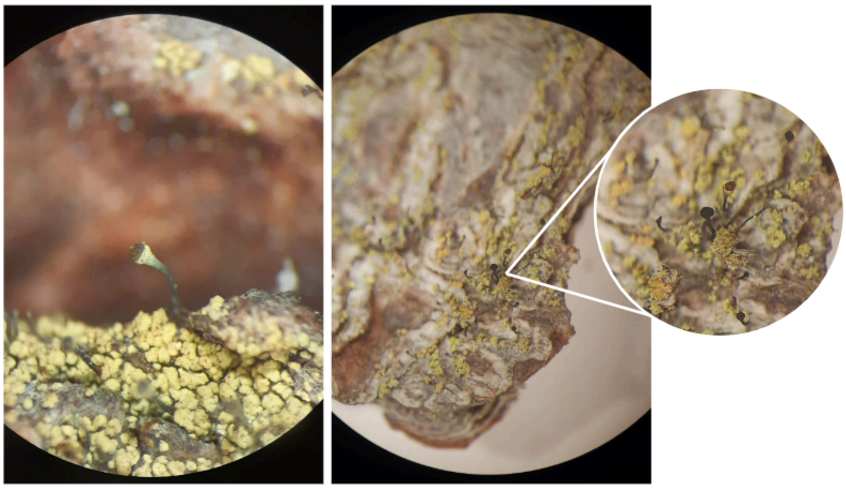
UNIVERSITY OF HELSINKI

Temporal and Geographical Distribution of *Chaenotheca chrysocephala* and *Chaenothecopsis consociata* in Europe

An investigation based on herbarium material and online databases GBIF and FinBIF



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Master's programme in Integrative Plant Sciences
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Master's thesis

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Abstract

Lichens are symbioses between fungi, photosynthetic algae and other organisms. The fact that several different fungi may occur in the same lichen thallus adds a further dimension to the diversity of these miniature ecosystems. Calicioids are a polyphyletic group of predominantly lichenised fungi which includes many species with stalked ascomata, topped with a persistent spore mass (mazaedium). One such species is *Chaenotheca chrysocephala,* a relatively common crustose lichen with a wide distribution. The lichenicolous fungus *Chaenothecopsis consociata* grows on the thallus of *C. chrysocephala* and is generally considered to be a parasite. This study aims to map the temporal and geographical distribution of *C. chrysocephala* and *C. consociata* in Europe in order to find out whether the parasite was present there before the year 1942, when the species was described, and to identify possible patterns which may affect the population dynamics of these two species. This study found that *C. consociata* was indeed present in Europe before 1942, at least in

Norway, Sweden and Finland. Additionally, the percentage of infected *C. chrysocephala* thalli seems to have increased in Europe since the parasite was first found. The GBIF dataset showed a significant increase in infected *C. chrysocephala* thalli in northern Europe (N-EU) compared to central-southern Europe (CS-EU). Although the exact reason is unclear, this increase may be related to differences in forest structure across Europe. Firstly, the host lichen seems to prefer *Picea* and *Pinus* as its substrate, these being typical trees of needleleaf forests in Europe. Furthermore, the decrease of old-growth forest stands in Sweden and Finland may have reduced suitable habitat for the host, while the concurrent increase of disturbed stands may have favoured the dispersal of the parasite.

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1. Introduction

Herbaria are vast sources of unexplored data. The mycological collection kept at the Botanical Museum of the University of Helsinki (H) include myriads of lichen specimens that deserve closer study. In 1869, Schwendener revolutionised biology by discovering that lichens are not single species, but rather mixed colonies of hundreds if not thousands of individuals of at least two different species. At the time, Schwendener wrote about a master that imprisons others and forces them to provide nutrition. The master was an ascomycete fungus while the 'slaves' were green algae (Schwendener, 1869). Evidence that the photobiont can also be a cyanobacterium, or a mixture of green algae and cyanobacteria eventually led to a broader definition that describes lichens as symbioses between a heterotrophic mycobiont (usually ascomycete) and at least one photobiont (green alga and/or cyanobacterium). Interestingly, together the mycobiont and photobiont of a lichen may often produce unique structures and metabolites which the symbionts are not able to produce independently (Calcott et al., 2018).

More recently the discoveries that lichen forming fungi also exist among the Basidiomycota (e.g., Lawrey & Diederich, 2003), that basidiomycete yeasts are found in the cortex of certain lichens (Spribille et al., 2016), and that many different types of heterotrophic bacteria are also involved (Bates et al., 2011), have prompted a broader definition of lichens to also include the multitude of microorganisms. Lichens are miniature ecosystems and an example of holobionts, a term used in different contexts to describe a host and its associated community of microorganisms or microbiome (Simon et al., 2019). Hawksworth and Grube (2020) offer the following description of the lichen symbiosis: "A lichen is a self-sustaining ecosystem formed by the interaction of an exhabitant fungus and an extracellular arrangement of one or more photosynthetic partners and an indeterminate number of other microscopic organisms". The fungus is seen as the main determinant of lichen phenotype and the photobionts provide the necessary energy. Because of their integral role, photobionts are usually less diverse, while the organisms associated with the outer layers, e.g., bacteria and yeasts, are more variable. The lichen symbiosis does not receive a unique name, but each organism within the symbiosis has an independent name appropriate for their species. Moreover, they are classified based on the lichenicolous fungi and are integrated in the fungal system. (Hawksworth & Grube, 2020).

Many of the thousands of species of so-called ‘lichenicolous fungi’ are categorised as saprophytes, which colonise dead or decaying thalli, but some are parasites and/or parasymbionts. Parasites cause visible damage to the host thallus, whereas parasymbionts establish an independent association with the photobiont and do not usually cause visible damage to the predominant host. The concept of a parasymbiont is derived from the observation that if a mycobiont can associate with multiple photobionts, yeasts and/or bacteria, then two or more mycobionts may also associate with the same microbiome. Furthermore, a parasymbiotic relationship can potentially change over time to become parasitic. Hence, the distinction between parasites and parasymbionts is rather an academic division than a natural one. (Hawksworth, 1982). Many parasitic or parasymbiotic lichenicolous fungi are host-specific, maintain their hosts long term and rarely kill their host (Lawrey & Diederich, 2003).

There remains much to be discovered in the field of lichens and lichenicolous fungi, particularly the mechanisms and drivers of these complex interactions. The close association of multiple organisms complicates genetic investigations and systematic classification. Their slow growth and specific growth requirements make lichens and lichenicolous fungi hard to isolate and study in controlled environments. (Lawrey & Diederich, 2003).

1.1. Lichens of interest

From the perspective of their phylogenetic relations, calicioids are widely a polyphyletic assemblage. Yet, the term calicioids is still used to represent a phenotypical group of both lichen-forming and non-lichenised ascomycetes. Many calicioids produce well-stalked ascomata and mazaedia. (Temu et al., 2019). The term ‘pin lichen’ is also used, which alludes to the distinct stalk and capitulum of the ascomata. A true mazaedium is a spore mass that arises from the early disintegration of the asci, whereupon the ascospores are clumped together with sterile filaments called paraphyses. The spores mature in the mazaedium and disperse passively. *Chaenotheca* is considered a representative taxon that forms such true mazaedia. Due to similar stalked apothecia, other species that do not form a true mazaedium, including the genus *Chaenothecopsis*, are included under the calicioid term. Although they may also form a spore mass, their ascospores mature within the asci and are actively dispersed through the ascus tip. (Schmidt, 1970). This distinction between passive and active dispersal refers to the spore release strategy, i.e. non-forced release through the disintegration of the ascus wall and forced discharge through apical apparatus, respectively. During the dispersal phase, in which ascospores travel to new habitats, both target species are subject to similar forces. The coarse surface of *Chaenotheca* ascospores helps them to clump together in wait for a favourable dispersal event that dislodges them and to adhere to dispersing agents, i.e. animals. After the ascospores disperse, they need to re-establish a symbiosis with the photobiont. In contrast, *C. consociata* does not form a true mazaedium and releases most of its ascospores into the air. Small spore size is often related to wide ranges as small spores can be carried long distances by wind. (Tibell, 1994). Yet, the thallus is small and friable, therefore it is possible that birds or insects that come into contact with the host can carry thallus bits to other suitable areas.

Specifically, the two calicioids of interest in this study are *Chaenotheca chrysocephala* (Coniocybaceae) and *Chaenothecopsis consociata* (Mycocaliciaceae), hereafter the host and parasite respectively (Fig. 1). The host was described scientifically as early as 1803 by E. Acharius, under the basionym name *Calicium chrysocephalum*. Theodor M. Fries reclassified it as *Chaenotheca chrysocephala* in 1860. In contrast, *C. consociata* was described under the basionym name *Calicium consociatum* by J. Nádvorník only in 1942. Later in 1970, A.F.W. Schmidt transferred it to the Mycocaliciales and gave it its current name. By 1970 there were only three places where *C. consociata* had been found; Slovakia, China and High Tatra (either Slovakia or Poland) (Schmidt, 1970). The holotype described by Nádvorník was collected in Slovakia in 1935. He published the finding in 1942 along with the observations from China. The third collection was published in 1962 by Tobolewski.

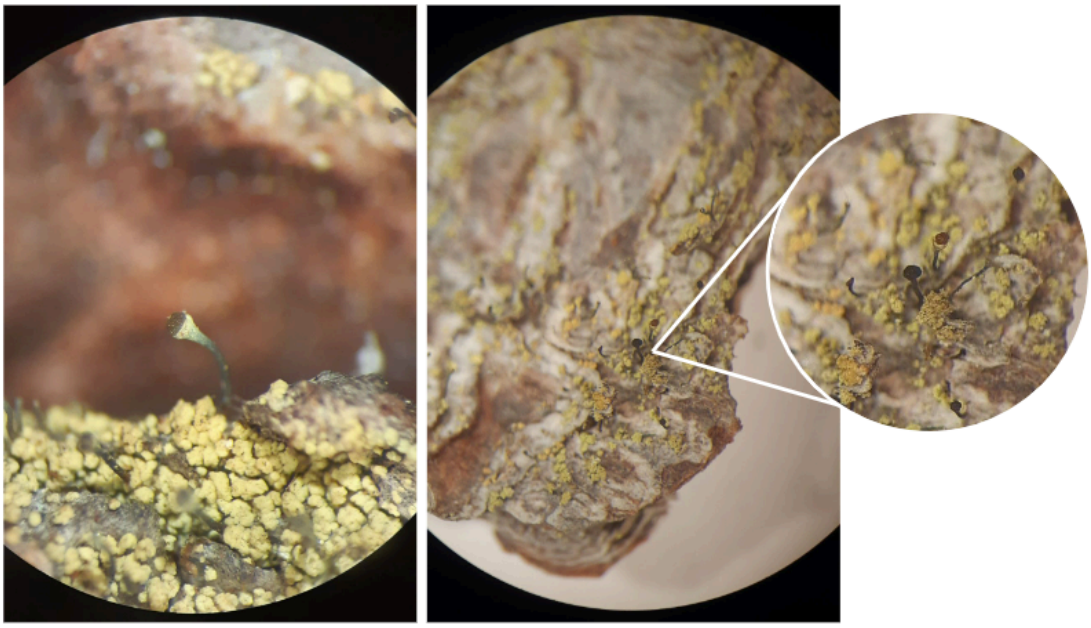


Figure 1. Left: *Chaenotheca chrysocephala*, bright yellow granular thallus and stalked ascoma with distinct yellow pruina. Right: *Chaenotheca chrysocephala* with black ascomata of *Chaenothecopsis consociata*. Both specimens grow on conifer bark. ©Gabriela Lemoine

Chaenotheca chrysocephala forms a crustose thallus, superficial or immersed in the substrate. The thallus texture is granular and ranges from a bright yellow to a greenish colour. The ascomata are stalked and black to pale brown; 0.6–1.3 mm high, ca. 9–22 times as high as the width of the stalk. The capitulum shape is obovoid to broadly obconical with a distinct dense yellow pruina on the outer surface of the excipulum. The asci are formed cylindrically with well developed stalks. Spores are short ellipsoidal to globose, 6–9 x 4–5 µm, with a coarse ornamentation and arranged uniserately within the asci. While *C. chrysocephala* does not react to spot tests with chemical reagents, the ascoma of *C. consociata* reacts to potassium ions (K^+), changing from red to green. The ascoma of the parasite is black and 0.7–1.2 mm in length. The capitulum is lenticular and often irregular. (Tibell, 1999).

Chaenotheca chrysocephala is described as a widespread, relatively common species that grows on bark and lignum of both conifers and deciduous trees. It is found in cool and temperate regions of the Northern Hemisphere and is considered a good representative of its genus. (Tibell, 1994). It prefers semi-open to closed forests in low elevations and is common on conifer trunks in mixed forests and edge habitats, particularly in relatively young stands (Rikkinen, 2003). It typically grows on trunks of *Picea*, but is also found on *Pinus*, *Juniperus* and *Larix* and on broadleaved species *Alnus, Betula* and *Quercus.* Besides bark, it is also found on decorticated stumps, timbered barns, dry twigs and lignum. *Chaenothecopsis consociata* can apparently only grow on the thalli of *C. chrysocephala*. (Tibell, 1999).

The host lichen produces secondary metabolites such as vulpinic acid, a derivative of pulvinic acid, which gives the pruina and thallus its bright yellow colour (Rikkinen, 1995). Although vulpinic acid has some antimicrobial activity (Lauterwein et al., 1995) and is able to inhibit germination of spores from competing lichens (Calcott et al., 2018), it is unlikely to deter *C. consociata.* There is evidence that some parasitic fungi are specialised to tolerate the secondary metabolites of their hosts (Lawrey, 1997).

Since the distinction between parasitic and parasymbiotic lichens is rather arbitrary, *C. consociata* is referred to as a parasite in this study. However, the exact nature of their association remains to be resolved. According to Tschermak-Woess (1980) *C. consociata* is neither a parasite nor a parasymbiont, but a lichen-forming fungus in its own right and associates with the green alga *Symbiochloris symbiontica* (basionym *Dictyochloropsis symbiontica*), while *C. chrysocephala* is in symbiosis with a different trebouxioid alga, *Trebouxia simplex*. Tschermak-Woess notes that whenever fruiting bodies of *C. consociata* are present only *S. symbiontica* is in the vicinity or that it strongly dominates over *Trebouxia*. Tschermak-Woess asserts that there are no discernible differences between the thallus texture and colour of the two species. Possibly the thallus of *C. consociata* tends more towards green-yellow. (Tschermak-Woess, 1980). Contrary to Tschermak-Woess' views, Schmidt (1970) speculates that the host apothecial growth is inhibited by the presence of *C. consociata*. Additionally, the green colouration is actually seen as evidence of damage to the otherwise bright yellow thallus of the host and not as an independent thallus (J. Rikkinen, personal communication, 18 December 2023). The mechanism between the photobionts and mycobionts has yet to be clarified. Regardless of their precise association, *C. chrysocephala* and *C. consociata* may belong to the same functional or photobiont-mediated guild, which reflects their common utilisation of resources (e.g., photobionts) and habitats. Guilds are ecologically delimited communities of lichen-forming fungi that exploit a common pool of photobionts, niches, dispersal vectors etc. (Rikkinen, 1995).

1.2. Objective

The goal of this study is to establish an overview of the temporal and geographical distribution of *Chaenotheca chrysocephala* and *Chaenothecopsis consociata* in Europe. A particular aim is to determine whether the parasite was present in Europe before 1942 and whether its range or prevalence has changed since then. By mapping the occurrence of the host and parasite, patterns may emerge that reveal ecological factors that influence the distribution of the target species and provide new information of the relationship between the two species. Does the parasite occur evenly across Europe? Are there areas with concentrated parasite presence? The study is done by investigating herbarium collections in Helsinki and Turku and on the basis of data from two databases: FinBIF (Finnish Biodiversity Information Facility Database) and GBIF (Global Biodiversity Information Facility). These are two online repositories for scientific data on biodiversity, supplemented by various experts, institutions and citizens.

The expectation is that there are few or none documented finds of *C. consociata* from Europe before 1942 and that the share of parasitised *C. chrysocephala* thalli has increased after 1942. The relatively recent discovery of *C. consociata* suggests that the parasite was not abundant before the 1940s. If the parasite arrived in Europe only recently, the host has probably required time to adapt to the invading species, and there may have been a rapid expansion of the parasite since the 1940s. However, the variety of biotopes and climates across Europe makes it likely that the host was never evenly distributed across the continent, and the parasite may not have been equally successful in all regions of Europe, partly due to inherent variation in host availability, but also other environmental factors.

2. Material & Methods

2.1. Herbarium dataset

For this study a total of 85 herbarium specimens were examined. These included 69 specimens labelled either *Chaenotheca chrysocephala* or *Chaenothecopsis consociata* from the collections of the Finnish Museum of Natural History (H) and 16 specimens from the herbarium collections of University of Turku (TUR). Per specimen the first step was to transcribe the labels into a spreadsheet. Every specimen received a unique identifier consisting of two digits (from 01 to 85) and a letter for the respective collection it originated from, H for Helsinki, T for Turku.

Firstly, each specimen was inspected for the host, *Chaenotheca chrysocephala* and then for the presence or absence of the parasite, *Chaenothecopsis consociata*. This was accomplished under a stereo microscope, Wild Heerbrugg M3 (Switzerland). In addition to an eye lens with 10x magnification, this microscope had three objectives with 6.4x, 16x and 40x magnification. The stereo microscope was used with a separate light source, Schott KL1500, which had five light settings at half or full intensity. The light was kept at full intensity on level three and generally kept in the same position. Notes were made for each specimen on the overall appearance, including colour, shape of thallus and relative abundance of ascomata of the two species. If there was any doubt on the species identity, the spores were inspected under the light microscope, Wild Heerbrugg 23200 (Switzerland). The eye lens had a magnification of 15x with four objectives: 4/0.10, 10/0.25, 40/0.65 d = 0.17 and Wild fluotar HI 100 1.30. In such cases one ascoma was taken from the specimen with fine tweezers and placed on a drop of water on a microscope slide. The ascoma was then sliced longitudinally with a razor blade. A cover glass was then placed on the water drop and the sample was viewed under the light microscope. Identification was achieved with the help of the Nordic Lichen Flora Vol. 1 (Tibell, 1999) and drawings from A.F.W. Schmidt (Schmidt, 1970). Note that the destructive sampling of the specimens was only performed on specimens from H. No such permissions were asked for the TUR specimens.

Photos were taken of all specimens to capture the original label, the entire specimen and magnified sections of the species. Photo names include the unique identifier, the number in the series of pictures and where relevant the objective that was used to magnify that section. Codes follow the template dd_[H/T]_dd or dd_[H/T]_dd_[magnification]. Pictures were taken through the eye lens of the microscope which adds a magnification of 10x to all images. Photos of the original label of all specimens are of the format dd_[H/T]_00.

The amount of available information varied between specimens. A total of 59 specimens lacked coordinates. In most cases, coordinates were approximated based on the location descriptions using Google Maps. If coordinates for the same locations were previously approximated in other databases, they were used. Furthermore, 15 specimens lacked the year of collection. For some collections it was possible to find the year of the expedition or publication. However, if no such sources were found the year the collector died was used. To retrieve this information the following digital databases were consulted: FinBIF (Suppula et al., 2023), JSTOR (*Global Plants on JSTOR*, n.d.), IPNI (*International Plant Names Index*, n.d.) and Index Fungorum (*Index Fungorum Home Page*, n.d.). Moreover, type specimen 28H was not accessible. Therefore, information was solely obtained from a photograph and description.

After initial inspection of the data, the samples were grouped into European and non-European specimens. As there were no specimens from Iceland, European specimens were defined based on coordinates that fell within 30°N–75°N and 10°W–60°E. The Ural Mountains mark the eastern limit. Hence, this subset includes specimens from western Russia and northeast Turkey. Datasets were further split based on the year of collection into 'before' or 'after' 1942.

2.2. Online datasets from GBIF and FinBIF

Specimen data was extracted from the online databases GBIF (GBIF.org) and FinBIF (Laji.fi). These open access databases contain extensive scientific information on biodiversity. GBIF is a vast global infrastructure of open data established through the collaboration of different countries and organisations. GBIF offers data from living, preserved and fossil specimens, material citations (a reference or citation to scholarly publications), human and machine observations. FinBIF is the Finnish Biodiversity Information Facility, a national initiative that aims to inventorize nature in Finland for the public, experts and government. FinBIF also contains data on living and preserved specimens as well as citizen observations. These two databases were filtered for entries of *Chaenotheca chrysocephala* and *Chaenothecopsis consociata*.

2.2.1. GBIF dataset

Online data of *C. chrysocephala* and *C. consociata* were separately retrieved from GBIF.org on 02 June 2023. Three filters were applied under 'basis of record': material sample, living specimen, and preserved specimen. This produced a list of collected specimens that are alive (e.g., in a botanical garden), or preserved and catalogued (e.g., in herbaria). It excluded fossil specimens, material citations, human (visual) observations and machine observations (e.g., from photos). This produced 2898 hits of *C. chrysocephala* and 235 of *C. consociata*, from 98 and 32 institutions respectively. These were downloaded as two separate folders and refined for analysis. There were multiple entries of parasitised host specimens that occurred in both the host and parasite datasets. However, for this analysis it was important to make the distinction between a 'clean' host observation and one with the parasite. Therefore, the datasets were corrected to contain observations of only the host or the host with the parasite.

Both host and parasite datasets contained many empty and irrelevant columns. These were removed and informative columns selected. In particular, of the 235 *C. consociata* specimens, 15 entries lacked a date. Due to the importance of these specimens, they were inspected separately to deduce the date from their additional information. However, 12 lacked fruitful information. The exact year of the remaining three could not be traced, but the collector names indicated that they were collected after 1942. In the end, the 15 date-less entries were omitted. Subsequently, entries without coordinates were filtered out. Of the 220, 187 included coordinates, and 33 did not. These 33 specimens were also inspected more closely. The majority had detailed location descriptions that were used to approximate coordinates with Google Maps, in the same way as for the herbarium material. The origin of four specimens observed after 1942 could not be located and were omitted. In addition, five specimens were obtained from the U.S.A. and also excluded from the dataset at this step. This left 211 observations of *C. consociata* that were handled further.

Similar steps were taken with the much larger *C. chrysocephala* dataset. Of the 2898 entries, 383 specimens lacked a date and were removed. Then, 503 lacked coordinates of which 170 were collected before 1942, half of them in Europe. However, none of these entries mentioned *C. consociata* in the supplemental notes. Despite the majority of these entries having location descriptions, due to the size of this subset no information was supplemented and, contrary to the parasite dataset, these entries were omitted. Of the remaining 2012 *C. chrysocephala* entries that included dates and coordinates, ten mention the presence of *C. consociata* in the supplemental notes. All but one were also in the *C.*

consociata dataset. The missing specimen was added to the *C. consociata* dataset, while the ten specimens mentioning the parasite were removed from the host dataset.

Like the herbarium material, also the GBIF dataset lacked specimens from Iceland. Thus, after refining the data, the specimens were split into European and non-European subsets based on the same demarcation as the herbarium material. At this point, duplicates within the GBIF dataset were removed, including one discernible duplicate in the *C. consociata* dataset, but none in the *C. chrysocephala* data. Lastly, the data was divided based on year of collection into ‘before’ or ‘after’ 1942 sets. Specimens collected in 1942 were added to the ‘after’ group.

Specimens from the herbarium and GBIF datasets were further divided into northern and central-southern European subsets, hereafter N-EU and CS-EU respectively. N-EU specimens were defined as having a latitude between 55°N–75°N and CS-EU specimens between 30°N–55°N. This division was used to compare the proportion of parasites in northern and central-southern Europe before and after 1942.

It was not possible to summarise the substrate species from the GBIF database as this is not handled as a separate field but included in the field notes together with other remarks about the collection site. This made enumeration of the substrate genus or species challenging. Furthermore, although many mention the scientific name, more often the colloquial name was used and written in the collector’s native language. The FinBIF database required individual inspection of each observation to track down substrate species, which due to the limited importance of the dataset was not done.

2.2.2. FinBIF dataset

Besides GBIF, entries of both host and parasite species were gathered from FinBIF on 02 June 2023. This search was restricted to national scientific collections. Observation reliability was limited to ‘expert verified’ and ‘unassessed’, while dataset origins included ‘professionals’ and ‘specialists’, but excluded citizen scientists. This resulted in a list of physical specimens that have been collected or identified by experts. The FinBIF database counted a total of 56 specimens of *C. chrysocephala* and *C. consociata*, of which 41 observations were from Europe and only three of these were reported to have the parasite. The information on the three parasite observations were complete. In contrast, while 34 host observations had dates and coordinates, three lacked a date entirely, and one had a date that ranged from 1940 to 1959. This prevents the classification into either the before or after 1942 subset. Hence, these four were removed, leaving a total of 37 entries from the FinBIF database.

2.3. Data analysis

The data was processed and visualised in order to compare the temporal and geographical distributions of the two species in the different datasets. The proportion of the parasite populations in Europe were compared before and after 1942. In addition, differences in the parasite proportions between N-EU and CS-EU before and after 1942 were tested. Proportions were analysed with a Fisher's exact test or Pearson's Chi-squared (X^2) test with a significance level of $\alpha = 0.05$. Fisher's exact test was used when at least one value of any category was less than five. Otherwise, the Pearson's Chi-squared (X^2) test was used.

For data processing and statistics R studio, R version 4.2.1 (2022-06-23 ucrt) was used (R Core Team, 2022). The following packages were used: ggplot2 (Wickham, 2016), ETLUtils (Wijffels, 2020), janitor (Firke, 2023) and tidyr (Wickham & Girlich, 2022). Mapping of the data points was performed in Jupyter Notebook (Kluyver et al., 2016) using Python version 3.9.13 (Van Rossum & Drake, 1995). The following packages were used: pandas (McKinney, 2010), numpy (Harris et al., 2020), geopandas (Jordahl, 2014), matplotlib {functions: pyplot, patches, colors} (Hunter, 2007), shapely {functions: geometry, Polygon} (Gillies et al., 2007).

3. Results

3.1. Data summary

The number of *C. chrysocephala* specimens from before and after 1942 and whether they contained *Chaenothecopsis consociata* or not was determined for all three datasets (Herbarium, GBIF, FinBIF), with the results summarised in Fig. 2. Of the 67 specimens, 35 were collected before and 32 after 1942. In this dataset, no specimens were collected during the year 1942 itself. The parasite was found in two specimens prior and in 14 specimens after 1942. The two occurrences were from Finland and Sweden (Table 1). Of the 16 specimens that were found to contain *C. consociata*, five did not mention the presence of the parasite species on the specimen label or envelope.

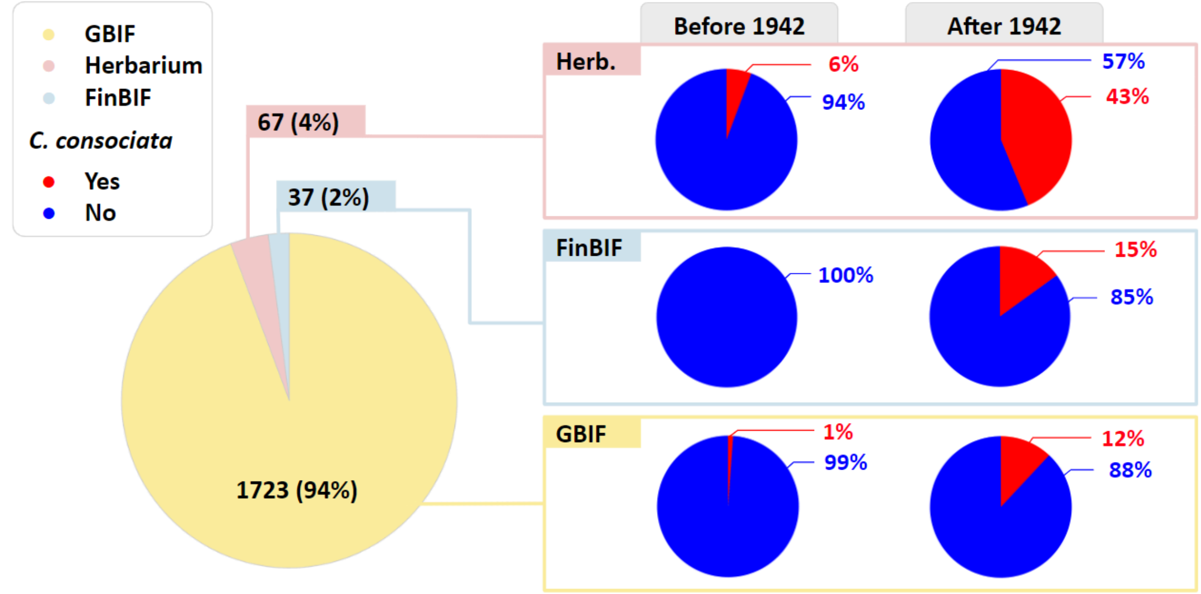


Figure 2. Schematic overview of the percentage of European specimens of *Chaenotheca chrysocephala* with (red) or without (blue) *Chaenothecopsis consociata*, before and after 1942, from herbarium (N = 67), GBIF (N = 1723) and FinBIF (N = 37) material. All specimens were collected between 30°N–75°N and 10°W–45°E.

Table 1. All specimens of *Chaenothecopsis consociata* (parasite) collected from Europe before 1942. Data obtained from herbarium material (Herb.) and GBIF dataset. FinBIF did not have any parasite observations before 1942.

Source	***Chaenotheca chrysocephala?***	***Chaenothecopsis consociata?***	**Country**	**Location**	**Collection**	**Year**	**Collector**
GBIF	Assumed	yes	Norway	Innlandet; Nordre Land	Lichen Herbarium, Tromsø, Norway	1880	J.M. Norma
Herb.	yes	yes	Sweden	Södermanland; Dunkers	Helsinki Herbarium	1890	O.G. Blomberg
GBIF	Assumed	yes	Sweden	Småland; Rumskulla, Kalmar län	Herbarium, Swedish Museum of Natural History	1933	G.O. Malme
Herb.	yes	yes	Finland	South Häme; Luhanka, Judinsalo	Turku Herbarium	1936	A. Koskinen

By far the largest dataset, GBIF contained a total of 1 723 observations of the two target species. The majority of specimens had been collected after 1942 and almost 90% represented solely *C. chrysocephala*. The portion of specimens that included *C. consociata* consisted of 187 observations. Two of these were collected before 1942 in Norway and Sweden (Table 1). Furthermore, a total of 11 specimens were collected during the year 1942, one of these including the parasite and collected in Sweden. The FinBIF dataset was the smallest and did not include any records of the parasite before 1942. The three parasite specimens that were collected after 1942 were all from Finland. Of the 34 host specimens, 17 were collected prior and 17 after 1942. These were all from Finland or Russia. Two specimens of *C. chrysocephala* occurred in all three datasets. In addition, GBIF and the herbarium material had ten specimens in common, seven of the host and three others of the parasite, all observed after 1942. The FinBIF dataset did not share any other specimens with the other two datasets.

In the herbarium material, 58 specimens *C. chrysocephala* grew on bark and nine on lignum of decorticated stumps or fence posts. More than one third of the specimens grew on *Picea*, with 17 mentioning spruce or *Picea abies* specifically (Fig. 3). Further host trees included *Pinus*, *Larix*, *Abies* and in one case each *Populus* and *Quercus*. 20 specimens did not include any information on the substrate. Moreover, it was difficult to get an accurate overview of the host tree species from the GBIF dataset. A simple text search of the 1536 entries resulted in 115 hits of *Picea*, 62 hits of *Pinus*, ten of *Larix* and five of *Quercus*. This leaves almost 90% of the records without any substrate description.

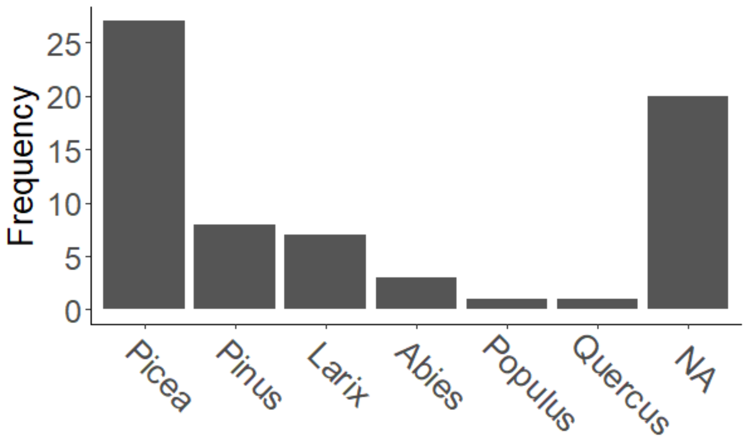


Figure 3. Frequency of substrate tree species observed with *Chaenotheca chrysocephala* from herbarium material (N = 67). The substrate information was not available (NA) for 20 specimens.

The thalli of the 84 herbarium specimens of *C. chrysocephala* (NB the type specimen was not inspected) consisted predominantly of coarse or smooth granular crumbs. The colour ranged from bright yellow to orange to green. The thalli of only a few specimens had a pale yellow or yellow-brown hue. In most cases the thallus was uniformly coloured. However, the colouration sometimes varied between different patches of the same thallus.

There was no decisive evidence indicating that colour correlated with the absence or presence of the parasite. Of the nine samples that had a dominant and clear green appearance, only one specimen was found to have ascomata of *C. consociata*, while the other eight specimens showed no signs of parasite presence. Of the 29 cases with some green tint as well as yellow and orange patches, 12 samples had *C. consociata* ascomata and 17 did not. For more than half of the specimens (N = 46) the thallus appeared clear yellow, without any green shade. Out of these, ten specimens contained *C. consociata* ascomata, these representing only one fourth of the total number of specimens.

3.2. Temporal patterns

The observations of each dataset were arranged into a timeline (Fig. 4) showing the temporal range and intensity of sampling of the two species. The first and most recent observations of both species were from the GBIF dataset. The oldest specimen, containing only *C. chrysocephala*, was collected in 1800 in Slovenia, while the most recent collection was from 2023. The oldest specimen of *C. consociata* was collected in 1880 in Norway by J.M. Norma while the most recent specimen of this species was collected in 2022. The herbarium specimens and FinBIF data contained records made from 1852 to 2011 and 1863 to 2021, respectively (Fig. 4). The vast majority of all specimens were collected after 1942 and most of the specimens collected before this year included only *C. chrysocephala*. Between 1990 and 2010 nearly 800 specimens were collected, which is almost half of all the records in the GBIF database.

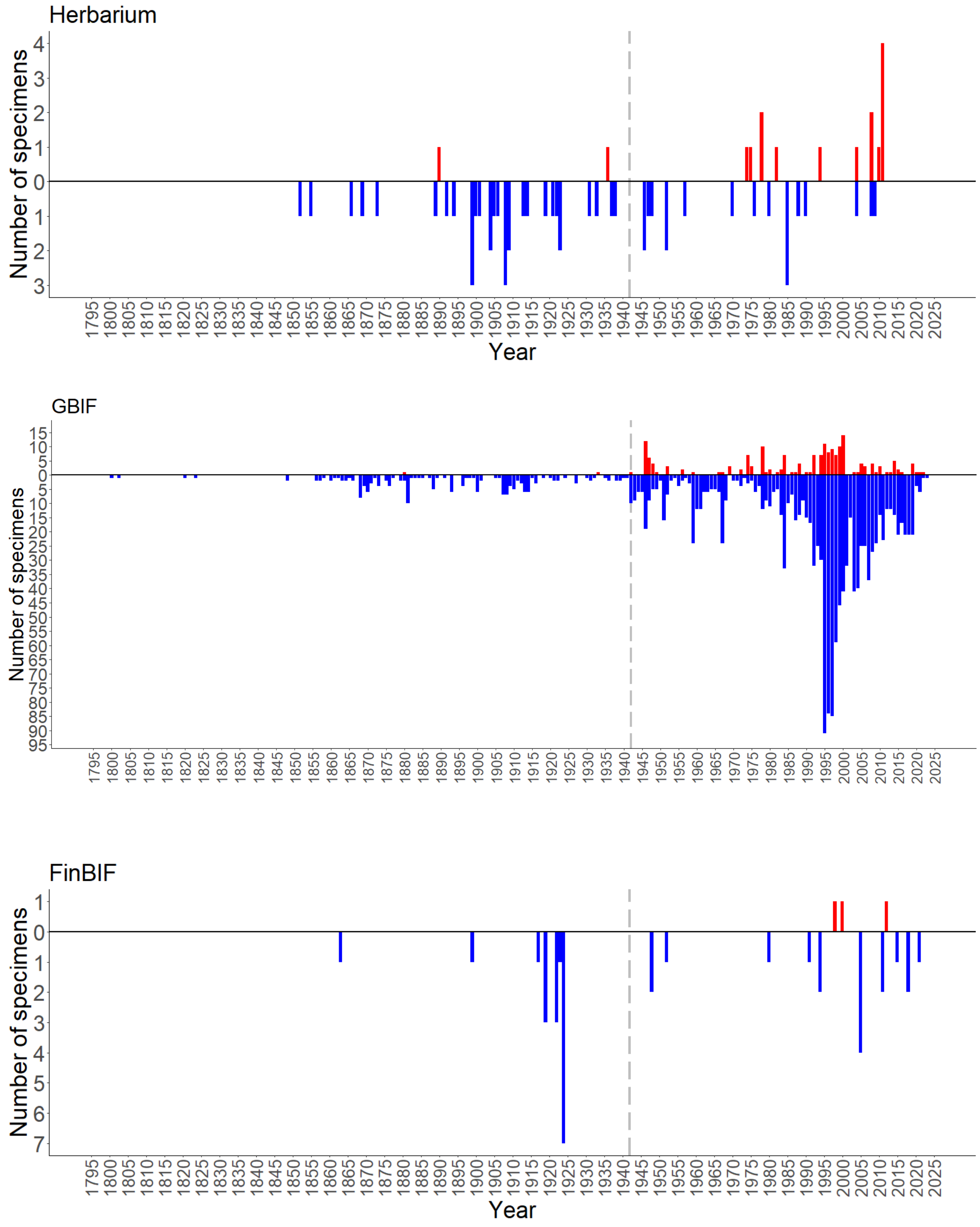
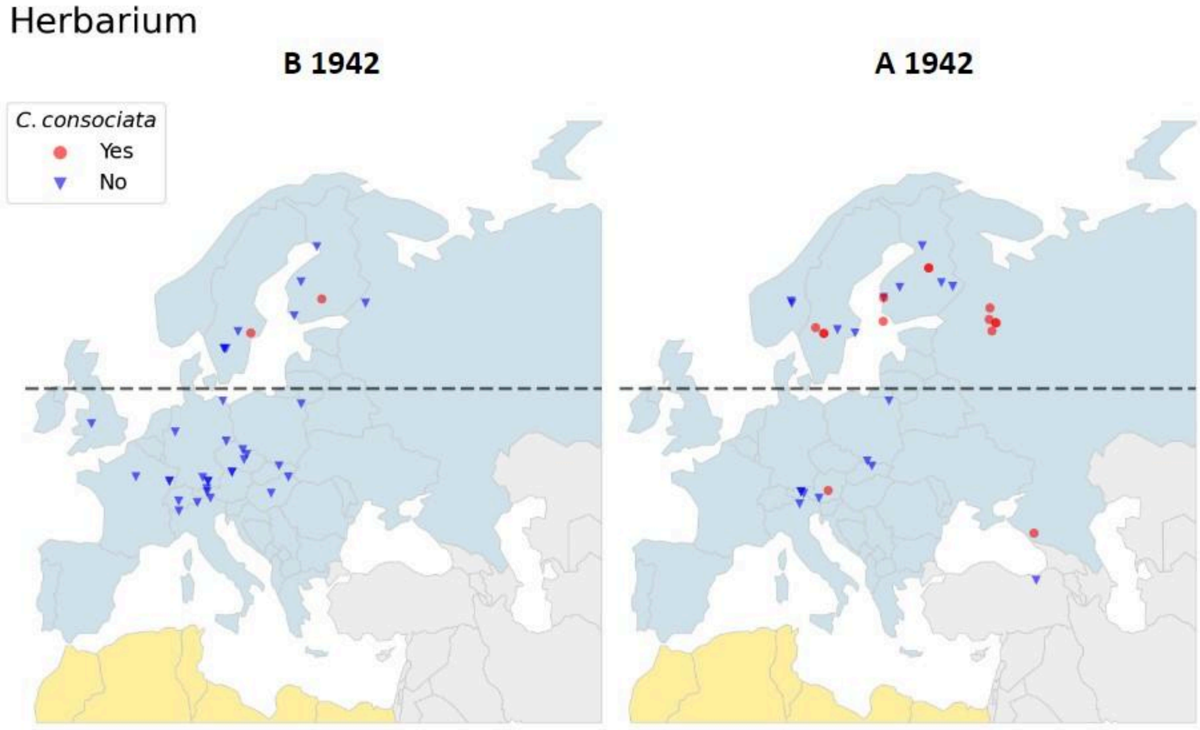


Figure 4. Temporal distribution of *Chaenotheca chrysocephala* with or without *Chaenothecopsis consociata* in Europe from three different datasets. Presence or absence of *C. consociata* is indicated by red (top bars) and blue (bottom bars) respectively. The dotted line marks the year 1942. Collection dates of herbarium specimens *C. chrysocephala* range from 1852 to 2011 (N = 67), including both specimens with (N = 16) and without (N = 51) *C. consociata;* GBIF records range from 1800 to 2023 (N = 1723), both with (N = 187) and without (N = 1536) *C. consociata;* FinBIF records range from 1863 to 2021 (N = 37), again both with (N = 3) and without (N = 34) *C. consociata*.

Statistical analyses of the datasets from both herbarium material and GBIF showed that the proportions of *C. chrysocephala* specimens infected by *C. consociata* were higher in specimens collected after 1942 than in those collected before the year 1942 (two-sided Fisher's exact test, both with p-value < 0.001). In both datasets the occurrence of *C. consociata* increased after 1942.

3.3. Geographical patterns

The herbarium and GBIF observations of the two species have been predominantly collected from the Alps and from the Nordic countries (Fig. 5). In contrast, most of the observations in the FinBIF data were from N-EU, in particular Finland and Russia (Fig. 5). Overall, *C. chrysocephala* had been collected in 26 different countries, ranging from the northernmost specimen in Tromsø in Norway to Andalucía in Spain. In contrast, *C. consociata* was collected in only nine countries, the northernmost observation being from Norrbotten in Sweden and the southernmost observation from Montenegro.



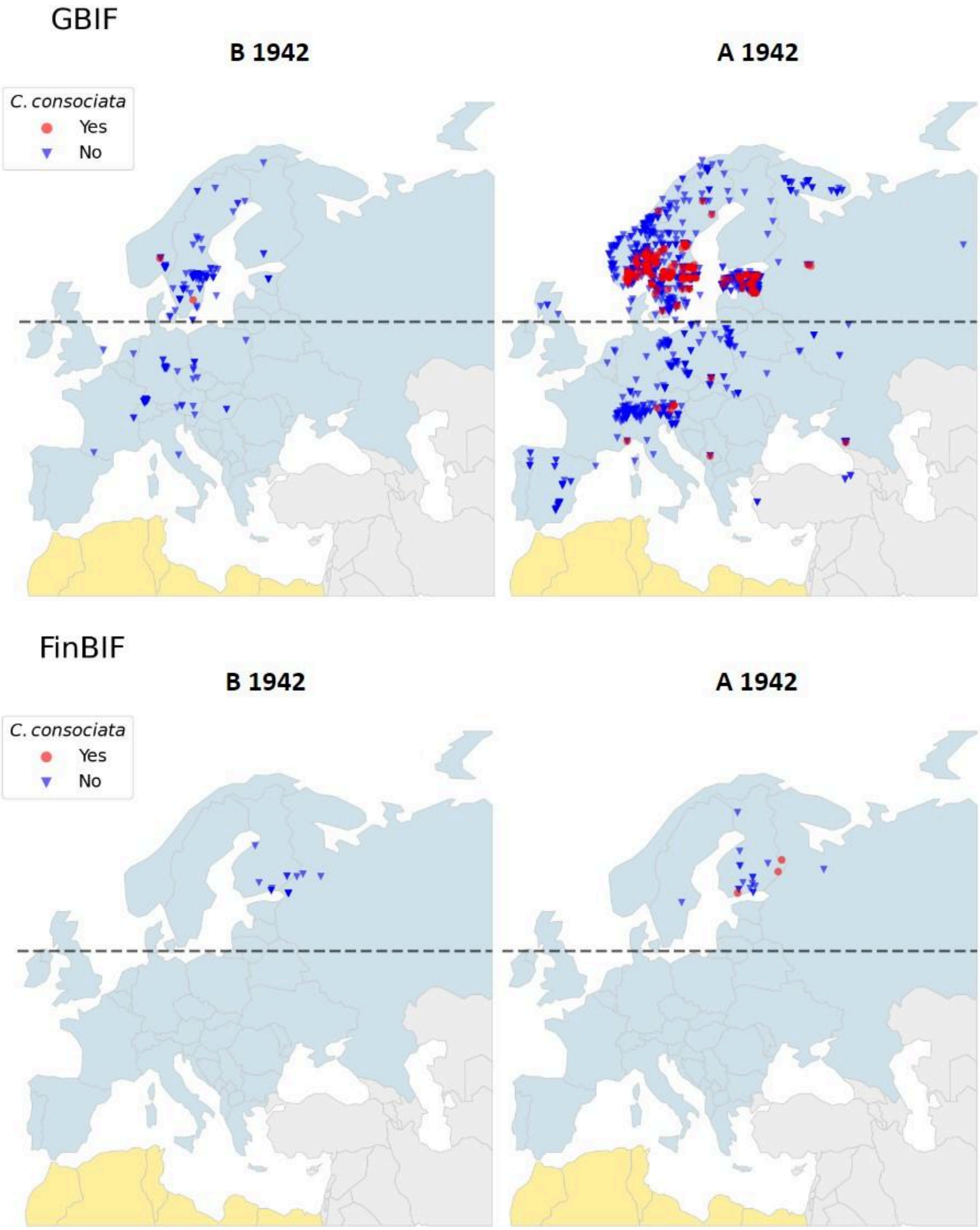


Figure 5. Distribution of *Chaenotheca chrysocephala* with and without *Chaenothecopsis consociata* before (B) and after (A) 1942 in Europe in the three datasets (herbarium, GBIF and FinBIF). Presence or absence of *C. consociata* is indicated by red dots and blue triangles respectively. The dotted line is at 55°N, denoting the division between northern and central-southern European specimens. Herbarium material before (N = 35) and after (N = 32); GBIF before (N = 173) and after (N = 1551); FinBIF before (N = 17) and after (N = 20) 1942. Due to geopanda map constraints some specimens appear to be collected from water when they actually are from islands off the mainland.

Statistical analyses of the herbarium dataset indicated that differences in the proportions of *C. chrysocephala* specimens with *C. consociata* between N-EU and CS-EU were not significant before (two-sided Fisher's exact test, p-value = 0.076) nor after (two-sided Fisher's exact test, p-value = 0.061) the year 1942 (Fig. 6). A similar result was inferred from the GBIF data collected before 1942 (two-sided Fisher's exact test, p-value = 1). However, after 1942, the proportion of *C. consociata* was greater in N-EU than in CS-EU (X^2 (1, N = 1550) = 44.529, p-value < 0.001) (Fig. 6).

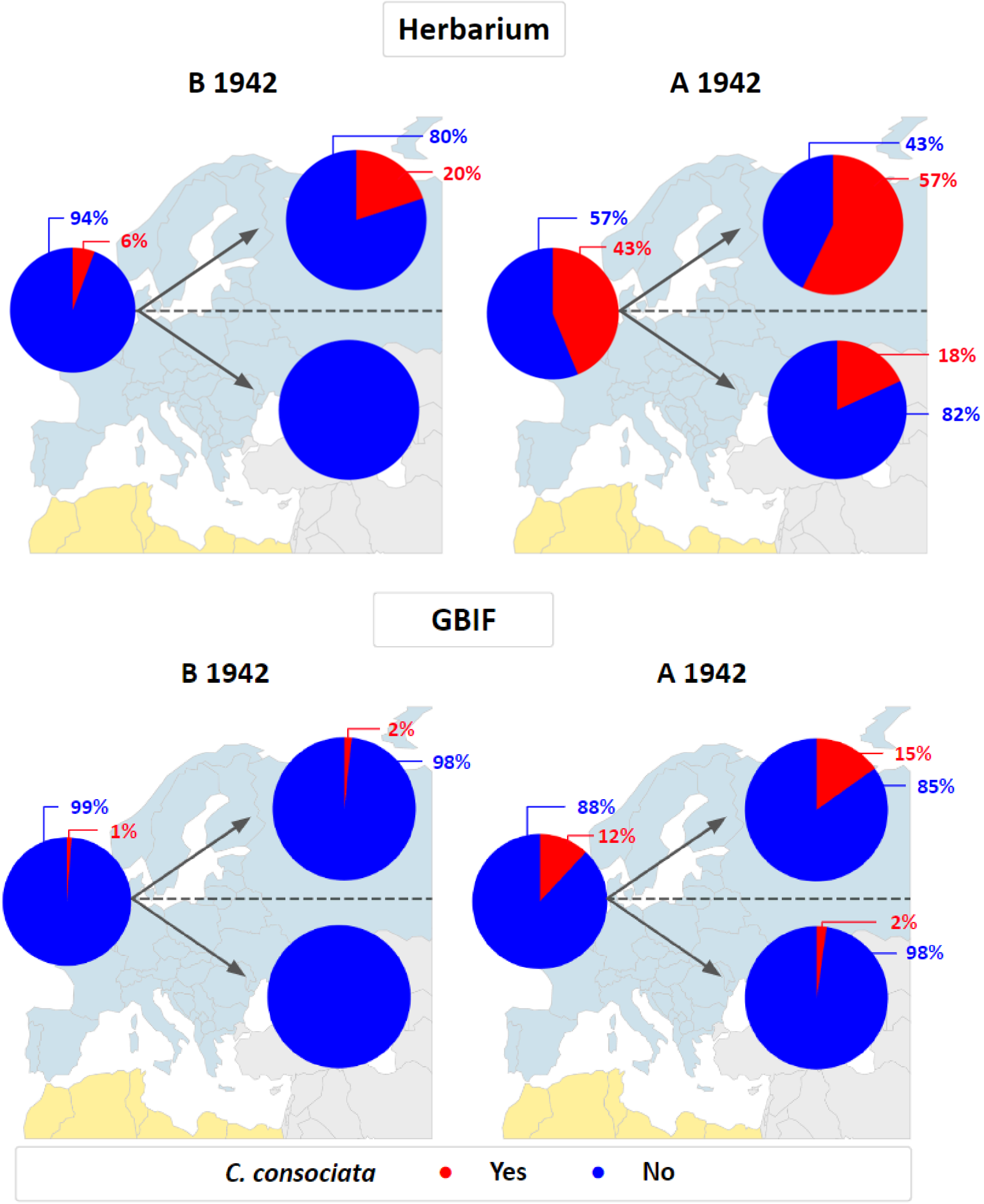


Figure 6. Proportion of *Chaenotheca chrysocephala* with and without *Chaenothecopsis consociata* before and after 1942 in Europe from the herbarium and GBIF dataset. Presence or absence of *C. consociata* is indicated by red and blue respectively. Pie charts show total host and parasite proportions (middle-left), host and parasite proportions in the North (top-right) and Central-South (bottom-right) of Europe (latitudinal border at 55°N).

4. Discussion

This study investigated the temporal and geographical patterns in the distribution of *Chaenotheca chrysocephala* and *Chaenothecopsis consociata* in Europe. As demonstrated by two herbarium specimens and two GBIF records, *C. consociata* was present in Europe before 1942 (Table 1), with the first specimen collected as early as in 1880. All of these specimens originated from northern Europe (N-EU).

No correlation was found between the thallus colour of *C. chrysocephala* and the presence or absence of *C. consociata*. A number of specimens with yellow thalli contained parasite ascomata, while multiple specimens with green thalli lacked parasite ascomata. Yet, the lack of ascomata should not be taken as an absolute absence of infection as they represent only surface structures. Besides, ascomata could have been broken off in the process of collecting or storage. The frequent lack of *C. consociata* ascomata on green thalli does not support the observation of Tschermak-Woess (1980) that the parasite would form green-yellow thalli and that host and parasite would form lichen thalli dominated by different trebouxioid algae. However, neither does it support the idea that the green colouration is a sign of infection damage.

The synthesis of cortical pigments is induced by UV radiation. These pigments, such as vulpinic acid, serve as photoprotection against damage caused by shorter wavelengths, e.g., blue light. (Phinney et al., 2019). Hence, prevailing light conditions affect thallus colouration so that shaded individuals would appear greener. On the other hand, studies also show that photosynthates stimulate the production of cortical pigments (Phinney et al., 2019). This suggests that competing lichenicolous fungi may have an effect on the colour of the thallus by influencing photosynthate levels. However, it is difficult to ascertain the cause of these colour variations since differences in colour are difficult to quantify and can reflect the results of various phenomena, including qualitative and quantitative differences in photobionts and/or epiphytic algae and in the production or breakdown of pigments (chlorophylls and carotenoids or pulvinic acid derivatives).

Of the 16 herbarium specimens that had *C. consociata*, five did not mention the presence of the parasite species on the specimen label or envelope. This includes the two parasite observations before 1942. Evidently, the parasite must have escaped notice or remained unidentified as its species identity was not known. Both the herbarium and GBIF datasets revealed that there may have been an increase in parasitism in Europe from before 1942 to the present and that this phenomenon seems to have been more pronounced in northern Europe than in southern Europe.

While host distribution matters for the occurrence of the parasite, it does not explain why after 1942 parasitism appears to have increased more strongly in northern Europe than in southern Europe. Before 1942, parasite observations were made in Norway, Sweden and Finland. If host apothecial growth is inhibited by the parasite as suggested by Schmidt (1970), then host dispersal may have been disadvantaged in northern Europe as compared to the Alps where the parasite remained unnoticed until after 1942. After 1942, many records of the parasite have been made both in Norway, Sweden and Estonia, but also in the Alps.

First it is prudent to consider the overall distribution of the host lichen, as this surely also influences the occurrence of the parasite. From the herbarium material, the host lichen grew most often on *Picea* (Fig. 3), in particular *Picea abies* (Norway spruce). *Pinus* was the second most abundant substrate. Host presence fits well in what is known about the natural range of *Picea* and *Pinus* across Europe (Fig. A1, Appendix I). There seems to be a general trend related to vegetation structure, with more observations of *C. chrysocephala* from regions dominated by needleleaf forests, as compared to those from broadleaf forests, which prevail in southern Europe (Fig. A2, Appendix I). Based on open data from the European Environment Agency (EEA) from 2018 (EEA, 2020a) less than 40% of European forests are needleleaf forests, compared to the 47% of broadleaf and 14% mixed forests (Fig. A2, Appendix I).

Fewer observations of *C. chrysocephala* and *C. consociata* were made in southeastern Europe, the west of the Iberian Peninsula and France, areas with little native needleleaf forests. It is probable that in these areas both target species are confined to restricted habitats. However, observations from Spain and southern Europe indicate that *C,* *chrysocephala* can grow on *Pinus nigra* and not only on *P. sylvestris*. Although *C. chrysocephala* is known to grow on multiple substrate species (Tibell, 1999), it seems to exhibit a strong preference for needleleaf forests and for Norway spruce and/or Scots pine. These two conifer species may have been important in expanding the potential range of *C. chrysocephala* and as a consequence also *C. consociata.* However, on the basis of existing information, it is difficult to assess whether the host lichen and its parasite have expanded their distribution into the introduced and naturalised areas of Norway spruce or into the native ranges of Scots pine. Yet, in Norway, after 1942 the host may have expanded into introduced spruce stands rather than into native pine stands. Parasite observations are confined to the southeastern forests of Norway, whereas the specimens of the host from the western coast appear to be without the parasite. In order to clarify patterns of substrate dependence, the GBIF dataset would need to be investigated more extensively and preferably supplemented with investigations in the field.

The distribution of the host lichen is unlikely to depend merely on the substrate tree species, but also on many other factors including forest structure, composition, density, etc. The apparent dependence on certain types of substrates makes the host lichen sensitive to changes in the forest landscape. European forests have undergone many human induced changes over the past centuries. In N-EU land use is marked by a long and intensive forest industry. In the 19th century, the increased demand for timber in Europe resulted in the removal of many old conifers (200–400 y/o), particularly in Sweden and Finland. (Karlsson, 2012). Over the next century, a shift from selective felling to clearcutting caused the loss of more old-growth forests (Östlund et al., 1997; Storaunet et al., 2000). Swedish forests went from consisting of more than 80% old-growth forests to a mere 3% (Östlund et al., 1997). Additionally, older deciduous trees were removed to make room for economically valuable conifers. (Linder & Östlund, 1998; Simola, 2006). Across the Baltic Sea, Estonian forests underwent similar losses of mature and overmature stands. After a forest minimum in the early 1900s, land conversion practices have seen an increase in forest cover, particularly in secondary deciduous forests. (Lõhmus et al., 2004). The loss of old-growth forests changed the forest structure from natural stands with uneven-aged trees, dead trees and fallen logs to young, even-aged stands (Östlund et al., 1997; Storaunet et al., 2000).

In contrast, studies in the Alps indicate that forest cover has increased since the mid-1800's (Bebi et al., 2017; Krumm et al., 2011; Mietkiewicz et al., 2017). One study estimates a 21% increase in Swiss forest cover between 1880–2000 (Ginzler et al., 2011). This is attributed to changes in land use, mainly due to urban migration, land abandonment and afforestation (Bebi et al., 2017; Fuchs et al., 2015; Ginzler et al., 2011). Depending on the elevation and the region, the Alps are composed of European larch, Norway spruce, Scots pine, beech, silver fir, oak and chestnut (Conedera et al., 2017; Mietkiewicz et al., 2017). Currently, the Alps are a patchwork of forests dating back before 1880 and so-called secondary forests that are not visible on historic maps before 1880. These younger secondary forests make up 43% of the current forests and are dominated by larch and a mix of broadleaved species. In the older forests, spruce, fir and beech are the dominant species. (Bebi et al., 2017).

Swedish and Finnish forests are clearcut over relatively short forest cycles and over relatively larger areas compared to the Alps (Nascimbene et al., 2010). Moreover, significant increases in harvested forest area are seen in northern Europe after 2015, notably in Sweden and Finland. Further increases were noted in the Baltic states, Poland and the Iberian Peninsula. In particular, needleleaf forests made up more than half of the harvested area as opposed to broadleaf and mixed forests. (Ceccherini et al., 2020). An analysis based on lower resolution data also shows a stark decrease in forest cover in Finland between 2000–2018, but not in Sweden or the Iberian Peninsula (EEA, 2020b). These differences in forest structure, composition and management may have led to a higher proportion of parasite infected *C. chrysocephala* thalli in northern Europe compared to those in the Alps.

The forest dynamics in Europe relate to the availability and state of suitable lichen habitat. Various studies of boreal forests find an increase in epiphytic lichen diversity with tree age of *Picea abies* and *Pinus sylvestris* (Bäcklund et al., 2016; Lie et al., 2009; Marmor et al., 2011; Lõhmus & Lõhmus, 2011). The denser canopy and habitat availability in mature stands appear to benefit calicioid colonisation and growth (Bäcklund et al., 2016). In the boreal zone, old and slow growing trees are important for species growing on stems (Lie et al., 2009). Similarly, in the Italian Alps epiphytic lichen species richness increases from young (<100 years) to old-growth stands (>200 years) (Nascimbene et al., 2010; Nascimbene et al., 2009). Certain species are associated exclusively with overmature trees (Nascimbene *et al.*, 2009). Although the host grows in old (150–200 yo) spruce and pine dominated forests, it is also found in younger (<100) forest sites (Tibell, 1992).

Nevertheless, one recent study notes that, in Sweden, *C. chrysocephala* together with other calicioid species is confined only to the oldest, 85 year-old, Norway spruce stands (Bäcklund et al., 2016). Despite its apparent preference for old forest stands, *C. chrysocephala* is not considered to be an indicator for forest continuity as it is a relatively common species on different aged conifers and on deciduous trees. (Tibell, 1992). It seems that the lichen does not grow on immature trees, yet it is not dependent on overmature trees. Therefore, the loss of old growth forests may reduce the amount of habitat available to the host lichen.

Furthermore, calicioid diversity is related to the availability of different substrate types, e.g., snags and root-plates of treefall mounds (Lõhmus & Lõhmus, 2011), which are more abundant in old-growth forests. In the literature, epiphytic lichen species richness is often studied with regard to tree age, stand age, size, DBH or circumference. Yet, identifying the causal variable is difficult as these variables are interconnected, e.g., surface area and BDH increase with tree age. Older trees have more surface area for higher lichen abundances and besides, older trees give lichens more time to colonise and establish (Nascimbene *et al.*, 2009; Bäcklund et al., 2016). Furthermore, properties such as bark expansion, bark texture, depth of bark furrows etc., appear to change with tree age (Bäcklund et al., 2016). It would be interesting to find out how these properties compare to other needleleaf and broadleaf substrate species of *C. chrysocephala* and whether these characteristics differ across European forests.

A lichen's life cycle can be divided into three phases: dispersal, establishment and growth (Sillett et al., 2000). Old-growth forests may be more important for dispersal and establishment rather than growth. How the three phases are affected by the environment is species dependent, as are the preferences, specificity and tolerance to changes in their microhabitat. Yet, the efficiency of dispersal is often associated with the distance of younger stands from old-growth forests that work as a source for propagules (Dettki et al., 2000). However, this may be more important for species that rely on larger propagules for their dispersal, e.g., *Lobaria oregana*, than for species that disperse by means of small spores (Sillett et al., 2000). Both host and parasite species have relatively small spores that can travel over long distances.

Calicioids are relatively mobile and aided by animal dispersal, namely arthropods and birds (Tibell, 1994). Besides, crustose calicioids are thought to rarely propagate by means of specialised asexual propagules (e.g., isidia, soredia, etc.), but instead reproduce by ascospores and need to re-establish a symbiosis after dispersal (Tibell 1994), which would affect the success of establishment rather than dispersal. Furthermore, Tibell (1994) mentions that some calicioid species germinate after several months of dry storage at room temperature, which points to a capacity for long distance dispersal through spore resilience. Therefore, host dispersal may not be negatively affected by the loss of old-growth forests. Disturbed forests may even aid dispersal since wind exposure increases near forest edges and thus can carry spores further away. In more open forests this could result in the simultaneous dispersal of the host and parasite, facilitating the success of parasite infestation.

Despite differences in light conditions, the establishment of some epiphytic lichens, e.g., *Lobaria scrobiculata, L. oregano* and *Platismatia norvegica,* does not differ between young and old forest (Hilmo & Såstad, 2001; Sillett et al., 2000). In the case of *C. chrysocephala*, establishment may be more dependent on suitable substrate availability such as old wood or coarse woody debris (Tibell, 1992). Old conifers have rougher bark than younger trees (Sillett et al., 2000). The host is also found on decorticated stumps and processed wood (e.g., fences). Managed forests often remove wood residues from the system. This loss of decorticated stumps, logs, snags etc. reduces habitat availability and could be detrimental to host establishment. Dense canopies of older forests protect against direct rainfall, create a stable microclimate (humidity and temperature) through insolation and wind protection in a forest even if macroclimate varies (Tibell, 1992). It seems that conditions in older forests are more desirable than those in young stands and their loss seems detrimental for the host. Yet, a decline in host establishment and growth is not necessarily beneficial for the parasite, who depends on the host thallus for survival. Moreover, changes to the habitat are likely to negatively impact the growth and development of the parasite as well.

Apart from a hypothesis that parasite dispersal increases in disturbed forests, there is little evidence that parasitism is enhanced by the loss of older stands. Rather, it affects host establishment through the loss of suitable habitat. Thus, the loss of old-growth forests does not fully explain why the parasite would do better in N-EU compared to CS-EU. Besides forest structure, there seems to be a difference in the density and connectedness of boreal coniferous forests and forests in the Alps (Fig. A2, Appendix I). Parasite observations in the eastern Alps are in a region with relatively dense needleleaf forests, whereas the western alpine forests are sparser and also lack parasite observations (Fig. A1 & Fig. A2, Appendix I). The homogeneity and connectedness of N-EU forests may facilitate the spread of the parasite, because hosts live closely together and thus it is more likely for parasite spores to encounter a new host thallus. In the Alps, the forests are more fragmented because of the mountains and the forest composition is less uniform. This hinders parasite colonisation through physical separation both between forests as well as within forests, where the chance of a parasite spore landing on the appropriate substrate tree with a host is lower than in homogenous forests. In other words, if host distribution is more unpredictable, parasite invasion should be less successful (Lawrey & Diederich, 2003).

5. Conclusion

Although using online databases comes with its limitations (Appendix II), this study has shed some light on the distribution trends of *C. chrysocephala* and *C. consociata* in Europe. Host distribution was associated with needleleaf forests, in particular Norway spruce and Scots pine. Furthermore, the data revealed the presence of *C. consociata* before 1942 in Norway, Sweden and Finland. An apparent increase in parasitism was noted in Europe and the GBIF dataset showed a stronger increase in N-EU compared to CS-EU. Although the initial parasite population in N-EU may have contributed to the greater parasitism across Europe, it seems insufficient to explain the magnitude. Differences in forest structure between N-EU and CS-EU are proposed to explain the increase in parasitism. The loss of older forests reduces suitable habitats impeding host establishment and it is hypothesised that parasite dispersal may be enhanced in disturbed forests. While in the Alps, where parasitism was proportionally lower, ageing and expanding mixed forests create stable conditions for host growth. Furthermore, the homogeneity and connectedness of N-EU forests compared to forests in the Alps may increase the success rate of parasites finding a host thallus.

It is easy to extrapolate between lichen groups and to assume that they behave similarly to environmental changes. However, many responses are species specific, reflecting the variety in lichen ecology and highlighting the importance of lichen specific studies. There is much to be studied in lichenology, especially ecology and physiology. Using open-source data and combining it with ecological trends across Europe can give valuable insights into the behaviour and preferences of these species. The information available in herbaria is vastly underrated. Although one specimen only contains a limited amount of information, if you look at entire collections across countries and continents a story emerges.

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Appendix I. Tree ranges and forest cover in Europe

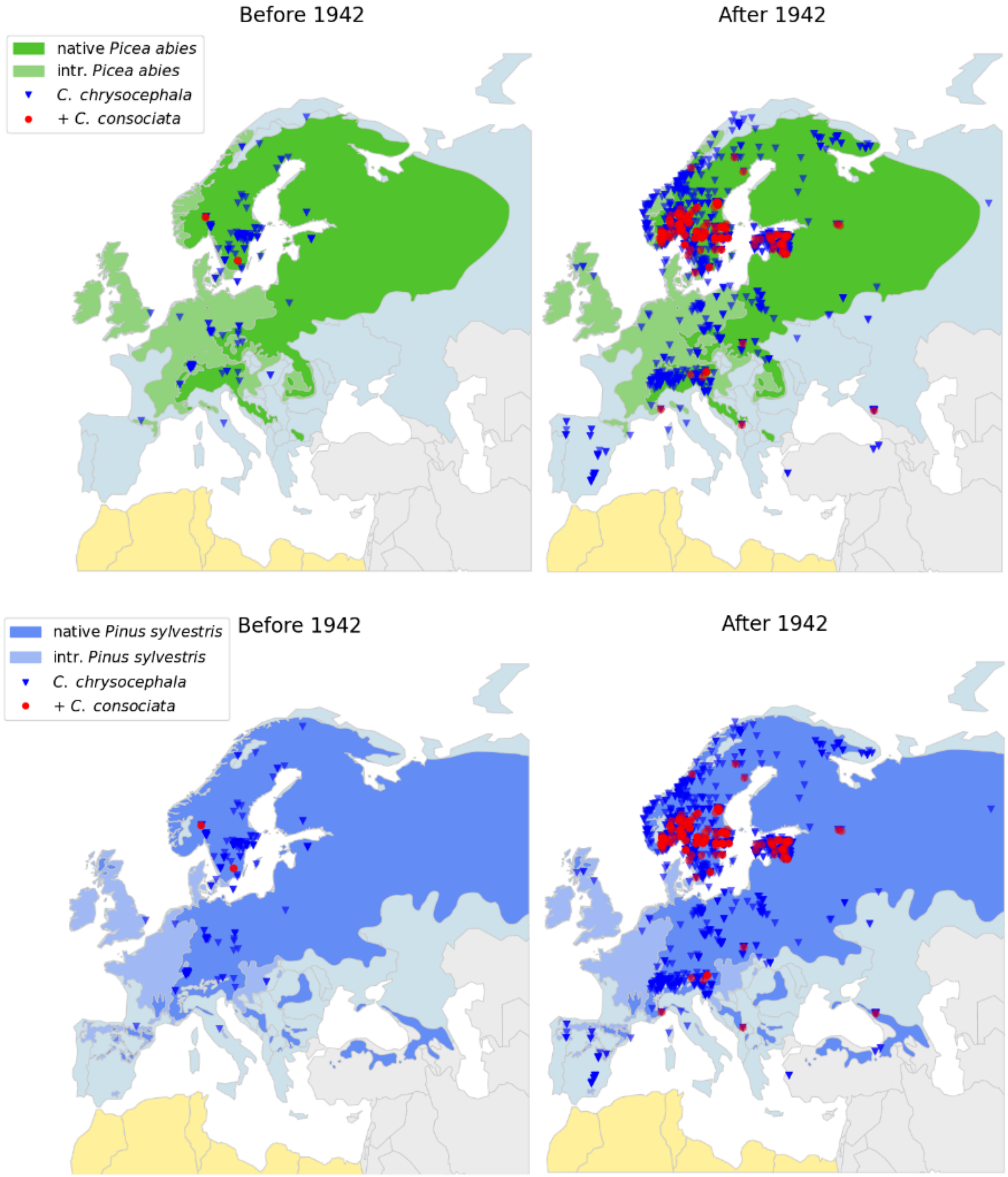

Figure A1. Native and introduced and naturalised (intr.) ranges of Norway spruce (*Picea abies*) in green hues and Scots pine (*Pinus sylvestris*) in blue hues in Europe with records of *Chaenotheca chrysocephala* (blue triangle) and *Chaenothecopsis consociata* (red dot) from GBIF, before and after 1942. Tree ranges data retrieved from (Caudullo et al., 2017).

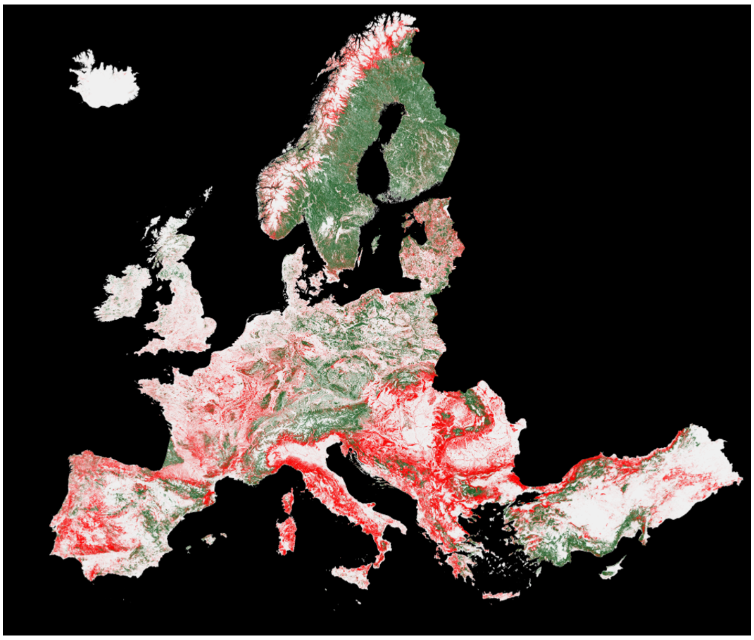

Figure A2. Distribution of needleleaf (green), broadleaf (red) and mixed (grey) forests in Europe based on 100 m grid of 2018 EEA open data (2020a).

Appendix II. Study limitations

Sampling bias

The datasets consisted of collected, physical specimens. Human observations, i.e. without physical evidence, of the target species were not included in the dataset. The GBIF had markedly more observations after 1942. This is in part due to an increase in technology after 1942 rather than just an increase in sampling. Older specimens are not always included in online databases because digitising herbarium material requires manual work and resources that not all herbaria have access to or prioritise, while newly collected material is uploaded more promptly. It is also possible that older specimens do not include enough information to be uploaded to online databases (missing dates, locations, collectors etc.). This difference in sampling size was not visible in the herbarium material, since this is a curated collection that strives to display representative observations of the species temporal and geographical ranges. In contrast, FinBIF is the national repository of Finland and thus this dataset only contained specimens collected in northern Europe.

Countries that lacked specimen observations, either reflect a true absence of the species or no sampling was done in those areas. Although forest types in Europe surely have an effect on host distribution, to fully rule out a lack of sampling, a more systematic sampling of Europe is proposed. Instead of random sampling, for each country representative grids of different biotopes would be selected for sampling.

Another factor that may be marginal, but still worth mentioning, is the difference in popularity of lichenology across Europe. This may influence the quantity of specimens collected and the accuracy of identification. Expeditions to other countries result in a limited number of specimens. A study mapping *Chaenothecopsis* species in Switzerland encountered similar issues with herbarium material and muses that 19th century lichenologists did not sample in the prealps as a common species is not present in old collections (Groner, 2006). Additionally, even though a lot of data points can be found in GBIF, many lichen specimens rest in personal herbaria or country specific collections that have not joined the GBIF network.

Duplicates

It was difficult to validate what qualified as a duplicate in the GBIF datasets. The database has a field for “associatedOccurences” that should keep track of the same specimen in different online locations. However, this only occurs when the specimen entered is an exact duplicate. The GBIF database consists of data provided by different institutions. Each institution adds their digitised data to this centralised platform. A specimen should in theory only be uploaded once by the institution that owns the specimen. Yet, when specimens are traded or moved to other institutions they may be uploaded again. Any variation in the entry of the same specimen creates a unique entry. Therefore, certain specimens appear as individual data points, when in reality they are duplicates. Nevertheless, during expeditions collectors obtain multiple specimens from the same location and on the same day. Hence it is possible that duplicates are indeed individual specimens with very similar collection information. This is difficult to distinguish and adds a degree of uncertainty to the dataset.

Missing coordinates

Removing entries with missing data could introduce a bias against older specimens which often lacked a date. A lot of information is contained in field notebooks that have not yet been digitised or have even been lost. Even though field notebooks are still common practice, nowadays the information is uploaded to online platforms immediately. Similarly, removing the observations without coordinates distorts the number of older specimens. While in the past it sufficed to note the location, nowadays it has become standard practice and often mandatory to include coordinates. In this analysis the GBIF dataset of *C. chrysocephala*, contained 292 European specimens that lacked coordinates but had some form of location (e.g., country codes). Of these, 99 were collected before 1942 and 193 after 1942. If they had been included, these specimens lacking coordinates would make up 36% of the before 1942 dataset and 12% of the after 1942 dataset. This indicates that a larger portion of samples with missing coordinates are observations from before 1942. Specimens with missing coordinates were also encountered in the *C. consociata* dataset. However, due to the marked size difference it was possible to go through these manually and fill in coordinates for these specimens either by finding more detailed sources or using the collector's year of death.

Yet, there are also differences between specimens that contain coordinates, namely the geo spatial system or the precision of the coordinates. Rounded off coordinates can cause overlaps. While coordinates that have been added to specimens lacking such information are precise but they are in fact approximations. Instead of precise coordinates other information may actually be more valuable. Keeping in mind the long-term purpose of herbaria, locations and coordinates only give a limited amount of information. One example, herbarium specimen #36H was collected at the Grünwaldpark on the outskirts of München, Germany in 1892. Since its collection, the population of München has grown considerably and although Grünwaldpark can still be located on a map, urbanisation has led to the disappearance of a lot of greenery that existed 130 years ago. Coordinates can give us information on the latitude, longitude and if they are accurate even the elevation of the species observation. However, coordinates tell us little of the relevant ecology. In the future, more emphasis should be put on the location description, including detailed information on the substrate (tree age, DBH/circumference, type of forest stand etc.), vegetation around the target species and abiotic characteristics of the environment (shade/light, humid/dry etc.).

Evidently, not all collections are equally complete or contain the same information. Besides lack of coordinates or dates, for the substrate tree species some included the scientific or the common name. However, in many cases only the genus was mentioned or the tree species was left out entirely. For specimens to become scientifically valuable, certain information is crucial.dd

Assumptions and inaccuracies

With online databases, one has to assume that the identification of the lichens is correct. Moreover, labels may not reflect the complete contents of a collected specimen. This became apparent with the herbarium material. In five herbarium specimens the parasite was present, but only the host species was mentioned on the label. This was the case for both specimens of *C. consociata* collected before 1942. Therefore, it is possible that a number of the database specimens labelled with *C. chrysocephala* also include the parasite. In particular, specimens collected before 1942 prior to the species description. Furthermore, various *C. chrysocephala* and *C. consociata* specimens included other species such as *Chaenotheca ferruginea* and *C. trichialis*. Accordingly, it is reasonable to find target species in non-target specimens.

Apart from these shortcomings, the data contained some basic errors. For example, the oldest *C. chrysocephala* GBIF observation from Slovenia dating back to 1800 was apparently recorded by M. Koch, H. Mayrhofer and F. Batič. This becomes interesting considering that Koch, Mayrhofer and Batič are still very much alive. Either they are enjoying immortality, or a mistake has occurred in the GBIF dataset. Other mistakes included mismatches between country of collection and country codes e.g., a specimen collected in Latvia with the country code EE, for Estonia.