Ann. Bot. Fennici 42: 351–363 ISSN 0003-3847
Helsinki 28 October 2005

Lichens of wooden barns and *Pinus sylvestris* snags in Dalarna, Sweden

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Received 5 May 2004, revised version received 21 Jan. 2005, accepted 29 Mar. 2005

Svensson, M., Johansson, P. & Thor, G. 2005: Lichens of wooden barns and *Pinus sylvestris* snags in Dalarna, Sweden. — *Ann. Bot. Fennici* 42: 351–363.

In Sweden, old wooden barns often host a diverse and threatened lichen flora including eight red-listed species, but this kind of barn has declined over the past 100 years. The barns have traditionally been made out of *Pinus sylvestris*, and it could be hypothesized that pine snags are the natural habitat for many lichens occurring on anthropogenic wood. We compared the lichen flora on old wooden barns in the village of Gärdsjö, Dalarna with that on snags of *P. sylvestris*. At α level, both species richness and lichen abundance were highest on snags, and for both substrates the north aspects had more species and higher abundance than E, S and W aspects. Overall species richness was similar on the substrates, with a slight tendency for higher γ-level diversity on barns. NMS ordination showed clear compositional differences between barns and snags, and also indicated a more heterogeneous vegetation on barns. Implications for conservation measures are discussed.

Key words: barns, buildings, lichens, red-listed, snags, wood

Introduction

The last 100 years have seen a decline of old, unpainted wooden buildings and fences in the agricultural landscape of Sweden. Not only are we risking the loss of an important part of our cultural heritage (Lange 1997, Larsson & Landström 2002), but also the loss of an important habitat for lichens. Although not much is known about the factors governing the distribution and ecology of the species living in this habitat, there are red-listed and rare lichens more or less restricted to this substrate. Because of this, there has been an increasing awareness of the need to investigate their status and ecology (Thor 2000).

Timber buildings in Sweden have traditionally been made almost exclusively of *Pinus sylvestris*, and it could be argued that many of the species occurring on wood in the agricultural landscape may have their natural habitats on snags in exposed situations in more 'natural' environments. On the other hand, anthropogenic wood, as barns, is known to assemble lichen species from a variety of habitats such as rocks and deciduous trees, besides the true lignicolous species. Therefore, old wooden buildings may also be expected to host a higher lichen diversity than *P. sylvestris* snags.

To examine these hypotheses, the aim of this study was to compare the lichen community of old wooden buildings in the agricultural landscape with the lichen community on nearby snags of *Pinus sylvestris*. We specifically asked if lichen species richness, abundance and species composition was different between old wooden barns and snags in a region located in the province of Dalarna, Sweden. This paper is based on a degree project at the Swedish University of Agricultural Sciences, Uppsala (Svensson 2003).

Wood in the agricultural landscape in Sweden

It has been estimated that there are 2.5 million buildings in Sweden that have some connection to agriculture. Of these, 0.5 million are dwelling houses and 2.0 million are various kinds of farm buildings like barns, outbuildings, etc. Their age varies, but 28% of the outbuildings are from the period 1850–1910 (Lange 1997). Older buildings are rare. Only 0.5% of all buildings in the agricultural landscape derive from the time before 1750. Most of these are found in the northern parts of the country, especially in provinces such as Dalarna, Hälsingland and Härjedalen. Though some old buildings are still utilized by the farmers of today, most of the old outbuildings are not in use anymore, and are therefore left unattended (Lange 1997). Thus, many buildings are condemned to slow decay, if not actively disposed of. When G. Degelius set out to investigate the occurrence of *Letharia vulpina* on wood and worked timber in the province of Jämtland, he found that in some areas most of the old barns had been demolished and sold to Stockholm as firewood during World War II (Degelius 1946).

Apart from buildings, another prominent feature of the past agricultural landscape was the presence of split rail fences (‘gärdsgårdar’). It has been estimated that the total length of these fences in Sweden was 560 000 km in 1750 (Stephansson 2003), obviously an enormous amount of potential substrate for lichens. Fences were usually made of *Picea abies* stakes, and were meant to keep cattle out of the fields. They demanded maintenance and received it regularly, with every farmer being responsible for a part of his village’s fence. When these fences were made obsolete by new cattle management systems, maintenance was discontinued, and as a result, old fences are now rare in the Swedish agricultural landscape (Cserhalmi 1997). New fences are seldom made of wood, and when they are, the wood has often been pressure-treated or painted, thus disqualifying it as a lichen substrate.

Earlier publications

The available literature concerning lichens growing on worked timber and wooden structures in the agricultural landscape of Sweden, as well as internationally, is scarce. In Sweden, early observations were made by Sernander (Sernander 1891, 1893). In a paper on saxicolous lichens growing on lignum, he mentioned several localities where such species were found on buildings, roofs, etc. Sernander visited three of these localities in the summer of 1889. The lichens of the churchyard of Njurunda, Medelpad, were treated in greatest detail (Sernander 1891). On an old wooden roof, which covered the stone wall surrounding the churchyard, Sernander found 33 lichen taxa, 28 of which were lignicolous and the remaining 5 growing on rusty nails. The substrates were described as ‘very old’ and ‘to some extent dust impregnated’. Sernander’s paper is also a source of even older references, though most of these have the character of short passages in works not primarily considering lichens on worked timber. This is indeed something that is characteristic of much of the available literature.

Degelius (1946) investigated the churchyard of Brunflo in Jämtland. He found an unusually rich occurrence of *Letharia vulpina*, where ‘several tens of thousands of specimens’ grew on an old wooden roof that covered the wall encircling the churchyard. Degelius found about 60 lichen taxa on this wall (ca. 10 on mortar and limestone, ca. 35 on wood and 15 on rusty nails), and he discussed the ecology of the lignicolous species. He also made observations concerning future conservational problems, considering the bad state of the roof.

In S. Ahlner's thesis on the biogeography of a selection of foliose and fruticose lichens growing on coniferous trees in the Nordic countries (Ahlner 1948: p. 131), man's impact on lichen distribution was discussed. He made the observation that lichens on coniferous tree bark, which can utilize lignum as a substrate in natural environments, sometimes were found growing on barns, split rail fences, roofs, etc. According to Ahlner, this was a quite uncommon phenomenon, most often observed in areas where these lichens were common on natural substrates in the vicinity. Ahlner (1948) concluded that man's impact on lichens growing on lignum was predominately negative, chiefly because natural substrates, such as decorticated snags, frequently were used as a source of firewood, but also because new wooden structures in the agricultural landscape were, to an increasing extent, painted or charred.

Brightman and Seaward (1977) published species lists of lichens that occur on worked timber in the British Isles. The species were divided into three groups:

A. Those commonly found on worked timber (56 species). These are mainly species with a wide ecological amplitude that are also found on various substrates apart from wood, e.g., bark and rock. Some of the species are predominantly found on wood and bark, but only one species is strictly lignicolous.
B. Those rarely found on worked timber (68 species). Many of these are common on bark or soil in Britain, but are only occasionally found on worked timber. Nine species on the list, *Calicium quercinum*, *C. trabinellum*, *Caloplaca furfuracea*, *Cliostomum corrugatum* (as *Catillaria graniformis*), *Cyphelium notarisii*, *Thelomma ocellatum* (as *Cyphelium ocellatum*), *Lecanora farinaria*, *L. subfuscata* (now included in *L. argentata*) and *Sphinctrina tubiformis* (as *S. microcephala*), have never been found on other substrates in the British Isles.
C. Normally saxicolous species, occasionally found on worked timber (44 species). The role of dust-impregnation in relation to this phenomenon is also discussed in the treatise.

Apart from serving as a substrate for lichens, old houses may sometimes function as sources of 'sub-fossil' lichen-remains, as stated by Coppins *et al.* (1985). When an old wooden 16th century house in Sussex was dismantled, samples of organic matter were taken in order to be biologically analysed. Among the samples were some ash staves, with eight identifiable lichen species still present on them. This allowed comparisons between the lichens of the ash staves and the present lichen flora of the region. Though all the species were still extant in Sussex, the lichen flora of the ash staves was more luxuriant and diverse than what is generally found there nowadays. Also, *Lecanora conizaeoides*, an air-pollution tolerant species which has increased its abundance during the 1900s, was absent from the staves.

Red-listed lichens on wood in Sweden

Eight red-listed species on the present Swedish Red List (Gärdenfors 2005) occur regularly or exclusively on wood in the agricultural landscape. These are: *Acarospora anomala* (Critically Endangered, CR), *Calicium abietinum* (Vulnerable, VU), *Caloplaca furfuracea* (Endangered, EN), *Cyphelium notarisii* (Critically Endangered, CR), *C. tigillare* (Near Threatened, NT), *C. trachylioides* (Critically Endangered, CR), *Letharia vulpina* (Near Threatened, NT) and *Sphinctrina anglica* (Critically Endangered, CR). Strikingly, four of these, *A. anomala*, *C. notarisii*, *C. trachylioides*, and *S. anglica* have not, or very rarely, been found in natural habitats in Sweden. Some recent publications concerning these species and their status in Sweden are Areskoug and Thor 2005 (*Cyphelium notarisii*), Arup 1999 (*C. trachylioides*), Oldhammer 2002 (*Letharia vulpina*), Thor 1996 (*Acarospora anomala*) and Thor and Arvidsson 1999 (all species except *Caloplaca furfuracea*).

Ingelög *et al.* (1993) focused on conservation problems in the agricultural landscape. In the lichen section of this book, the importance of old wood in the agricultural landscape as a substrate for red-listed lichens was addressed (Ingelög *et al.* 1993: p. 396). Properties that make wooden buildings suitable for lichen colonisation were listed; the building should (1) be made of coarse timber, (2) not be heated and, (3) not be painted or impregnated. The lichens of such habitats are threatened as old wooden buildings are getting fewer, and few new buildings with the properties listed above are being built. As a way of increasing the amount of wood suitable for lichen colonisation, subsidising the building of new split rail fences around natural pastures has been suggested. In a recent information booklet about the history and conservation of old barns (Ekeland *et al*. 1999), a short survey of lichens on barns is included. Thor (2000) stressed the importance of old wooden buildings as habitat for red-listed lichens, and that more knowledge concerning the status of these species is needed. Co-operation between conservation biologists and authorities dealing with the preservation of old buildings is suggested for successful protection of this vanishing habitat.

Material and methods

Study area

The inventory of old wooden buildings was conducted in the village of Gärdsjö (60°55´N, 15°13´E), 10 km NW of Rättvik, in the province of Dalarna. In this village, there are almost 350 barns still left, dating from medieval times to about 1930. Most of them are not used anymore and have suffered from decades of neglect. During the 1990s a restoration was made, involving people in the village and the County Board of Dalarna, during which most of the old barns were given new roofs (Peres *et al*. 1996). A guide to the barns of Gärdsjö exists (Peres *et al.* 1996), which includes a map and a classification of the barns into five different age classes, based on dendrochronological dating and timber techniques. The inventory of *Pinus sylvestris* snags was made at a randomly chosen mire (61°00´N, 15°10´E) about 10 km W of Gärdsjö, 7 km N of Vikarbyn, along the road from Vikarbyn to Tövåsen. The fieldwork was carried out during January and February 2003 by M. Svensson. His collections will be deposited in herbarium UPS. The nomenclature follows Santesson *et al.* (2004).

Selection criteria for barns and snags, and lichen sampling

Not every building included in this inventory may strictly be defined as a 'barn', i.e., a building where hay was stored. At least two buildings have been used as houses where farmers lived periodically, mostly during harvest ('slåtterstugor'). They have been built using the same techniques as the barns, and since they are not in use anymore (and hence not heated), the difference to the lichens growing on them should be scant. In the following, they are referred to as barns. To be included in the inventory, a barn had to fulfil the following criteria: (1) belonging either to age class 1600–1700 or 1750–1850, according to Peres *et al*. (1996); (2) a clear north–south orientation — for example, if the supposed northern wall of a barn in fact had a directional stance of NW, it was excluded; (3) unpainted; and (4) the barns should be exposed (exposition values of 1 or 2 on all walls, *see* below). Barns excluded by this criterion were surrounded by full-grown trees. However, some barns included had one wall that was not exposed. Exposition was estimated using a scale invented for this investigation: (1) completely exposed, e.g., in a field, (2) partly exposed, e.g., in a field but with a big tree next to it, (3) partly shaded, e.g., at edge of a forest, and (4) shaded, e.g., situated in a forest. Four vertical sample lines were established on each wall of the building. To determine the distance between the lines, the length of the wall was measured and divided into five parts. The lines were positioned on the four 'borders' between those parts. If an obstacle (window, door, etc.) was encountered, the sample line was put beside it. The plot consisted of a 16-square plastic net with the dimensions 10 × 10 cm, with individual squares measuring 2.5 × 2.5 cm (subplots). The plots were attached along the sample lines with the first plot at ground level. The total number of subplots in which a species occurred, was noted for each plot. The distance between the plots was 50 cm, measured from low middle point to low middle point of each respective plot. If possible, the walls were inventoried from ground level up to 2.5 m (6 plots). The decay stage was estimated using the scale of Areskoug and Thor (2005): (1) new wood free from surface cracks and obvious signs of decay, (2) wood intact, firm, cracks < 1 mm wide, (3) wood of a silver hue, firm, surface fleeced, cracks between 1–3 mm wide, (4) wood beginning to soften, cracks between 3–5 mm wide, and (5) wood in later stages of decay, cracks > 5 mm wide. The directional exposure of each wall was measured using a handheld compass. Small fragments of species not possible to identify in the field were collected to be examined later.

To be included in the inventory, the snag had to fulfil the following criteria: (1) the snag should be exposed — snags having exposition values of 3 or 4 according to the scale above, were not included; (2) the snag should have an old and weathered appearance and no bark should be left; and (3) the snag had to be at least 10 cm in diameter 1.5 m above ground level. Sample lines were placed on the north side and the south side of each snag. The centre of each plot was positioned facing north or south, using a handheld compass. Plots were applied in the same way as on the barns. The snags were inventoried from ground level up to 2.5 m (6 plots).

Data analyses

The statistical analyses aimed to compare lichen species richness, abundance and composition between the barns and the snags, and we used the sample lines (transects) as sample units in these analyses. Transects with missing sample-plots and transects without any lichen records (which only occurred on barns) were excluded. Standard methods were used for species richness and abundance analyses, which were performed in the GLM procedure in SAS (SAS Institute 2000). Lichen abundance was estimated as the total number of records per transect for all species combined, and was square-root transformed before analyses.

Species composition was examined by non-metric multidimensional scaling (NMS) by ordinating the transects in species space, using the PC-ORD software (McCune & Mefford 1999). NMS is a suitable ordination technique for community data with a large number of zero-values, such as in the present paper, and does not have assumptions of normality or linearity (McCune *et al.* 2002). NMS uses ranked distances in the original multidimensional space to find a solution which reduces the dimensions but keeps the relationship with the original space as high as possible. We used the Sørensen distance measure and the slow and thorough autopilot mode provided in PC-ORD. This mode uses an instability criterion of 0.00001, and up to 400 iterations to reach that stability. Since our hypothesis was that species present on barns occur naturally on snags, we chose to compare species presence rather than using species abundances. We excluded species found in only 1–2 transects since these introduced some instability, leaving 28 species in the data matrix used in the ordination and subsequent MRPP. We repeated the ordination several times, and we also compared the results using presence–absence data with results using square-root transformed abundance data. In all ordinations a three dimensional solution was selected by the autopilot mode and the ordinations were very similar between the runs. The mean stress level in the final solution presented in this paper was 15.1% and significantly lower than 50 randomized runs ($p < 0.05$). The instability criterion was reached after 222 iterations.

To test for differences between barns and snags, and between the individual barn walls, we used multi-response permutation procedures (MRPP), using the Sørensen distance measure and again excluding rare species (occurring in 1–2 transects). As for the NMS ordination the PC-ORD software was used for the MRPP.

Results

General results

In all, 11 barns and 16 snags were included in this study. On the barns we found 41 lichens and 3 calicioid fungi in 848 sample-plots. On the snags, 27 lichens and 2 calicioid fungi were found in 192 sample-plots (Tables 1 and 2). Two unidentifiable species belonging to the genus *Lecanora*, referred to as *Lecanora* sp. 1 and *Lecanora* sp. 2, were found on the barns. They may represent atypical or damaged specimens. According to the criteria (*see* Data analyses), we used 42 transects

(18 on north facing walls, 8 on E, 12 on S, 4 on W) from 7 barns and all 32 transects from the 16 snags in the data analyses of species richness, abundance and composition. Seven species, *Chaenothecopsis pusiola*, *Cyphelium tigillare*, *Lecanora polytropa*, *Parmelia sulcata*, *Physcia stellaris*, *Protoparmeliopsis muralis* and *Xanthoria parietina*, found on the barns, were not present in any transects fulfilling the criteria, leaving 54 species for the subsequent analyses.

Table 1. Frequencies of all species found on the barns. The columns named 'Subplots' give the number of subplots in which a certain species was found. The cardinal point is also given. The columns named 'North total' etc. give the number of walls facing a certain direction on which the species in question was found.

Species	Subplots North	Subplots East	Subplots West	Subplots South	North total	East total	West total	South total
Amandinea punctata	86	53	8	0	6	2	1	0
Bryoria furcellata	12	0	0	0	6	0	0	0
Buellia arborea	2	0	0	0	1	0	0	0
Calicium glaucellum	0	9	0	0	0	2	0	0
Calicium viride	117	9	0	0	4	2	0	0
Caloplaca holocarpa	20	0	0	3	3	0	0	1
Candelariella vitellina	119	49	73	0	5	4	7	0
Chaenotheca chrysocephala	27	2	0	0	3	1	0	0
Chaenotheca phaeocephala	212	13	0	0	9	3	0	0
Chaenotheca trichialis	37	0	0	0	5	0	0	0
Chaenothecopsis pusilla	4	12	18	0	1	2	2	0
Chaenothecopsis pusiola	0	8	0	0	0	1	0	0
Chaenothecopsis savonica	43	100	10	0	8	7	2	0
Cyphelium inquinans	205	54	0	0	4	2	0	0
Cyphelium notarisii	0	7	0	12	0	1	0	1
Cyphelium tigillare	0	5	0	0	0	1	0	0
Evernia prunastri	2	0	0	0	2	0	0	0
Hypocenomyce scalaris	56	140	7	43	4	7	1	3
Hypogymnia farinacea	1	0	0	0	1	0	0	0
Hypogymnia physodes	158	9	0	0	5	2	0	0
Lecanora hagenii	0	0	0	1	0	0	0	1
Lecanora polytropa	4	0	0	0	1	0	0	0
Lecanora pulicaris	78	11	0	0	4	1	0	0
Lecanora varia	573	185	4	23	9	9	1	4
Lecanora sp. 1	23	0	0	0	3	0	0	0
Lecanora sp. 2	0	16	16	54	0	2	2	1
Mycoblastus affinis	2	0	0	0	1	0	0	0
Ochrolechia microstictoides	2	0	0	0	1	0	0	0
Parmelia sulcata	6	0	0	0	2	0	0	0
Parmeliopsis ambigua	21	0	0	1	2	0	0	1
Parmeliopsis hyperopta	0	1	0	0	0	1	0	0
Phaeophyscia nigricans	58	0	1	0	2	0	1	0
Physcia dubia	0	0	7	0	0	0	2	0
Physcia stellaris	0	10	0	0	0	1	0	0
Placynthiella icmalea	0	4	0	0	0	1	0	0
Platismatia glauca	1	0	0	0	1	0	0	0
Protoparmeliopsis muralis	0	1	0	0	0	1	0	0
Psilolechia lucida	3	0	0	0	1	0	0	0
Pycnora sorophora	267	42	0	1	5	4	0	1
Rinodina pyrina	45	2	4	3	5	1	1	1
Usnea hirta	16	0	0	0	4	0	0	0
Xanthoria candelaria	38	3	4	0	4	1	1	0
Xanthoria parietina	0	2	0	0	0	1	0	0
Xanthoria polycarpa	2	2	1	0	1	1	1	0

Red-listed species

Two red-listed species occurred on the barns, but none on the snags. *Cyphelium notarisii* (Critically Endangered, CR) was found on the southern walls of two barns standing close to each other (only one of these included in the study, Table 1), and on the eastern wall of a third. It was most abundant on one of the southern walls, where it covered more than 1 dm^2. On the same barn, it also occurred on an old wooden sledge, which was leaning against the western wall. On the other two barns the species was very scarce. All specimens were sterile with abundant pycnidia, making this population equivalent to the Hallands Väderö population reported by Arup and Ekman (1997). The locality for *C. notarisii* in Gärdsjö is new, and it is one of the northernmost occurrences in Sweden (Janolof Hermansson, pers. comm.). *Cyphelium tigillare* (Near Threatened, NT) was found on the eastern wall of one barn. It was represented by at least two distinct thalli, though both were small. It was fertile, and no pycnidia were found. *Cyphelium notarisii* and *C. tigillare* did not occur on the same barn.

Species richness

Mean species richness per transect was higher for the snags than for the barns (7.8 *vs*. 4.2 species, $t = 5.98$, $p < 0.001$). This difference was mainly due to the low number of species occurring on the east, west and south facing walls of the barns (Fig. 1). To account for differences between the individual barns, we included both

Table 2. Frequencies of all species found on the snags. The columns named 'Subplots' give the number of subplots in which a species was found. The cardinal point is also given. The columns named 'Northern sides total' and 'Southern sides total' give the number of sides facing a certain direction on which the species in question was found.

Species	Subplots North	Subplots South	Northern sides total	Southern sides total
Alectoria sarmentosa	1	0	1	0
Bryoria fremontii	4	0	1	0
Bryoria furcellata	127	47	14	8
Buellia arborea	2	0	1	0
Calicium denigratum	249	267	13	14
Calicium trabinellum	35	39	8	4
Chaenothecopsis fennica	0	14	0	2
Chaenothecopsis savonica	21	95	3	3
Cladonia botrytes	0	10	0	1
Cladonia carneola	0	4	0	2
Cladonia cenotea	2	0	1	0
Cladonia digitata	13	8	2	3
Hypocenomyce anthracophila	0	3	0	1
Hypocenomyce scalaris	9	2	3	1
Hypogymnia physodes	230	31	15	8
Lecanora pulicaris	3	0	3	0
Mycoblastus alpinus	13	0	1	0
Mycoblastus sanguinarius	9	2	2	2
Ochrolechia microstictoides	12	3	5	2
Parmeliopsis ambigua	547	256	16	15
Parmeliopsis hyperopta	464	453	15	15
Platismatia glauca	4	0	2	0
Pseudevernia furfuracea	0	2	0	2
Pycnora sorophora	500	432	15	13
Pycnora xanthococca	22	19	1	1
Pyrrhospora elabens	14	2	2	1
Trapeliopsis flexuosa	4	0	1	0
Usnea hirta	151	63	12	10
Vulpicida pinastri	9	4	2	3

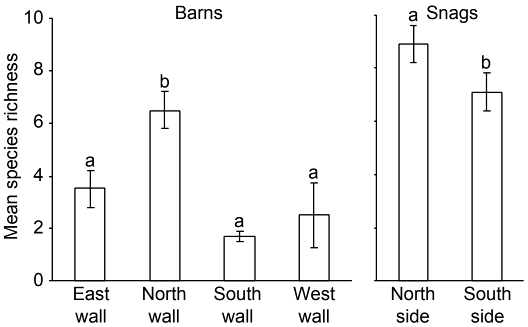

Fig. 1. Species richness (and standard error) per transect for barn walls and snags. The barn walls and snags were tested separately in a GLM with Tukey adjusted post-hoc test for differences among groups, and the paired *t*-test, respectively. Different letters denote significant differences ($p < 0.05$) between barn wall cardinal points in the GLM, and between the northern *vs.* southern sides of the snags in the paired *t*-test.

barns and walls in a General Linear Model, which showed wall directional stance to have the strongest effect on richness (GLM: $r^2 = 0.78$, type 3 F value for barns = 6.86, $p < 0.001$, type 3 F value for walls = 22.76, $p < 0.001$). The north walls had significantly higher species richness than the other walls, which did not differ in this respect (Fig. 1). On snags, the north sides had more species than the south sides (Fig. 1; paired *t*-test: $t = 2.7$, $p = 0.02$).

The incidence graphs indicate that the inventory led to a reasonably good estimate of the total species number, and a similar species accumulation rate across the transects for both the barns and the snags (Fig. 2). There was, however, a slight tendency towards a higher initial accumulation rate but a lower overall (γ) species richness on the snags.

Lichen abundance

As for species richness, mean species abundance was higher on the snags than on the barns, but more pronounced (131.2 *vs.* 32.7 mean number of records, $t = 10.42$, $p < 0.001$). Again, the north walls had a higher lichen abundance than the other walls among the barns (Fig. 3, GLM: $r^2 = 0.85$, type 3 F value for barns = 12.84, $p < 0.001$, type 3 F value for walls = 39.3, $p < 0.001$). On the snags the north sides had higher abundance than the south sides, and this difference was also more pronounced than the difference in species richness (Fig. 3; paired *t*-test: $t = 7.35$, $p < 0.001$).

Species composition and characteristic species for barns and snags

The NMS ordination showed that species composition was clearly different between barns and snags (Fig. 4). The MRPP within-group agreement (A) comparing barns and snags was 0.23 ($p < 10^{-9}$), which is high and confirms this compositional difference. The ordination graph also illustrates compositional differences between the barn walls, which was further confirmed by the within-group agreement for the barn wall cardinal directions ($A = 0.18$, $p < 10^{-9}$). The cumulative r^2 between the ordination distances and the distances in the n-dimensional space was 0.867 (axis one = 0.406, axis two = 0.28, axis three = 0.181).

The most frequently occurring species on the barns in terms of number of transects were *Amandinea punctata*, *Calicium viride*, *Candelariella vitellina*, *Chaenotheca phaeocephala*, *Chaenothecopsis savonica*, *Cyphelium inquinans*, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Lecanora pulicaris*, *L. varia* and *Pycnora sorophora* (Table 1). The most frequently occurring species on the snags were *Bryoria furcellata*, *Calicium denigratum*, *C. trabinellum*, *Chaenothecopsis savonica*, *Hypogymnia physodes*, *Parmeliopsis ambigua*, *P. hyperopta*, *Pycnora sorophora* and *Usnea hirta* (Table 2). Thus, only three species were among the most common species both on barns and snags.

Species abundances were variable between the walls of the barns, typically being much higher on the north facing walls (Fig. 5). On the north sides of the barns, *Amandinea punctata*, *Calicium viride*, *Candelariella vitellina*, *Chaenotheca phaeocephala*, *Cyphelium inquinans*, *Hypogymnia physodes*, *Lecanora pulicaris*, *L. varia* and *Pycnora sorophora* were most abundant (Fig. 5). On snags, *Bryoria furcellata*, *Hypogymnia physodes*, *Parmeliopsis ambigua*, *P. hyperopta*, *Pycnora sorophora* and *Usnea hirta* were most abundant on the north sides of

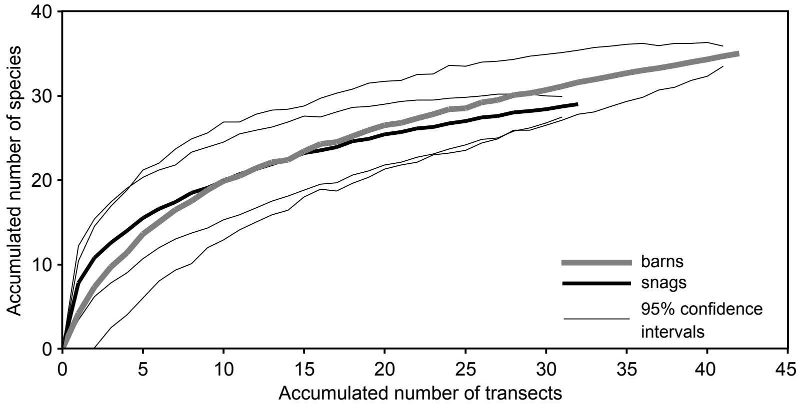

Fig. 2. Species accumulation curves across the transects on barns ($n = 42$) and on snags (32). The curves were constructed in PC-ORD (McCune & Mefford 1999).

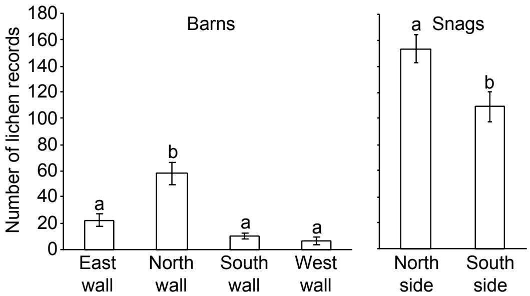

Fig. 3. Total lichen abundance (and standard error) estimated as the number of records per transect, for barn walls and snags. The barn walls and snags were tested separately in a GLM with Tukey adjusted post-hoc tests for differences among groups, and the paired *t*-test, respectively. Different letters denote significant differences ($p < 0.05$) between barn wall cardinal points in the GLM, and between the northern *vs.* southern sides of the snags in the paired *t*-test.

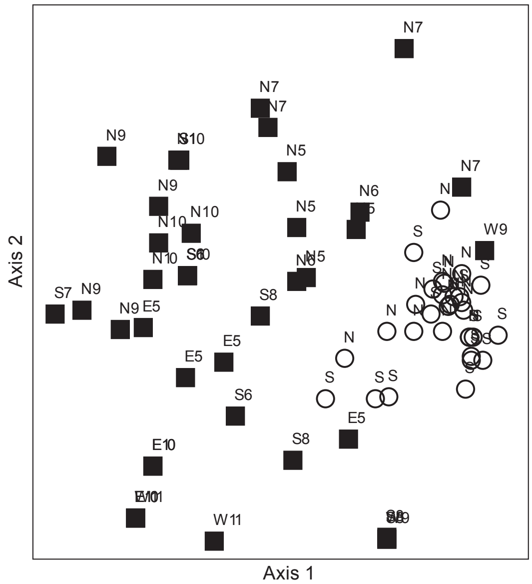

Fig. 4. NMS ordination graph of transects in species space based on presence–absence of 28 species in 42 transects on seven barns (■), and 32 transects on 16 snags (○).The labels denote cardinal points (N, E, S, W), and in the case of barns the number refers to the barn identity. Axis one accounts for 41% of the variation in the data, and the vertical axis accounts for 28%.

the snags (Fig. 6). We found small effects on the MRPP results using species abundance instead of species presence–absence.

Discussion

General comparison of species composition, richness and abundance

We examined the hypothesis that the lichen community on old, wooden buildings is found in its natural habitat on exposed snags of *Pinus sylvestris*. The results did not support this hypothesis. Instead, we found a strong compositional difference between the barns and snags, with few species in common between these substrates. We had, however, anticipated some differences between barns and snags, based on earlier observations which have recognized that anthropogenic wood accumulates species from a wide variety of substrates (Sernander 1891, Brightman & Seaward 1977). Therefore, we had expected a higher diversity of lichens on the barns than on the snags. But this hypothesis was not supported by the results either. At α level, represented by the sample-lines, snags harboured a markedly

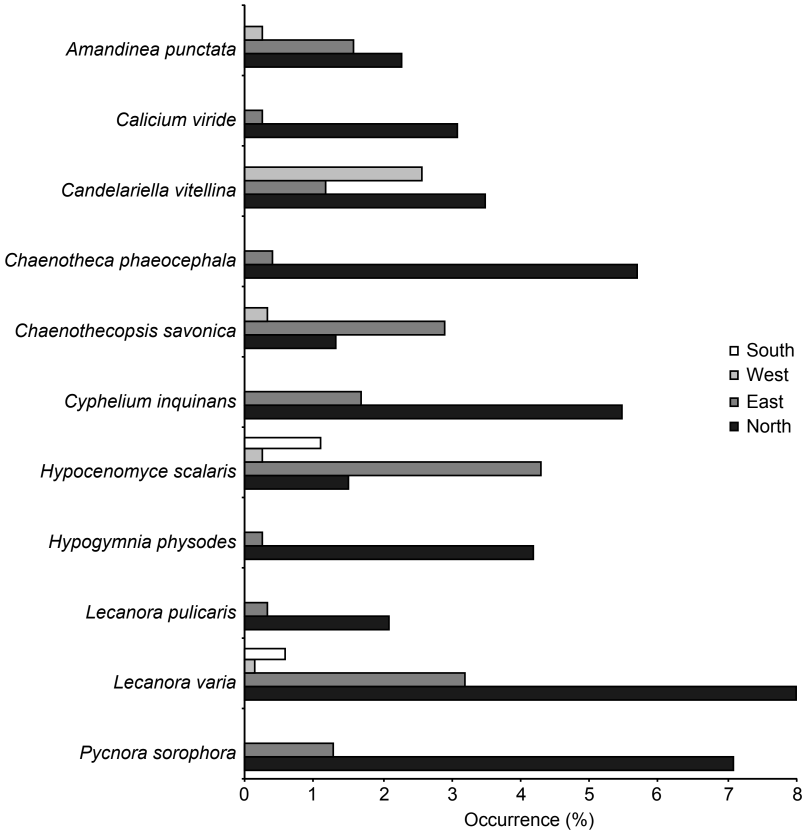

Fig. 5. Occurrence of common species on barns. The occurrence of species on a wall with a certain directional stance is given as a percentage of the total number of subplots investigated on all walls with the same directional stance. (Note: *L. varia* occurred in 17.4% of the subplots of northern walls.)

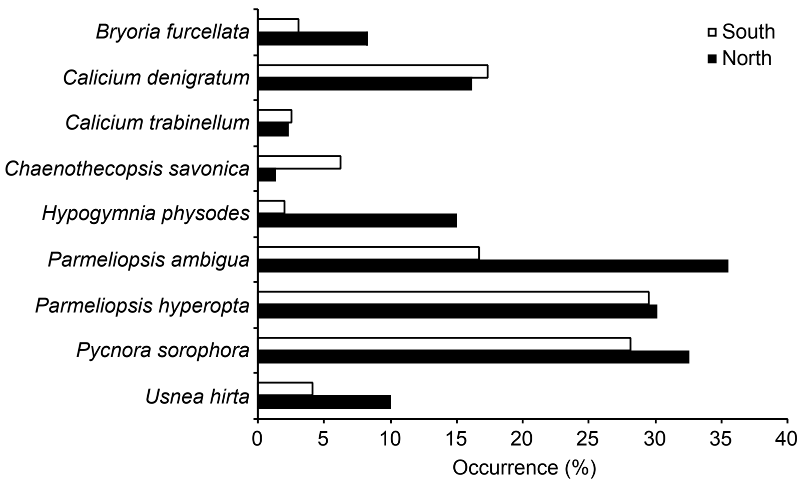

Fig. 6. Occurrence of common species on snags (for explanation *see* Fig. 5).

higher number of species than the barn walls. Extrapolating the species accumulation curves there was a slight tendency towards an overall higher lichen diversity on barns, indicating a more diverse lichen flora on this substrate, although comparing the same number of sample-units did not show any differences in overall diversity.

The NMS ordination did, however, indicate a more heterogeneous lichen flora on the barns than on the snags, in accordance with that anthropogenic wood assembles lichens from a variety of habitats such as rocks and deciduous trees, besides the true lignicolous species. The strong differences in species composition between snags and barns might indicate that the natural habitat of rare and red-listed lichens on barns is not only snags, but also rocks, dust impregnated trees and aggregations of fallen trees ('timmerbrötar'). The latter are sometimes formed after wildfires, by flooded streams and rivers as well as by whirlwinds.

The lichen abundance showed the same pattern as the species richness. Lichens were more abundant on snags than on barns, and the northern aspects had more lichens than the other aspects. Taken together, the results indicate that lichen cover and species density per surface area was higher on the snags than on the barns, which should account for the tendency towards a faster species accumulation rate on the snags.

On both barns and snags, the northern aspects harboured the greatest number of lichens, both in terms of species and occurrences. The explanation may be that northern walls and snag sides hold humidity longer during the day, which allows net growth of lichens for a longer time. In southern, western and eastern aspects, light exposure may dry out these surfaces more quickly after sunrise. This may be particularly important on intact wood with low water holding capacity.

Even if the northern walls of the barns had a higher lichen diversity than the other walls, excluding the east, south and west walls would have led to a reduction by approximately 25% in the total number of lichens found on barns. Also, both the red-listed species would have been missed.

Differences in species composition between barns and snags

The most striking differences between the respective lichen floras of barns and snags were the frequency of nitrophilous and facultatively saxicolous species. Eight species found on the barns are nitrophilous and/or favoured by the presence of mineral dust (e.g., Hallingbäck 1995, Foucard 2001, Moberg 2002a, 2002b, Santesson *et al.* 2004), *Candelariella vitellina*, *Lecanora hagenii*, *L. polytropa*, *Phaeophyscia nigricans*, *Physcia dubia*, *Protoparmeliopsis muralis*, *Xanthoria candelaria* and *X. parietina*. On the snags, no such species were to be found. It should be noted that most of these species were rare on the barns. Furthermore, 15 species on the barns are often or occasionally found on rock (Foucard 2001, Santesson *et al.* 2004), *Amandinea punctata*, *Candelariella vitellina*, *Caloplaca holocarpa*, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Lecanora polytropa*, *Mycoblastus affinis*, *Parmelia sulcata*, *Phaeophyscia nigricans*, *Physcia dubia*, *Platismatia glauca*, *Protoparmeliopsis muralis*, *Psilolechia lucida*, *Xanthoria candelaria* and *X. parietina*. Among the species found on snags, only five are frequently or occasionally found on rock, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Mycoblastus sanguinarius*, *Platismatia glauca* and *Pseudevernia furfuracea*. Three of these were present on the barns as well.

Several factors may explain the observed differences in lichen composition between barns and snags, and no single factor is likely to explain them all. Instead, any combination of the seven factors listed below may have caused the difference. (1) Dust. At the site in Gärdsjö, there are several gravel roads, and also some fields that are still being cultivated. The dust is probably alkaline, since Gärdsjö is situated on the base-rich soil typical of the Siljan area in Dalarna (Peres *et al.* 1996). The presence of dust might explain why there was a greater proportion of saxicolous species growing on the barns, as well as the occurrence of nitrophilous species. (2) Differences in dispersal ability. The barns might be older than the snags. In that case, species that disperse slowly have had more time to colonise the barns. The snags may, however, be at least as old as the barns, though that seems unlikely. (3) Differences in age could give rise to substrates that may have different chemical or structural properties. (4) The microclimate may differ between the sites. (5) Unlike snags, the logs of the barns are placed in horizontal position. This, together with a protruding roof, causes a difference in the extent and duration of exposure to rain water. This difference may be beneficial to some species and deleterious to others. (6) Acid rain caused by air pollution may have changed the character of the substrate. Wood is an acid substrate in itself (Arup &

Ekman 1997), so species sensitive to low pH are perhaps only able to persist in an environment where alkaline dust serves as a buffer. However, the influence of acid rain is most noticeable in southern Sweden. (7) Sometimes one finds bird's nests under roofs. Faeces emanating from these may explain the local abundance of species such as *Candelariella vitellina*.

Decay stage and age

The data on the decay stage were not evaluated, because this parameter was found to be ambiguous. The decay stage was often very variable, with different logs on the same wall being in different states of decomposition. It was common to find that a wall assumed to be old, in fact consisted of a mixture of newer and older logs. This is hardly surprising, since the farmers replaced rotten logs. To analyse the relationship between the decay stage and abundance of lichen species or individual species, one would have to note the decay stage of each individual plot rather than taking a mean value for a whole wall, as was the case in this study. Furthermore, some of the newer logs were upon closer examination found to be *Picea abies* rather than *Pinus sylvestris*. Whether or not this fact affects the lichens is unknown, but it is possible that the difference may be quite small (Lõhmus & Lõhmus 2001).

Here, only barns belonging to the age classes 1600–1700 and 1750–1850 were inventoried. These barns were similar to each other in terms of building material and techniques. Barns of the age classes 1800–1900 and 1870–1930 often had walls made of deal boards, a lichen substrate that might differ from the logs used in older barns. As for barns belonging to the age class 1200–1600, in our experience, they often had a very weathered appearance with very few lichens growing on them. Another problem was the vague character of the age classes themselves. As mentioned above, an individual barn may consist of logs of varying age. For example, one barn of age class 1500–1600 mentioned in Peres *et al*. (1996) had three walls dating from the 16th century and one from the 18th century. Also, barns were often moved from one place to another. Obviously, this may cause problems when estimating their age.

Management recommendations

Management recommendations for the conservation of lichens and red-listed species on barns and other kinds of wood in the agricultural landscape, based on present knowledge, might be summed up as follows:

1. *Maintenance and restoration*. In the case of barns, a reasonably watertight roof is certainly the most important single factor. When the roof caves in, decay accelerates. Split-rail fences not seen to will fall, but just erecting them again might prolong their life as lichen substrates by many years.
2. *Paint*. Old buildings made of untreated wood should never be painted. Buildings that have been painted long ago with Falu red may be painted again, but attention should be paid to the possible presence of species such as *Acarospora anomala*, which prefers growing on buildings with faded Falu red paint. Only thin layers of paint should be appplied.
3. *Exposure*. Trees and bushes growing close to a barn might shade it, thus making it less suitable for red-listed species. This is often the case when meadows etc. slowly turn into forest, a common process today. This results in more shaded and humid conditions that will also increase the risk of degradation caused by wood-decaying fungi. An open space should be kept around the barns.
4. *Dust*. If possible, old gravel roads near old wooden buildings with lichens should not be covered with asphalt. Dust from roads and fields is probably important to these lichens.
5. *New substrate*. Continuous replenishment of suitable habitats (barns, etc.) must be maintained over time. If new buildings or split rail fences are to be built, untreated wood should be considered. Also, when replacing rotten logs, it is important to use wood that has not been painted or pressure treated. Actually, removing a few logs and replacing them with new ones might be a good conservation measure, since it will provide rare species with new substrate, which they can easily colonize. It should be noted that it might take hundreds of years for the wood to acquire the desired characteristics.

It should be emphasised that the barns of Gärdsjö are, by comparison, unusually well kept. Many of the old wooden buildings still remaining in Dalarna and elsewhere in Sweden have probably been left to decay. Hence, the number of places where these very rare lichens can survive is slowly decreasing. If we wish to keep these species, urgent measures are required. The first step must be to protect the few buildings still standing, as has been done in Gärdsjö.

Further investigations on lichens on wooden barns are needed, and would have important implications for the management of these habitats to ensure the survival of the lichen species occurring there, some of which are red-listed.

Acknowledgements

We thank Janolof Hermansson, for suggesting Gärdsjö as a suitable place for the inventory and for general advice, and Anders Nordin for the help with the identification of some samples, and herbarium UPS for access to their facilities.

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