Preslia 94: 579–605, 2022
doi: 10.23855/preslia.2022.579

Preslia

DaLiBor: Database of Lichens and Bryophytes of the Czech Republic

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Abstract: Digital data on the distribution of species are crucial for vegetation studies, monitoring and nature protection. Despite the existence of databases, the majority of bryophyte and lichen occurrences in the Czech Republic are not widely available in a standard and machine-readable form. Therefore, we created a Database of Lichens and Bryophytes (DaLiBor; https://dalibor.ibot.cas.cz) under Creative Commons license (CC-BY-SA). DaLiBor provides an infrastructure for recording standardizing, validating and enhancing data, e.g. neural network record classification. The database is also a tool for sharing and analysing records. Here, a descriptive analysis of 596,935 DaLiBor records, composed of 473,690 (79.4%) bryophytes and 123,245 (20.6%) lichens, is presented. There are bryophyte records for the whole Czech Republic, but there are no lichen records for large areas. The records of the spatial distribution of bryophytes and lichens in the Czech Republic were evaluated, which confirmed the importance of protected areas for biodiversity. There were more records of epiphytic and epixylic species at high elevations than of saxicolous and terricolous species, which are mainly recorded at low elevations. *Fagus sylvatica* was the tree with the highest number of recorded taxa for both bryophytes and lichens. The highest number of records, including Red-listed species, originates from natural beech and managed coniferous forests. Three cases that benefited from DaLiBor standardized data are presented: (i) the species distribution model helped find six new localities for *Dicranum majus* and *Polytrichastrum alpinum* within a single field visit; (ii) analysis of bryophyte and lichen species abundances in time revealed a high percentage of acidophilous species and spread of nitrophilous species in current bryophyte and lichen communities; (iii) DaLiBor is the main source of data for the online interactive Atlas of Czech lichens (https://dalib.cz).

Keywords: biodiversity, bryophytes, epiphytic lichens, eutrophication, *Fagus sylvatica*, habitat suitability, lichenized fungi, nature protection, occurrence database, species distribution model

Received: 9 Jul 2022, Revised: 26 Sep 2022, Accepted: 15 Oct 2022, Published online: 29 Dec 2022

Introduction

Data on species occurrence are fundamental for vegetation research, biodiversity protection and biogeography. Scientific interest in plant occurrences resulted in the publication of many distribution atlases at a continental scale (e.g. Jalas & Suominen 1972), national scale (e.g. Zając 1978, Preston et al. 2002, Bartha et al. 2015, Kaplan et al. 2015, 2020, 2021, Vangjeli 2017) and local scale (e.g. Chmiel 1993, Jongepier & Pechanec 2006, Van Landuyt et al. 2006, Turis & Košťál 2019, Mirek 2020). Many records are also included in digital databases on global (e.g. GBIF – GBIF.org 2021, WFO – Borsch et al. 2020), continental (e.g. EVA – Chytrý et al. 2016) and national scales (e.g. Pladias – Wild et al. 2019).

The effort expended in gathering bryophyte, lichen and fungal occurrences lags far behind that for vascular plants, with several exceptions (SLU Swedish Species Information Centre 2021, CNABH 2021, NBIC 2021, Swissbryophytes 2022). Atlases of lichen (Cieśliński & Fałtynowicz 1993, Roux et al. 2017, Arcadia 2021, Nimis & Martellos 2021, Stofer et al. 2021, British Lichen Society 2022) and bryophyte distributions (Ochyra et al. 1994, Meinunger & Schröder 2007, Blockeel et al. 2014) are still scarce. Although published data on distribution exist in the Czech Republic, the most comprehensive being the distribution of liverworts by Duda and Váňa published between 1967 and 1996, the intensive effort to gather all known moss, lichen and fungal occurrences has not yet been summarized in a publication or recorded in a specialized database.

Recent efforts to gather digital data on bryophyte and lichen occurrences have been rather sporadic. The majority of bryophyte and lichen records in databases are in different formats because they were collected for various purposes and by various methods. Existing digital records are spread in isolated databases maintained with various accessibility, licences, nomenclature, information density and quality. The richest source of Czech bryophyte/lichen digital records is the Species Occurrence Database (NDOP) of the Nature Conservation Agency of the Czech Republic (AOPK ČR 2021) with ~350,000/81,000 records, followed by the Czech National Phytosociological Database (Chytrý & Rafajová 2003) with ~150,000/8,000 records. Most of the bryophyte records in the literature need to be incorporated into a database. Similarly, most herbarium specimens of both bryophytes and lichens collected from the Czech Republic have never been digitized or put on a database.

To overcome the problem of data heterogeneity and complicated accessibility of occurrence records for bryophytes and lichens, a Database of Lichens and Bryophytes in the Czech Republic (DaLiBor; https://dalibor.ibot.cas.cz) was developed. DaLiBor has been available since 2019 and is not only a tool for gathering and standardizing existing digital records of bryophytes and lichens, but also for sharing the data with the community. Furthermore, DaLiBor uses Creative Common license, which enables further analysis, validation and enhancing of records and the development of new applications based the records. In this paper, a descriptive analysis of currently available data in DaLiBor is presented. In addition, three cases in which DaLiBor records are used are presented: (i) identification of the localities with the highest potential for finding rare bryophytes as a support for field floristic research, (ii) analysis of the temporal changes in the abundance of bryophytes and lichens and (iii) creation of an interactive, online distribution atlas of lichens in the Czech Republic.

Methods

Database structure and data-handling

The Database of Lichens and Bryophytes (DaLiBor) was developed using the same concept and infrastructure as the Pladias database of vascular plants (Wild et al. 2019, Chytrý et al. 2021). The basic unit of common infrastructure is a record, which consists of certain required fields: the scientific name of the taxon, point coordinates (WGS84), date of record, author's name and source of data. Each record can be supplemented with optional fields, such as the herbarium, altitude, coordinates source and precision or literature reference. Database infrastructure provides the tools for expert validation of records, control tools help the user to upload correctly formatted data aligned with a database's taxonomic concept, and tools for generating and printing distribution maps.

DaLiBor inherited many of its features from Pladias, the technical aspects of which are described by Novotný et al. (2022). Though these two databases are largely compatible, several significant modifications were made for bryophytes and lichens. In DaLiBor we created database fields for: (i) Substrate1 – rough classification of the five major substrate categories (epiphytic, saxicolous, terricolous, lignicolous, other); (ii) Substrate2 – subcategories for each of the Substrate1 categories, such as the list of species of trees for epiphytes or substrate rock for saxicolous species (see Supplementary Table S1 a complete list of subcategories); (iii) substrate – description of a substrate as provided by the original source; (iv) chemical data – chemotaxonomic notes, such as secondary metabolites detected mainly by thin-layer chromatography (TLC), which is especially important for identification of lichens. In contrast to Pladias, Creative Commons Licence (CC-BY-SA) is used mandatorily for data management in DaLiBor. This allows for easier data sharing, mining and analysis.

DaLiBor species lists

The list of bryophyte taxa is derived from Kučera et al. (2012), with minor updates reflecting the additions of new taxa and correction of nomenclatural errors discovered since then. A major update of this list based on the slightly updated taxonomy and nomenclature of Hodgetts et al. (2020) is envisaged for 2023.

The species list of lichens used in the DaLiBor database was derived from the last national checklist published by Liška & Palice (2010) with additions by Malíček et al. (2018b) and several other recent studies. The nomenclature is continuously updated according to new taxonomic concepts, but mostly follows Nimis et al. (2018). Besides lichens, we included also some non-lichenized fungi within mostly lichenized genera (e.g. *Thelocarpon*), species closely associated with algae, or with an indistinct degree of lichenization (e.g. *Epigloea*, *Ramonia*) and calicioid fungi traditionally studied by lichenologists (e.g. *Chaenothecopsis*, *Microcalicium*, *Mycocalicium*, *Stenocybe*). These taxa are usually recorded during lichenological surveys and many of them are known as important bioindicators.

Both the bryophyte and lichen lists of species in DaLiBor are curated, maintained and updated by experts. Current DaLiBor species lists are back-compatible with earlier DaLiBor lists. DaLiBor provides a semi-automatic tool for name conversion during data import. If the imported taxon was not found in the actual DaLiBor species list, but was in the synonym lists, the algorithm offers a valid taxon name; the user can accept or decline it manually.

Imports and standardization

The majority of both bryophyte and lichen records in DaLiBor come from large databases, mainly Species Occurrence Database of Nature Conservation Agency of the Czech Republic (AOPK ČR 2021), Database of Czech Forest Classification System (Zouhar 2012) and Czech National Phytosociological Database (Chytrý & Rafajová). Bryophyte records from large databases are supplemented with the personal databases of several researchers (Jan Kučera, Milan Marek, Pavel Dřevojan, Petra Hájková, Ivana Marková) and published data (Hájková et al. 2018). Lichen records supplementing the above-named large databases came from the literature, unpublished field inventories and ecological studies, a few public herbaria [PL, digitized specimens from PRA and PRC] and personal database of Jiří Malíček (Table 1). During the initial import of records of bryophytes and lichens from existing resources, many records with wrong identification or wrong coordinates were discovered. With the large data providers, protocols for further DaLiBor updates were negotiated. Based on these protocols, incomplete or unreliable records were reported to the data providers. The gathering of records in one database resulted in numerous duplicate records, which were manually assessed. To support duplicity eradication, the records were automatically tagged with the identical species' name, geographic coordinates (tolerance 200 m), date and substrate. Almost all lichens records in DaLiBor were expertly validated, i.e. an expert decision on the credibility based on original source, the name of author, locality and substrate. Usually the records were not physically revised (in herbaria). For bryophytes, the validation is still in process.

Table 1. Number of DaLiBor records for bryophytes and lichens obtained from each source. DaLiBor includes data from institutional and personal databases and the literature. Based on the data in DaLiBor in July 2021.

Source	bryophytes	lichens
Species' occurrence database of NCA CR	190,691	45,428
Database of Czech Forest Classification System	146,973	4,336
Czech National Phytosociological Database	112,141	7,401
Personal databases	23,011	15,142
Public herbaria	0	4,790
Literature excerption	874	46,148
Total	473,690	123,245

Explorative analysis and enhancement of records

For the explorative analysis in this study, DaLiBor data as of July 2021 were used. To reduce spatial bias in the presented analysis, duplicate records were filtered out and only unique ones kept. There were 36,729 (5.7% of total) records with identical species name, geographic coordinates, date and substrate. After filtering out duplicates, 596,935 unique DaLiBor records were left. In the explorative analyses, common and uncommon species were distinguished based on the Red list categories used in national red lists: CR, DD, DD-va, EN, LC, LC-att, NE, NT, RE, VU for bryophytes (Kučera et al. 2012) and CR, DD, EN, LC, NE, NT, RE, VU for lichens (Liška & Palice 2010). Considering differences between bryophytes and lichens Red-list classification, the species were divided ad-hoc into Red-listed (uncommon), defined as those in RE, CR, EN or VU categories, and all other Red-list categories (common).

To show the spatial structure of DaLiBor data, a number of records and number of species were projected onto the cells of the central-European mapping grid (KFME grid, (Niklfeld 1971). We used the first-order quadrants cells of ~6 × 6 kilometres. The ID of the mapping cell was automatically assigned to all records during import. Based on the sum of records in grid mapping cells, the top 10 bryophyte and 10 lichen taxa recorded in mapping cells and most frequent taxa over all DaLiBor records, were identified. To inspect the effect of protected areas on record frequency and identify non-protected areas with high local bryophyte and lichen diversity, each record was supplemented with attributes defining whether it came from a protected area or not, based on its coordinates. Spatial data defining the borders of protected areas was provided by the NCA CR (https://gis-aopkcr.opendata.arcgis.com).

To review DaLiBor species according to the substrate on which they occur, substrate categories classification was used. Substrate classes were assigned based on the existing text description of substrate and locality. The classification occurred either manually, based on expert knowledge and automatically using neural text mining. Classification using the neural network was done using a Python script with MLP Classifier from scikit learn library (Pedregosa et al. 2011). It provides a multi-layer perceptron classification (Longstaff & Cross 1987). In our case, five neural networks were used for the classification of substrates; one network for Substrate1 category (epiphytic, saxicolous, terricolous, lignicolous) and another four for Substrate2 subcategories (102 classes, see Supplementary Table S1). Input of the neural network consisted of textual description of substrate and taxon name. Textual substrate was encoded with TF-IDF feature, extraction technique (Robertson 2004). Taxon was encoded with One-hot encoder from scikit learn library. A sigmoid activation function was used. Experiments with the count of neurons in the hidden layer resulted in very similar results so we kept to the commonly used 100 neurons. DaLiBor database contained 88,960 records with manually classified Substrate1 category, 47,964 with Substrate2 subcategory of Epiphytic category, 15,752 with Substrate2 subcategory of Saxicolous category, 3,804 with Substrate2 subcategory of Terricolous category and 11,936 with Substrate2 subcategory of the Lignicolous category. These were used for neural network training. The trained network was applied to 17,260 DaLiBor records with no substrate class, but a textual description of the substrate, which was available for machine classification.

Substrate classification was part of data enhancement, similar to the extraction of environmental factors based on record coordinates. For all records, altitude was obtained from a fine-scale digital terrain model, precipitation and air temperature from interpolated historical weather station data (for technical details on altitude and meteorological data used here see Supplementary Tables S2, S3). The average air temperature, precipitation, altitude and coordinates in DaLiBor were compared with the average values in the climatic atlas and statistical yearbook of the Czech Republic (Tolasz 2007, Rojíček 2020). This was done separately for bryophytes and lichens Substrate1 category in order to reveal the potential links between substrate and environmental preferences. Besides comparing the average values, the difference in environmental gradient coverage was visualized by plotting the density of temperature, precipitation and altitude records in DaLiBor together with the density of one million randomly generated background occurrences in the Czech Republic. At the landscape scale, habitat preferences of bryophytes and lichens were explored using Chytrý et al. (2010). The habitat mapping layer updated to 2019, as provided by NCA CR (Härtel et al. 2009), was used. The intersection of coordinates revealed that the records of 23% of bryophytes and 15% of lichens were for areas with no habitat class and were excluded from habitat preference exploration. Analysis was done using R 4.0.3 (R Core Team 2016).

Case 1: Species distribution modelling

DaLiBor data was used to increase the efficiency of field research focused on two regionally uncommon species in the Bohemian Switzerland National Park. The park is known for its heterogeneous topography, with cold narrow valleys and sunny steep rocks, resulting in a steep environmental gradient in the area. Despite low altitude, cold valley bottoms experience moist and cold montane conditions (Wild et al. 2013). Therefore, the area is rich in bryophytes (~300 species, i.e. one-third of the national species pool), including many locally and nationally rare and endangered species (Kučera et al. 2003, Härtel et al. 2007). *Dicranum majus* [VU] and *Polytrichastrum alpinum* [LC] were selected as two examples of locally uncommon species. Many of their localities have yet to be discovered because they are in barely-accessible landscapes and there is a lack of skilled bryologists surveying this region. To increase the efficiency of field research, the probability of occurrence of suitable habitats in the area of the park was computed. Based on our experience, we did not presume a linear response of species to environmental conditions and used a Random Forest algorithm for habitat suitability modelling: ranger package (Wright & Ziegler 2017) in R (R Core Team 2016). To describe the main environmental gradient, potentially important for the distribution of target species, we used six low colinear, ecologically relevant factors represented by continuous grids of 10 metres (normalized difference vegetation index, altitude, canopy height model, potential insolation, topographic position index, topographic wetness index). For technical details of environmental factors see Supplementary Table S2. DaLiBor was the source of the recent records of target species reported from the Bohemian Switzerland National Park. The records selected were those with a position error below 50 m. For *D. majus*, there were 43 records and for *P. alpinum* 31 records. The small multiplier strategy (Liu et al. 2019) and randomly generated four times more pseudoabsence for each species (172 and 124 for *D. majus* and *P. alpinum)* were used. Pseudo-absences were generated at least 200 m from known presences. For model building, a 10-fold repeated cross validation (100 model runs) was used. To assess model performance, confusion matrices, Cohen's kappa and true skills statistics were used (Allouche et al. 2006). To assess the importance of the environmental factors for the distribution of suitable habitats for the target species, we used the Gini index (Liu et al. 2020), i.e. the sum over the number of splits (across all trees in Random Forest) that include the environmental variable, proportionally to the number of input occurrences (presences/absences) it splits. To verify the model's performance and potentially discover new localities for the target species, 20 randomly selected localities (10 for each species) within the highest (90th percentile) potential habitat suitability were selected, which were then visited. As a control, 20 localities selected at random within the area with lower than the 90th percentile of potential habitat suitability were also visited.

Case 2: Changes in the abundance of species over time

During the last two decades there was a rapid change in lichen communities in the Czech Republic. Therefore, the focus was on the changes in the abundance of species that occurred after the year 2000. This threshold date was established based on the significant decrease in acid rain deposition due to the desulphurization of coal-fired power stations during the 1990s (Hruška & Kopáček 2005, 2009). Desulphurization was followed by environmental eutrophication. Both desulphurization and eutrophication strongly affected the distributions of bryophytes and lichens. This analysis focused mainly on epiphytic lichens, which are well-known as sensitive indicators of air quality. Both the total number of records and the number of occupied mapping grid cells (~6 × 6 km) were analysed.

Case 3: Atlas of Czech lichens

Data from the DaLiBor database were used to create the national online atlas of lichens (https://dalib.cz/en). The concept used is similar to that used by Pladias (https://pladias.cz/en): a taxon fact sheet, composed of a dynamic distribution map, a text description supplemented by photographs and a list of characteristics. Data for the public portal are updated in the PostgreSQL database once a day via materialized SQL views in the database, maps are generated using Geoserver and the OpenLayers library and the portal itself is based on the PHP framework Nette. DaLiBor, like Pladias, uses the hierarchical structure of the taxon list for the automatic transfer of occurrence information between different taxonomic levels (Chytrý et al. 2021). This ability allows a more complete view of the distribution in the case of higher taxa such as aggregates. The atlas of lichens aims to make the data available in a clear form not only for conservation purposes but also for the informed public, for example, students or teachers.

Results

Explorative analysis

As of July 2021, there was a total of 633,664 records in the national database of bryophytes and lichens (DaLiBor). After filtering for duplicate data, 596,935 records remained and are analysed here. Of the 596,935 unique records, there were 473,690 (79.4%) records for bryophytes and 123,245 (20.6%) for lichens.

The biggest provider of data on bryophyte records (71.2%) was the Species Occurrence Database of the NCA CR (Table 1), while for the lichens this source provided only 37.5% of the total and was outnumbered by records from the literature (38.1%). The Database of Czech Forest Classification System – DCFCS (Zouhar 2012) of the Forest Management Institute (FMI), formally a part of NCA CR Species Occurrence Database, but treated independently in this analysis, is the second most important source of data on bryophytes. The ratio between common and Red-listed species and their spatial distribution was different for bryophytes and lichens based on the data in DaLiBor. There were

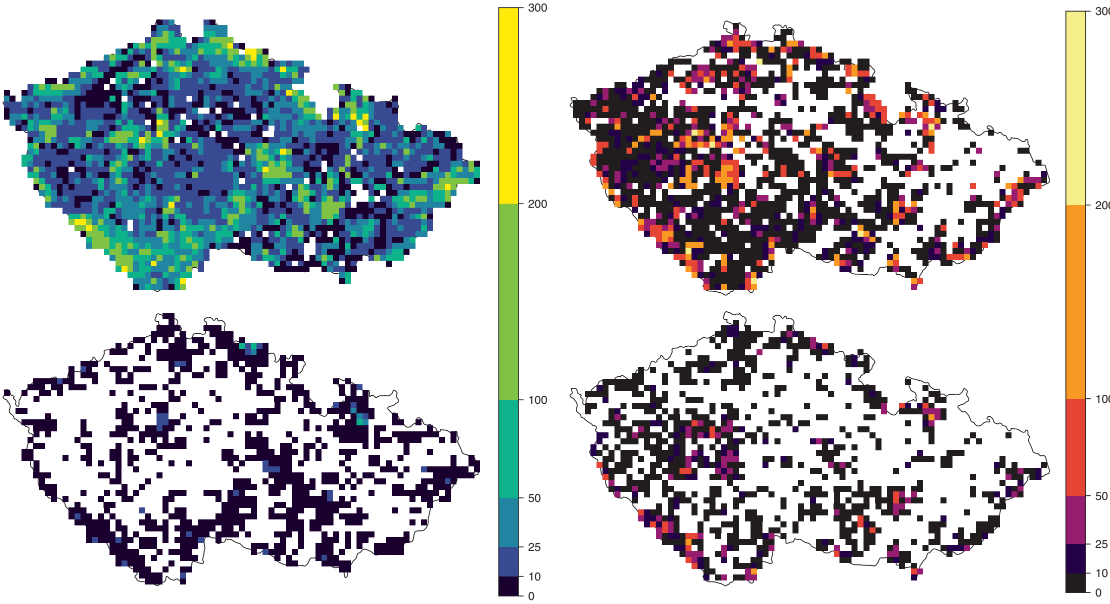

Fig. 1. Maps showing the number of species of bryophytes (left) and lichens (right) recorded in quartered KFME mapping grids (~6 × 6 km) in the Czech Republic. Red-listed (bottom; red list evaluation CR, EN, RE, VU) and common species (top; all other than Red-listed) are presented separately.

9,134 and 17,227 records of Red-listed bryophytes and lichens, respectively, which accounted for 2% and 14% of all bryophyte and lichen records. Common bryophyte species were recorded in almost all mapping cells in the Czech Republic, as opposed to the lichens, for which there were no records for many of the mapping cells in DaLiBor. In contrast, Red-listed bryophytes and lichens were reported from a similar number of mapping cells. Nevertheless, lichen records, including those of Red-listed taxa are clearly concentrated in the south-western part of the country (Fig. 1).

The most frequent bryophytes were common forest taxa, which are easy to identify in the field (and are regularly reported by a broad spectrum of field researchers), such as *Polytrichum formosum* (627 of 697 mapping cells occupied), *Hypnum cupressiforme* (626), *Plagiomnium affine* (624), *Pleurozium schreberi* (615), *Dicranum scoparium* (606) and *Atrichum undulatum* (603). A similar pattern in the most abundant species appeared while analysing the total number of records instead of records in mapping cells (Table 2A). The most frequent lichens were *Cladonia fimbriata* (337), *Cladonia rangiferina* (326), *Cladonia arbuscula* agg. (297), *Cladonia coniocraea* (291), *Hypogymnia physodes* (288) and *Cetraria islandica* (277). According to the total number of records, *Hypogymnia physodes* was the most common species (Table 2B).

Based on DaLiBor metadata, the majority of records, particularly for lichens, originate from the last two decades (Fig. 2A). The older records are usually not yet digitized. For lichens, there is only a low number of records of between 1950–2000, which reflects the low research effort in this period. Concerning the substrate, the majority of lichens with a categorized substrate were epiphytes, while the bryophyte records were almost equally distributed across epiphytic, saxicolous, and lignicolous substrates (Fig. 2B)

Table 2. The most frequent species in DaLiBor ranked in terms of the number of mapping grids they occupy and total number of records.

Bryophytes				
Rank	Species	Grid cells	Species	Records
1	*Polytrichum formosum*	627	*Polytrichum formosum*	33,199
2	*Hypnum cupressiforme*	626	*Dicranum scoparium*	29,146
3	*Plagiomnium affine*	624	*Pleurozium schreberi*	24,074
4	*Pleurozium schreberi*	615	*Hypnum cupressiforme*	19,854
5	*Dicranum scoparium*	606	*Plagiomnium affine*	12,375
6	*Atrichum undulatum*	603	*Polytrichum commune*	12,197
7	*Plagiomnium undulatum*	567	*Atrichum undulatum*	10,299
8	*Pohlia nutans*	542	*Pohlia nutans*	9,757
9	*Brachythecium rutabulum*	520	*Leucobryum glaucum*	8,229
10	*Leucobryum glaucum*	517	*Hylocomium splendens*	7,803

Lichens				
Rank	Species	Grid cells	Species	Records
1	*Cladonia fimbriata*	337	*Hypogymnia physodes*	2,924
2	*Cladonia rangiferina*	326	*Cladonia coniocraea*	2,730
3	*Cladonia arbuscula* agg.	297	*Cladonia rangiferina*	2,369
4	*Cladonia coniocraea*	291	*Cetraria islandica*	2,244
5	*Hypogymnia physodes*	288	*Cladonia fimbriata*	2,185
6	*Cetraria islandica*	277	*Coenogonium pineti*	2,101
7	*Cladonia pyxidata*	247	*Cladonia digitata*	2,018
8	*Cladonia furcata*	242	*Lecanora conizaeoides*	1,910
9	*Hypocenomyce scalaris*	220	*Cladonia arbuscula* agg.	1,775
10	*Lecanora conizaeoides*	219	*Hypocenomyce scalaris*	1,668

Using 6,146 and 41,841 records of epiphytic bryophytes and lichens, respectively, revealed that the tree hosting the highest diversity in the Czech Republic is *Fagus sylvatica*, with 97 bryophyte and 406 lichen taxa. *Fagus sylvatica* was also the most frequent substrate according to DaLiBor epiphytic records with 3,165 and 7,542 records for bryophytes and lichens, respectively (Fig. 3).

Data enhancement

Using Artificial Neural Network (ANN) the substrate class was predicted for 17,503 records based on the text description of the substrate or habitat. After machine classification, all newly classified records were manually checked and only those with prediction reliability higher than 97% accepted. This threshold resulted in highly reliable substrate classifications, providing 9,214 records with Substrate1 class and 4,189 records with Substrate2 class. The neural network correctly classified 52% of records with only a description of the substrate. Such enhancement helped, for example, to identify the tree species hosting the highest bryophyte and lichen diversity (Fig. 3). Artificial Neural Network was not only used to predict substrate from the text description, but also to check all records with a substrate class assigned by the author of the record. The cases where the neural network assigned a different class than the author was examined, which revealed several mistakes in author-classified records that were subsequently corrected. Enhancing

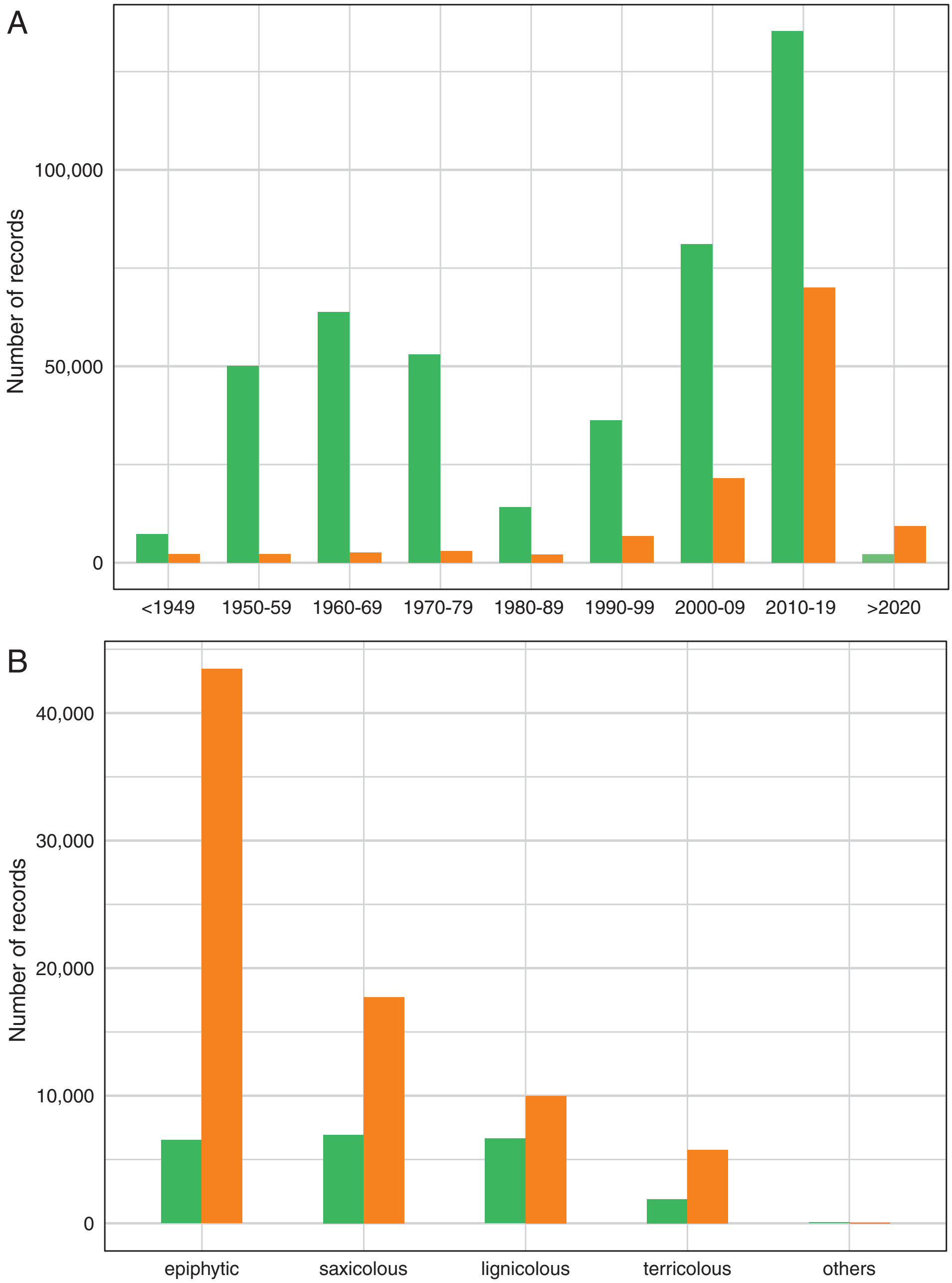

Fig. 2. Analysis of the number records in DaLiBor for bryophytes (green) and lichens (orange). (A) number of records per decade; (B) number of records for specific substrates.

DaLiBor data geographically by associating them with protected areas revealed that most bryophyte and lichen records originate from protected areas, although the percentage of records from protected areas differed for bryophytes and lichens (Table 3).

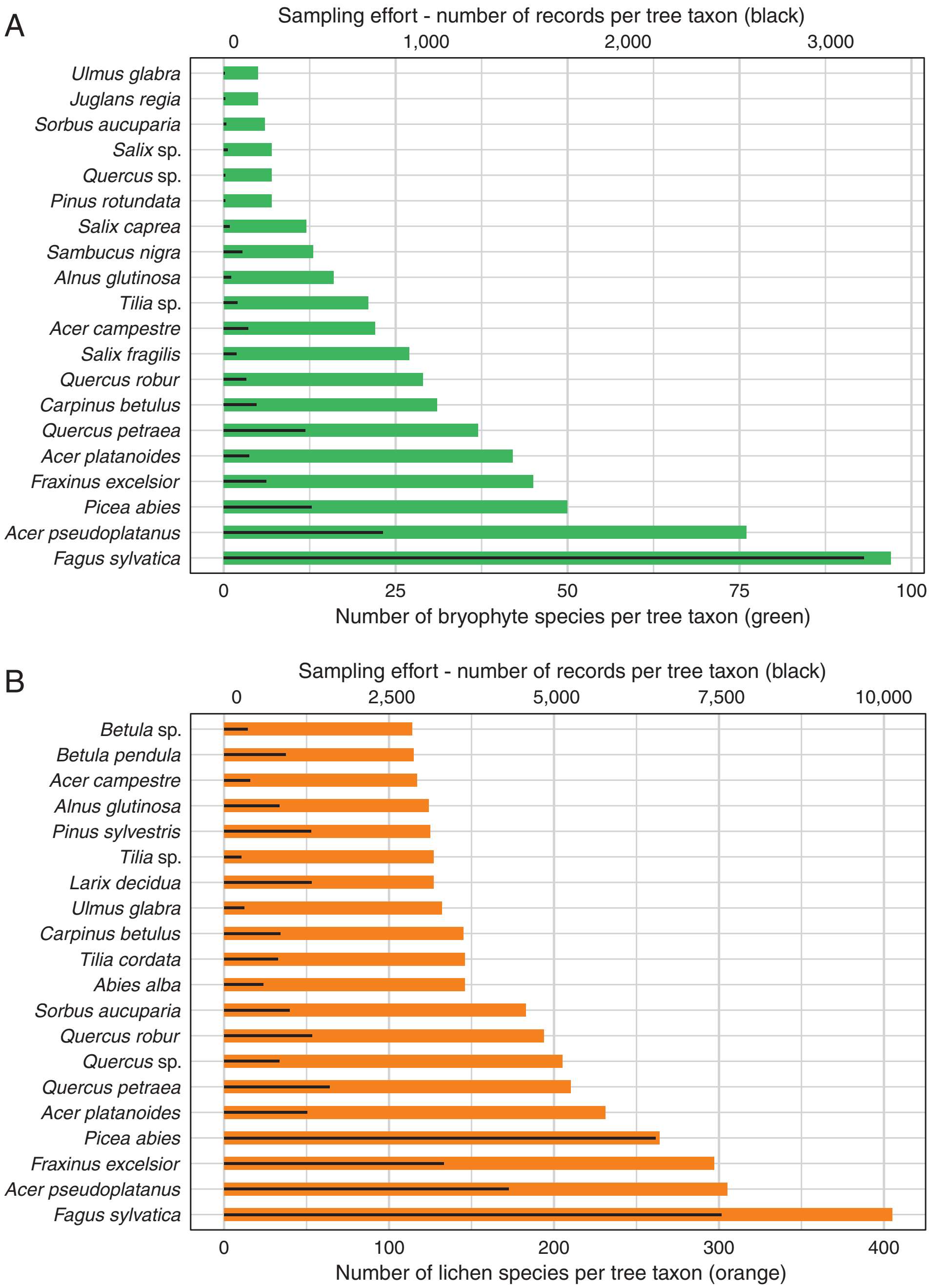

Fig. 3. The top 20 trees hosting the highest diversity of (A) bryophytes and (B) lichens. Sum of bryophytes/lichens per species of tree (x axis at the bottom) is shown together with the number of records for a specific tree (x axis at the top).

Table 3. Bryophytes and lichens records from protected and non-protected areas of the Czech Republic.

	Protected areas	Non-protected areas
Bryophytes	283,390 (59.8%)	190,300 (40.2%)
Lichens	95,677 (77.6%)	27,568 (22.4%)

Environmental gradients

Both bryophytes and lichens were recorded more frequently at high altitudes with lower temperatures and higher precipitation than in the rest of the Czech Republic (background, Fig. 4A, C). Epiphytes and species growing on dead wood occurred more frequently at high altitudes, in areas with higher precipitation and lower temperatures, in contrast to saxicolous and terricolous species, which are mainly recorded in drier and warmer regions (Table 4).

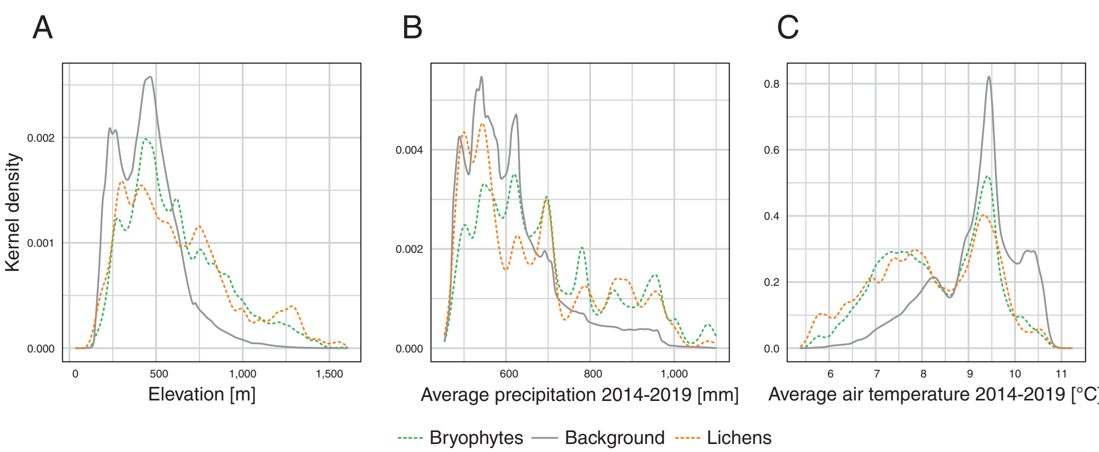

Fig. 4. Density of bryophytes and lichens at different altitudes (A), areas with different average precipitation (2014–2019) (B) and average temperatures (2014–2019) (C) compared to background average for these conditions in the Czech Republic. Background density is based on a random area sampled at one million points

Table 4. Comparison of average environmental conditions recorded for four ecological groups of bryophytes and lichens with the average conditions recorded for the Czech Republic (CZ; precipitation and air temperature according to Tolasz 2007, altitude from Rojíček 2020)

Group	Precipitation (mm)			Air temperature (°C)			Altitude		
	Lichens	Bryophytes	CZ	Lichens	Bryophytes	CZ	Lichens	Bryophytes	CZ
Epiphytic	724	669	700	7.8	8.2	8.1	702	621	430
Lignicolous	733	715		7.7	7.7		744	753	
Saxicolous	648	641		8.7	8.3		469	570	
Terricolous	690	628		8.7	8.4		511	566	

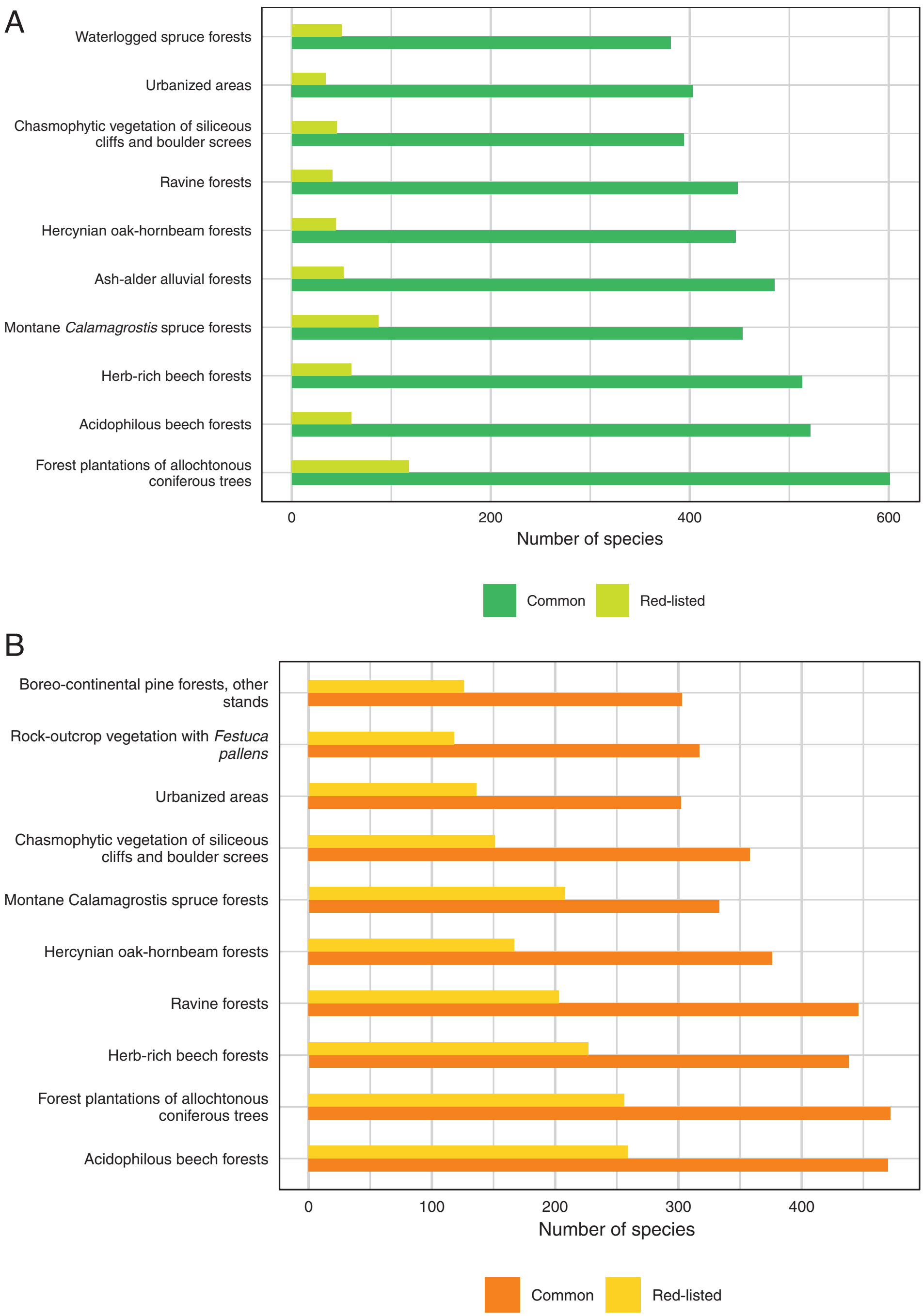

Fig. 5. Number of species in DaLiBor recorded in the ten richest habitats. (A) Number of common and Red-listed species of bryophytes, (B) number of common and Red-listed species of lichens. There were 23% of bryophyte and 15% of lichen records reported from an area with no information on the habitat. Records for unclassified habitats are not shown.

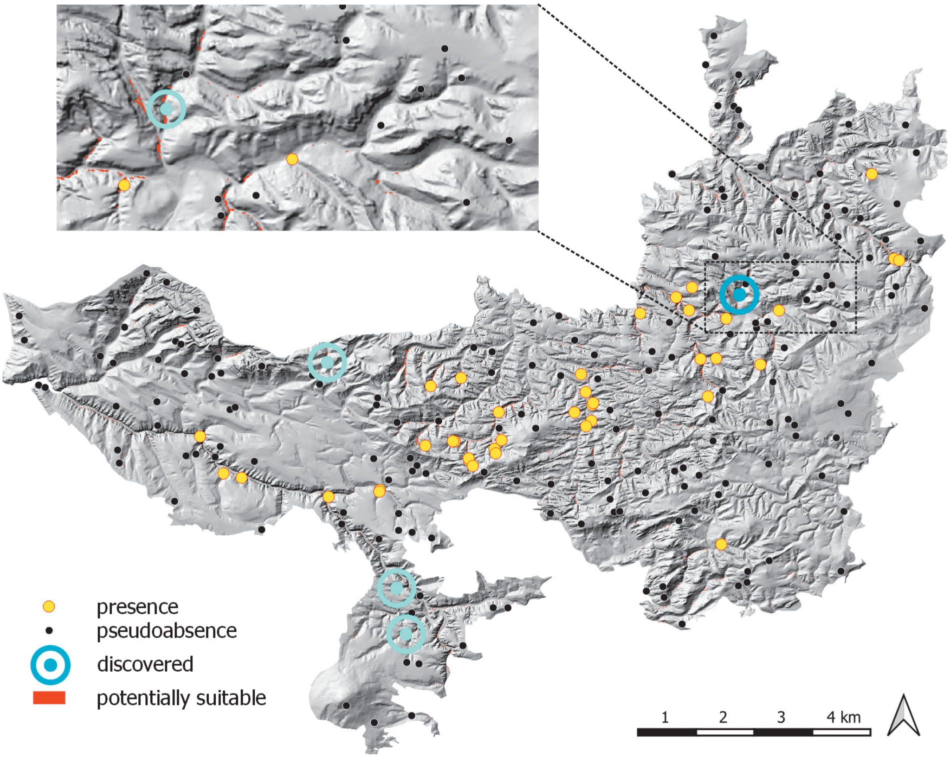

Fig. 6. The map of potential habitat suitability for *Dicranum majus* in the National Park Bohemian Switzerland. Known (used for model training) presence is yellow, random pseudoabsence points for model calibration black. Newly-discovered localities during field validation are highlighted in blue. Potentially suitable localities (red) are 90th percentile of the habitat suitability in the area are shown. The background map is the hill shading based on a digital elevation model.

Based on DaLiBor records enhanced with national habitat mapping data revealed that the majority of DaLiBor records originate from forests. Moreover, forests include eight habitats with the highest bryophyte and seven with the highest lichen diversity. The highest diversity in forest is the case for both common and Red-listed species. The vast majority of bryophyte and lichen records were reported from plantations of coniferous trees and acidophilus beech forests (Fig. 5).

Case 1: Species distribution modelling

The maps showing the probability of occurrence of suitable habitats for target species were used to focus field research in a barely-accessible terrain. The performance of habitat suitability models was: *Dicranum majus* – kappa = 0.46, TSS = 0.41; *Polytrichastrum alpinum* – kappa = 0.42, TSS = 0.38. The most important environmental factor determining the potential suitability of habitats measured by using the Gini importance predicted by Random Forest models was the topographic position index for both *D. majus* and *P. alpinum* (Table 5). Despite the relatively low performance, the results of the models

Table 5. Gini importance of the environmental factors predicted by the Random Forest based habitat suitability models for *D. majus* and *P. alpinum.* The higher the Gini-coefficient value the more important the variable.

Species	Environmental factor	Gini
Dicranum majus	topographic position index	27.08
	topographic wetness index	10.57
	potential insolation	8.59
	normalized difference vegetation index	8.26
	elevation	7.89
	canopy height model	6.27
Polytrichastrum alpinum	topographic position index	21.10
	elevation	8.91
	topographic wetness index	7.63
	potential insolation	4.78
	canopy height model	3.86
	normalized difference vegetation index	3.17

were used to focus the field survey on uncommon species, which resulted in two new localities for *P. alpinum* and four for *D. majus* (Fig. 6). All new records were discovered at 20 localities, for which the model predicted the highest habitat suitability, and no target species were found in 20 randomly selected control localities in the national park.

Case 2: Changes in the abundance of species over time

Before and after 2000, there were 228,786 and 214,643 records of bryophytes and lichens, respectively. In contrast, there was a distinct imbalance between historical and recent DaLiBor records of lichens, with 19,522 records of lichens before 2000 and 100,481 after that date. The number of occupied mapping grids (~6 × 6 km) before and after 2000 were comparable for both bryophytes and lichens. Coincidently the numbers of historical (before 2000) and recent (after 2000) bryophyte records were similar. The criteria for selecting the year 2000 were changes in air quality. A decreasing trend in occupied quadrants after 2000 was recorded for bryophytes (compare x-axes of Fig. 7A, B), while for lichens the number of records increased (Fig. 7D as compared to Fig. 7B)

For bryophytes, there was a decrease in forest species (*Dicranum polysetum, Leucobryum glaucum*) and pioneer species (*Pohlia nutans, Polytrichum juniperinum, Atrichum undulatum*), and an increase in aquatic species (*Fontinalis antipyretica*) and air quality-sensitive species (*Lewinskya speciosa, Orthotrichum pumilum*; Fig. 7A, B and Supplementary Fig. S1). For lichens, there were noticeable differences in the number of species recorded over time. Historical records before 2000 (Fig. 7C, D and Supplementary Fig. S1) are mainly for various species of *Cladonia*, while those after 2000 are mainly for acidophilous and nitrophilous epiphytes.

In addition, the list of the most common epiphytic species of lichen in grids before 2000 significantly differs from that after 2000 (Fig. 8). For example, the historical list contains more macrolichens (13/8) and more species of *Lecanora* (5/3). It also includes three epiphytes that are now rare (*Ramalina fastigiata*, *R. fraxinea* and *Pleurosticta acetabulum*) but were more common and more frequently recorded before 2000.

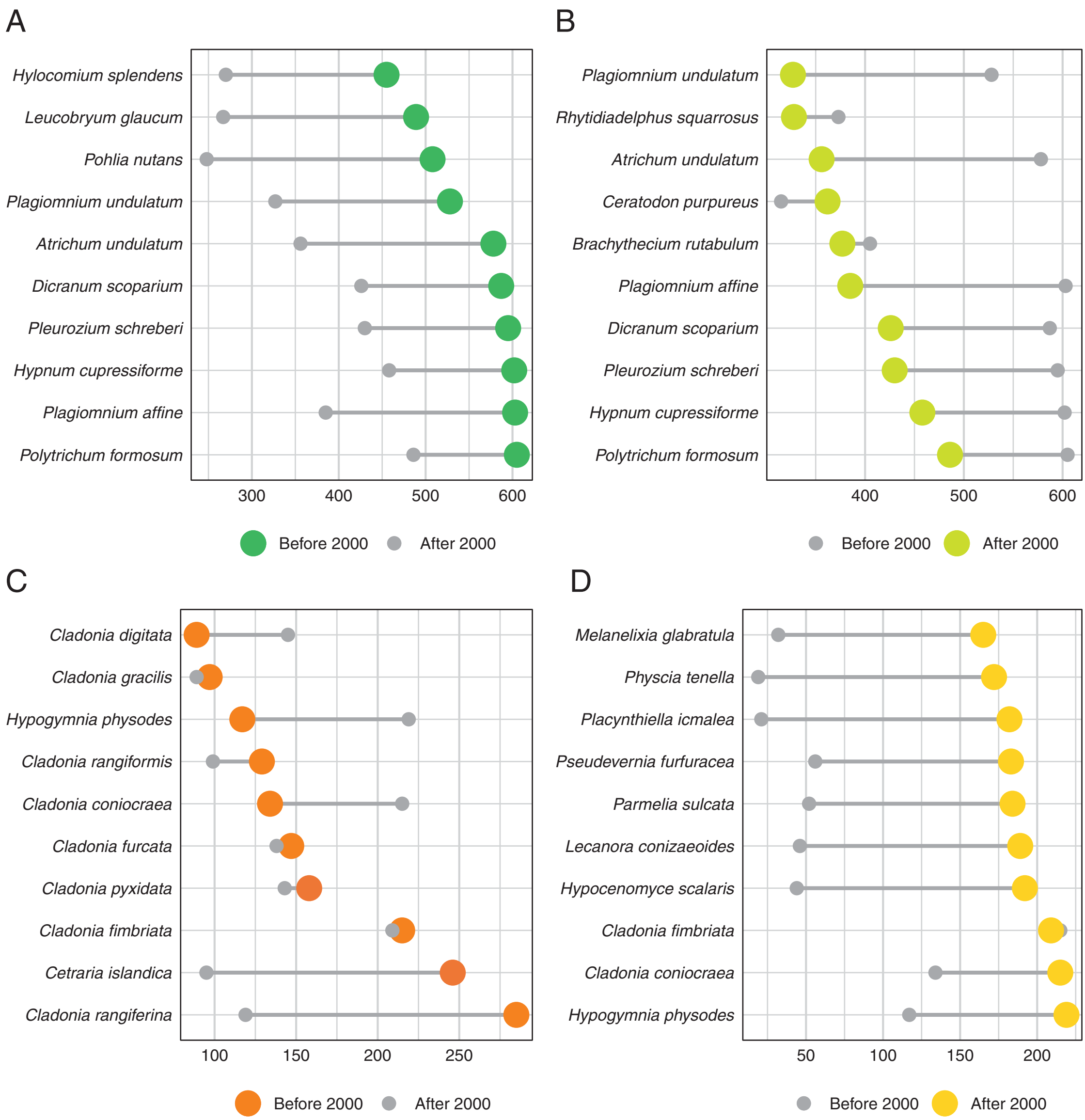

Fig. 7. The 10 most abundant bryophytes (green) and lichens (orange, yellow) recorded in the quadrants in the Czech Republic (697) before 2000 (A, C) and after 2000 (B, D). Horizontal lines together with smaller points represent the increase/decrease of the species before/after 2000.

Case 3: Atlas of Czech lichens

The public portal (dalib.cz) including all of the 1,765 species (1,820 taxa) occurring in the Czech Republic, was created for better accessibility and comprehensibility of data on lichen occurrence and ecology. The portal is sourced directly from DaLiBor and publicly available from 2020. General functions include maps of biodiversity, identifying for

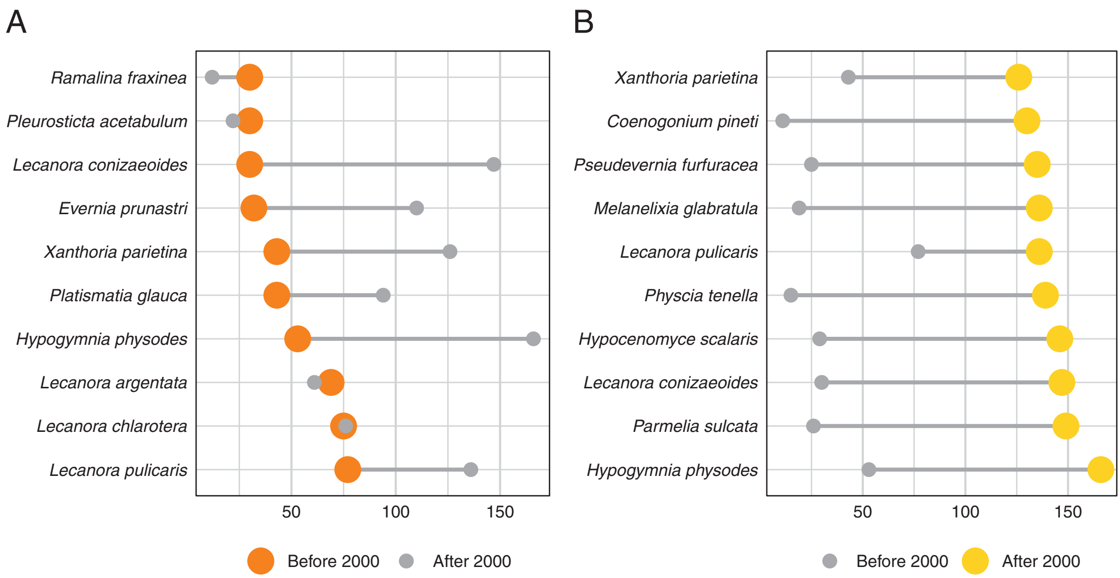

Fig. 8. The 10 most abundant species of epiphytic lichens recorded in the quadrants before 2000 (A) and after 2000 (B) in the Czech Republic. Horizontal lines together with smaller points represent the increase/decrease of the species before/after 2000.

example national hotspots, gallery of photographs of lichens, taxonomic tree, database of lichen secondary metabolites detected in samples from the Czech Republic and general information on Czech lichens. A major part of the atlas includes current Red-list categories, the most common synonyms, taxonomic classification, dynamically generated maps of distribution, description of ecology and substrate preferences, pictures of individual species, etc. Each record can be displayed by clicking on the map and includes the quadrant number, locality, altitude, substrate, date and authors of the record, original species name and source. In addition to the automatic, dynamic generation of information from DaLiBor, further 2,500 macroscopic and microscopic photographs of 853 species were added manually. For 1,370 species there are brief descriptions of their ecology, distribution and morphology, and chemotaxonomic data for >1,600 samples (the numbers as of December 2022).

Discussion

A national database of bryophytes and lichens (DaLiBor) recorded up to July 2021, including ~634,000 records from nearly all existing digital resources supplemented with our own literature and herbaria records, has been established. A major limitation of the DaLiBor data is that it does not include non-digitized records from herbaria. It is estimated that less than 10% of bryophytes and lichens recorded in national herbaria are digitized (with few exceptions such as fully digitized CBFS). This is a major potential source of further data for DaLiBor, especially the digitization of collections of national and regional museums (e.g. BRNM, MJ, ZMT, PR, PRC). Literature excerption and future floristic research are also big challenges. Currently, there are four times as many records for bryophytes than lichens in the database and only about 2% of the bryophyte and 14% of the lichen records are for Red-listed species. This imbalance was still notable after correction taking in account the different concepts of the Red-listing processes for bryophytes and lichens. Bryologists categorized 34% of the national species pool in the categories CR, RE, VU or EN, whereas lichenologists categorized 50% in these categories. Even after considering this, one would still expect a higher number of records of Red-listed species of bryophytes in DaLiBor than is the case. This difference could be due to the generally better knowledge of field researchers, such as botanists and forest inventory workers, of common bryophytes than common lichens. This could increase the number of common bryophytes compared to Red-listed species and therefore lichen data could seem to be more focused on Red-listed species. The majority of records for lichens in DaLiBor come from the literature, which is more focused on Red-listed than common species.

The most common species in the Czech Republic

The most common species are based on both the number of occupied mapping cells and the total number of records in DaLiBor (Table 2). The occupation of mapping cells is sensitive to sampling effort, which may be focused on specific taxa or vegetation types and thus the spatial distribution of available habitats. This indicates, for example, that *Polytrichum commune* is often recorded in wetlands and peatlands. These habitats are, however, present in a limited number of mapping cells. Therefore, *P. commune* was not listed in the top 10 most common taxa based on their presence in mapping cells. On the other hand, based on the total number of records, *P. commune* was the sixth most common taxon, because it is recorded by a variety of field workers, sometimes unfortunately also based on misidentifications.

The list of the 10 commonest species contains mainly macrolichens, especially members of the genus *Cladonia*, which are often reported by non-lichenologists and were included in large databases. This is also the case for bryophyte records, which are dominated by large forest taxa reported in forest inventories or phytosociological surveys. In contrast, ubiquitous microlichens or small leafy liverworts are mostly only recorded by specialists.

The majority of lichens in DaLiBor were recorded during the last two decades, which limits an historical comparison. Compared to lichens, several thousands of bryophytes were recorded every decade starting from the 1950s, with a notable decrease in the 1990s (Fig. 2B). These four decades are represented in DaLiBor mainly by records of common forest bryophytes coming from the Database of Czech Forest Classification System (Zouhar 2012), which was included in the Species Occurrence Database of NCA CR and then in DaLiBor.

Importance of substrate

In DaLiBor metadata, only 10% of the bryophytes have a substrate assigned to them, whereas for lichens it is more than 60%. Substrate is a very important ecological character and is routinely recorded by expert bryologists and lichenologists. A substantial part of lichen data comes from the literature and personal databases, which include the substrate. In contrast, most of the bryophyte records came from large databases with no or a limited option to record a substrate. This is also connected to the different purposes for gathering the records. For example, none of the 151,309 records in DCFCS include substrate because the purpose was to produce a forest inventory. This is in contrast to curated research databases, e.g. CBFS, in which 92% of the records include substrate, and the personal database of Jiří Malíček with 99% of records with a substrate. Using Artificial Neural Network (ANN) resulted in an additional 13,000 (75%) records with data on substrate. Text mining of existing databases on distribution should be applied more widely as in other fields (Ghiassi et al. 2013, Hughes et al. 2017).

In the ecological analysis, the focus was on epiphytic species, because they are known as very sensitive bioindicators (Conti & Cecchetti 2001, Thormann 2006) and can thus be used to assess environmental changes over time. Beech (*Fagus sylvatica*) is the tree hosting the highest bryophyte and lichen diversity in the Czech Republic. This tree was the most common broadleaf tree in Czech forests in 2019, covering almost 9% of forested land. In addition, stands of *Fagus sylvatica* were intensively explored in the last few years, so the number of records is higher than for other trees. Beech is followed by sycamore (*Acer pseudoplatanus*), which is a natural admixture in various, mainly montane woodlands, including old-growth and primeval forests very rich in epiphytes. Spruce (*Picea abies*), the third/fourth richest tree for bryophytes/lichens, was the most common conifer in 2019, making up about 50% of Czech forests (Anonymous 2019). Surprisingly the high number of species on spruce is due to the relatively high number of epixylic bryophytes growing on spruce, especially in dense forests in rocky areas. Consistent with our results, beech is repeatedly reported to be generally very important for epiphytic bryophytes and lichens in temperate and boreal regions (Friedel et al. 2006, Jüriado et al. 2009, Fritz & Brunet 2010, Ódor et al. 2013, Hofmeister et al. 2016, Malíček et al. 2018a). The analysis of epiphytic records was robust, especially for lichens based on 41,841 records, which was not entirely true for bryophytes based on 6,146 records. Thus, the interpretation is limited, especially for bryophytes.

Environmental gradients and habitats

Unlike in lichens there is a notable peak in bryophyte records for places with the most common air temperature and altitude in the Czech Republic (Fig. 4A, C). Bryophyte density peak could be in line with the background density peak because bryophytes are stronger competitors of vascular plants than lichens, especially in areas with high vascular plant cover, where bryophytes can coexist with vascular plants, but lichens are excluded (Löbel et al. 2006). Besides the biological reason, there is still a possibility of a bias in the DaLiBor data due to better spatial coverage of bryophyte records than of lichens or stratified location of forest inventory plots, which could shift bryophyte distribution towards random background sampling.

Epiphytic, lignicolous lichens and lignicolous bryophytes were more often recorded at high altitudes, i.e. areas with generally lower temperatures and higher precipitation, compared to saxicolous and terricolous lichens and saxicolous, terricolous and epiphytic bryophytes (Table 4). At least in the case of lichens, this result is connected with the currently increasing species diversity of the epiphytic and lignicolous species with altitude in continental Europe (Nascimbene & Marini 2015, Bässler et al. 2016). In addition, primary data were collected preferentially in protected areas and old-growth forests (Fig. 5,

Table 3), which are more abundant in mountain areas in the Czech Republic. The proportion of forested landscape is generally lower at low altitudes (Romportl et al. 2013), where woodlands are more fragmented due to much stronger historical as well as recent influence of forest management. These parameters are closely associated with bryophyte and lichen species diversity. On the other hand, rocky habitats seem to be more frequent in lowland and at middle altitudes, for example in river valleys, karst and sandstone areas, in contrast to many densely forested highlands poor in exposed rocky substrates.

Natural beech forests and coniferous plantations in the Czech Republic are dominated mostly by *Picea abies*, and are the two richest habitats in terms of the number of records for both common and Red-listed bryophytes and lichens (Fig 5). Beech forests are naturally very rich in lichens, especially *Fagus sylvatica* (see Fig. 3 and the discussion section Substrate strategy above). In contrast, managed forests are usually poor in bryophyte and lichen diversity. Therefore, three possible explanations are proposed for the high number of bryophyte and lichen records: (i) coarse habitat classification, (ii) species-rich managed forests in some areas, (iii) rich occurrence of Red-listed species on *Larix decidua* (lichens only). Coniferous plantations may often include groups of old trees or even fragments of old-growth forests that are important substrates for Red-listed species. In addition, the plantations can also include many species rich microhabitats such as dead trees, other trees intermixed, streams and rocks. Managed spruce forests may in some cases harbour a high diversity due, for example, to the spreading of rare species from surrounding old-growth stands, or maybe the first generation of a forest after the cutting down of old-growth forest. *Larix decidua,* which is a common tree in coniferous plantations, may be quite rich in a number of Red-listed lichens. It is one of the favourable substrates for several genera of macrolichens (Otte 2012, Šoun et al. 2017).

Finally, our data may be biased as coniferous plantations are the most common type of forest in the Czech Republic. This could play a significant role, especially when planted spruce cover complex landscapes with streams and rocky habitats, which would be rich regardless of the type of forest. However, there is a big difference between spruce monocultures (e.g. mountains, wetlands) and stands with other tree species, typical of low altitudes, which usually harbour a much lower diversity and number or Red-listed species (Fig. 9). This is similar to vascular plants reflecting landscape history (Divíšek et al. 2020).

Case 1: Species distribution modelling

In line with other studies (Bourg et al. 2005, Guisan et al. 2006, Callaghan & Ashton 2008, Spitale & Mair 2015), habitat suitability models were useful for increasing the effectiveness of field surveys. Despite the poor performance of the models using Kappa and TSS (Landis & Koch 1977), in a single day in the field, six new localities of two target species were recorded. The low performance could be due to the relatively low number of records used for training, which could bias model performance (Reese et al. 2005, Hirzel et al. 2006). It is, however, shown that despite the small number of records used for training, habitat suitability predictions are ecologically plausible and useful (Proosdij et al. 2016, Mi et al. 2017, Støa et al. 2019). The importance of topographic position and wetness indices together with altitude makes good ecological sense in the sandstone landscape of Bohemian Switzerland. These variables reflect the main gradient in the area between two extremes: cold and wet valley bottoms and exposed rocky tops. Target

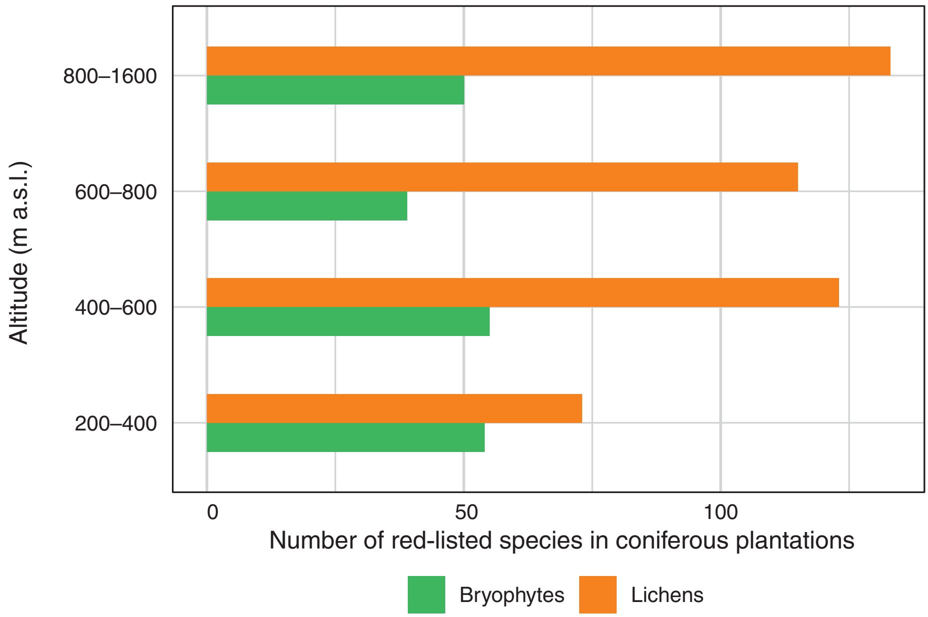

Fig. 9. The number of Red-listed bryophyte and lichen species recorded in "Forest plantations of allochthonous coniferous trees" see Fig. 5. The number of species in coniferous plantations (dominated by spruce trees) is further sorted into 4 bins based on altitude. Especially for lichens, the highest number of species were recorded in forests at high elevations, which are natural stands of spruce.

species occurred mainly in localities on slopes relatively low down in cold, narrow valleys. The distribution of highly suitable habitats on steep slopes in narrow valleys is also visible in the map of habitat suitability (Fig. 6). Such distribution seems to be ecologically relevant based on the expert-based map assessment. This indicates the potential of DaLiBor data for modelling habitat suitability, which could be useful especially at high resolution for large areas and when there is a high number of predictors as the expert-based assessment then starts to be extremely time-consuming or even impossible.

Case 2: Changes in the abundance of species over time

Changes in the distribution of bryophyte and lichen taxa over time in DaLiBor, were recorded. There was an unexpected decrease in occupied quadrants of the mapping grid after the year 2000, which is more likely to be an artefact than attributable to their ecology. The decrease in bryophytes in quadrants after 2000 could be connected to a decrease in bryological surveys recorded in the Database of Czech Forest Classification system. This explanation is further supported by the significant decrease in the records of forest species (e.g. *Dicranum polysetum, Leucobryum glaucum*) after 2000. In contrast, with the decrease in the number of records after 2000 there was an increase, for example, in aquatic moss *Fontinalis antipyretica* and air quality sensitive species such as *Lewinskya speciosa*, *Orthotrichum pumilum* and *O. diaphanum* (see Fig. 7C, D and Supplementary Fig. S1). The increase in these species could have ecological reasons (environmental pollution decreased after 2000), which were also important for lichens.

Epiphytic lichens with the highest number of occupied quadrants recorded before 2000 are three members of the *Lecanora subfusca* group (Fig. 8A), which is a bias resulting from the national revision of this group by Malíček (2014). The rest of the list contains a large proportion of common and easily recognizable macrolichens of the family *Parmeliaceae* and two species of *Ramalina*. In contrast, the list of the commonest epiphytic lichens after 2000 represents very well the current picture of communities in central-European landscapes, which are dominated by ubiquitous, acidophilous and nitrophilous species. The frequent occurrence of acidophilous lichens (e.g. *Lecanora conizaeoides*, *Hypocenomyce scalaris*, *Coenogonium pineti*) is associated mainly with widespread coniferous plantations and boosted by acid rain in the past (Hruška & Kopáček 2005). Spreading of nitrophilous species (e.g. *Physcia tenella*, *Xanthoria parietina* and *Amandinea punctata*) is favoured by strong eutrophication, especially from a dry deposition dispersed by wind, which recently seems to be one of the most important determinants of lichen communities (Łubek et al. 2018).

The results on the distributions of species could be strongly influenced by the character of the data in DaLiBor. For example, in the case of lichens, DaLiBor after 1990 includes many detailed records, whereas before 1990 they are very fragmented. Therefore, the most abundant lichens before 2000 (Fig. 7) are mainly various species of *Cladonia* and *Cetraria islandica*, which originated from the Database of forest typology and the Czech National Phytosociological Database. This is also the case for bryophytes for which the number of records is influenced by forest inventories, containing mainly large, easily identifiable forest taxa. The list of the most common lichens after 2000 seems to be closer to reality and there is no important bias in the data.

Case 3: Atlas of Czech lichens

Online atlases of lichens are available mainly for European countries and larger regions. A more or less interactive interface is available for Belgium, Luxembourg and northern France (Diederich et al. 2022), Italy (Nimis & Martellos 2021), the Netherlands (NDFF 2022), Switzerland (Stofer et al. 2021) and the Alps (Nimis et al. 2018). By comparison, the Czech atlas is more detailed and complex. For example, the resolution of distributional maps is very high (quadrants of ~6 × 6 km) and it is possible to examine individual records (locality, substrate, date, source, etc.) in both Czech and English. In addition, records are marked in colour, according to their credibility and recent/historical records can be distinguished on maps using the moveable timescale.

Conclusions

The database of Lichens and Bryophytes of the Czech Republic (DaLiBor) is the first Czech database specialized on bryophytes and lichens. It is administered by experts in bryology, lichenology, using information technology. In addition to the basic benefit of unifying the records into a standardized form, they were also enhanced using advanced methods, such as Artificial Neural Network substrate classification or GIS analysis. The three case studies reveal how integration of occurrence records from fragmented national sources can be beneficial. DaLiBor is likely to be the most important source of floristic and biodiversity data for research at a national scale and also for studies on ecology, biogeography and taxonomy.

Supplementary materials

Table S1. – DaLiBor Substrate2 sub-categories.
Table S2. – Environmental factors used for species' distribution modelling.
Table S3. – Meteorological data used in the gradient analysis.
Fig. S1. – Increase/decrease in DaLiBor species after the year 2000.

Supplementary materials are available at www.preslia.cz

Acknowledgements

We thank Milan Chytrý and Ilona Knollová for help with incorporating the Czech National Phytosociological Database records and Jan Kučera for expert consultations. We thank Zdeněk Palice, Jan Rydlo, Zuzana Sejfová, Ilona Sommerová, Jan Vondrák, Jak Kučera, Milan Marek, Ivana Marková, Táňa Štechová, Pavel Dřevojan, Petra Hájková, Michal Hájek, Eva Holá, Martina Procházková, Václav Šulc and Zdeňka Konopová for providing and processing data. This study was supported by the long-term research development project no. RVO 67985939 and by projects TH03030469 and TH02030644 provided by the Technology Agency of the Czech Republic.

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DaLiBor – Databáze lišejníků a mechorostů České republiky

Údaje o výskytu druhů centralizované v elektronických databázích jsou v současné době základním zdrojem dat pro účely ochrany přírody a vědecké výstupy v různých biologických disciplínách. Většina údajů o mechorostech a lišejnících z ČR doposud nebyla snadno dostupná, což byl hlavní impulz k vytvoření Databáze lišejníků a mechorostů České republiky (DaLiBor; https://dalibor.ibot.cas.cz), která je volně dostupná s podmínkou uvedení zdroje v souladu s licencí Creative Commons (CC-BY-SA). Prostředí databáze DaLiBor poskytuje infrastrukturu pro standardizaci, validaci a editaci záznamů, a to mimo jiné i s využitím neuronových sítí. Zároveň umožňuje jejich sdílení a analýzu. Pro účely tohoto článku jsme pracovali s 596 935 údaji dostupnými v databázi DaLiBor k červenci 2021, konkrétně s 473 690 (79,4 %) záznamy o mechorostech a 123 245 (20,6 %) záznamy o lišejnících. Mapové výstupy ukázaly, že data o mechorostech pokrývají celé území ČR, zatímco ta o lišejnících zcela chybí v poměrně rozsáhlých oblastech. Potvrzen byl význam chráněných územích, jejichž diverzita v rámci studovaných skupin byla výrazně vyšší. Analýzy také poukázaly na větší počet epifytických a epixylických druhů ve vyšších polohách oproti saxikolním a terikolním taxonům, k nimž existuje více údajů z níže položených území. Pro mechorosty i lišejníky byl stromem s nejvyšším počtem zaznamenaných druhů buk lesní (*Fagus sylvatica*). Nejvyšší počet údajů, a to včetně druhů z Červeného seznamu, pochází z přirozených bučin a hospodářských jehličnatých lesů. Mimo tyto popisné analýzy uvádíme navíc tři příklady využití standardizovaných dat z databáze. Prvním je predikční model rozšíření druhů, který pomohl najít šest nových lokalit mechorostů *Dicranum majus* a *Polytrichastrum alpinum* během jediné návštěvy terénu. Druhým je analýza abundancí mechorostů a lišejníků v čase, která odhalila vysoký podíl acidofilních druhů a šíření nitrofilních druhů v současných společenstvech. Posledním příkladem využití dat z DaLiBora je online interaktivní Atlas lišejníků ČR (https://dalib.cz), jehož cílem je shrnutí dostupných informací o přibližně 1750 druzích známých z ČR.

How to cite: Man M., Malíček J., Kalčík V., Novotný P., Chobot K. & Wild J. (2022) DaLiBor: Database of Lichens and Bryophytes of the Czech Republic. – Preslia 94: 579–605.

Preslia, a journal of the Czech Botanical Society

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