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Decline in lichen biodiversity on oak trunks due to urbanization

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Abstract: Biodiversity often suffers from urbanization. In the present study, we focused on how the length of urbanization affects the richness of 17 epiphytic lichen species and their cover on large oaks in urban environments in a city of 100 000 inhabitants in SE Sweden. We also surveyed trees in adjacent rural areas, selected to have similar distributions of tree trunk circumference and surrounding oak density (within 300 m). Lichen richness and cover were lower on urban trees compared to rural trees. Furthermore, richness and cover decreased with the length of time that urban trees had been surrounded by houses. Most of the species that were analysed demonstrated a decline in occurrence with respect to the duration of housing development. The reduction in the probability of occurrence varied from 60% (*Calicium viride*, *Evernia prunastri*), 80% (*Chrysothrix candelaris*) to 90% (*Ramalina* spp. Ach.) during the 160-year period of urbanization considered. Therefore, even if valuable trees survive over the course of development, their lichen biota is likely to become depleted over time.

Key words: housing; landscape; lichens; *Quercus*; spatial; Sweden; urbanization

Introduction

Urbanization alters the natural environment in a number of ways and causes local extinction of species (McKinney, 2006). Urbanization is considered to be one of the worst threats to endangered species (Czech *et al.* 2000). Many studies have shown that when moving from rural areas to the central parts of a city, there is a gradual decrease in species richness in a number of organismal groups, such as butterflies (Blair and Launer 1997; Blair 1999), beetles (Ishitani *et al.* 2003; Niemelä and Kotze 2009; Su *et al.* 2011), birds (Blair 1999; Gagne and Fahrig 2011), amphibians (Price *et al.* 2006; McKinney 2008), reptiles (McKinney 2008), mammals (McKinney 2008), and plants (McKinney 2008). In contrast, there are a few studies that show that urbanization has no effect on biodiversity. For instance, Carabidae assemblages showed no changes across urban gradients in three cities in Finland, Bulgaria and Canada with three different levels of urbanization (Niemelä *et al.* 2002). A study in the lower Florida Keys concluded that the native ant fauna were not, at the moment, negatively affected by length of urbanization (Forys and Allen 2005). Nevertheless, with a few exceptions, urbanization generally seems to reduce biodiversity.

Urbanization affects various environmental factors that in turn affect survival and reproduction of species. The mechanisms involved in species loss varies, spanning from habitat loss and fragmentation (Robinson *et al.* 2005) to assumed shifts in biotic interactions and possible adverse effects of pollution (Tarhanen *et al.* 2000). One group that is particularly sensitive to pollution is lichens. In urban areas, sulphur and nitrogen oxides (SO_x, NO_x) primarily cause the greatest damage to lichens (Giordani 2007). Over the last century, air pollution in urban areas has been subject to substantial changes, both in composition and quantity (e.g. Fenger 2009; Agnan *et al.* 2013), which is probably a main driver for the changes documented for the urban lichen flora (e.g. Munzi *et al.* 2007; Lisowska 2011).

Lichens also have different tolerances and preferences for substrates. Some lichens are restricted to large trees (Washburn and Culley 2006) that usually have a coarse bark structure. Such specialised lichens have declined as the density of that substrate has diminished due to agriculture and forestry (Hedenås and Ericson 2008; Belinchón *et al.* 2009). However, trees are often an important feature of cities and are often allowed to grow old for a number of reasons, including human well being, economic value, aesthetics, shade production, and in some circumstances, fire prevention (Lohr *et al.* 2004; Donovan and Butry 2010, 2011). An example is the large number of *Quercus robur* L. trees, which have been maintained throughout urbanization, in urban Linköping, a city with 100 000 inhabitants in southeastern Sweden. Mobile organisms can escape urban habitats, while trees (and lichens) are inevitably incorporated into the urban environment. Lichens on the remaining trees are thus isolated, and their dispersal and establishment may be negatively affected. However, the future prospects for epiphytic organisms are better than those of many other elements of urban biodiversity as trees will continue to be an important feature of cityscapes.

In the present study, a selection of lichen species were surveyed on *Q. robur* trees in urban and rural environments. The objectives of this study can be divided into four questions: Is there any difference with regard to (i) species richness and (ii) cover of epiphytic lichens on *Q. robur* in urban or rural environment? How are (iii) species richness and (iv) cover of epiphytic lichens on *Q. robur* affected by the length of urbanization? To make these comparisons, we matched a population of urban oaks with a selection of rural oaks based on tree circumference and the density of surrounding oaks because oak lichens are sensitive to both the size of their host tree (Johansson *et al.* 2009) and the density of surrounding oaks (Westerberg, Muhammadi, Bergman and Milberg unpublished data).

Materials and Methods

Study area

The study was conducted in the city of Linköping and surrounding rural areas south of the city, in the province of Östergötland, Sweden (Fig. 1). The area north of Linköping municipality was avoided due to differences in soil and vegetation characteristics from the urban areas. The area is located at an altitude of 30 to 125 m above sea level and consists of the urban city centre of Linköping, urban district and surrounding rural environments. The city of Linköping is the seventh largest city in Sweden with a population of 104 232 in 2010 (Linköpings kommun 2011). It was founded in the 11th Century, but the majority of buildings have been built since the mid-1800s. The annual average temperature at the nearest meteorological station (urban district Malmslätt) is 6.1 °C, with an average temperature of – 3.2 °C in January and 16.2 °C in July; and the average precipitation is 516 mm per year (Statistics Sweden 2011). Linköping has expanded concentrically (Fig. 2), and the city centre consists largely of three to five storey buildings with shops at the street level. Blocks with flats and one to two-storey houses make up the greater part of the residential areas in the urban district. Squares, parks and paved roads are both in the city centre and urban district. The surrounding rural areas consist mainly of a mixed landscape with deciduous forests, planted conifers, arable land and pastures.

Selection of *Quercus robur* and lichen species

We studied the lichen flora on pedunculate oak (*Quercus robur*). *Quercus robur* is common in and around Linköping, and urban trees were selected for study from an existing tree database. The database contains the position and circumference of all large *Q. robur*, as well as several other tree species in the province of Östergötland, and was developed by the County Administration Board in Linköping (available at <http://gis.lst.se/lstgis/>). Using

ArcMap 9.3 (ESRI, 2011), all *Q. robur* within the municipality of Linköping with a circumference >250 cm were chosen because these trees can be assumed to be old enough to host a high diversity of lichen species (e.g., Johansson *et al.* 2009). The age of the sampled trees can be estimated from dendrological studies in the area (Berg 2006) to be at least 180 to 240 years; therefore, most trees included would have established 100-150 yrs before the onset of urbanization. A 250 m by 250 m grid was added over the urban area, and in each cell in the grid where *Q. robur* trees were present, the oak tree closest to the centre of the cell was chosen. This meant that the minimum distance between included trees were at least 250 m. From the database, we selected 105 urban trees, which were matched with a population of rural trees (Fig. 1). The criteria for matching urban trees with rural trees were that (i) the distribution of trunk circumference and (ii) the density of trees within 302 m should be similar. Some selected rural trees were excluded during the fieldwork because they had been cut down, or were in private gardens; others were substituted with similarly sized trees for the same reasons. In the end, we used 105 and 109 trees in urban and rural environments respectively.

The seventeen lichen species selected for our survey are shown in Table 1 together with their red-list category (Gärdenfors 2005) and, when appropriate, if the species are used as an indicator species for forests of conservation value (Nitare 2010), as well as with substrate preference (Santesson *et al.* 2004). Species were selected to represent relatively easily identified species, or a group of species within a genus (in two cases when it was difficult to accurately identify to species level), that are either habitat specialists or common and widespread. The nine common species occur more or less throughout all of Sweden, and some of them are considered resistant to air pollutants. The eight rare lichens are red-listed by the threat categories near threatened (NT) or vulnerable (VU), and/or are indicator species for high nature conservation and are thought to be sensitive to air pollution. Two additional

lichen species were initially included but were excluded at the beginning of the fieldwork as they proved too difficult to reliably identify in the field. After finishing fieldwork it turned out that three species (*Calicium quercinum* Pers., *Lecanographa amylacea* (Ehrh. ex Pers.) Egea & Torrente and *Schismatomma decolorans* (Turner & Borrer ex Sm.) Clauzade & Vezda in Vezda) had not been found.

Field survey

The fieldwork was conducted during April, May, October and November, 2011. For every oak, circumference at breast height was measured to the nearest centimetre. The depth of tree trunk bark crevices was measured on the north, east, south and west sides of the trunk to the nearest millimetre. Based on these four measurements, a mean bark crevice depth was calculated for each tree. Sun exposure was estimated by assessing how much sun in percent to the trunk was received, taking into account the shade cast by nearby buildings, shrubs and trees. On each tree trunk, lichens were examined from 50 to 150 cm above the ground; the bottom of the trunk was avoided because they varied greatly between individual trees. For each of the target lichen species, covered was estimated to the nearest cm² and expressed as a percentage of the inspected trunk area.

Additional parameters

Some complementary explanatory variables were also considered (Table 2). The number of *Q. robur* trees around each tree, including the tree being examined, was used as an explanatory variable. Six different radii were used: 150, 250, 350, 500, 700 and 1 000 m. The same range of radii was also used to determine the area of buildings around each studied *Q. robur*. The data on buildings were drawn from the GSD-Topographic Map (Lantmäteriet, ©Lantmäteriet license number I2012/0021) and combined four different classes of buildings (industrial buildings, one and two storey houses, apartment buildings and city blocks). Length

of urbanization was estimated from the average year of construction of the five buildings closest to the target tree, using a radius of approximately 200 m (data from the municipality of Linköping). Fewer buildings were used if the year of construction was not available for all five buildings or if fewer than five buildings were within 200 m of the tree. For the city centre (Fig. 2), where some older buildings have been demolished and replaced with newer ones, the above approach would underestimate the age. We therefore assigned the age 1900 to seven buildings that were erected by 1950 or later (hence replacing older buildings). One tree associated with buildings in the area dated to the eighteenth century (Fig. 2) was given the age 1850. In total, these age assignments affected the urban length estimates of eight trees in the city centre, and are most likely underestimates of the true ages.

Statistical analyses

The number of urban and rural trees of *Q. robur* used in the statistical analyses was 105 and 109, respectively, and in total, 14 lichen taxa were observed: nine common and five rare.

To evaluate the data, regression analyses (generalised linear model, GLM) were run in Statistica 10 (Statsoft 2011). The first set of analyses involved the number of target species per tree on urban vs. rural trees (normal distribution; identity link), and the total cover of the target lichens per tree for urban vs. rural trees (normal distribution; log link). Rural trees were not included in any further analyses.

The second set of analyses evaluated the relationship between (i) the number of target species per tree (normal distribution; identity link), and (ii) the total cover of target lichen per tree (normal distribution; log link), as related to number of years in an urban setting (i.e., the average age of the five closest buildings).

The third set of analyses involved the species-wise occurrence of the eight most frequent species (binomial distribution; logit link). For each radius (150–1 000 m), a model was made and included the following candidate explanatory variables: (i) length of urbanization, (ii) tree

circumference, (iii) average bark crevice depth, (iv) sun exposure, (v) density of oaks, and (iv) cover of buildings. Using Akaike information criterion (AIC), explanatory variables, including radii, were selected. Depth of bark crevices was chosen as it is often considered a better proxy for tree age than is tree circumference (Barkman 1958; Pedersen 1980; see Johansson *et al.* 2009). However, as the depth and circumference were poorly correlated, both were considered as candidate variables. Tree circumference and density of oaks were log transformed before the analysis.

Finally, six attributes of the fourteen species were analysed in relation to their average cover (square-root transformed) on urban oaks: spore size (length/2*width/2* π ; normal distribution; identity link function); diaspores (binomial; logit); growth form and photobiont (multinomial; logit); spores and pycnidium (ordinal multinomial; logit).

Results

In total, 214 trees of *Quercus robur* were studied, of which 105 and 109 were in urban and rural environments, respectively. Of the 17 lichen species included in the study, three rare and red-listed species (*Calicium quercinum*, *Lecanographa amylacea* and *Schismatomma decolorans*) were not found (Table 1). The number of lichen species per tree varied between 0 and 9. The total number of observations of lichen species was 954, with 400 observations in urban areas and 554 in rural areas.

Species richness and cover: urban vs. rural

There were clear differences in the occurrence and cover of individual lichen species between the urban and rural areas (Fig. 3). Four taxa were found only in the rural areas (*Calicium adpersum* Pers., *Cyphelium inquinans* (Sm.) Trevis., *Sclerophora coniophaea* (Norman) J. Mattsson & Middelb. in Middelb. & J. Mattsson and *Usnea* spp. Dill. ex Adans.).

All taxa, except *Lepraria incana* (L.) Ach., occurred more frequently on rural oaks than on urban oaks (Fig. 3a). All taxa (including *Lepraria incana*) had a higher cover on rural than urban oaks, both when looking at averages over all trees (including zero cover observations) and when considering only trees on which lichens were present (Fig. 3b and c).

The number of target species per tree and the cover of target lichens were significantly higher on oaks in rural environments than on oaks in the urban area ($P < 0.0001$ in both cases) (Fig. 4a and c). Mean species richness was 34% higher on rural oaks than urban oaks (5.1 and 3.8 lichen species, respectively) (Fig. 4a). When looking at the total cover of the 14 species, the differences between urban oaks and rural oaks were even more pronounced, with a mean cover many times higher on rural versus urban oaks (0.041% and 0.007%, respectively) (Fig. 4c).

Species richness and cover: effects from length of urbanization

The number of species per tree decreased significantly with the increasing age of the surrounding buildings ($P = 0.00031$) (Fig. 4b). The average number of target species in the most recently urbanized areas was four times higher than in the oldest areas (Fig. 4b), and a similar decline was found in the cover of target lichens (Fig. 4d).

Species-wise responses to environmental factors in urban areas

Out of the 14 species, eight were sufficiently frequent to be analysed individually in consideration of all explanatory variables. The selected models proved significant for seven of the eight species (Table 3). The majority of the species were affected by urbanization factors or oak size factors, while few species were affected by the other biotic factors such as oak density. The length of urbanization had a significant negative effect on five species and the area covered by buildings on two species. *Chrysothrix candelaris* (L.) J. R. Laundon and *Hypogymnia physodes* (L.) Nyl. were positively affected by the area covered by buildings

(Table 3). Species responded mostly to area covered by buildings at larger scales, ≥ 350 m. A higher tree circumference or deeper bark crevices had a significant positive effect on the occurrence of four species and a negative effect on one. Sun exposure had a significant negative impact on two species (Table 3). Oak density significantly affected only one species negatively and none positively.

For the four species where the length of urbanization significantly affected their occurrence, separate binomial (logit link) GLMs were conducted. All species showed a decrease in prevalence in the older parts of the city in comparison to newer areas. The models predicted a reduction of 60% (*Calicium viride* Pers., *Evernia prunastri* (L.) Ach.), 80% (*Chrysothrix candelaris*) and 90% (*Ramalina* spp.) probability of occurrence during the 160 years of urbanization (Fig. 5).

Out of the six tested species attributes (Table 4), only one had a significant association with cover on urban trees: ‘spores’, i.e., to what extent a species relies on spore dispersal for reproduction ($P = 0.039$).

Discussion

This study showed a clear reduction in species richness and cover on oaks in urban versus rural areas. Likewise, the length of urbanization reflects the same pattern, a finding that is consistent with studies of other organismal groups (Blair and Launer 1997; Blair 1999; Ishitani *et al.* 2003; Price *et al.* 2006; McKinney 2008; Niemelä and Kotze 2009; Gagne and Fahrig 2011; Su *et al.* 2011; Coffey and Fahrig 2012). Our results also support that dispersal mode may be an important factor in predicting which lichen species are affected by urbanization.

Lower richness and cover on urban oaks

Species in urban areas are affected by a complex interaction between factors, such as pollution, temperature, moisture, disturbance and habitat configuration (McDonnell *et al.* 1997). Generally habitat loss and fragmentation are among the most important factors in urban areas (McKinney 2006; Niemelä 1999), which for most species is negative. A high density of large oak trees has proved to be important for species richness and the occurrence of some lichens (e.g. Paltto *et al.* 2010), and shows that habitat configuration (or connectivity) is important (Coffey and Fahrig 2012). The sample populations of urban and rural oaks were matched for both circumference and surrounding tree density, thereby allowing for comparison while controlling for habitat quality (circumference) and connectivity. Several species are generalists and not confined to oaks, but because previous studies emphasized the importance of oaks (Paltto *et al.* 2010; Westerberg, Muhammadi, Bergman and Milberg, unpublished), we argue that our sample design can control for differences in habitat connectivity. Thus, by controlling for habitat length and habitat composition (density of surrounding oaks), we were able to isolate the effects of urbanization, from that of a general decrease in habitat. In cases where it was possible to analyse species, our study showed that urbanization had a clear effect on cover (Table 3). The explanatory variable, i.e., length of urbanization, showed that five species were negatively affected, while area covered by buildings showed that three species were negatively affected and one species was positively affected.

A factor we did not control for was air and dust pollution. Lichen declines in urban environments were reported very early with the industrialisation of Europe (Grindon 1859; Nylander 1866). The main factor for the decline was SO_x generated by industries and traffic (Gilbert 1968). SO_x peaked during the 1960s and 1970s, and lichen deserts in urban areas were reported at elevated emission levels (Hawksworth and Rose 1970). However, air quality

has recently improved in many urban areas (Lisowska 2011, Lackovicova *et al.* 2013). In Tampere, Finland, sulphur dioxide levels were reduced from $160 \mu\text{g m}^{-3}$ in 1973 to $2 \mu\text{g m}^{-3}$ in 1999, which coincided with an increase in the richness of lichen epiphytes and their cover since 1980 (Ranta 2001). For the municipality of Linköping, SO_x decreased with 85% and NO_x with 60% from 1990 to 2010 (RUS 2013). The improvement in the local lichen flora is supported by our research as shown by the fact that there were no differences between the number of oaks without target species in urban and rural areas (4 out of 105 urban oaks without target lichens and 3 of 109 rural oaks). However, there were nevertheless large differences in species diversity and the cover of individual species between urban and rural oaks. Our results show that species that disperse by spores were often absent or had low cover, while those that were vegetative dispersed were among those with the highest cover (Table 4). Species dependent on the process of re-lichenisation involving contact between spores and an appropriate photobiont, after successful dispersal, seem less likely to succeed in urban areas. The species most sensitive to urbanization in our study all belong to this group. *Calicium adpersum*, *Cyphelium inquinans*, *Sclerophora coniophaea* and *Usnea* spp. were not found on oaks in the urban environment, but were present in the rural environment. *Calicium adpersum*, *C. inquinans* and *S. coniophaea* are classified as indicators of forest areas with high conservation values (Nitare 2010), while *Usnea* spp. are known to be sensitive to air pollution (Hawksworth and Rose 1970). In addition to the dispersal mode, the photobiont may be important. Tarhanen *et al.* (2000) demonstrated that the green alga *Trebouxia* is sensitive to air pollution. Their results showed that high concentrations of air pollutants increased plasmolysis and mitochondrial changes in cells. Furthermore, degenerated cells showed altered chloroplasts and electron-translucent pyrenoglobuli as far as 35 to 50 km from the pollutant source. Low lichen cover on many urban oaks compared to rural oaks suggests that something is having a negative effect on lichens in urban areas, even though the air quality

has improved. Armstrong and Bradwell (2010) reviewed 52 studies with reported growth rates for crustose lichens, and 33 of the surveys had been performed in Europe. If we adopt an average European radial growth rate of 0.92 mm per year, which seems reasonable, lichen thalli would need 6 years to reach one centimetre in diameter and thus become clearly visible to the naked eye. Of the five foliose and fruticose lichens, growth rates are available for *Hypogymnia physodes*: approximately 3 to 5 mm in diameter per year (Gorbach and Kobzar 1981; unpublished data), with a corresponding shorter time to reach visibility. Given that levels of sulphur and nitrogen dioxides have steadily decreased over the last 30 years, there should have been ample time for regrowth for most lichens, assuming that they are not dispersal or photobiont limited and that current SO_x and NO_x levels are sufficiently low.

Another potentially important factor is the higher temperature/lower humidity in urban areas. Lichens are known to be sensitive to changes in temperature such as might be seen with global warming (van Herk *et al.* 2002). Most lichen species also seem to favour moist conditions in urban areas (Coffey and Fahrig 2012). Therefore, shifts in temperature and moisture might be limiting to urban lichens. Several studies have shown that temperatures are generally higher in urban versus rural areas (George *et al.* 2007; Bulut *et al.* 2008; Liu *et al.* 2009), a phenomena known as the “urban heat island effect”. Hughes (2006) investigated the “urban heat island effect” in four cities in the United Kingdom of varying population size. Norwich had on average urban temperatures 0.5°C higher than surrounding rural areas. Because the population size of Norwich is similar to Linköping’s, we can assume the latter has a similar temperature difference. Relative humidity (RH) is, to a large extent, a function of temperature, so we would expect the urban heat island effect to coincide with lower RH. Furthermore, hard surfaces, efficient canalisation of runoff water, and small volumes of vegetation (low evapotranspiration) in urban areas also suggest lower RH values.

Nevertheless, the data are conflicting (George *et al.* 2007 found no differences, while Liu *et al.* 2009 did).

Loss rate over the course of urbanization

Numerous studies have investigated how a spatial gradient from rural, suburban to urban areas affects the diversity and abundance of organisms. Most studies have concluded that the number of species and their abundance generally decreases with increasing urbanization (Mercado Cárdenas and Buddle 2009), but there are exceptions particularly when invasive species are involved (Dolan *et al.* 2011) and generalist (Magura *et al.* 2008; Tóthmérész *et al.* 2011). The same reduction in species and their abundance toward the city centre can also be observed in temporal studies. For instance, Fattorini (2012) reconstructed the extinction trends of four insect groups in urban Rome, Italy from 1885–1999. Her results showed a clear decline in species richness in each group of insects. Price *et al.* (2006) examined the incidence of species from the vertebrate family Salamandridae near Davidson, North Carolina, USA, for a period of 30 years and found that the populations declined over time.

Our results showed a clear effect on species number and cover of lichens with the increasing length of urbanization. Of all 14 lichens, eight were analysed individually (Table 3). Length of urbanization, or the area covered by buildings around the trees, affected seven species negatively. We estimated a decrease in species richness and the total cover of target lichen species per tree (Fig. 4b and 4d) and a lowering probability of occurrence by 3.7–5.6% per decade depending on lichen species (Figure 5). In summary, the relatively slow but steady loss of biodiversity confirms the assumption of Hahs *et al.* (2009) that modern cities potentially carry a large extinction debt; however, the interpretation is complicated by the return of lichens following recent improvements in air quality (see above).

Conclusions

We have shown major differences in lichen species richness and cover between urban and rural environments, as well as a clear decrease with the length and degree of urbanization on remnant large oaks in a city. Therefore, even if the prospects are good for a continuous supply of epiphytic substrate in cities – where trees are likely to exist – their value for epiphytic lichens seems limited. For the urban planner, this means two things. First, retaining valuable individual trees during urbanization does not automatically contribute to lichen biodiversity. Second, the preservation of lichen biodiversity is most likely best achieved if urban development leaves large contiguous areas of trees with rich lichen populations intact with plans for connecting fragments of old trees instead of embedding them within densely urbanized areas.

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FIGURES

Figure 1. The study area location. A, Map of the southern parts of Sweden, where the diamond indicates the position of the survey area. B, Position of the rural oaks (triangles) around Linköping (grey). C, Urban (circles) and rural oaks (triangles) in and around Linköping (grey).

Figure 2. The concentric expansion of Linköping, SE Sweden, over the past 300 years. Reproduced with kind permission from the municipality of Linköping.

Figure 3. A comparison of the 14 investigated lichen species' occurrence and cover on oaks in urban and rural environments. A, shows the proportion of trees with occurrence. B, shows the average cover (%) on trees when present. C, shows the average cover (%) based on all oaks. Error bars show 95% confidence intervals (binomial ditto in A). Lines show the corresponding GLM solutions.

Figure 4. A and C, the median number of lichen species (of the 14 target species) and the percent of the trunks of *Quercus robur* covered by these lichens in rural and urban areas. In B and D, the cover of target lichen species on urban oaks is shown as a function of when urbanization occurred (based on the average age of the five closest buildings).

Figure 5. The predicted values based on results from a logistic regression of finding *Calicium viride*, *Chrysothrix candelaris*, *Evernia prunastri* and *Ramalina* spp. on trees in relation to the length of urbanization.

- 1 Table 1. The 17 target lichens searched for on *Quercus robur*. Nine of the lichens are common, and eight are red-listed and/or indicator species
- 2 with varying substrate requirements

Lichen species	Status			Substrate preference ³
	Common	Threat ¹	Indicator ²	
<i>Calicium adspersum</i>	.	.	X	On rough bark of <i>Quercus</i> , rarely on old wood.
<i>Calicium quercinum</i>	.	VU	.	Corticolous on <i>Quercus</i> , etc., sometimes on old wood.
<i>Calicium viride</i>	X	.	.	Corticolous (<i>Alnus</i> , <i>Quercus</i> , <i>Betula</i> , <i>Pinus</i> , etc.) and lignicolous.
<i>Chaenotheca phaeocephala</i> (Turner) Th. Fr.	.	.	X	On lignum and bark of various trees (<i>Quercus</i> , etc.).
<i>Chrysothrix candelaris</i>	X	.	.	Corticolous and lignicolous.
<i>Cliostomum corrugatum</i> (Ach.: Fr.) Fr.	.	NT	X	On rough bark of <i>Quercus</i> , <i>Ulmus</i> , etc., also lignicolous.
<i>Cyphelium inquinans</i>	.	.	X	Lignicolous, rarely corticolous (on <i>Picea</i> , <i>Quercus</i> and <i>Betula</i>) and saxicolous.
<i>Evernia prunastri</i>	X	.	.	Corticolous or sometimes lignicolous, rarely saxicolous.
<i>Hypocenomyce scalaris</i> (Ach.) M. Choisy	X	.	.	Corticolous (esp. on <i>Pinus</i>) and lignicolous. Toxitolerant.
<i>Hypogymnia physodes</i>	X	.	.	Corticolous, lignicolous and less often saxicolous.
<i>Lecanographa amylacea</i>	.	VU	.	Corticolous on <i>Quercus</i> .
<i>Lepraria incana</i>	X	.	.	Corticolous and lignicolous, also saxicolous (under overhangs).
<i>Parmelia sulcata</i> Taylor	X	.	.	Corticolous, lignicolous and saxicolous, often on rocks manured by birds.
<i>Ramalina</i> spp.	X	.	.	—
<i>Schismatomma decolorans</i>	.	NT	X	Corticolous, esp. on old <i>Quercus</i> .
<i>Sclerophora coniophaea</i>	.	NT	X	Corticolous on <i>Quercus</i> , <i>Ulmus</i> , etc., in northern areas usually lignicolous on conifers.
<i>Usnea</i> spp.	X	.	.	—

3 ¹ Gärdenfors (2005). VU = vulnerable; NT = near threatened

4 ² Nitare (2010).

5 ³ Santesson *et al.* (2004).

7 Table 2. Characterisation of the urban and rural oak populations studied, and the explanatory variables used when modelling the occurrence of
8 target lichens on *Quercus robur* in urban environments. The average depth of bark crevices is based on averages from each tree measured from
9 the north, east, south and west. The summarised number of oak trees (including the focal tree) and summarised density of buildings; industrial
10 area, high, low and enclosed buildings surrounding the focal tree on six different radius distances were calculated from a tree database and maps,
11 respectively

	Urban (n=105)			Rural (n=109)		
	Average	Min	Max	Average	Min	Max
Oaks circumference at breast height (cm)	341	230	574	351	250	530
Depth of bark crevices (mm)	24·8	8·8	57·5	29·2	12·6	60·0
Sun exposure (%)	36·8	0	63·0	32·6	4·0	60·0
Density of oaks (ha ⁻¹) within:						
150 m	0·85	0·14	3·96	0·57	0·14	2·55
250 m	0·41	0·05	1·58	0·36	0·05	1·53
350 m	0·29	0·03	1·01	0·29	0·03	1·35
500 m	0·20	0·01	0·71	0·22	0·01	1·04
700 m	0·18	0·01	0·56	0·18	0·01	0·91
1000 m	0·13	0·02	0·36	0·15	0·00	0·71
Area covered by buildings (%) within:						
150 m	35·9	0·0	88·2	0·2	0·0	15·8
250 m	39·8	0·0	78·7	0·5	0·0	24·8
350 m	40·8	0·0	77·0	0·7	0·0	28·3
500 m	40·6	5·1	71·8	0·9	0·0	35·3
700 m	38·6	7·1	75·6	1·1	0·0	30·9
1000 m	35·8	10·4	66·3	1·4	0·0	19·8

14
15 Table 3. The occurrence of eight lichens species on urban trees was analysed in relation to the explanatory variables shown. The P-values of
16 (partial) regression coefficients are displayed for variables included in the best model for each species (based on AIC). Plus and minus signs
17 indicate a positive or negative association with the response variables

	<i>Hypogymnia physodes</i>	<i>Chaenotheca phaeocephala</i> ^a	<i>Ramalina spp.</i>	<i>Parmelia sulcata</i>	<i>Evernia prunastri</i>	<i>Chrysothrix candelaris</i>	<i>Calicium viride</i>	<i>Lepraria incana</i>
Length of urbanization	0·13 –	·	0·013 –	·	0·046 –	0·0043 –	0·0033 –	·
Tree circumference	·	·	·	·	·	0·0014 +	0·069 +	0·036 +
Bark crevices	0·14 –	0·013 +	·	·	·	0·061 +	0·033 +	·
Sun exposure	0·12 –	·	·	·	·	·	0·017 –	0·022 –
Density of oaks within:								
150 m	·	·	·	·	·	·	·	0·16 +
250 m	·	·	·	·	0·044 –	·	·	·
350 m	·	·	·	·	·	·	·	·
500 m	·	·	·	·	·	·	·	·
700 m	·	·	·	·	·	0·099 +	·	·
1000 m	·	·	·	·	·	·	·	·
Area covered by buildings within:								
150 m	·	·	·	·	·	·	·	·
250 m	·	·	·	·	·	·	·	·
350 m	0·014 +	·	·	·	·	·	·	·
500 m	·	·	·	0·039 –	·	·	·	·
700 m	·	·	0·055 –	·	·	·	·	·
1000 m	·	0·00076 –	·	·	·	·	·	·
P-value for the selected model	0·078	0·000043	0·00066	0·034	0·021	<0·00001	0·00007	0·0037

18 ^a indicator lichen.

19

20 Table 4. Percent cover of 14 lichen species on urban oak trees as affected by six traits, i.e. if they mainly disperse by spores or diaspores, the
 21 spores area, if pycnidium are present or not, the group to which the photobiont belongs and the growth form. The vegetative dispersal mode is
 22 also indicated either by soredia or isidia

Species	Cover (%)	Spores	Diaspores	Spore size (μm^2)	Pycnidium	Photobiont	Growth form
<i>Calicium adspersum</i>	0	Yes	No	82.5	Yes	<i>Trebouxia</i>	Crustose
<i>Cyphelium inquinans</i>	0	Yes	No	123	Yes	<i>Trebouxia</i>	Crustose
<i>Sclerophora coniophaea</i>	0	Yes	No	21.6	No	<i>Trentepohlia</i>	Crustose
<i>Usnea</i> spp.	0	Rarely	Yes	42.4	No	<i>Trebouxia?</i>	Fruticose
<i>Cliostomum corrugatum</i>	6.66 E-08	Yes	No	23.6	Yes	<i>Trebouxia?</i>	Crustose
<i>Hypocenomyce scalaris</i>	5.62 E-07	Rarely	Yes	20.6	Rarely	<i>Chlorococcus?</i>	Crustose
<i>Hypogymnia physodes</i>	1.60 E-06	Rarely	Yes	29.4	Yes	<i>Trebouxia?</i>	Foliose
<i>Ramalina</i> spp.	2.02 E-06	Yes	Yes	66.3	Rarely	<i>Trebouxia?</i>	Fruticose
<i>Chaenotheca phaeocephala</i>	2.22 E-06	Yes	No	33.2	No	<i>Trebouxia</i>	Crustose
<i>Parmelia sulcata</i>	4.75 E-06	Rarely	Yes	68.7	Rarely	<i>Trebouxia?</i>	Foliose
<i>Evernia prunastri</i>	6.14 E-06	No	Yes	—	No	<i>Trebouxia?</i>	Fruticose
<i>Chrysothrix candelaris</i>	8.41 E-06	No	Yes	—	No	Green algae	Crustose
<i>Calicium viride</i>	1.19 E-05	Yes	No	63.8	No	<i>Trebouxia</i>	Crustose
<i>Lepraria incana</i>	2.89 E-05	No	Yes	—	No	<i>Trebouxia?</i>	Crustose
P-value	—	0.039	0.19	0.95	0.16	NA	0.27