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Tree and site quality preferences of six epiphytic lichens growing on oaks in southeastern Sweden

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Oaks (*Quercus robur*) can reach a considerable age, which makes them an important substrate for many epiphytic lichens, including several red-listed species. We studied the importance of tree size and other environmental factors for the occurrence of six epiphytic lichens at two sites, in southeastern Sweden, differing in quality as judged by tree size distribution and number of old trees. The effects of tree circumference, light availability, trunk inclination and site were analysed. Results showed that different lichen species responded differently to these factors, but, overall, tree size was most important for lichen occurrence. Five species showed a positive relation to tree size, but the 50% probability of occurrence was reached at different tree sizes among these species and there were also site differences. This study shows that the maintenance of old trees is crucial for several lichen species, which highlights the importance of long-term management plans.

Key words: *Calicium*, *Chaenotheca*, *Chrysothrix*, *Cliostomum*, *Evernia*, occurrence probability, *Parmelia*

Introduction

Old growth deciduous forests have declined all over Europe to only a fraction of their original extents (Hannah *et al*. 1995) and old trees have become scarce. Old trees have also declined in wooded pastures due to changing land use and management. This has had a negative effect on several species groups associated with old trees and today these species groups only exist in remnant populations (Harding & Rose 1986). One such group is epiphytic lichens associated with old oaks (*Quercus robur*). Today, only a few extensive areas with oak are left and one of them is situated in Östergötland, in southeastern Sweden. Even though the number of oaks has declined also here, the province is still considered to be one of the most important oak areas in northern Europe (Ek & Johannesson 2005).

Oaks change as they age and a good example of this is the bark structure, going from being smooth on young trees to very rough with deep fissures on old ones. With increasing age, the chemical properties, hardness and water-holding capacity of the bark changes (Barkman 1958, Pedersen 1980). These changes are involved in causing a characteristic succession of the epiphytic lichens on an aging oak. Young oaks are dominated by common, easily-established generalist species, but with increasing age, the lichen flora change towards more oak-specific species (Rydberg 1997). The oak is an important substrate for epiphytic lichens with, e.g., over 300 species being recorded on oak in England (Rose 1974) and about 260 species in Sweden (Arup 1997). Due to the scarcity of old oaks and their rapid decline during the 19th century (Niklasson *et al*. 2002, Eliasson & Nilsson 2002), a large number of old-oak specialist are red-listed in Sweden (Gärdenfors 2005). In the province of Östergötland, 23 red-listed, oak-associated lichen species have been reported and several of these lichens have a large proportion of the total Swedish population, or even European, in Östergötland (Ek *et al*. 2001).

Many studies have shown the importance of tree size and/or number of old trees for the occurrence of specific lichen species (Gustafsson *et al*. 1992, Johansson & Ehrlén 2003, Ranius *et al*. 2008), the total density of lichen biomass (Esseen *et al*. 1996) and overall species richness (Kantvilas & Jarman 2004). However, models predicting specific tree sizes for different lichen species' occurrence and how these models differ over sites of different quality (e.g. the density of potential dispersal sources) seem to be lacking. Knowledge about how tree size, as an easily obtainable proxy for age, and other factors affect occurrence of different lichen species could give information about how an oak stand should be planned and managed to maintain populations of sensitive and demanding lichen species.

The aim of this study was to describe the tree size preferences of six epiphytic lichens, known to represent different stages of the succession of lichens on oak, and to investigate how the occurrence of these species are related to different environmental factors. The six species were also selected to represent different levels of abundance; from two common and widespread species to more rare ones, including three that are red-listed in several countries in northern Europe one of which is red-listed in Sweden. Models for predicting occurrence in relation to tree size were created and two sites differing in quality (tree size distribution) were compared.

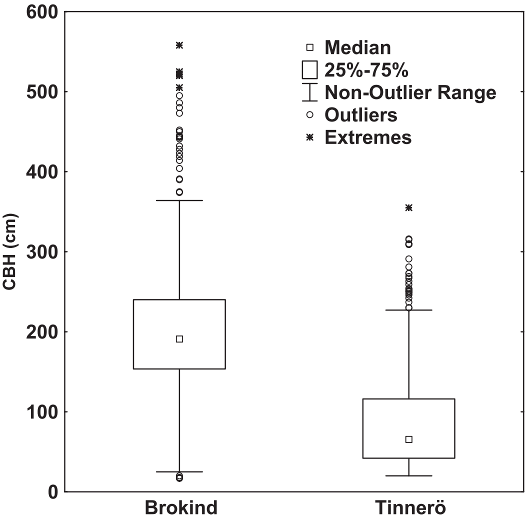

Fig. 1. Tree size distribution at the two studied sites; Brokind ($N = 400$) and Tinnerö (458).

Material and methods

Study sites

The two study sites are situated in the province of Östergötland, southeastern Sweden. Both sites are nature reserves representing parts of the oak district of Östergötland, an area with many oak stands and old trees. The sites were chosen to be as similar as possible except for tree size composition and number of old trees (Fig. 1 and Table 1), an attribute of quality expected to be important.

Skolhagen in Brokind (58°12´N, 15°39´E) is a wooded pasture with deciduous trees characterized by widely-spaced old oaks. The area has a long continuity of oaks and today it has a high proportion of old trees. Tindrafältet in Tinnerö (58°22´N, 15°36´E) has been used as pasture or meadow at least since the 1600s. The area has a long continuity of deciduous trees where oak is the dominating species. Today, the area has a large proportion of young oaks. The spatial distributions of trees for both sites are given in Fig. 2.

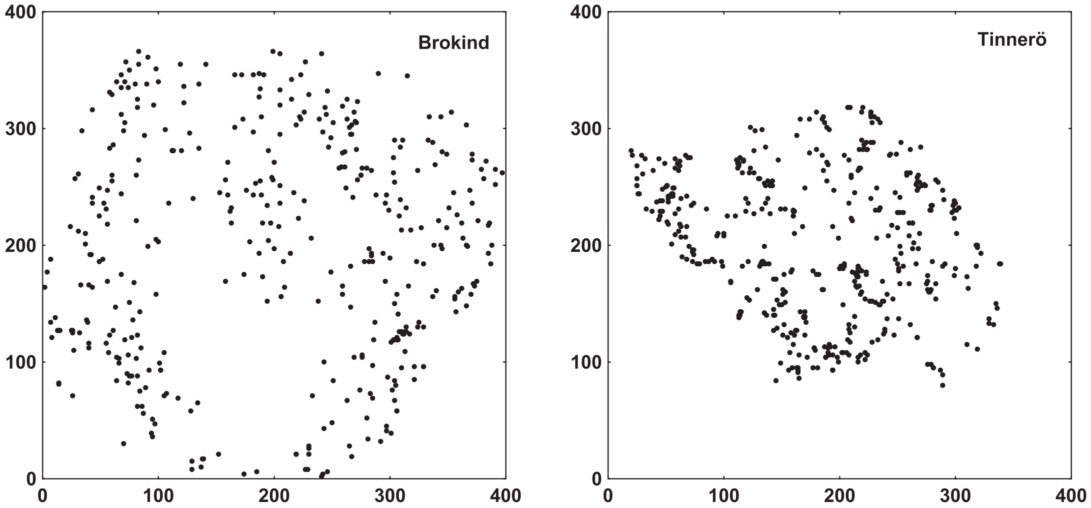

Fig. 2. The spatial distribution of oaks at the study sites. Scales are in metres.

Field work

The field work was conducted between May and September in 2006. Six epiphytic lichen species, differing in abundance and known, from field experience, to represent different stages of the succession of lichens on oak, were chosen: *Calicium adspersum*, *Chaenotheca phaeocephala*, *Chrysothrix candelaris*, *Cliostomum corrugatum*, *Evernia prunastri* and *Parmelia sulcata* (Table 2).

The occurrence of the six species were recorded for all oaks with circumference > 17 cm at breast height (CBH), within a delimited area at both sites (Table 1 and Fig. 2).

Lichens occurrence was examined from the end of the bryophyte border, at the base of the trunk, and 150 cm upwards. Circumference was measured at breast height, CBH, (130 cm) using a measuring tape. The time spent searching for lichens on each oak followed a function, based on data from a pilot study testing the time needed for finding different lichen species on trees of different sizes. The time (t) needed was dependent on the CBH of the tree: $t = 0.0307\text{CBH}$. Hence, more time was spent on larger oaks because of their larger trunk area. The smallest trees, CBH < 70 cm, did not follow the equation because the minimum time spent was set to 2 minutes. Some-

Table 1. The proportion of trees with occurrence of the studied lichen species and site information. Numbers in parentheses indicate standard deviation and range.

	Brokind	Tinnerö
Number of trees	400	458
Parmelia sulcata	88.5%	95.4%
Evernia prunastri	98.8%	73.8%
Chrysothrix candelaris	88.5%	19.4%
Chaenotheca phaeocephala	58.0%	15.9%
Calicium adspersum	68.3%	14.2%
Cliostomum corrugatum	14.0%	3.9%
Tree circumference (cm)	202.8 (93.11; 17.0–558.0)	90.3 (67.26; 20.0–355.0)
Light availability (%)	32.5 (5.87; 15.0–55.0)	32.6 (7.68; 15.0–60.0)
Trunk inclination (°)	4.7 (4.71; 0–24.0)	5.6 (5.62; 0–51.0)
Approximate study area (ha)	12	6
Trees ha^{-1}	33	76
Trees > 150 cm ha^{-1}	26	14

times more time had to be spent to ensure correct species' identification of difficult specimens, but the total search time remained unaffected.

Fissure depth was measured by putting a metallic ruler into the fissure, at breast height, and reading it against a straight object held over the fissure. This was made in all four cardinal points and a mean value was calculated per tree.

The inclination of the trunk was measured by attaching a 100-cm-long string, on the side of the tree where the lean was largest, at an approximate height of 150 cm. At the other end of the string, the distance at right angle in to the trunk was measured with a ruler. The lean angle was then calculated: arcsine × (distance to trunk/length of string).

Light availability was based upon a visual assessment of the proportion clear sky that lighted up the trunk. The area used was in the shape of 1/6 of a sphere, going from E to W, with S as midpoint, where the vertical angle (60° from the horizon) is largest. The area considered was first divided into two parts (S to W and S to E) and a mean value calculated based upon the subjective estimates from each part.

Data analyses

Effects of CBH, light, inclination of the trunk and site on each species' occurrence were analysed with a generalized linear model (GLM); binomial distribution, logit link function (logistic regression), using R 2.6.2 (R development core team 2008). Because *E. prunastri* occurred on 99% of the trees in Brokind (Table 1), this case was excluded from analyses. Furthermore, the effect of CBH was also analysed separately, and

Table 2. Details of the studied lichen species.

Species	Habitat	Rareness and distribution	Reference
Parmelia sulcata	Mostly on bark, but also on wood and mossy rocks, in both sun and shade	Common and widespread	Brodo *et al.* 2001, Hallingbäck 1995, Dahl & Krog 1973
Evernia prunastri	Growing on all kinds of trees in both sun and shade	Common and widespread	Brodo *et al.* 2001, Hallingbäck 1995, Dahl & Krog 1973
Chrysothrix candelaris	Mostly on rough bark of oak and other deciduous trees but also on spruce. Prefer shaded bark	Quite common. Widely distributed in old forests	Arup 1997, Brodo *et al.* 2001, Hallingbäck 1995
Chaenotheca phaeocephala	Mostly on old oaks but also occasionally on a few other deciduous trees and rarely also on pine. Often on sun exposed parts of the trunk	Scattered distribution all over Sweden, locally common in the southeastern parts. Indicator of trees of high conservation value in Sweden. Red-listed in Norway, Finland, England and Germany	Tibell 1978, Hultengren 1995, Nitare 2000, Kålås *et al.* 2006, Rassi *et al.* 2001, Woods & Coppins 2003, Ludwig & Schnittler 1996
Calicium adspersum	Mostly on old oaks but also occasionally on a few other deciduous trees. Often on the north side but avoiding moist substrates	Follows the distribution of oak in Sweden. Indicator species for oaks that often have other rare lichen species in Sweden. Red-listed in Norway, Finland, England and Germany	Tibell 1977, Nitare 2000, Kålås *et al.* 2006, Rassi *et al.* 2001, Woods & Coppins 2003, Ludwig & Schnittler 1996
Cliostomum corrugatum	Mainly on old oaks but also rarely on other deciduous trees with rough bark. Prefers sun exposure	Occurs mainly in southeastern Sweden and is very rare outside the range of oak. Also spread in Europe. Red-listed in Sweden, Denmark, Norway, Finland, England and Germany	Gärdenfors 2005, Hultengren 1995, Kålås *et al.* 2006, Ludwig & Schnittler 1996, Nitare 2000, Rassi *et al.* 2001, Woods & Coppins 2003

the predicted values with prediction bands were plotted using STATISTICA 7.0 StatSoft Inc. (2004). Calculations of CBH needed for 50% probability (P_{50}) of lichen occurrence was made using an approach similar to that often used in toxicology when modelling dose response relationships and predicting the LD50 (lethal dose 50; Kerr & Meador 1996).

Results

Altogether 858 trees were included in the analysis (400 in Brokind and 458 in Tinnerö). The mean CBH was distinctly higher in Brokind than in Tinnerö (Fig. 1 and Table 1). In Tinnerö, the mean tree inclination was higher ($F_{1,856} = 7.762$, $p = 0.005$), but the light availability did not differ between sites (Table 1). The area of Tinnerö was approximately half of that of Brokind and thereby the number of trees per hectare was higher in Tinnerö. In contrast, the number of large trees, (CBH > 150 cm) was higher in Brokind (Table 1). The number of trees with occurrences of the different lichen species is shown in Table 1; four of the species, *C. adspersum*, *C. phaeocephala*, *C. candelaris* and *C. corrugatum* were much more frequent at Brokind than at Tinnerö.

Effects of environmental variables

Occurrence of lichens were related to tree size, local environmental factors and site (Brokind or Tinnerö), and the effects differed between species (Table 3). Tree size (CBH) had a significant effect on all species (Table 3) and was, for at least four species, by far the most important factor and for one of these the only factor of significant importance in the GLM (Table 3).

For one species, *E. prunastri*, light condition and inclination had a significant effect: positive and negative, respectively. Site was of significant importance for all species except *C.*

Table 3. Likelihood ratios and *p* values from species-wise analyses using four explanatory variables, and a binomial response variable (occurrence of the species).

	Circumference at breast height (CBH)	Site[1]	Light	Tree inclination
P. sulcata				
p	0.041	0.034	0.928	0.937
Likelihood ratio	4.17	4.48	0.01	0.01
Relationship	–	+ (Tinnerö)		
E. prunastri				
p	0.014		< 0.001	0.010
Likelihood ratio	5.99		18.21	6.70
Relationship	+		+	–
C. candelaris				
p	< 0.001	< 0.001	0.090	0.873
Likelihood ratio	538.39	60.65	2.87	0.03
Relationship	+	– (Tinnerö)		
C. phaeocephala				
p	< 0.001	0.543	0.651	0.380
Likelihood ratio	384.85	0.15	0.20	0.77
Relationship	+			
C. adspersum				
p	< 0.001	0.003	0.646	0.083
Likelihood ratio	278.95	8.79	0.21	3.08
Relationship	+	– (Tinnerö)		–
C. corrugatum				
p	< 0.001	0.034	0.182	0.215
Likelihood ratio	228.57	4.5	1.53	1.78
Relationship	+	+ (Tinnerö)		

[1] Not evaluated for *E. prunastri* where only data from one site was included.

phaeocephala. Fissure depth was not included in the model because of the strong correlation with CBH ($R^2 = 0.90$, $n = 858$).

Tree size preferences

To describe the relationship of lichen occurrence and CBH, models (GLM, binomial distribution and logit link function) were created for each species. One species, *C. phaeocephala*, did not display a site difference (Table 3), which is why the graph for this species is based on data from both sites together (Fig. 3d and Table 4). For remaining species, data from the two sites were analysed separately (Fig. 3 and Table 4).

Five species had a positive relationship with an increasing CBH (Table 3). Of these, *Evernia prunastri* was the one found, to a large extent, on smaller trees. For the remaining four species, the probability of occurrence increased on smaller trees for *C. candelaris* as compared with that on the others, and this species also had the lowest P_{50} (and steepest slope). *Chrysothrix candelaris* was also found on smaller trees in Brokind and the confidence intervals of P_{50} are clearly separated when comparing the two sites (Fig. 3c and Table 4).

Calicium adspersum was also found on trees with smaller CBH in Brokind and furthermore had a flatter slope at this site, but the P_{50} estimates were relatively similar at the two sites (Table 4). *Chaenotheca phaeocephala* (Fig. 3d) had quite similar tree size preferences as *C. adspersum* (Fig. 3e), especially when comparing the results from Brokind for the latter. *Cliostomum corrugatum* had the highest P_{50} values for occurrence (Table 4) and showed a tendency to occur on slightly smaller trees in Tinnerö (Table 3 and Fig. 3f). *Parmelia sulcata* was most frequently present on small trees and the only species showing a negative relationship with increasing CBH (Fig. 3).

Discussion

There are numerous factors affecting the occurrence of lichens (Barkman 1958). In this study, effects of tree size, light availability, bark fissure depth, inclination of the trunk and site quality were investigated and these factors were indeed shown to affect the occurrence of six lichen species differently. The most important factor overall was tree size and, as expected, the shape of the relationship differed between species.

Table 4. Coefficients (b_1 and b_2) describing the logistic curve $y = e^{(b_1 + b_2)x/\left[1 + e^{(b_1 + b_2)x}\right]}$ and the CBH (cm) giving a 50% probability of lichen occurrence (P_{50}) with 95% confidence interval.

	N	b_1	SE	b_2	SE	P_{50}[1]	95% CI	*p*
P. sulcata								
Brokind	354	–2.56	0.375	0.00246	0.001554	–	–	0.113
Tinnerö	437	–3.46	0.385	0.00429	0.002834	–	–	0.130
E. prunastri								
Tinnerö	338	–0.544	0.183	–0.00586	0.001907	–	–	0.002
C. candelaris								
Brokind	354	5.32	0.878	–0.0543	0.007101	98	85–108	< 0.001
Tinnerö	89	9.82	1.206	–0.0666	0.008375	147	140–156	< 0.001
C. phaeocephala								
Both sites	305	5.48	0.381	–0.0311	0.002168	176	170–184	< 0.001
C. adspersum								
Brokind	237	2.34	0.373	–0.0143	0.001946	163	145–179	< 0.001
Tinnerö	65	7.37	0.783	–0.0410	0.004664	180	169–193	< 0.001
C. corrugatum								
Brokind	56	7.72	0.818	–0.0242	0.003103	319	299–347	< 0.001
Tinnerö	18	9.24	1.466	–0.0346	0.006261	267	247–303	< 0.001

[1] Not calculated for *P. sulcata* and *E. prunastri*, as that would extrapolate outside the range of CBH measurements.

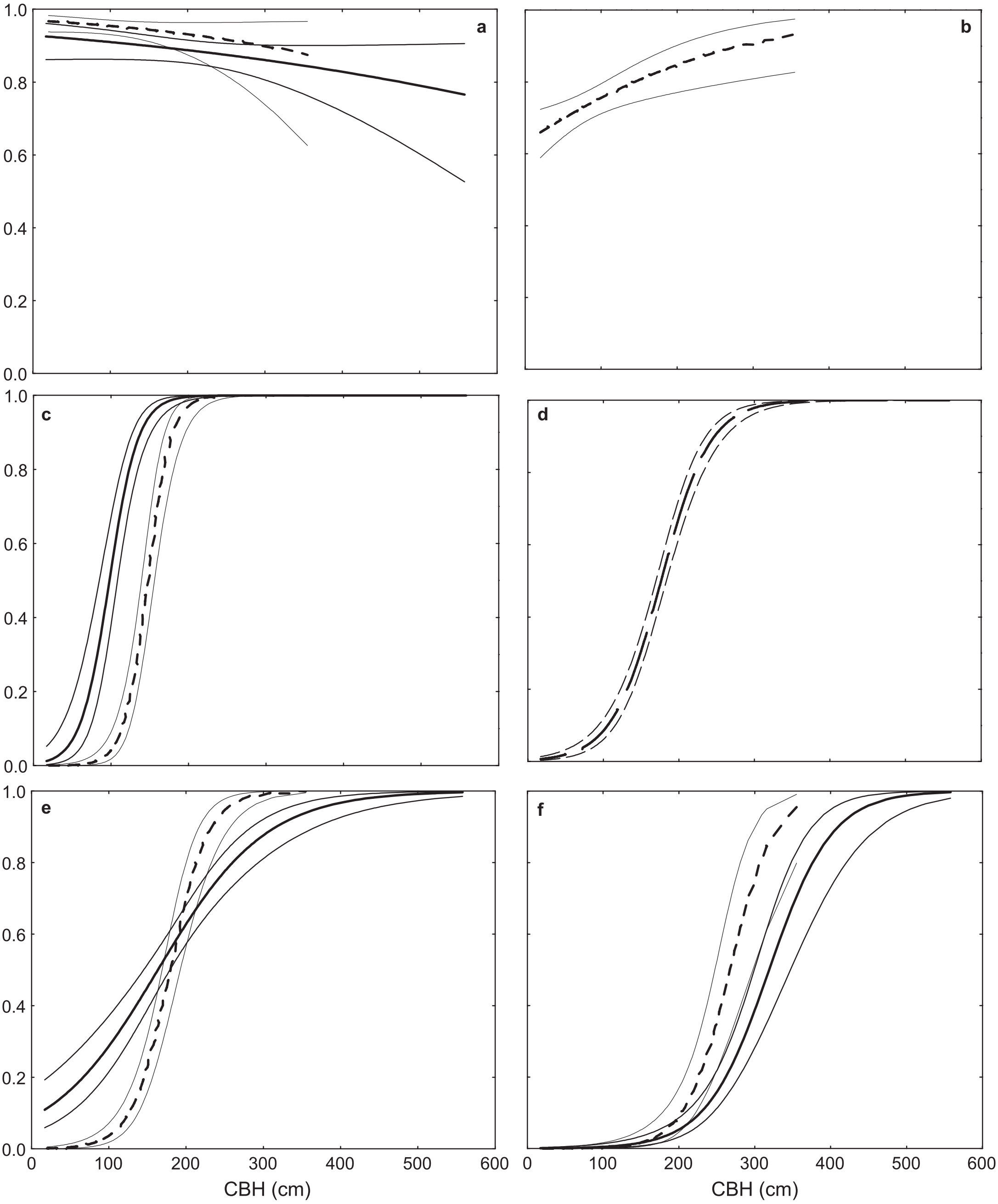

Fig. 3. Probability, with 95% prediction bands, of lichen occurrence by circumference at breast height (CBH) according to the models presented in Table 4. **a**: *Parmelia sulcata*, **b**: *Evernia prunastri*, **c**: *Chrysothrix candelaris*, **d**: *Chaenotheca phaeocephala*, **e**: *Calicium adspersum*, **f**: *Cliostomum corrugatum.* Solid lines represents Brokind and dashed Tinnerö. For *C. phaeocephala* there was no significant site difference, so the dashed line in **d** indicates a model based on data from both sites.

Tree size preferences

All species had a significant relationship (one negative and five positive) with increasing tree size. Several studies have revealed a positive relationship between tree size and the occurrence of individual epiphyte species (e.g. Uliczka & Angelstam 1999, Gu *et al.* 2001) but there are also reports of a negative relationship (Hedenås & Ericson 2000). The positive relation between habitat patch size and species occurrence is well established, as large patches are likely to harbour large populations, which are less extinction-prone (metapopulation theory: Hanski 1999). However, results from a study of an epiphytic moss indicates that extinctions of epiphytes on standing trees may be rare (Snäll *et al.* 2005) and thereby the occurrence of a species will depend more on the mechanisms behind its colonisation probability. Tree size was shown to explain very little of the variation in recent colonisations according to Snäll *et al.* (2003) who instead, in line with Rose (1992) and Gu *et al.* (2001), stress the importance of time (age) under which the tree has been exposed to lichen dispersal. In the present study we could not separate the effect of size and age, as the latter was not estimated. Nevertheless, we want to stress the complexity of the issue, beyond the dichotomy of age versus size. For example, bark properties change, structurally and chemically (Barkman 1958, Rydberg 1997) as trees age, affecting the microclimate (Pedersen 1980, Ranius *et al.* 2008) and lichen propagule survival (Armstrong 1990). Furthermore, the lichens themselves also affect each other and the substrate they live on. Competition and facilitation have been suggested to affect the lichen community over time, involving a change from "ruderal" to a more competitive species pool (Rogers 1988). This may explain why "ruderal", early colonisers can show a negative relationship to tree age: they lack success in competition and decrease when the tree ages. In our study, only one species, *P. sulcata*, showed a negative relationship which, even if it is weak, corroborates previous reports for this species (Harris 1971, Pedersen 1980). It should be remembered that early-successional species not present on the lower parts of the trunk may still persist higher up on the trunk (Hedenås & Ericson 2000).

In conservation biology, it is useful to be able to make predictions of species' occurrence from environmental factors. Thus, knowledge about the time (or size) when different lichen species start to colonise the oak could give information about how stands should be managed and what time frame the management plans have to consider. In the present study, we used tree size as a simple proxy for tree age, making the models more user friendly, as age of large trees is difficult to estimate (e.g. Rozas 2003).

This study showed that the probability of occurrence of *C. adspersum*, *C. candelaris*, *C. corrugatum* and *C. phaeocephala* increased with tree size. As the tree size increases, the first species to appear of these four was *C. candelaris* with a P_{50} value of 98 cm for Brokind and 147 cm for Tinnerö (Table 4). As tree size increases further, the probability of finding *C. adspersum* and *C. phaeocephala* increased, both with P_{50} values between 163 and 180 cm for occurrence. For the most demanding species, *C. corrugatum*, the oak had to reach a considerable size, CBH > 300 cm, before the probability of occurrence reached 50%. Tree coring made in Brokind has shown that a tree in this size class is probably over 200 years old (calculated from Ranius *et al.* 2009).

The different curves (Fig. 3) could give information about how specific the tree size preferences are. A steep slope as in the case of *C. candelaris* (Fig. 3c), may indicate a threshold in tree size (or age) that must be passed, because a small change in tree size, seems to make establishment of this species possible.

Effects of light and inclination

The majority of lichens found on oak are considered light-demanding (Rose 1974), e.g. *C. phaeocephala* and *C. corrugatum* (Hultengren 1995). Even so, the light availability did not have a significant effect on most species in the current study, except for *E. prunastri* showing a positive relationship to increasing light availability. It is worth noting, however, that the light availability did not differ much within or between the study sites (Table 1). So we cannot rule out light as an important factor under other conditions, e.g. overgrowth of formerly open oak stands.

The inclination of the trunk is often neglected in studies of epiphyte occurrence. In this study, the increased inclination was shown to have a negative effect on *E. prunastri* occurrence. Snäll *et al.* (2005) showed that strongly leaning trees were less likely to become colonised by a bryophyte species. Leaning trunks may develop a clear differentiation in moisture condition and bark chemistry between the upper and lower sides as a tree ages (Barkman 1958), which most likely cause the lichen distribution to differ from non-leaning trunks. One possible reason for the negative correlation in this study is that leaning trees may contain smaller areas of suitable habitat than straight-grown trees.

Site quality

Several lichen species are dependent on large and old trees to be able to colonise and seem to need certain substrate properties (as discussed above). In addition, the overall stand quality might also be important. In this study, overall stand age and the number of large trees was used as a measure of quality, with Brokind then being the higher-quality area.

The results (Table 3) showed that for four out of five species, site was of significant importance. For most species, the site differences were small (similar curves and P_{50} values). However, for at least *C. candelaris* the site difference was clear and the probability of occurrence increased on smaller trees in Brokind than Tinnerö. This could be interpreted in relation to the number of dispersal sources (old trees), which was higher in Brokind (Table 2), increasing the load of dispersal propagules. Either, more dispersal leads to higher probability of establishment under suboptimal conditions, or the probability of empty optimal sites decrease (or a combination of both). The number of potential dispersal sources (old trees) per hectare was higher in Brokind (Table 2), which also decrease the dispersal distances and enhance the connectivity between sources and suitable patches. Several studies have suggested that epiphytes are restricted in their dispersal ability (e.g. Dettki *et al*. 2000, Sillett *et al*. 2000, Walser *et al*. 2001) and that the occurrence (Johansson & Ehrlén 2003, Snäll *et al*. 2004) and colonisation probability (Snäll *et al*. 2005) increase with increasing connectivity.

For two species, there was no or only small site differences (*C. phaeocephala* and *C. corrugatum*). Hence, it seems that there are no local dispersal limitations in the area of lower quality. Occurrence of old trees seemed to be the “only” factor that affects the presence of these species. This may indicate that the models for these species have a good transferability between sites, at least to areas of similar productivity. For species with larger site differences, site-specific models might be needed for well-founded management guidelines. It should also be noted that the models based on tree size may differ even more at sites with slower tree growth. Results from Ek *et al*. (1995) indicate that the species considered in our study may appear on smaller, more slowly growing oaks living on south-exposed precipices in Sweden.

Conservation implications

Old oaks are one of the most important trees for red-listed lichens in Sweden but detailed knowledge of habitat demands have been lacking. This study has indicated thresholds in tree sizes for occurrence of several lichen species. The studied red-listed *C. corrugatum* was shown to require trees of about 200 years of age for a high probability of occurrence. Several other red-listed oak lichens are known to prefer even older oaks (Ranius *et al*. 2008). To conserve species with this kind of habitat demands, long-term management plans considering time frames of several hundred years (Drobyshev *et al*. 2008). The conservation management is further complicated by the restriction of old oaks to semi-natural habitats. Oak recruitment in these habitats is dependent on an optimal balance between sufficient light availability and sufficient protection against grazing cattle (Bakker *et al*. 2004). A management plan should have to consider the age structure where trees of different sizes, without age gaps, have to be present for long-term supply of old oaks. The density of old trees within a stand also seems to be important for some species, because the number of sources and a shorter distance to suitable trees increase the probability of other trees to become colonised.

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