**INTRODUCTION**

The lungwort lichen, *Lobaria pulmonaria* (L.) Hoffm., is one of the most conspicuous lichens having a characteristic morphology; therefore, it is frequently observed also by non-lichenologists. Many advanced studies have been undertaken to understand its distribution and ecology (e.g. Wirth, 1968; Farmer et al., 1991; Rose, 1992; Gauslaa & Solhaug, 1999; Wolseley & James, 2000; Edman et al., 2008; Jüriado & Lüra, 2009; Jüriado et al., 2011; Gauslaa et al., 2017, 2020; Beckett et al., 2019; Jüriado & Paal, 2019; Phinney et al., 2019), but there is still a lack of knowledge that explains its ecological and climatic requirements, since it occurs in a wide range of environments. *Lobaria pulmonaria* is widely distributed in the northern hemisphere (Litterski, 1999; Brodo et al., 2001; Jørgensen & Tønsberg, 2007; Urbanavichus & Andreev, 2010; Widmer et al., 2012; Grimm et al., 2021), but has decreased remarkably since the 19th century, becoming rare and threatened in, for example, the Central European lowland (Diederich & Sérasiaux, 2000; Ciesliński et al., 2006; Aptroot et al., 2011; Wirth et al., 2011), and southernmost Scandinavia (Hallingbäck, 1986; Hallingbäck & Olsson, 1987; Jørgensen & Tønsberg, 2007; Schiefelbein et al., 2016, 2017; Schiefelbein & Thell, 2018; Thell & Schiefelbein, 2018). In this study we follow the changes in its distribution and frequency in the southwestern Baltic and Kattegat area over different time periods since the mid-19th century. Earlier studies have shown that it suffered a decline for a long time, mainly due to agriculture, intensive forestry and emissions (e.g. Farmer et al., 1992; Gustafsson
et al., 1992; Farmer, 1997; Wolseley & James, 2000; Pykäla, 2004; Seaward & Coppins, 2004; Kalwij et al., 2005; Edman et al., 2008; Jüriado & Liira, 2010; Schiefelbein & Thell, 2018). However, it still occurs in places where it is difficult to explain its existence, such as in those close to intensive agricultural activities. Four questions were formulated: (1) where did *L. pulmonaria* grow in the southwestern Baltic area in the past, (2) where is it still present, (3) in which habitats is it still present, and (4) how healthy is it? To answer these questions, literature, herbaria and databases were consulted, as well as the actual localities where it occurred in the recent past. The answers to these questions can help with a successful long-term conservation of *L. pulmonaria*. Some results of this study in Sweden have already been published (Schiefelbein et al., 2016, 2017; Schiefelbein & Thell, 2018; Thell & Schiefelbein, 2018).

**MATERIAL AND METHODS**

**Study area**

The study area in the southwestern Baltic Sea and Kattegat area covers Denmark, the nemoral zone of Sweden including most of Skåne, coastal regions of Bohuslän, Halland, Blekinge, the southernmost Kalmar region and the southern part of Öland, northwestern Poland including the voivodeship Western Pomerania, Pomerania and adjacent regions, and northern Germany including the federal states Mecklenburg-Vorpommern and Schleswig-Holstein. The study area has been divided into eight geographical regions (Fig. 1): central and northern Jutland (J), Danish Islands incl. Bornholm (DÍ), coastal region along Kattegat (Halland, Bohuslän; BH), Skåne (Sk), coastal region of Blekinge and southernmost Kalmar (BK), Pomerania and Kashubia (Pom), Mecklenburg-Western Pomerania incl. Wolin island (M-V).

**Fig. 1.** Distribution of *Lobaria pulmonaria* in the studied regions of Denmark, Sweden, Germany and Poland.
and Schleswig-Holstein including also northern
Schleswig, which is a part of Denmark (S-H).

The study area is actually predominated by ag-

cultural landscapes. Large forested areas only
occur in Poland and Mecklenburg-Vorpommern
on terminal moraines and in nutrient poor sand
areas, as well as in Sweden at the northern
ege of the study area and in the transition to
the boreal vegetation zone (Fig. 2). The natural
vegetation of the study area would have been
mainly mesophytic species-rich beech, species-

poor acidic beech, species-poor oak, and mixed
oak-hornbeam forests (Bohn & Neuhäusl,
2000/2003). In addition, alluvial and wet low-
land forests would have been distributed in the
Elbe river valley and along the North Sea coast
of Schleswig-Holstein, at swamps and fen for-
ests in river valleys, non-forest coastal vegeta-
tion and some raised bogs (Bohn & Neuhäusl,
2000/2003). The distribution of the different
potential natural vegetation types can be seen
in Fig. 2 & 4.

The climate is temperate and characterized by
moderate temperatures. The average annual

temperature ranges from 5.6 to 9.0°C, and the
average annual precipitation from 480 to 1060
mm (Fick & Hijmans, 2017). Regions with lower
average annual temperatures are in Pomerania,
in central Skåne and at the border to the boreal
vegetation zone.

Compilation of distribution data

For historical and recent records, the databases
Danmarks svampeatlas (www.svampeatlas.
dk), Artportalen (www.artportalen.se) and
Sweden’s Virtual Herbarium (www.herbarium.
emg.umu.se) were consulted, as well as lit-

erature sources (Krawiec, 1933; Saxen, 1963;

Fig. 2. Distribution of Lobaria pulmonaria in the study area and potential natural vegetation
Izydorek, 1987; Søchting & Christensen, 1989; Fałtynowicz, 1992; Christensen & Søchting, 1996; Fałtynowicz & Kukwa, 2000; Fałtynowicz et al., 2000; Dolnik, 2004; Schiefelbein et al., 2016, 2017; Schiefelbein & Thell, 2018; Thell & Schiefelbein, 2018; Neumann & Dolnik, 2018). Some Polish records were personally communicated by W. Fałtynowicz (Wrocław), A. Ryś (Strzałowo) and M. Kukwa (Gdansk). The records were divided into four time periods: 19th century including 1900, 1901–1975, 1976–2000, and 2001 onwards.

Inventory work in 2015–2018

Between 2015 and 2018, 124 localities of *L. pulmonaria* were visited; in Denmark and Germany only localities that were recently known at the beginning of the study, in Sweden, all sites reported to Artportalen in Skåne, southern Blekinge and southern Kalmar region since 1990, except for few difficult to reach remote sites, and in Poland, those sites recorded in the 1980s by Izydorek (1987) and those after 1990 personally communicated by W. Fałtynowicz, A. Ryś and M. Kukwa.

These studies were carried out as a part of an on-going population genetic study. Therefore, the main goal was not to check all known recent and historical localities, but to find as many specimens as possible. The species was searched for not only at the original locality, but also in suitable surroundings. The size of the study area at the localities depended on the accuracy of the information. The more precise information, the smaller area examined.

For those trees with *L. pulmonaria*, the habitat type, the host tree species and viability of the population on the host tree were determined. The habitats are classified into six classes: species-poor oak forests, species-poor acidic beech forests, mesophytic species-rich beech forests, *Tilio-Acerion* forests, mixed oak-hornbeam forests or wooded meadows. Four classes of viability of the population on the host tree have been distinguished: (1) specimens of populations with poor viability were strongly damaged; there were no young thalli, populations were of few small specimens; (2) specimens of populations with moderate viability were with partly damaged specimens or lobes, respectively; healthy lobes were only few at the edge of the thalli and younger thalli were almost absent; (3) specimens of population of good viability bore isidia, phylidia or soredia in abundance; most thalli looked healthy, younger thalli were usually present; (4) population with specimens bearing apothecia on the thalli were considered to be of very good viability.

RESULTS

Historical and recent distribution of *Lobaria pulmonaria* in the study area

As a result of the inventory, 332 historical and/or recent localities could be identified in the study area. The number of records in the different regions and periods can be seen in Table 1. The localities are spread over the whole area and occur in almost all parts of the study area (Figs 1 & 2). Most localities are in central and northern Jutland and in Skåne, and least in Mecklenburg-Vorpommern and on the Danish Islands. According to the famous Danish botanist Emil Rostrup, *L. pulmonaria* occurred here and there on beeches on Lolland in the mid-19th century (Rostrup, 1864), but no other reports or collections are known from the southern Danish Islands. The number of localities in the Blekinge/Kalmar region is also very low, but this region is very small.

Regarding the number of localities since 2000, the situation is similar, the only difference being that the number of localities in Schleswig-Holstein were reduced to three. The proportion of the recent localities out of total known localities is high in central and northern Jutland, all Swedish regions and in Pomerania. In contrast, the percentage of recent localities of all known ones is low in the German regions and on the Danish Islands.

There has been a significant shrinkage in the distribution of *L. pulmonaria*. It has disappeared almost completely in Schleswig-Holstein, on the Danish Islands, in southwestern Skåne, in Mecklenburg-Vorpommern and in the western part of Pomerania (Fig. 1, Table 1). The only recent localities in these regions are in the Old Drift landscape (Geest) of Schleswig-Holstein, on the northern coast of Rügen, the Darß-Zingst Peninsula in Mecklenburg-Vorpommern, and in northern Zealand where it became extinct in 2015. In central and northern Jutland, it occurs almost exclusively in the centrally located
large forest complexes and in coastal regions. In Pomerania, the current area reaches from Słupsk in the west to Kashubia (west of Gdansk) in the east. The localities in Bohuslän/Halland, northern and eastern Skåne, Blekinge and the Kalmar region declined in the past, but a reduction of the distribution area is not recognizable.

The localities of *L. pulmonaria* are mainly in areas where the potential natural vegetation are oak and beech forests (Figs 2 & 3). Only few localities are in areas with other potential vegetation types, 6 in nemoral pine forests, 4 in alluvial and wet lowland forests, and 2 in raised bogs. The percentages of records between mesophytic (mesophytic species-rich beech forests, mixed oak-hornbeam forests, mesophytic pedunculate oak forests) and acidic forest types (species-poor acidic beech forest, species-poor oak forests) have changed over time (Fig. 3). Before 1900, most records were in areas with potentially mesophytic forests. Since then, the percentage of records in mesophytic forests has continuously declined; today, only 10 localities are located in areas of these forest types, 4 in Skåne, 4 in Blekinge/Kalmar, 1 in Pomerania and 1 in Mecklenburg-Vorpommern.

**Table 1.** Number of records in the different regions and periods. Abbreviations: J – central and northern Jutland, DI – Danish Islands incl. Bornholm, BH – coastal region along Kattegat (Halland, Bohuslän), Sk – Skåne, BK – coastal region of Blekinge and southernmost Kalmar, Pom – Pomerania and Kashubia, M-V – Mecklenburg-Western Pomerania incl. Wolin island, S-H – Schleswig-Holstein including also northern Schleswig.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Number of records</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>J</td>
</tr>
<tr>
<td>≤1900</td>
<td>8</td>
</tr>
<tr>
<td>1901–1975</td>
<td>26</td>
</tr>
<tr>
<td>1976–2000</td>
<td>34</td>
</tr>
<tr>
<td>&gt;2000</td>
<td>30</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>79</td>
</tr>
</tbody>
</table>

**Fig. 3.** Percentage of the localities in different potential natural vegetation types according to Bohn & Neuhäusl (2000/2003).

**Inventory work in 2015–2018** – Between 2015 and 2018, the occurrence of *L. pulmonaria* could be confirmed at 64 localities (see Appendix 1) of the 124 visited localities (Fig. 4). At these localities, 150 trees inhabited by *L. pulmonaria* were found, but the search ceased at most localities after five trees with *L. pulmonaria* had been discovered.
Sixty-two (of 64) investigated localities and 148 (of 150) host trees are located in forests; only two localities and two host trees are in wooded meadows. 46 localities and 117 host trees occurred in species-poor acidic forests (species-poor acidic beech forests, species-poor oak forests) and 15 localities and 31 host trees in mesophytic forests (mesophytic species-rich beech forests, lime-maple forests, mixed oak-hornbeam forests; Table 2).
Lobaria pulmonaria occurred in all regions except Schleswig-Holstein in species-poor acidic beech forests. Most localities in this forest type were found in central and northern Jutland (Table 2). The localities in oak forests with a species poor ground floor vegetation were mainly situated in the western part of the study area, whereas the localities in mixed oak-hornbeam forests and lime-maple forests were, with one exception, of each forest type, in the northwestern part of the study area. The only locality in mixed oak-hornbeam forests outside Sweden was in Schleswig-Holstein, and the single locality in lime-maple forests was in Pomerania. However, the basic conditions are different, as the localities in Sweden are in rocky places whereas the Pomeranian locality was entirely without stones. Localities on wooded meadows were exclusively found in Blekinge.

The most inhabited tree species in the study area was Fagus sylvatica, followed by Quercus species (mainly Q. robur), and Acer platanoides (Table 3); very few occurrences were on Fraxinus excelsior and Tilia cordata and only one on Carpinus betulus.

Lobaria pulmonaria specimens on about two thirds of the colonized trees were in a healthy condition, five of them even with apothecia (Fig. 5). The situation was less favourable in Schleswig-Holstein and on the Danish Islands where the few specimens found were in bad condition. At the locality on Zealand, c. 6 km NE of Hillerød, Nedebo Holt (De 21), the only remaining L. pulmonaria had fallen to the ground and thus became extinct in eastern Denmark during this study. The situation was slightly more favourable in Mecklenburg-Vorpommern and Pomerania, because the number of colonized trees was slightly higher and the occurrences in good condition dominated. Even more colonized trees could be found in Skåne and Blekinge/Kalmar, but the healthiest specimens were seen on trees in Blekinge. The best situation in

Table 3. Number of studied occurrences of Lobaria pulmonaria on different host tree species. (For abbreviations, see Table 1)

<table>
<thead>
<tr>
<th>Tree species</th>
<th>J</th>
<th>DI</th>
<th>Sk</th>
<th>BK</th>
<th>Pom</th>
<th>M-V</th>
<th>S-H</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer platanoides</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>61</td>
<td>1</td>
<td>8</td>
<td>5</td>
<td>3</td>
<td>6</td>
<td>0</td>
<td>84</td>
</tr>
<tr>
<td>F. excelsior</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Quercus spec.</td>
<td>29</td>
<td>0</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>43</td>
</tr>
<tr>
<td>Tilia cordata</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>90</td>
<td>1</td>
<td>20</td>
<td>23</td>
<td>7</td>
<td>6</td>
<td>3</td>
<td>150</td>
</tr>
</tbody>
</table>

Fig. 5. Viability of Lobaria pulmonaria in the studied area.
respect of both the number of colonized trees and health condition of the specimens was in central and northern Jutland.

**DISCUSSION**

The findings by Schiefelbein & Thell (2018) in southernmost Sweden can be applied to the whole southwestern Baltic – Kattegat area. *Lobaria pulmonaria* was formerly widespread in the study area but disappeared from many regions. Today, it is almost restricted to regions where forest communities on rather nutrient-poor soils naturally dominate. In regions, where eutrophic beech forests or mixed oak-hornbeam forests would form the natural vegetation cover, *L. pulmonaria* is almost absent. These regions are of greater interest to agriculture; consequently, forests in these regions are proportionally less represented and stronger affected by eutrophication (and hypertrophication in some cases) and atmospheric pollution (Schiefelbein & Thell, 2018). Andersson & Appelqvist (1987) also noted that *L. pulmonaria* had disappeared from the central part of their study area in SW Sweden due to the fact that this area was deforested for a long period which ended a century ago.

The major reasons for its decline are air pollution by sulphur dioxide (e.g. Hawksworth & Rose, 1970; Hawksworth et al., 1973; Hallingbäck & Olsson, 1987; Farmer et al., 1991; Gauslaa, 1995; Farmer, 1997), and later, nitrogen (e.g. Farmer, 1997; Wolseley & James, 2000; Seaward & Coppins, 2004, Hauck & Wirth, 2010). In addition, forestry practices have strongly influenced *L. pulmonaria* in different respects over a long period of time (e.g. Wirth, 1968; Andersson & Appelqvist, 1987; Gustafsson et al., 1992; Gauslaa & Solhaug, 1996; Gu et al., 2001; Öckinger et al., 2005; Gauslaa et al., 2006, 2007; Edman et al., 2008; Gustafsson & Milberg, 2008; Carlsson & Nilsson, 2009; Johansson et al., 2007; Jüriado & Liira, 2009, 2010; Öckinger & Nilsson, 2010; Jüriado et al., 2011; Schiefelbein & Thell, 2018).

In addition to the above-mentioned anthropogenic causes, climatic factors influence the distribution of *L. pulmonaria*. Eaton & Ellis (2012) found a significant relationship between thallus growth measured for experimental forest microhabitats and macroclimatic variables (total precipitation and annual mean temperature). This relationship was validated through a comparison with *L. pulmonaria*’s North American range for which projected growth rates were higher and lower where the species tended to be present and absent, respectively. In the study area, the natural climatic conditions seem to be more suitable for *L. pulmonaria* in some regions than in others. It cannot be justified by other reasons why most recent localities of *L. pulmonaria* are concentrated in central and northern Jutland and on the Scanian horsts, which run in the north-west to south-east direction, marking the south-west border of Fennoscandia, at the edge to the boreal vegetation zone and in Pomerania and why *L. pulmonaria* is absent today in most of Mecklenburg-Vorpommern and western part of Pomerania. However, the climatic data by Fick & Hijmans (2017) show that the climate of these regions is rather different; for example, the annual mean temperature is rather low on the Scanian horsts, at the border to the hemiboreal zone and in Pomerania and rather high in the western part of central and northern Jutland, in Schleswig-Holstein and at the Mecklenburg-Vorpommern coast. The lowest mean temperature in the warmest quarter is in central and northern Jutland, on the Scanian horsts, and in the eastern part of Pomerania. The regions with the highest mean annual precipitation, where *L. pulmonaria* was recently found, are in Schleswig-Holstein, in the western part of central and northern Jutland, in Halland/Bohuslän and on the Scanian horsts. In Schleswig-Holstein, Bohuslän/Halland and in the western part of central and northern Jutland, the annual rainfall can reach up to 900 mm (Fick & Hijmans, 2017). The most eastern part of central and northern Jutland, northeastern Skåne, Blekinge/Kalmar, Mecklenburg-Vorpommern and a large part of Pomerania are rather dry, but the mean precipitation in the warmest quarter in Pomerania is much higher than the other regions.

According to Gauslaa (2014), rain, dew, and humid air are drivers of morphology, function and spatial distribution in epiphytic lichens. Thus, it is clear that precipitation is very important for the distribution of *L. pulmonaria*, but it is not obvious to which amount in general and at what time the rainfall is necessary, and how the rainfall will be compensated if the required amount does not fall. Temperature and air humidity undoubtedly play important roles for *Lobaria*,
but which temperatures are most suitable for *L. pulmonaria* during the year, in the driest and in the warmest periods in relation to air humidity and vice versa.

In coastal regions, the Baltic Sea provides rather humid air, but Pentecost (2020) assumes that sea water also influences *Lobaria* spp. sites. *Lobaria pulmonaria* tends to grow on trees with alkaline bark preferably growing in alkaline soils far from the coast. Thus, all parameters that makes the water more alkaline seem beneficial for *L. pulmonaria*.

Mention should also be made to the unnatural climatic conditions induced by global warming which impact upon lichens (e.g. van Herk et al. 2002, Aptroot & van Herk, 2007, Ellis et al. 2007, 2014, Aptroot et al., 2021), and more specifically to *Lobaria* species (Rose & Purvis, 2009).

Another aspect related to the distribution of *L. pulmonaria* is the land cover in the vicinity of the occurrences. Skagerberg (2011) already noted that the presence of *L. pulmonaria*, the size of its thalli and the height of the lichen patches on the trunks were positively influenced by habitat size and adversely affected by habitat exposure. During the inventory between 2015 and 2018, it was conspicuous that most occurrences in central and northern Jutland, Mecklenburg-Vorpommern and Pomerania were in extensive forests or forest complexes. The explanation is that forests protect *L. pulmonaria* against sulphur dioxide, eutrophication/hypertrophication to a certain extent (Seaward & Coppins, 2004). One remaining question is how large a forest must be to neutralize the emissions.

In conclusion, many natural and anthropogenic factors influence the recent distribution in the Baltic Sea – Kattegat area, but interaction between the factors is still little known and needs to be studied in more detail.

**ACKNOWLEDGEMENTS**

We are very grateful to M. R. D. Seaward (Bradford) for linguistic revisions and improvements to drafts, and to The Ove Almborn Foundation for financial support. We thank W. Faltynowicz (Wrocław), A. Ryś (Strzalowo) and M. Kukwa (Gdansk) for the provision of data. Furthermore, we are also indebted to the Nature Conservation authorities in Mecklenburg-Vorpommern (Nationalparkamt Vorpommern), Skåne (Länsstyrelsen, Söderåsen Nationalpark) and Poland (Regional Directorate for Environmental Protection in Gdansk) for permission to conduct the study in protected areas.

**REFERENCES**


Abschlussbericht. AG Geobotanik in Schleswig-Holstein und Hamburg, 8 pp + 1 map.


APPENDIX 1

List of localities of *Lobaria pulmonaria* studied between 2015 and 2018
(Number of studied trees at the localities are in brackets. These numbers represent the number of trees on which *L. pulmonaria* was found.)

Denmark, North Jutland region, Rebild, Rold Skov, Torstedlund Skov, Lillevangvejen, c. 2,3 km SSW of Åresestrup, 56°47'N, 09°43'E, alt. c. 65 m, narrow strip of old growth, species-poor acidi beech forest between coniferous plantations, 29 May 2016 (3)

Denmark, North Jutland region, Rebild, Rold Skov, Torstedlund Skov, Langemose, c. 1,8 km SSE of Åresestrup, 56°48'N, 09°45'E, alt. c. 80 m, old growth, species-poor acidic beech forest surrounded by clear cuttings and spruce forests and single beech trees along peatland, 29 May 2016 (2)

Denmark, North Jutland region, Mariagerfjord, Rold Skov, RoldVesterskov, Roldkilden, c. 0,25 km N of the road No. 535, 56°46'N, 09°47'E, alt. c. 55–65 m, old growth, species-poor acidic beech forest on N-exposed slope, 29 May 2016 (3)

Denmark, North Jutland region, Mariagerfjord, Rold Skov, Kærbjerg Skov, N of Måldrupvej, 56°47'N, 09°54'E, alt. c. 45–55 m, old growth, species-poor acidic beech forest on a NW- to N-exposed slope, 29 May 2016 (7)

Denmark, North Jutland region, Rebild, Rold Skov, Kærbjerg Skov, Aspvej, E of the crossroad, 56°48'N, 09°54'E, alt. c. 45 m, single beech at a roadside surrounded by larch forests, 29 May 2016 (1)

Denmark, North Jutland region, Rebild, Rold Skov, Store Øksse, Twillingskov, E of the railway, 56°48'N, 09°52'E, alt. c. 75–85 m, old growth, species-poor acidic beech forest, 29 May 2016 (4)

Denmark, Central Jutland region, Viborg, Hald Sø, Indens Skov, north western edge of the peninsula, 56°22–23'N, 09°20'E, alt. c. 15–25 m, old growth, species-poor acidic beech forest at lake side, 30 May 2016 (10)

Denmark, Central Jutland region, Viborg, Trøldeslugten, c. 0,6 km W of Niels Bugges Kro, 56°23'N, 09°19–20'E, alt. c. 40–45 m, old growth, species-poor oak forest at edge of a deeply incised valley, 30 May 2016 (4)

Denmark, Central Jutland region, Skive, Kås Skov, c. 1,9 km N of Kås Hovedgård, 56°23'N, 09°19–20'E, alt. c. 25–30 m, old growth, species-poor oak forest on sandy plain, 30 May 2016 (7)

Denmark, North Jutland region, Rebild, Rold Skov, Buderupholm, c. 1,4 km W of Skørping, 56°51'N, 09°52'E, alt. c. 70 m, old growth, mesophytic species-rich beech forest, 31 May 2016 (1)

Denmark, Central Jutland region, Ikast-Brande, Stenholt N, c. 1,2 km N of Klosterlund Museum, 56°11'N, 09°21'E, alt. c. 110 m, old growth, species-poor oak forest, 31 May 2016 (8)

Denmark, Central Jutland region, Ikast-Brande, Stenholt S, c. 0,8 km NNW of Klosterlund Museum, 56°11'N, 09°20'E, alt. c. 110 m, old growth, species-poor oak forest, 31 May 2016 (7)

Denmark, Central Jutland region, Silkeborg, Vesterbosk, c. 1,3 km S of Funderholme, 56°08'N, 09°34'E, alt. c. 55 m, old growth, species-poor acidic beech forest (with *Ilex*), 31 May 2016 (3)

Denmark, Central Jutland region, Silkeborg, Virklund, Avnsø, c. 0,7 km E of the transit station Horsensvej/Uglesøvej, 56°08'N, 09°34'E, alt. c. 35 m, old beeches at lake side near spruce plantation, 31 May 2016 (2)

Denmark, Central Jutland region, Silkeborg, Velling, Velling Skov E, c. 1,3 km SW of the transit station Vellingvej/Lystruphavevej, 56°02'N, 09°31'E, alt. c. 90 m, old growth, species-poor acidic beech forest (with *Ilex*), 1 June 2016 (3)

Denmark, Central Jutland region, Silkeborg, Velling, Velling Skov W, c. 1,9 km SE of the transit station Vellingvej/Lystruphavevej, 56°02'N, 09°29'E, alt. c. 95–110 m, old growth, species-poor acidic beech forest (with *Ilex*), 1 June 2016 (4)

Denmark, Central Jutland region, Silkeborg, Addit Skov, c. 0,35 km SE of castle Løndal, 56°03'N, 09°35'E, alt. c. 75 m, small old growth, species-poor acidic beech forest (with *Ilex*) surrounded by spruce forest and grassland, 1 June 2016 (1)

Denmark, Central Jutland region, Silkeborg, Gjessø, Gjessø Skov, Kjellerup Dal, c.
km WSW of the transit station Egebakken, 56°07’N, 09°30’E, alt. c. 60 m, old growth, species-poor acidic beech forest in ravine, 1 June 2016 (3)

Denmark, Central Jutland region, Silkeborg, Virklund, Knagerne, c. 1,1 km W of the transit station Virklund Gunihøjvej/ Rundkersel, 56°08’N, 09°32’E, alt. c. 85 m, old growth, species-poor acidic beech forest (with Ilex), 1 June 2016 (1)

Denmark Central Jutland region, Silkeborg, Frederik den syvendes hjøst, c. 1,7 km S of Funderholme, 56°08’N, 09°30’E, alt. c. 100 m, old growth, species-poor acidic beech forest (with Ilex), 1 June 2016 (1)

Denmark, Capital region, Hillerød, c. 6 km NE of Hillerød Nørre Ådal, 55°58’N, 12°21’E, alt. c. 15 m, species-poor acidic beech forest at lake side, leg. U. Søchting, 25 Dec. 2015 (1)

Denmark, Central Jutland region, Viborg, Lindum Skov, c. 10 km SW of Hobro, 56°35’N, 09°40’E, alt. c. 25 trees, small stand of beeches on acidic soil surrounded by small lake, spruce and larch plantations, 4 June 2016 (2)

Denmark, Central Jutland region, Viborg, Sedal Egekrat, c. 8 km NE of Viborg, 56°30’N, 09°31’E, alt. c. 35 m, old growth, species-poor oak forest mixed with beech and hazel, 6 July 2016 (1)

Denmark, North Jutland region, Holstebro, Troldtoft Egekrat, Stråsø Plantage, c. 13 km SW of Holstebro, 56°14’N, 08°31’E, alt. c. 50 m, species-poor oak forest mixed with few Populus tremula, 15 July 2016 (1)

Denmark, North Jutland region, Mariagerfjord, Tofte Bogø, Tofte Skov, Lille Vildmose, c. 20 km SE of Aalborg, 56°50’N, 10°11’E, alt. c. 15–25, old growth, species-poor acidic beech forest towards raised bog, 28 July 2016 (3)

Denmark, North Jutland region, Mariagerfjord, Sønderup Adal, Skivum Nørrekrat, c. 1,5 km E of Vegger, 56°53’N, 09°36’E, alt. c. 25 m, species-poor oak forest with beech and Populus tremula, 11 Aug. 2016 (1)

Denmark, North Jutland region, Mariagerfjord, Hellum Skov, Rold Skov, c. 1 km E of parking place of Madum Sø, 56°47’N, 10°57’E, alt. c. 70 m, old growth, species-poor acidic beech forest, 23 Aug. 2016 (3)

Denmark, North Jutland region, Mariagerfjord, Knebel Bakker, Rold Skov, c. 1,5 km ESE of Skørping station, 56°49’N, 09°54’E, alt. c. 60 m, old growth, species-poor acidic beech forest and forest margin, 25 Aug. 2016 (3)

Germany, Schleswig-Holstein, Jörl, Pobüller Bauernholz, 54°37’N, 09°15’E, alt. c. 20 m, mixed oak-hornbeam forest, 28 Nov. 2015 (1)

Germany, Mecklenburg-Vorpommern, Born, Darß Peninsula, beech forest c. 3,5 km N of the youth hostel Born-Ibenhorst, 54°26’N, 12°29’E, alt. c. 5 m, species-poor acidic beech forest, 11 Sept. 2015 (4)

Germany, Mecklenburg-Vorpommern, Born, Darß Peninsula, beech forest c. 5,9 km N of the youth hostel Born-Ibenhorst, 54°27’N, 12°23’E, alt. c. 5 m, species-poor acidic beech forest, 12 Sept. 2015 (1)

Germany, Schleswig-Holstein, Schleswig-Flensburg, Handwitt, Handewitter Forst, 54°45’N, 09°19’E, alt. c. 40 m, acidophilous oak forest, 16 Feb. 2018 (2)

Germany, Mecklenburg-Vorpommern, Vorpommern-Rügen, Rügen Island, Stubnitz, S of Stubbenkammer, 54°34’N, 13°40’E, alt. c. 100 m, calcareous beech forest, 29 Nov. 2018 (1)

Poland, Kujawy-Pomerania, Świece, Tuchola forest, c. 2,5 km NE of Stara Rzeka, 53°39’N, 18°19’E, alt. c. 90 m, Tilio-Acerion forests on non-stony soils, 30 July 2017 (2)

Poland, Pomerania, Łupawa, c. 1,7 km ESE Łupawa, forest section 76c, 54°25’N, 17°26’E, alt. c. 85 m, species-poor oak forest, 10 Nov. 2017 (1)

Pomerania, Wejherowo, c. 1,5 km ESE Pińskie, forest section 74g, 54°32’N, 18°20’E, alt. c. 125 m, species-poor acidic beech forest, 10 Nov. 2017 (1)

Pomerania, Bytów, Gostkowo, Gołębia Góra, c. 0,4 km NE of the parking place Gołębia Góra, forest section 396a, 54°15’N, 17°29’E, alt. c. 95 m, species-poor acidic beech forest, 11. Nov. 2017 (1)

Pomerania, Bytów, Borzytuchom, c. 3,0 km W of Jutrzenko, forest section 227a, 54°12’N, 17°16’E, alt. c. 75 m, species-poor oak forest, 11. Nov. 2017 (1)

Pomerania, Skarszów, c. 1,6 km E of Dębica Kaszubska, forest section 162a, 54°22’N, 17°13’E, species-poor acidic beech forest, 12. Nov. 2017 (1)

Sweden, Skåne, Simrishamn, Norr om Måsalycke, c. 0,6 km S of St. Olof, 55°38’N, 14°08’E, alt. c. 125 m, old growth, species-rich, eutrophic beech forest, 30 June 2016 (1)
Sweden, Skåne, Häsståleholm, Göingeholm, c. 0.7 km SSE of Göingeholms Gård, 55°57'N, 13°42'E, alt. c. 125 m, old growth, species-poor acidic beech forest with oaks, 01 July 2016 (1)

Sweden, Skåne, Klippan, Färingsktofta, c. 2.8 km SSE of Färingsktofta, 56°01'N, 13°23'E, alt. c. 55 m, old growth, mixed mixed oak-hornbeam forest, 02 July 2016 (1)

Sweden, Skåne, Klippan, Skäradal, Söderåsen National Park, c. 1.7 km WSW of the “Naturum Söderåsen”, 56°01'N, 13°13'E, alt. c. 110 m, old growth, species-rich, eutrophic beech forest on N-(NW-) exposed steep slope, 03 July 2016 (3)

Sweden, Skåne, Klippan, Skäradal, Söderåsen National Park, c. 4.2 km SW of the “Naturum Söderåsen”, 56°01'N, 13°12'E, alt. c. 110 m, old growth, damaged *Tilio-Acerion* forest, on N-exposed steep, rocky slope, 03 July 2016 (1)

Sweden, Skåne, Höganäs, Kullen, N of the golf course, 56°18'N, 12°28'E, alt. c. 30 m, *Tilio-Acerion* forest on N-exposed steep, rocky slope, 04 July 2016 (2)

Sweden, Skåne, Hallaröd, Allarpsbjär, 56°00'N, 13°25'E (all specimens around this point, alt. c. 100 m, *Tilio-Acerion* forest on rocky ground, 27 July 2016 (4)

Sweden, Blekinge, Sölvesborg, forest N of the E 22, SW of the exit to Gammlastorp, 56°04'N, 14°35'E, alt. c. 20–50 m, species-poor acidic beech forest, 11 May 2017 (3)

Sweden, Blekinge, Sölvesborg, forest S of Leingyrdsvägen, E of Sondre Vång, 56°08'N, 14°32'E, alt. c. 50 m, species-poor acidic beech forest, 11 May 2017 (1)

Sweden, Blekinge, Sölvesborg, forest S of Leingyrdsvägen, NE of Finkelman, 56°08'N, 14°33'E, alt. c. 80 m, species-poor acidic beech forest, 11 May 2017 (1)

Sweden, Blekinge, Sölvesborg, forest E of Leingyrdsvägen, E of crossover NE of Leingyrdsvägen/Hagstads byväg, Täppet, 56°08'N, 14°34'E, alt. c. 80 m, species-poor acidic beech forest, 11 May 2017 (1)

Sweden, Blekinge, Karlshamn, Stensnäs, peninsula E of Pukavik, 56°09'N, 14°42'E, alt. c. 0–15 m, species-rich, eutrophic beech forest, 12 May 2017 (3)

Sweden, Blekinge, Karlshamn, Stensnäs, peninsula E of Pukavik, 56°10'N, 14°42'E, alt. c. 5 m, species-poor acidic beech forest, 12 May 2017 (1)

Sweden, Blekinge, Ronneby, Bökevik, peninsula W of Trolleboda, 56°09'N, 15°10'E, alt. c. 20 m, species-poor acidic beech forest, 12 May 2017 (1)

Sweden, Blekinge, Ronneby, Kjättertorp, SW Ronneby, W Kjättertorp, 56°14'N, 15°14'E, alt. c. 40 m, *Tilio-Acerion* forest on rocky ground, 12 May 2017 (2)

Sweden, Blekinge, Ronneby, Näsudden, Bräkne-Hoby, peninsula in the lake Nässjön, 56°14'N, 15°12'E, alt. c. 30 m, free-standing tree on pasture, 12 May 2017 (1)

Sweden, Blekinge, Ronneby, Näs, Bräkne-Hoby, 56°14'N, 15°12'E, alt. c. 30 m, mixed oak-hornbeam forest, 13 May 2017 (3)

Sweden, Blekinge, Ronneby, Listerby, Tromtö, Ringholmens, 56°09'N, 15°30'E, alt. c. 5 m, mixed oak-hornbeam forest, 13 May 2017 (1)

Sweden, Blekinge, Ronneby, Listerby, Hjortshamberga, Johannishus åsar, 56°09'N, 15°29'E, alt. c. 40 m, free-standing tree on pasture, 13 May 2017 (1)

Sweden, Blekinge, Karlskrona, Nättraby, Skalla-hult, 56°14'N, 15°30'E, alt. c. 40 m, *Tilio-Ace- rion* forest on rocky ground, 13 May 2017 (4)

Sweden, Skåne, Kristianstad, Vånga, Orehagen, 56°09'N, 14°25'E, alt. c. 55 m, species-poor, *Tilio-Acerion* forest on rocky ground, 14 May 2017 (2)

Sweden, Skåne, Bromölla, Näsum, between Vånga and Näsum, 56°10'N, 14°26'E, alt. c. 150 m, species-poor acidic beech forest, 14 May 2017 (2)

Sweden, Skåne, Kristianstad, Nosaby, Österslöv, 56°08'N, 14°14'E, alt. c. 50 m, species-poor acidic beech forest, 15 May 2017 (1)

Sweden, Skåne, Hässleholm, Västra Torup, W Häktorp, Häktorpsshall, 56°07'N, 13°28'E, alt. c. 130 m, species-poor acidic beech forest, 15 May 2017 (1)

Sweden, Småland, Mortorp, forest between Mor- trop and Väntorp, 56°35'N, 16°06'E, alt. c. 25 m, species-poor acidic beech forest, 15 April 2018 (1)