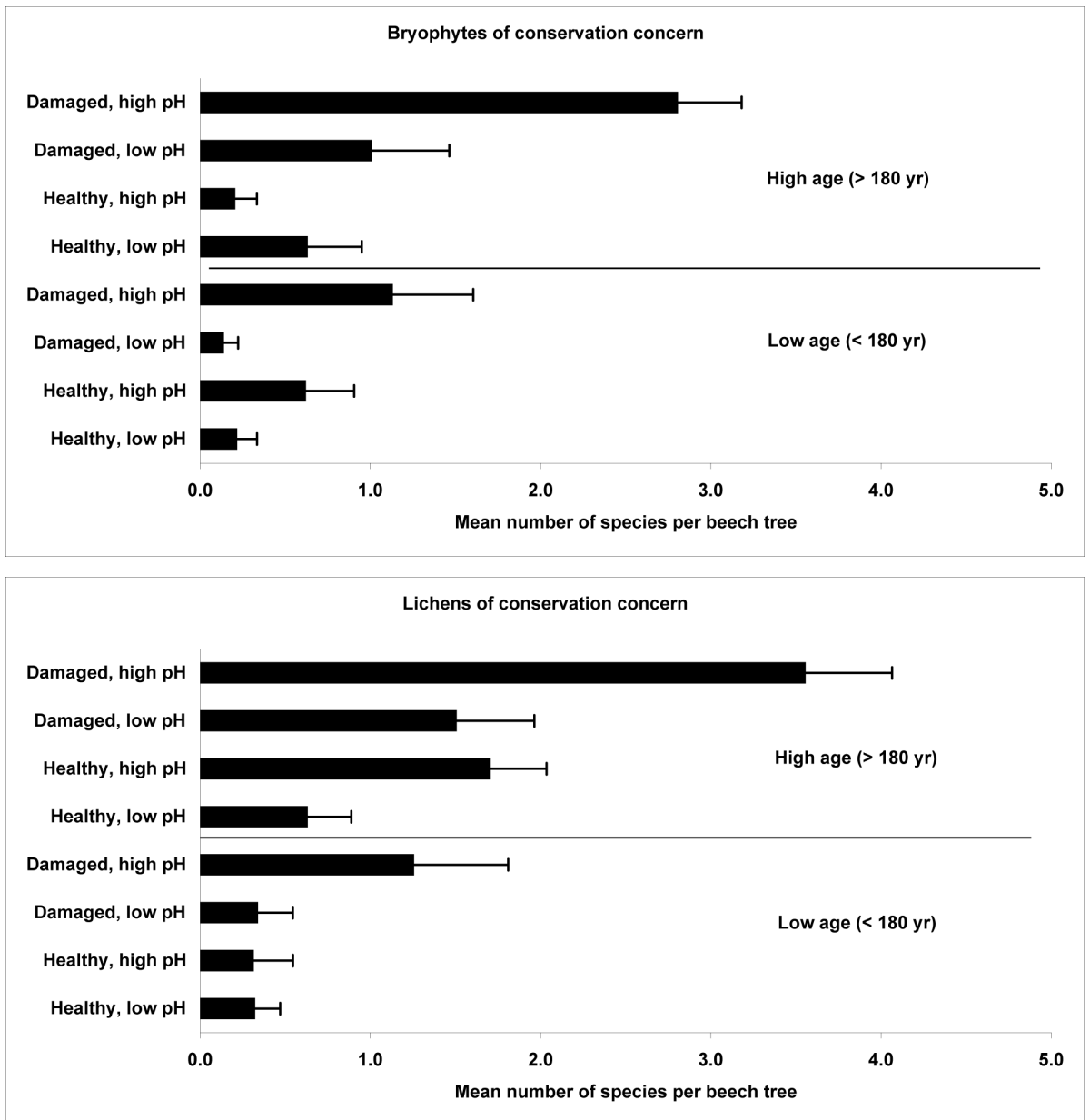


Figure 6. Mean number (\pm SE) of species of conservation concern, bryophytes and lichens respectively, on surveyed beech trees ($n = 101$) at Biskopstorp for combinations of tree age (low < 180 yr, high > 180 yr), tree vitality (damaged, healthy) and bark pH (low < 5.96, high > 5.96).

importance therefore, of rainfall chemistry and leaching from stem damage for bark pH increases on acid soils.

Study 5: rare epiphytes prefer damaged beech trees with rot holes

In the final study of the project at Biskopstorp, different types of stem damage at tree and at microhabitat level were

related to bark pH, tree age, size, growth and the occurrence of epiphytes (Fritz and Heilmann-Clausen 2010). 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 and surface rot (Fritz and Heilmann-Clausen 2010).

The incidence of rot holes was highest on trees with a low growth rate during the last 50 yr, but was unrelated

to tree size or age per se. Bark pH was significantly higher below than above rot holes, whereas no such relationship was found for cankers and surface rot. Wood mould extracted from rot holes had a very high pH H₂O (median 8.2), which probably explains the higher bark pH below this type of stem damage, and the preference of certain CC lichens and bryophytes for this microhabitat. Species number of CC bryophytes and of CC lichens was strongly positively related to rot holes and high bark pH (Fritz and Heilmann-Clausen 2010).

The fungus *Psathyrella cernua* was associated with rot holes and may be the main primary decay fungus creating this microhabitat, below which many CC epiphyte species grow (Fritz and Heilmann-Clausen 2010).

Conclusions

Important factors for the occurrence of epiphytes in beech forests

1) Stand age is a key factor regulating the availability of the tree substrates required for the habitat specialists studied. Effects of habitat quality and forest continuity per se could not be separated because old stands (>200 yr) were only found in areas which also had long forest continuity.

2) Plots confined to the base of slopes with old, unmanaged forest were particularly rich in CC epiphyte species. This pattern probably reflected the preference of many beech epiphytes for sheltered humid conditions and their sensitivity to air pollution and forestry activities.

3) For single trees, species succession was largely age-structured. Species number of CC epiphytes was best explained by high tree age in combination with stem damage and a high bark pH.

4) At the microhabitat level rot holes created patches with high bark pH conditions which favoured many CC species.

Which new results emerged from the project?

1) A unique data set of age-determined beech trees was used to demonstrate a close relationship between the occurrence of epiphytes and tree age. The results showed that beech trees have to be much older than previously assumed to host rich epiphyte communities.

2) The first systematic analysis of entire beech stems showed that the vertical distribution of epiphytes was greatly influenced by tree age. CC species were recorded high up the stems only on the oldest trees emphasizing their importance in conservation.

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

4) 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 CC epiphytes.

As a result of this project, a conceptual model is proposed for one of the most important processes influencing the occurrence of epiphyte species of conservation concern on beech trees (Fig. 7).

Implications for conservation and management

Conservation and restoration in beech forest landscapes

Tree ages of at least 180–200 yr are required for the most demanding red-listed lichens (Fritz et al. 2009a). Old broadleaved forests of that age may serve as source areas from which species populations can expand to new suitable stands, and have therefore a very high conservational value. The results show that some red-listed lichens were recorded in newly matured stands on formerly open land. If habitat availability increases the populations of at least

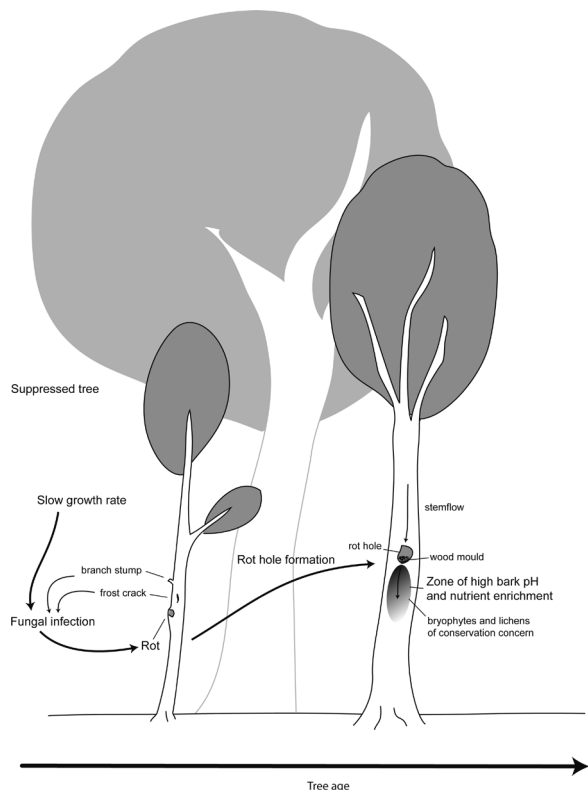


Figure 7. Conceptual figure showing processes influencing the occurrence of CC epiphyte species on beech trees.

some species will respond positively, in particular adjacent to source areas.

However, most of the remaining suitable beech habitats are relatively small and thereby largely influenced by edge effects (Gignac and Dale 2005). In addition, they are located in a strongly fragmented beech forest landscape, and often more or less isolated in a hostile matrix of conifer plantations. All this increases the risk for local extinctions. Larger areas or concentrations of woodland key habitats offer therefore, better conditions to develop viable populations. These areas are also currently prioritised in Swedish forest conservation (SEPA and NBF 2005).

Conservation of epiphytes in shelterwood forestry is problematic

The results of this project indicate that a combination of conventional shelterwood beech forestry and conservation of a rich epiphyte flora is not possible at stand level. The relatively short rotation period in beech forestry excludes the survival of species depending on old-growth substrates. Comparisons also show lower total numbers of epiphyte species or fewer specialist species in beech forests managed by traditional shelterwood forestry than in unmanaged or less intensively managed forests (Aude and Poulsen 2000, Friedel et al. 2006, Nascimbene et al. 2007). It is mainly the removal of most of the mature trees at regeneration felling (Bardat and Aubert 2007), and the regular cutting of slow-growing and/or suppressed damaged trees that adversely affect epiphytes.

Retention of suitable habitat trees may increase the possibility for demanding species to remain (Boudreault et al. 2000). The sensitive species on retention trees dispersed throughout the area would however, be vulnerable for rapid shifts in microclimate. There would also be practical problems during management in identifying the retention trees. To improve the conservation of epiphytes in managed shelterwood forests, we suggest a spatial separation within the beech stands in production units and set aside areas for sensitive and substrate demanding epiphytes. The set asides should ideally have a mixed age structure and should be located in the most sheltered and humid sites.

Substrate creation

Many protected old beech forests are currently developing suitable substrates for epiphytes. The existing beech forest in Halland has however, a skewed age distribution with few young stands. 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 and regeneration 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.

Suppressed or slow-growing trees with rot holes are important for the conservation of epiphyte diversity. In managed forests these trees are often cut, but should be selected as retention trees instead. In forest nature reserves, the association of conservation demanding epiphyte species with rot holes highlights a potential for habitat restoration by inducing artificial damage and inoculation of decay fungi in beech trees.

The damage and inoculation should preferably be applied high up the stem in order to have an impact on a larger area of bark on the stem. Field experiments and surveillance of the effects are urgently needed to develop recommendations for active habitat restoration to favour epiphytes in beech forests.

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