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MGR. MATĚJ MAN

Forest bryophytes and microclimate

Lesní mechorosty a mikroklima

Doctoral thesis / Disertační práce

Supervisor / Školitel: doc. Ing. Jan Wild PhD.

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PROHLÁŠENÍ

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem řádně uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla využita jako závěrečná práce k získání jiného nebo obdobného druhu vysokoškolské kvalifikace.

Pro jazykové korektury a zlepšení čitelnosti textu této práce jsem využil jazykový model GPT 4.o. Prohlašuji, že jsem tento nástroj nevyužil k nahrazení žádných výzkumných úkolů, jako je interpretace dat nebo vyvozování vědeckých závěrů.

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Motivation

Since childhood, I have been interested in nature. I remember the moment I got my first magnifying lens at age five. From that moment, I have been fascinated by all the tiny aspects of nature. My passion for these tiny creatures even increased when I received my first kid's microscope. I distinctly remember the feeling when I saw plant cells for the first time in my life: the cells of a Mnium moss leaf. Many years later, at university, I rediscovered those old memories while participating in bryology and lichenology lectures, which captivated me. I was fascinated by the micro-universe of bryophytes and lichens, leading me to focus on bryophytes in my further studies.

A pivotal moment was meeting the great people from the Department of Geoecology, Institute of Botany, whose course on geographic information systems I attended during my studies. I started to work with them, and they introduced me to the fascinating world of forest ecology and spatial analysis with microclimate data. Then, I started asking questions connected to ecological processes and microclimate below the forest canopy, considering bryophytes as ideal model organisms.

At the beginning of my journey, I did a lot of bryophyte sampling myself and compiled bryophyte and lichen records from existing digital resources. I was surprised by how fragmented the data on the occurrence of Czech bryophytes and lichens was. Another surprise was the level of effort required to gather and standardize the occurrence data, but this effort paid off. The resulting standardized DaLiBor occurrence database allowed me to start answering some significant questions.

Connecting bryophyte occurrences with microclimate data requires handling microclimate time series, which was quite challenging for me. Fortunately, I could build upon the extensive knowledge of my colleagues, who had developed various methods, scripts, and routines for cleaning, pre-processing, validating, joining, and aggregating microclimate data. They also had ideas and approaches for calculating relevant microclimate variables. Being someone who values open research and skill-sharing, I collected existing knowledge, connected the right people, and together we created myClim, an R package dedicated to handling microclimate time series and calculating relevant microclimate variables.

After dealing with the maintenance and data handling of over a thousand localities equipped with one or more microclimate loggers across the Czech Republic, I began to question whether there was a suitable, cheaper, and easier-to-obtain proxy that could capture the effect of microclimate on forest understory bryophytes. Going deeper into this fundamental question, we also specifically asked which microclimate variables are most important in affecting temperate forest understory bryophyte diversity and community composition. From physiological and experimental studies, it is well known that bryophytes are generally sensitive to local conditions, their physiological processes are coupled with available liquid water on their surfaces, and they are more limited by high than low temperatures. However, very little is known from in situ measurements and observations. What role do soil moisture, relative air humidity, or vapor pressure deficit play, respectively? These were the questions I aimed to resolve in my dissertation.

Dedication

The work on my dissertation allowed me to meet inspiring people worldwide, make lifelong friends, gain skills I never thought I could achieve, and visit many beautiful places. I am very grateful to the special people from the Institute of Botany, Department of Geoecology, who helped me grow in research by sharing their ideas, skills, and code, giving me critical and constructive feedback, and providing the background for developing my own ideas and projects. First and foremost, I would like to thank Jan Wild and Martin Kopecký, who supervised my dissertation research from my first steps in academia to now. From them I have learned many valuable skills and habits that I will try to follow lifelong.

Thank you, Áňo, for your helpfulness and passion for bryophytes. Thank you, Čingisi, for your inspiring statistical and scripting skills. Thank you, Honzo, for your enthusiasm and inspiring scientific management skills. Thank you, Jano, for showing me that scientific politics and gender aspects are also important parts of our work. Thank you, Jirko, for your help with geocoding and remote sensing. Thank you, Martine, for your ability to generate great research questions and master critical thinking. Thank you, Pepíku, for your encouraging feedback and HW/SW help. Thank you, Terko, for your unbelievable organizing skills and knowledge of local beers. Thank you, Vítku, for your inspiring approach to interpersonal interactions in research. Thank you, Vojto, for your friendly 24/7 support and your programming skills, which allowed us to shine in the global microclimate community. Thank you, Zdenko, for your optimism and the hours of manual work you invested into the tasks I asked for.

A big thank you goes to the group of great people from Charles University, Department of Botany, who allowed me to stay in close touch with the university community and students. Teaching and supervising student theses and attending many field excursions and social events were among the greatest experiences of my study years. Thank you, Fando, for reminding me that nature is powerful and beautiful. Thank you, Davide, for your accurate but friendly feedback. Thank you, Hajnej, for introducing me to the universe of micro lichens. Thank you, Ivko, for inspiring assertive communication in research. Thank you, Jirko, for showing me a completely different way of writing papers than I had ever experienced. Thank you, Kubo, for all the great music you played for me during our studies. Thank you, Lado, for all the coffee and discussions we had together and the beautiful places you showed me. Thank you, Ondro, for supporting and letting me develop my teaching ideas. Thank you, Patriku and Tomáši, for your enthusiasm and help in the moments I wanted to give up writing. Thank you, Zdeňku, for the most formative experience in the field that drove my attention to bryophytes.

I would also like to thank the great people from the Czech Bryological and Lichenological Section of the Czech Botanical Society. Thank you, Betty, Eliško, Evčo, Evko, Honzo, Ivko, Jitko, Julko, Peksiči, Pepo, and Svatko, for great company on field excursions, many inspiring discussions, and useful feedback.

I am very grateful to my family for their constant support and encouragement, even when scientific conferences or field trips took precedence over family holidays, and especially when work-life balance was not well balanced at all. Thank you, Žando, Lotko, and Ludvo.

Abstract

Bryophytes, often overlooked yet crucial and sensitive components of terrestrial ecosystems, play essential roles in forest understories by providing ecosystem services such as moisture retention and nutrient cycling. Their high sensitivity to environmental conditions makes them ideal model organisms for studying ecological processes under forest canopies. Forests cover a significant portion of terrestrial ecosystems and possess unique microclimate that buffer climatic extremes, differing substantially from open land. However, most climate data originate from meteorological stations outside forests, creating a potential blind spot in understanding climate change effects within forest interiors. Despite the potential for advancing forest understory ecology by combining bryophyte records with microclimate time-series, such data have rarely been available together until recently. The advent of affordable microclimate loggers has increased data availability but introduced new challenges, such as the lack of standardized measurement guidelines and common practices for calculating microclimate variables. Consequently, significant gaps remain in our understanding of microclimate effects on forest understory organisms.

To address the gap in bryophyte data availability, we established the Database of lichens and bryophytes of the Czech Republic (DaLiBor), which compiles and harmonizes all available digital data, resolves different taxonomic concepts, and validates metadata, including partial validation of occurrences themselves (Paper 4). To standardize microclimate time-series data handling, we developed myClim, an R package that provides reproducible methods for handling microclimate time-series data from loggers (Paper 3). A key question in microclimate ecology is whether in-situ measurements, which are expensive and demanding, are necessary or if cheaper proxies suffice. Our research demonstrates that no proxy fully captures the microclimate effects on forest understory bryophytes. The most critical drivers shaping bryophyte communities are growing degree days, maximum air temperature, and mean soil moisture (Paper 1). We also found that vapor pressure deficit, particularly its temperature component, significantly influences bryophyte communities at the landscape scale (Paper 2).

In conclusion, we found that near-ground microclimate is a crucial driver of temperate forest bryophytes. Specifically, we identified vapor pressure deficit, growing degree days, maximum air temperature, and mean soil moisture as the most important factors. Our findings are novel because they are based on field studies with in-situ measured variables, contrasting with existing knowledge primarily derived from physiological and manipulative experiments. Our results fill a gap in understanding the processes in forest understories affected by climate change and disturbances, traditionally based on macroclimatic data from weather stations, which are largely irrelevant for forested areas.

Abstrakt

Mechorosty, často přehlížené a zranitelné, přesto velmi důležité, hrají zásadní úlohu v terestrických ekosystémech, a to zejména v lesích. Zajišťují totiž nepostradatelné ekosystémové služby jako například zadržování vody či koloběh živin. Jejich vysoká citlivost na vnější podmínky prostředí z nich činí ideální modelové organismy pro studium ekologických procesů v lesním podrostu. Lesy pokrývají významnou část souší naší planety, a hostí unikátní mikroklimatické podmínky s mírnějšími výkyvy v porovnání s klimatem mimo les. Avšak naprostá většina našich poznatků o klimatu je postavena na datech z meteorologických stanic, které jsou cíleně umisťovány mimo les. To může vést ke zkreslenému porozumění působení globální změny klimatu v lesních ekosystémech. Přestože výzkumy mechorostů v kombinaci s měřeným mikroklimatem mají potenciál přinést v lesní ekologii nové poznatky, výskytová data mechorostů a měřeného mikroklimatu nejsou zpravidla dostupná. Současný rozmach levných senzorů pro měření mikroklimatu výrazně zvýšil množství terénních dat, což přineslo ve výzkumech i nové výzvy. Chybí například společný standard pro měření a výpočty mikroklimatických proměnných. Nedostupnost dat a chybějící metody tak dlouho bránily širšímu porozumění mechanismům působení mikroklimatu na organismy v lesních ekosystémech.

Kvůli dosavadní nízké dostupnosti výskytových dat mechorostů jsme vytvořili Národní výskytovou databázi mechorostů a lišejníků ČR (DaLiBor), kde jsme shromáždili veškerá dostupná digitální data, sjednotili a pročistili jejich nomenklaturu včetně metadat, část dat jsme také expertně validovali (článek č. 4). Pro práci s mikroklimatickými daty jsme pak vytvořili R knihovnu myClim která umožňuje standardizované, reprodukovatelné zpracování časových řad z mikroklimatických senzorů (článek č. 3). Základní otázkou v mikroklimatické ekologii je, zda skutečně potřebujeme drahá a složitá měření mikroklimatu in-situ, nebo existuje nějaká levnější alternativa? V našich výzkumech jsme zjistili, že není žádná dostupná, levnější proměnná, která by mohla plně nahradit vliv měřeného mikroklimatu na lesní vegetaci. Nejvýznamnější proměnné pro lesní mechorosty jsou: suma efektivních teplot, maximální teplota vzduchu a průměrná půdní vlhkost (článek č. 1). Dále jsme zjistili, že sytostní doplněk, specificky jeho teplotní složka, má na krajinné škále významný vliv na složení společenstev mechorostů v temperátním lese (článek č. 2).

Z mé práce vyplývá že, přízemní mikroklima má určující vliv na společenstva mechorostů v temperátním lese. Zejména sytostní doplněk, efektivní suma teplot, maximální vzdušná teplota a průměrná půdní vlhkost hrají v lesích klíčovou roli. Naše zjištění jsou nová zejména proto, že vycházejí z terénních měření mikroklimatu na rozdíl od dosavadních znalostí postavených na fyziologických a skleníkových experimentech. Naše výsledky doplňují dosavadní porozumění procesům v lesním podrostu v kontextu globální změny klimatu a disturbancí, tradičně založené na měření z meteorologických stanic. Meteorologická data však mohou být pro lesní ekosystémy irelevantní, protože pochází většinově z oblastí mimo les.

Aims

This thesis aims to enhance our understanding of the processes occurring under the tree canopy in temperate forests by using in-situ measured microclimate and bryophytes as model organisms. Forest microclimate is a critical driver that influences the diversity, community composition, and physiological processes of bryophytes. However, its study has been limited due to measurement and data handling challenges. This research aims to bridge the gap between existing findings, which are mainly based on macroclimate data from weather stations, and the real-world conditions experienced by understory organisms.

The second aim of this thesis is to address the methodological challenges associated with measuring and analysing forest microclimate data and bryophyte records. This includes: 1. The development and application of standardized protocols for microclimate data processing. 2. The creation of a harmonized, ready-to-use database of bryophyte records in the Czech Republic.

Overall, the thesis seeks to provide a detailed understanding of how microclimate influences forest bryophytes, thereby contributing to broader ecological knowledge. By establishing robust methodologies and showcasing the importance of in-situ measured microclimatic data, this research aims to advance the field of forest microclimate ecology and its applications.

Introduction

1. The bryophytes

1.1. Bryophytes as research objects

Bryophytes are traditionally understudied, and their role in ecosystems has been underestimated compared to vascular plants (Kutnar *et al.*, 2023). It is evident across many research fields. For example, the Global Biodiversity Information Facility (GBIF) hosts approximately 450 million records of vascular plants (around 390,000 known species) but only about 14 million records of bryophytes (approximately 20,000 known species). Similarly, the most comprehensive database of vascular plant occurrences in the Czech Republic, PLADIAS, contains around 15 million records (about 3,500 species on the national checklist). In contrast, the bryophytes and lichens database DaLiBor, the most complete national resource (Paper 4), hosts about 0.6 million records of bryophytes (approximately 900 species on the national checklist).

The imbalance between research focused on bryophytes and vascular plants could be attributed to the much smaller community of bryologists compared to those studying vascular plants in most countries (with exceptions such as the British Bryological Society). Although the national species pool of bryophytes is usually lower than that of vascular plants, bryophytes are typically more challenging to identify (Renner *et al.*, 2017), often requiring microscopic examination and leaf or stem cross sections. Furthermore, bryophytes lack the attractive features of vascular plants, such as colorful, fragrant flowers, tasty fruits, or nutrient-rich roots, and they do not produce commercially valuable secondary metabolites. The lack of interest in bryophytes is evident in nearly all scientific fields, where bryophyte research generally lags far behind that of tracheophytes.

1.2. Importance in ecosystems

Despite receiving less research attention, bryophytes provide important ecosystem services **Fig. 1**, especially in boreal areas and under forest canopies (Lindo & Gonzalez, 2010; Eldridge *et al.*, 2023). In boreal regions, they play a crucial role in nitrogen fixation through their symbiosis with cyanobacteria, responsible for about 65% of the total available nitrogen fixation in the ecosystem (DeLuca *et al.*, 2002). Additionally, they significantly contribute to global carbon sequestration, particularly through peatlands, which cover only about 3% of terrestrial ecosystems but hold up to 33% of global organic carbon (Yu *et al.*, 2011; Yu, 2012). Beyond their role in nutrient cycling, bryophytes influence water circulation and local microclimate (Jaroszynska *et al.*, 2023). For instance, epiphytic bryophytes in tropical forests can retain more than 15 tons of water per hectare, which would otherwise run off, causing a significant cooling effect on the entire ecosystem (Pypker *et al.*, 2006).

In temperate forests, the water-holding capacity of epiphytic bryophytes is also significant, reaching about 1 ton of water per hectare (Porada *et al.*, 2018; Hembre *et al.*, 2021). Besides retaining water, bryophytes have been proven to prevent soil erosion in temperate forests (Gall *et al.*, 2022), play an important role in nitrogen fixation (DeLuca *et al.*; Arróniz-Crespo *et al.*, 2022), and contribute to carbon sequestration (Turetsky, 2003; Elbert *et al.*, 2012; Janyszek *et al.*, 2015; Yang *et al.*, 2023). These essential environmental services provided by temperate forest bryophytes may be at risk due to ongoing climate change. Existing studies have shown that bryophytes' response to climate change (warming) can be very different from that of vascular plants (Kiebacher *et al.*, 2023; Virtanen *et al.*, 2024). Bryophytes seem to be more sensitive to warming than vascular plants and thus indicate changes earlier and more explicitly (Zellweger *et al.*, 2015; Becker Scarpitta *et al.*, 2017; Becker-Scarpitta *et al.*, 2022). Contrary to the prevalent view about bryophytes' sensitivity to climate change, there are also indications that, like tracheophytes, bryophytes have the capability to buffer against climate change (Slate *et al.*, 2024). Assessing the impact of climate change on temperate forests and their understory is a key argument for involving bryophytes in research. The absence of bryophytes from many macro- and microclimate studies represents a significant gap in microclimate ecology. My dissertation research aims to fill this gap.

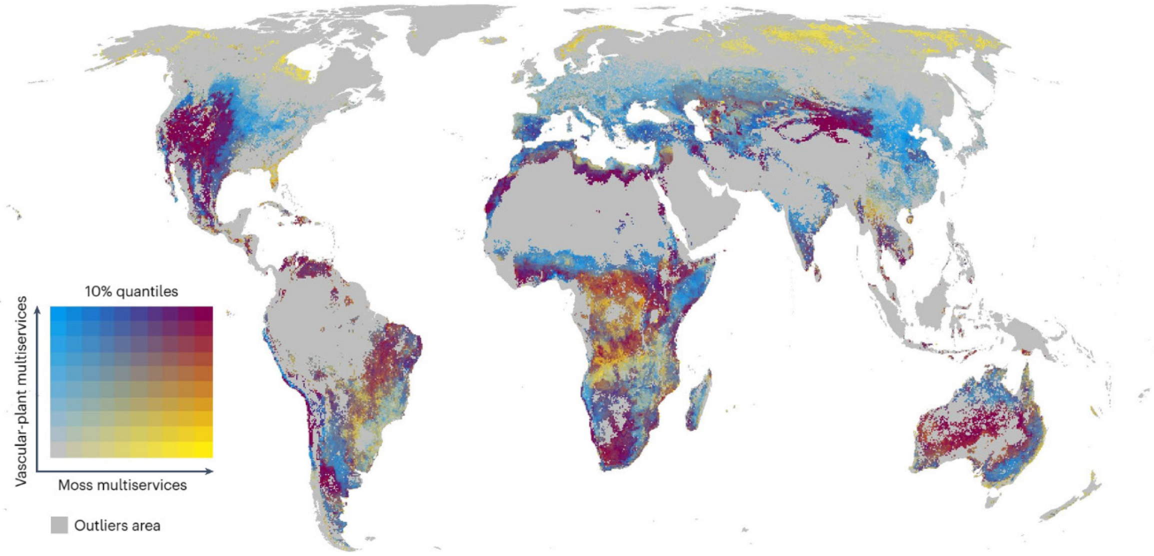

Figure 1 Predicted contribution of vascular plants and mosses to global ecosystem multi-services. According to Eldridge et al. (2023).

1.3. Bryophytes as model organisms

The high sensitivity of bryophytes to climate change and local microclimate (Giaccone *et al.*, 2019; Tinya *et al.*, 2021) stems mainly from their unique strategies to deal with drought stress, which differ significantly from those of vascular plants (Proctor *et al.*, 2007b). Bryophytes lack a fully connected, internal, lignified water-conducting system, internal water and sugar storage organs, and active stomata to regulate water loss (Schofield, 1981). The combination of these features, along with their shade tolerance (Martin & Adamson, 2001) and ability for long-distance diaspore dispersal (Wolf *et al.*, 2001; Muñoz *et al.*, 2004), makes them ideal models for studying forest understory processes connected to environmental factors.

However, there are other features typical of bryophytes that need to be considered when using them as model organisms, such as the influence of substrate availability and diversity (Söderström, 1993; Chen *et al.*, 2017) and the strong effect of substrate pH (Mills & Macdonald, 2005; Zellweger *et al.*, 2015; Ilić *et al.*, 2023). Despite the crucial role of substrate in bryophyte studies, this information is usually missing in occurrence databases that are not specifically dedicated to bryophytes or lichens. Addressing this gap was one of the key motivations for creating a separate national database for bryophytes and lichens, DaLiBor, rather than using the existing database for vascular plants, PLADIAS.

The latter cannot store information on substrate type, category, or chemical data. Information about substrate categories allowed us to filter species growing on specific substrates, such as soil, and analyse only those guilds to filter out substrate influence (Papers 1 and 2). This information is also potentially useful as a covariate in ecological analysis.

Despite the challenges with substrate and pH, studies using forest bryophytes as model organisms have recently emerged, helping to increase our understanding of processes under forest canopies. Bryophytes are useful models for gaining insights into the thermal heterogeneity of small-scale forest stands, estimating the modification of local microclimate by plants (Canali *et al.*, 2024), critically assessing ecological indicator values used for inferring understory microclimate (Gril *et al.*, 2024), and estimating which global change factors most affect forest understory plants (Virtanen *et al.*, 2024). All these studies build on the assumption that bryophytes are sensitive to forest understory microclimate due to their morphological, physiological, and ecological characteristics.

Interestingly, existing studies with bryophytes and microclimate often do not focus on the specific microclimatic factors affecting bryophyte community composition and diversity (e.g., maximum, mean, minimum temperature, moisture and humidity of air or soil). Identifying these specific factors can help direct further research and applications, such as mapping specific factors or managing forests to maintain microclimate in nature conservation. One of the main aims of my dissertation research was to fill this gap and identify the microclimatic factors the most affecting the communities of forest bryophytes (Papers 1 and 2).

1.4. Relevance of microclimate

Although most studies relate forest bryophytes to free air macroclimate (Ruas *et al.*, 2015; Dahlberg *et al.*, 2020; Collart *et al.*, 2023), a better approach would be using near-ground microclimate data, as it is more relevant in forest interiors (Bramer *et al.*, 2018) and more directly affects understory organisms (Guisan & Zimmermann, 2000; Dahlberg *et al.*, 2020). Macroclimate is usually measured by weather stations and is traditionally used for bioclimatic variables calculation (Fick & Hijmans, 2017; Karger *et al.*, 2017), which are rather proxies for the conditions experienced by organisms under the forest canopy (De Frenne *et al.*, 2019; Zellweger *et al.*, 2019a).

The lower relevance of weather station data for forest bryophytes is also due to methodological guidelines that exclude forested areas as suitable sites for placing weather stations (World Meteorological Organization, 2008). It causes a lack of weather station data from forest interiors (De Frenne & Verheyen, 2016). Moreover, understory microclimate is highly variable in space, creating a fine-scale mosaic of various temperature and moisture conditions in contrast with free air conditions. I can confirm this based on my ecological analysis of the influence of microclimate on forest understory bryophytes for Papers 1 and 2. We found that the explained variation in bryophyte community composition and species richness was always slightly higher at fine scales when compared to larger phytocoenological samples, e.g., 1 m² versus 3 or 6 m² (unpublished results).

Research on bryophytes as model organisms has demonstrated that their physiological processes are directly influenced by the microclimatic conditions they encounter, such as temperature and moisture levels in the air or substrate (Shaw & Goffinet, 2000). Most evidence about specific microclimatic factors affecting bryophytes comes from laboratory or greenhouse manipulative experiments. The largest number of studies dealt with temperature, as it is the easiest variable to measure but not necessarily the most important. Temperature affects bryophyte photosynthetic rate, respiratory rate, reproductive timing, growth, development, and productivity (Glime, 2017b). An interesting fact about bryophytes, known mainly from controlled condition experiments, is that they can have photosynthetic gain at temperatures below 0°C, with some species even as low as -10°C (Rutten & Santarius, 1993), which is a significant difference compared to tracheophytes. The photosynthetic temperature optimum of bryophytes is generally lower than that of tracheophytes, ranging between 15°C and 25°C (Furness & Grime, 1982; He *et al.*, 2016), even for tropical species or those adapted to very hot conditions (Frahm, 1990). Most of bryophytes stop their photosynthesis during hot summer events and become dormant, waiting for colder conditions. Therefore, forest understory bryophytes benefit from the tree and shrub canopy's buffering effect on microclimate (De Frenne *et al.*, 2019; Zellweger *et al.*, 2019a; Kašpar *et al.*, 2021; Stickley & Fraterrigo, 2021).

Accepting the thesis that microclimate is more relevant for forest understory bryophytes than macroclimate introduces many new unknowns. Recent discussions have highlighted the unresolved nature of the effect of microclimate data sources. The debate centres on whether it is necessary to invest in direct in-situ measurements or if statistically (Haesen *et al.*, 2021) or mechanistically (Maclean *et al.*, 2019) modelled microclimate data, or other affordable proxies, are sufficient. My dissertation research significantly contributed to this ongoing discussion, showing that the effect of microclimate on forest understory bryophytes cannot be fully captured by any affordable proxies, such as topography or canopy structure (Paper 1).

The role of in-situ measured microclimate in shaping the diversity and distribution of forest bryophytes has become more studied and shown to be crucial with the recent boom in using microclimate loggers, not only those measuring temperature (Kemppinen *et al.*, 2024). Affordable, durable loggers have allowed for much more intensive microclimate measurement within forest interiors than ever before. The use of in-situ measuring automatic microclimate loggers confirmed our knowledge on the effects of temperature, moisture, and light on bryophyte physiology and ecology from previous controlled condition experiments. Furthermore, in-situ microclimate data appeared to be an indispensable part of forest bryophyte ecology (Gril *et al.*, 2024), allowing us to investigate which microclimatic variables are the strongest drivers of diversity, community composition and distribution of forest bryophytes (Paper 1 and 2).

2. The microclimate

Studying microclimate is essential for understanding how forest understory ecosystems respond to climate change. Microclimate plays a major role in shaping local biodiversity and the makeup of ecological communities. However, there are several challenges in this field, especially when it comes to measuring microclimate in forests, managing the data collected, and calculating microclimatic variables.

2.1. Insufficient microclimate data

Historically, obtaining in-situ measured microclimate data, especially in forest interiors, was extremely demanding. Consequently, microclimatic studies, particularly those focusing on bryophytes, were rare (Cantlon, 1953; Troják, 1960; Billings & Anderson, 1966). Researchers had to rely on analogue measuring devices for temperature or radiation (e.g., thermometers, pyranometers), which required regular visits depending on the desired temporal resolution. Laboratory processing was needed for soil moisture measurements (e.g., gypsum blocks, Kopecky's cylinders). The advent of automatic digital measuring devices allowed ecologists to collect microclimate data more intensively. Early forest microclimate observations with digital loggers utilized either a small number of expensive, precise scientific loggers developed for laboratory purposes (Frego & Carleton, 1995a,b) or a larger number of affordable but less precise, devices developed for industrial use (Hubbart *et al.*, 2005; Dahlberg *et al.*, 2014; Oishi, 2019; Greiser *et al.*, 2020). Devices specifically designed for biological or ecological research were scarce for a long time.

2.2. Excessive microclimate data

However, there has been a significant surge in in-situ microclimate measuring in recent years thanks to the increasing availability of small-sized, affordable equipment. Besides the growing usage of industrial or agricultural loggers due to the decrease in their price, the rise of microclimate ecology owes much to the advent of microclimatic loggers designed specifically for measuring microclimate variables relevant to organisms, which emerged just in last few years (Mickley *et al.*, 2019; Wild *et al.*, 2019b) and are still emerging e.g., (https://electricblue.eu/; https://x.com/HawksheadDesign). Especially TOMST TMS loggers resembling small herbaceous plant (Wild *et al.*, 2019b) have become prevalent due to their relatively low cost, high durability, and extended battery life. The spread of such devices resulted in the establishment of various microclimate measuring networks, including forest study plots or urban gardens in citizen science projects (e.g., https://curieuzeneuzen.be). The increasing number of researchers measuring in-situ microclimate has led to the foundation of the international initiative SoilTemp (Lembrechts *et al.*, 2020). The recent boom in using microclimate loggers is evident from the metadata of the SoilTemp database **Fig. 2.**

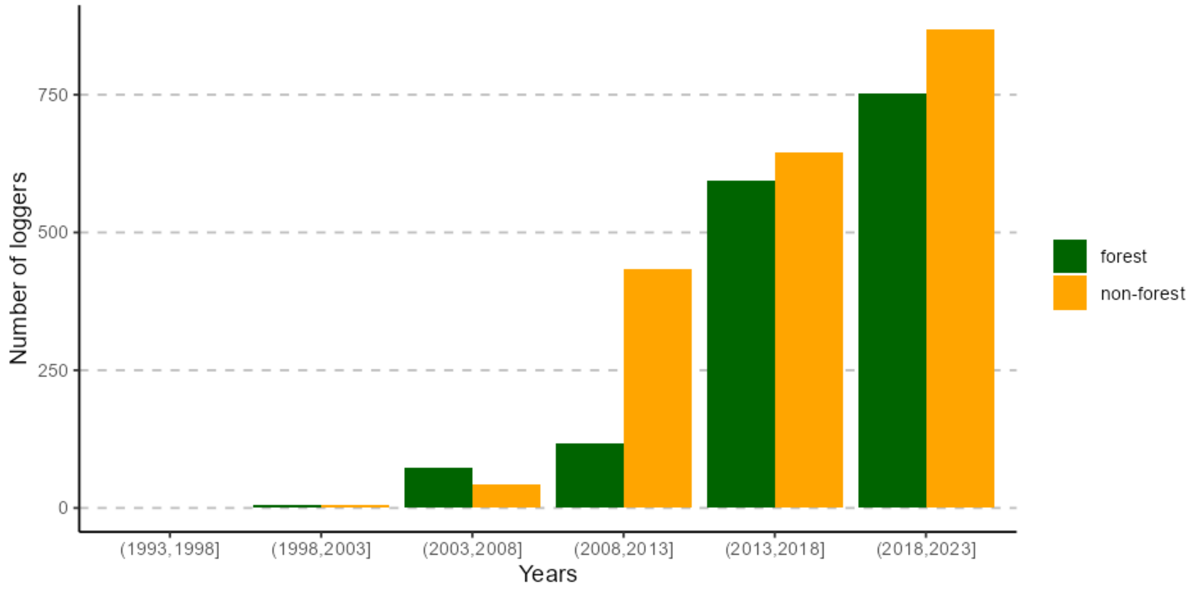

Figure 2 The number of microclimate loggers measuring temperature over time, based on SoilTemp metadata (excluding the "curieuzeneuzen" Belgium citizen science project), illustrates the recent boom in microclimate ecology. The use of microclimate loggers would probably be much more intensive, because not all researchers are willing to be part of SoilTemp and those who are, often does not share all their data.

2.3. Standardized microclimate data handling

The recent boom in affordable loggers has completely changed the landscape of microclimate ecology. What was once a problem of expensive and unavailable in-situ records has transformed into a challenge of missing standards and methods for field research (Holden *et al.*, 2013; Aalto *et al.*, 2024). Researchers now face gigabytes of microclimate time-series data that lack human resources to handle, check, validate, and derive relevant variables. The need for standardization and meta-analysis has become evident (Ilić *et al.*, 2023). To address this gap, we developed myClim, an R package designed to cover the complete workflow for microclimate data handling. It includes reading logger files, validating time-series data, joining and aggregating data, and calculating microclimate variables (Paper 3).

A significant problem in microclimate studies is that each research group or individual researcher employs different approaches to calculate microclimate variables. Although these calculations seem straightforward at first glance, detailed examinations of methods sections in some of the microclimate studies reveal several methodological inconsistencies. For instance, the calculation of maximum temperature varies widely; some researchers may use the simple yearly maximum, others the mean of daily maxima over the year, or some form of yearly or daily percentile like the 95th or 99th. The timeframes used can also differ, with calculations based on single or multiple calendar years, hydrological years, or vegetation seasons.

Similarly, the methods for calculating mean or minimum temperature, soil moisture, and relative air humidity show significant variation. Soil moisture might be reported using raw logger units or converted to some measure of water content, with or without logger calibration and consideration of soil type. For relative air humidity, some studies might use the humidity data directly, while others calculate vapor pressure deficit instead, using varying formulas and records. While some aspects of these methodologies are occasionally well-documented, they are often not, with authors simply noting that they calculated mean or maximum values without further detail.

These issues can now be resolved using myClim, which allows for proper referencing of specific functions used. Thanks to myClim, we can derive microclimate variables for our studies efficiently and reproducibly. The package introduces a set of calculations and equations designed to establish standards for microclimate variable calculations. I have benefited from using myClim in two of my most important ecological studies to date, relating bryophytes with microclimate (Papers 1 and 2). In these studies, we faced the challenge of handling microclimate data from hundreds of loggers and calculating biologically relevant microclimate variables, including air and soil temperatures, air and soil moisture, and vapor pressure deficit (VPD).

3. Key results

My dissertation research highlighted the pivotal role of near-ground measured microclimate in shaping temperate forest bryophyte communities. We identified the key microclimatic factors affecting understory bryophyte communities. Additionally, we significantly contributed to the global microclimate ecology community by creating an R package for the standardised handling of time-series from microclimate loggers. On a national level, my dissertation research led to the development of the much-needed open-source, Creative Commons-licensed database DaLiBor, which compiles almost all digital records of bryophyte and lichen occurrences in the Czech Republic.

Can high-resolution topography and forest canopy structure substitute microclimate measurements? Bryophytes say no.

High-resolution topographic and canopy structure variables are increasingly used in ecological studies, assuming they are a good proxy for the effects of microclimate on organisms. However, clear information on whether this practice is reliable is missing. The poor understanding of how well topographic proxies and vegetation structure can substitute for microclimate effects on species communities has limited ecological research and conservation efforts.

My research addressed this by directly comparing the effects of in-situ measured microclimate with high-resolution topographic data and vegetation structure on forest understory bryophytes. The findings reveal that microclimate, particularly growing degree days, maximum air temperature, and mean soil moisture, are the primary drivers of bryophyte assemblages in temperate coniferous forests. This demonstrates that topographic variables and vegetation structure, even when derived from advanced methods using high-resolution data, cannot fully replace the effects of in-situ measured microclimate.

Temperature-driven variability in vapor pressure deficit controls bryophyte community composition within a temperate forest landscape

The role of atmospheric vapor pressure deficit (VPD) in forest plant communities is largely unknown, creating a significant gap in our understanding of forest understory plant ecophysiology, productivity, and distribution. VPD is becoming a central topic of microclimate ecology due to its direct effect on plant physiology and the increasing availability of microclimate loggers that measure relative air humidity, needed for VPD calculation.

My dissertation research investigated how VPD variability affects forest bryophyte communities across topographically rugged terrain. We also explored which component of VPD has the strongest effect at the landscape scale. Our findings reveal that forest understory VPD varies significantly across the landscape, primarily driven by temperature-induced differences in saturated vapor pressure. Bryophyte species composition closely follows VPD variability, with mesophytic bryophytes in high VPD areas and hygrophilous, boreal, and Atlantic species in low VPD areas. We demonstrate that VPD is a critical driver of bryophyte community assembly, emphasizing its importance in microclimate ecology.

myClim: Microclimate data handling and standardised analyses in R.

In the field of global change biology, microclimate is starting to play a pivotal role. However, the lack of standardised workflows for handling microclimate time-series hampers synthesis across studies and impedes progress.

To address this challenge, we developed myClim, an R package designed for comprehensive microclimate data processing, storage, and analysis. myClim supports the entire workflow—from reading and preprocessing raw logger data to aggregating time-series, calculating ecologically relevant variables, and exporting data for further analysis. It includes features for data aggregation, error detection, measurement calibration, and time-series joining or correction. By enabling standardised data handling and enhancing data sharing, myClim promotes large-scale synthesis efforts, fosters comparability across studies, and enhances the reproducibility of microclimatic research, thereby advancing global change biology.

DaLiBor: Database of Lichens and Bryophytes of the Czech Republic.

Digital data on species distribution are essential for vegetation studies, monitoring, and conservation efforts. Despite the existence of databases, a significant portion of bryophyte and lichen occurrences in the Czech Republic were not widely accessible in standard, machine-readable formats.

To resolve this issue, we developed the Database of Lichens and Bryophytes (DaLiBor; dalibor.ibot.cas.cz) under Creative Commons (CC-BY-SA), serving as an infrastructure for record standardisation, validation, and enhancement, including neural network-based classification. DaLiBor facilitates data sharing and analysis, supporting biodiversity research and conservation. In the paper introducing DaLiBor, we illustrate three case studies utilising DaLiBor's standardised data: 1) species distribution modelling identified new localities of uncommon species; 2) temporal analyses highlighted shifts in bryophyte and lichen community compositions over time; and 3) DaLiBor serves as the primary data source for the online interactive Atlas of Czech lichens (dalib.cz).

4. Discussion

This dissertation addressed several critical gaps in microclimate ecology. Most importantly, we demonstrated that microclimate significantly influences forest bryophyte communities across topographically diverse landscapes. We identified the microclimate variables that are the most ecologically relevant drivers shaping understory bryophyte assemblages. Besides providing new insights into ecological processes, we developed two new tools that significantly facilitate ecological analysis with microclimate time-series and bryophytes.

Following previous successes in the co-development of the widely used microclimate loggers TOMST TMS (Wild *et al.*, 2019b) and the establishment of the largest national database of vascular plant occurrences, PLADIAS (Wild *et al.*, 2019a; Chytrý *et al.*, 2021; Novotný *et al.*, 2022), our focus on methodological development sometimes outpaces our capacity to resolve biological or ecological questions. However, the ability to produce efficient scripts for handling highly complex microclimatic data, establish and maintain SQL databases, and use computation clusters for analysing large spatial datasets is, in my opinion, one of the greatest skills early-career ecologists can gain from their dissertation projects. Such skills promote collaborative and reproducible research, enable fast and efficient analysis and meta-analysis, and allow for the easy upscaling of studies to continental and global scales.

4.1. Ecologically relevant microclimate variables

The relevance of in-situ measured microclimate, especially for sessile and small organisms under the forest canopy, has been traditionally acknowledged. However, studies that empirically proved this assumption based on in-situ measured variables were missing. Therefore, our findings in Paper 1 are pivotal and received significant attention from the microclimate ecology community. Published at the end of 2022, Paper 1 has been cited several times by respected microclimate ecology researchers as evidence that in-situ measured microclimate is crucial for understory organisms. In Papers 1 and 2, we showed that in-situ measured microclimatic VPD, air temperature, and soil moisture are the most important variables driving bryophyte communities.

Similar results were reported from Canadian boreal forests, where vapour pressure deficit, soil moisture, and near-ground air temperature were the key factors influencing understory forest communities (Stewart & Mallik, 2006). Although the authors did not measure microclimate continuously as we did, and their approach differed by using bryophyte growth and vitality rather than community composition and diversity as dependent variables, the general message about the importance of in-situ measured microclimatic variables was consistent across both studies.

Identifying soil moisture as an important microclimatic factor affecting forest bryophyte communities could be surprising, given that bryophytes lack roots capable of absorbing and conducting water like tracheophytes. Therefore, soil moisture likely serves as a proxy for the general humidity conditions of the locality. Water-related microclimatic variables are crucial predictors in forest ecology, particularly for bryophytes. These variables are often correlated and interconnected, making them significant in predicting ecological outcomes. However, they frequently act as proxies for one another. Indirect but easy-to-measure variables often mask the effects of direct factors influencing bryophyte physiology. Considering that my study focuses on temperate forests with some overlap into boreal forests, where soil moisture is a good proxy for overall moisture conditions. This is because the precipitation, which often reaches the soil, and the distance from the water are the main factors driving moisture conditions in this system and they are well mirrored in soil moisture. This contrasts with tropical or cloud forests, where soil and air moisture can be decoupled, because precipitation may not reach the soil through dense vegetation, and high air humidity may not be detected in high soil moisture (Hall *et al.*, 2013; Darby *et al.*, 2016). In temperate forests, soil moisture works well as a proxy, even though bryophytes are more directly connected to air humidity.

The pivotal role of relative air humidity for bryophyte communities has been demonstrated in several recent microclimatic studies. In temperate managed forests, the most important in-situ measured microclimate factors structuring epiphytic bryophyte richness and community composition were relative air humidity and air temperature measured 1.3 m above the ground (Tinya *et al.*, 2009; Király *et al.*, 2013; Ódor *et al.*, 2013). Summer air moisture was identified as the most important driver of epixylic bryophyte community composition in old-growth temperate forests (Táborská *et al.*, 2020).

Although relative air humidity is more relevant than soil moisture for forest bryophytes, its use in ecological studies has also been criticized (Anderson, 1936; Seager *et al.*, 2015). Relative air humidity does not directly indicate the amount of moisture the air can hold or how it affects ecological processes, and it can vary significantly with temperature, making it less reliable in fluctuating environments. Therefore, using vapour pressure deficit (VPD) is preferable because it remains a consistent indicator of moisture stress regardless of temperature changes. This rationale led us to explore VPD in our studies (Paper 2), where we showed its significant influence on bryophytes, consistent with several existing studies. Our research showed that the temperature component of VPD plays a pivotal role on the landscape scale, affecting bryophyte communities. This underlines the importance of temperature on small to medium scales. The importance of near-ground temperature has not only been shown for bryophyte community composition but also for the bryophyte soil diaspore bank of temperate forests (Kövendi-Jakó *et al.*, 2016) and for the precise identification and protection of refugia for forest understory bryophytes, such as old-growth forests in topographically shaded areas (Greiser *et al.*, 2020).

Despite microclimate being a crucial driver shaping forest bryophyte distribution, other known factors, such as substrate or pH, and yet unknown factors, may play important roles, especially in forests with homogeneous topography and canopy structure (Frego & Carleton, 1995a). Therefore, it is desirable to design research on forest bryophytes and microclimate that stays within a small spatial scale while capturing the maximum possible variation of microclimate and habitats in the study system.

4.2. The tools in microclimate ecology

Like many branches of ecological research, microclimate ecology increasingly relies on big data handling. In numerous research fields, new standardized databases have emerged, enabling synthesis and meta-analysis of study subjects, such as occurrence data of lichens (Martellos *et al.*, 2023), the bryophytes trait database (van Zuijlen *et al.*, 2023), or locally in the Czech Republic, the database of pollen profiles (Kuneš *et al.*, 2009) and vascular plants PLADIAS (Wild *et al.*, 2019a). Our database DaLiBor (Paper 4) follows this global trend by being a standardized, machine-readable, Creative Commons resource of occurrence data, enabling further synthesis and application development (e.g., online atlas of Czech lichens, dalib.cz).

Records of bryophytes and lichens are unfortunately often absent from global databases (**Fig. 3**), remaining in local repositories or not being digitalised at all. However, due to their specific environmental requirements, bryophytes and lichens serve as ideal model organisms, particularly valuable for assessing the effects of various microclimate variables. The lack of records in global databases significantly limits the usefulness of platforms such as GBIF for ecological analysis involving bryophytes and lichens, as most results would be artefacts of poor or uneven data coverage. This is especially problematic in analyses of environmental niches that rely on well-sampled occurrences. Figure 3 demonstrates that the absence or low abundance of common forest bryophytes in the Czech Republic, as indicated by GBIF data, does not reflect a true biological pattern when compared with DaLiBor data, which shows these species as widely distributed. This situation is likely similar to that of many other European countries. Therefore, it is crucial to build local and national databases, collect all possible occurrences, and share them with the global community.

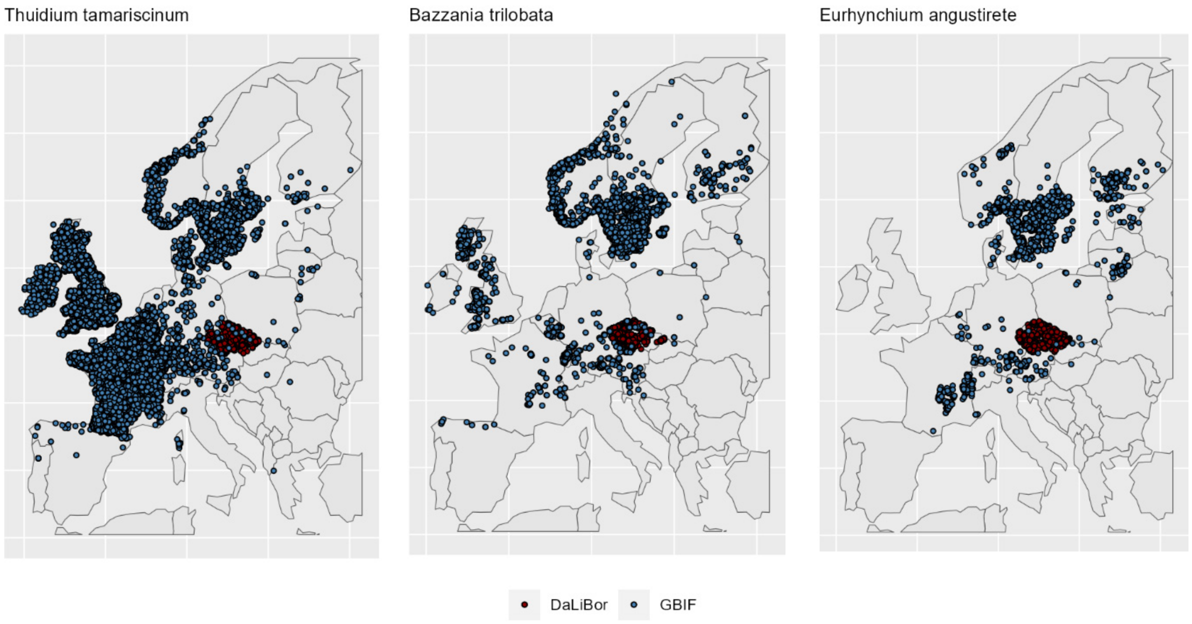

Figure 3 The example of three selected common forest understory bryophyte species occurrence data from GBIF (steel blue) and DaLiBor (dark red) to show the pattern of missing records in the global database hampering global analysis and synthesis. Specifically, in the case of GBIF, many (European) countries are not sharing their national data about bryophyte occurrences due to political, technical or license issues.

The limited data flow of bryophytes and lichens from national to global databases is primarily due to political, technical, or licensing issues, as well as the absence of local databases. The Czech Republic faces similar political and technical challenges that hinder this data transfer, making it no exception among other countries. However, we have taken initial steps to address this problem: we have developed a well-organised local database, DaLiBor, and are preparing to join the Charles University transfer facility, JACQ, which will help overcome these obstacles. The jointly administered herbarium management system and specimen database, JACQ, will facilitate the connection between DaLiBor and GBIF. Without the JACQ infrastructure initiative at Charles University, transferring data from DaLiBor to GBIF would be much more challenging.

Besides gathering, organizing, and sharing occurrence data of model organisms in microclimate ecology, there are numerous challenges related to microclimate time-series. This includes not only in-situ study plot setups (logger types, heights, depths, shielding, disturbance protection) but also handling microclimate data already downloaded from loggers. The increasing number of researchers using microclimate loggers is expanding microclimate data into the realm of big data (**Fig. 2**). Advancing microclimate research towards meta-analysis and big data analysis requires efficient, ready-to-use scripts and open-source software for data handling. Fortunately, many microclimate ecologists share their scripts and ideas for data handling and maintenance, such as:

- https://github.com/poniitty/kilpisjarvi_microclimate
- https://github.com/RyanLab/microclimloggers
- https://github.com/OlivaresLD/TOMST_data_handling

However, a ready-to-use package for microclimate data handling was long missing. Our package, myClim (Paper 3), fills this gap. By presenting this open-source tool to the research community, we have opened the door to new collaborations through user contacts, helping them with issues and organizing workshops. Since the first publication of myClim, we have received hundreds of messages from users, which have helped to polish the package, improve function's help and tutorials, and generate ideas for further development and cooperation proposals. We observed a similar added value with the DaLiBor database, which opened new channels to local research groups and fostered new topics for cooperation and further development.

The primary reason for developing both methodological tools was to bridge specific gaps hampering our research. However, the gains from community interactions and networking hold equal or perhaps even greater value for my future research endeavours.

5. Conclusion

In my dissertation research, we demonstrated the pivotal role of near-ground microclimate in shaping temperate forest bryophyte communities. We disentangled the key microclimatic factors, including vapor pressure deficit (especially its temperature component), growing degree days, maximum air temperature, and mean soil moisture. Our findings, derived from in-situ measurements, fill the gap in previous knowledge predominantly based on macroclimatic data from weather stations and laboratory or garden experiments. Our results underscore the inadequacy of using proxies instead of in-situ microclimatic time-series to comprehend the relationship of climate and forest understory vegetation. Our work highlights the necessity of standardized methods for handling microclimate data, as exemplified by the development of myClim R package. This approach makes a significant contribution to the microclimate ecology towards increasing research reproducibility and possibilities for meta-analysis. Similarly significant was the establishment of the Database of the lichens and bryophytes of the Czech Republic (DaLiBor), which dramatically improved accessibility of standardised, validated occurrence data and thus enabled deeper analysis together with their use for education and popularisation. The presented studies demonstrated that integrating microclimatic data with bryophytes as model organisms has advanced our understanding of forest ecology. This highlights the need for continuous and precise in-situ microclimate monitoring to inform conservation strategies and ecological predictions.

6. Outlook

Moving forward, future research should aim to expand the geographic scope of these studies to include bryophyte occurrences across Europe. This expansion should involve networking with local researchers and gathering local digital data to enable a continental meta-analysis. Future research directions should also include lichens, fungi, and potentially soil microorganisms, relating them to microclimate and comparing the effect of microclimate with previously used macroclimate variables.

The next steps should focus on expanding the availability of high-resolution microclimate data by combining forest records from microclimate loggers with weather station data from open areas. While pivotal products have recently emerged (Haesen *et al.*, 2021), they still have limited resolution and biotope coverage. In addition to statistical approaches, mechanistic modelling can help generate high-resolution, high-quality data. However, mechanistically modelled microclimate layers require critical validation not only in terms of spatial and resolution accuracy but also across various depths and heights, as well as over time.

To deepen our understanding of factors affecting cryptogam communities, future studies should incorporate microclimate into niche modelling and species distribution modelling. This approach can enhance conservation efforts by increasing our understanding of distribution limits and, with the help of high-resolution microclimate grids, identify potential refugia that provide environmental spaces for survival amid ongoing climate change.

The broader implications of this research extend to forest and landscape management, climate change mitigation, and biodiversity conservation. Gaining insights into microclimate dynamics allows us to shape policies and practices that help conserve forest ecosystems and bolster their resilience against climate change. Specifically, researchers play a crucial role in clearly and simply interpreting the results from microclimatic studies and providing them to the administrations of protected areas. This helps defend and discuss conservation actions with local stakeholders and the general public.

I also see my future role in the popularisation and communication of the importance of forest microclimate to the general public. This involves helping to change the traditional view of climate change, which is often based solely on weather station data and tends to ignore forested areas.

Statement of contribution

For this thesis, I selected four of my most relevant, recent studies, which form a consistent block of ideas dealing with microclimate and forest understory bryophytes from methodological and ecological perspectives. I am the first author of three of those papers and co-author of the last one. Hereby, I specify my contributions to each of the studies.

1. **Man, M.**, Wild, J., Macek, M., & Kopecký, M. (2022). Can high-resolution topography and forest canopy structure substitute microclimate measurements? Bryophytes say no. Science of The Total Environment, 821, 153377. https://doi.org/10.1016/j.scitotenv.2022.153377

Contribution of Matěj Man: Conceptualisation, data collection, statistical analysis, interpretation of results, figures creation, draft manuscript preparation, manuscript revisions.

2. Růžičková, A., **Man, M.**, Macek, M., Wild, J., & Kopecký, M. (2024). Temperature-driven variability in vapor pressure deficit controls bryophyte community composition within a temperate forest landscape [Manuscript submitted for publication]

Contribution of Matěj Man: Conceptualisation, draft manuscript preparation, manuscript revisions, figures creation, statistical analysis.

3. **Man, M.**, Kalčík, V., Macek, M., Brůna, J., Hederová, L., Wild, J., & Kopecký, M. (2023). myClim: Microclimate data handling and standardised analyses in R. Methods in Ecology and Evolution, 14(9), 2308–2320. https://doi.org/10.1111/2041-210X.14192

Contribution of Matěj Man: Conceptualisation, software development, statistical analysis, interpretation of results, figures creation, draft manuscript preparation, manuscript revisions.

The maintainer and main code developer of the myClim package, professional programmer Vojtěch Kalčík, is responsible for the back-end infrastructure, including coding, testing, versioning, and package deployment.

4. **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(4), 579–605. https://doi.org/10.23855/preslia.2022.579

Contribution of Matěj Man: Conceptualisation, database development, data gathering and pre-processing, statistical analysis, interpretation of results, figures creation, draft manuscript preparation, manuscript revisions.

On behalf of all the co-authors, I declare the keynote participation of Matěj Man in completing the research and writing the papers, as described above.

doc. Ing. Jan Wild PhD.

Complete list of publications

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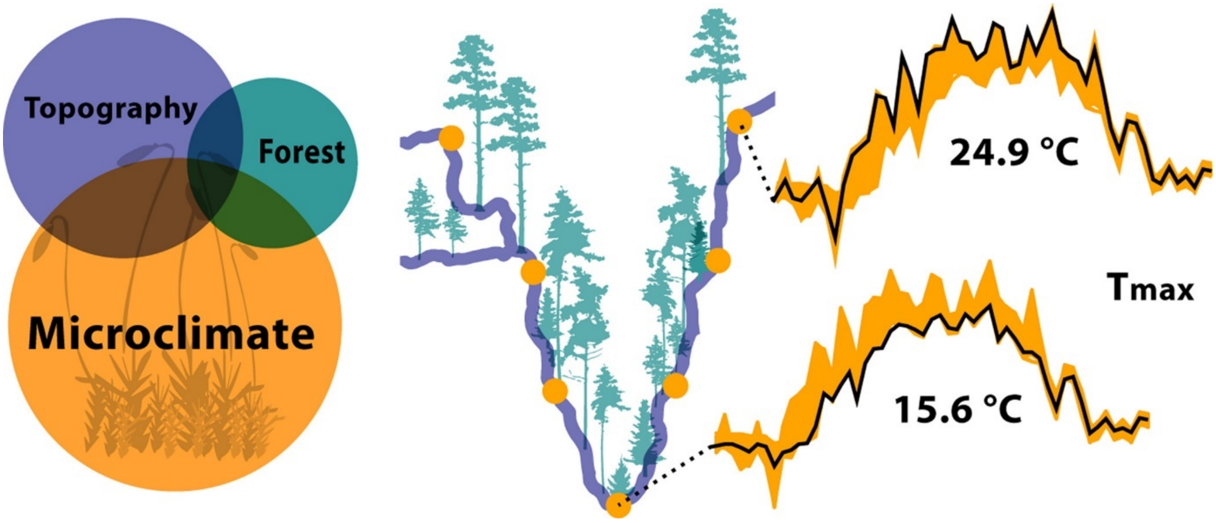
PAPER 1



Graphical abstract from paper 1. Author: Matěj Man

Can high-resolution topography and forest canopy structure substitute microclimate measurements? Bryophytes say no

Matěj Man, Jan Wild, Martin Macek & Martin Kopecký

Man, M., Wild, J., Macek, M., & Kopecký, M. (2022). Can high-resolution topography and forest canopy structure substitute microclimate measurements? Bryophytes say no. Science of The Total Environment, 821, 153377. https://doi.org/10.1016/j.scitotenv.2022.153377

Abstract

Increasingly available high-resolution digital elevation models (DEMs) facilitate the use of fine-scale topographic variables as proxies for microclimatic effects not captured by the coarse-grained macroclimate datasets. Species distributions and community assembly rules are, however directly shaped by microclimate and not by topography. DEM-derived topography, sometimes combined with vegetation structure, is thus widely used as a proxy for microclimatic effects in ecological research and conservation applications. However, the suitability of such a strategy has not been evaluated against in situ measured microclimate and species composition. Because bryophytes are highly sensitive to microclimate, they are ideal model organisms for such evaluation.

To provide this much needed evaluation, we simultaneously recorded bryophyte species composition, microclimate, and forest vegetation structure at 218 sampling sites distributed across topographically complex sandstone landscape. Using a LiDAR-based DEM with a 1 m resolution, we calculated eleven topographic variables serving as a topographic proxy for microclimate. To characterize vegetation structure, we used hemispherical photographs and LiDAR canopy height models. Finally, we calculated eleven microclimatic variables from a continuous two-year time- series of air and soil temperature and soil moisture. To evaluate topography and vegetation structure as substitutes for the ecological effect of measured microclimate, we partitioned the variation in bryophyte species composition and richness explained by microclimate, topography, and vegetation structure.

In situ measured microclimate was clearly the most important driver of bryophyte assemblages in temperate coniferous forests. The most bryophyte-relevant variables were growing degree days, maximum air temperature, and mean soil moisture. Our results thus showed that topographic variables, even when derived from high-resolution LiDAR data and combined with in situ sampled vegetation structure, cannot fully substitute effects of in situ measured microclimate on forest bryophytes.

1. Introduction

Climatic conditions experienced by organisms often differ from climatic data derived from weather stations (Geiger *et al.*, 2009; Potter *et al.*, 2013; Wild *et al.*, 2019b; Zellweger *et al.*, 2019a). In contrast to the free-air conditions recorded by weather stations, local microclimate is modified by vegetation and land-surface topography (Geiger *et al.*, 2009), and it is therefore highly variable in space and time (Suggitt *et al.*, 2011). Using weather station data, and from them derived coarse-scale (~1 km) climatic grids, e.g. (Fick & Hijmans, 2017; Karger *et al.*, 2017) may thus significantly bias the results of studies based on the relationship between species occurrence and climate (Graae *et al.*, 2012; Potter *et al.*, 2013; Slavich *et al.*, 2014). For example, it has been shown that omitting microclimatic data leads to an overestimation of species vulnerability to climate change (Suggitt *et al.*, 2017), and misleading identification of plant refugia (Meineri & Hylander, 2017) and plant distribution (Franklin *et al.*, 2013; Lembrechts *et al.*, 2019). Therefore, the microclimate is the key to more realistic predictions of climate change effects on biodiversity (Zellweger *et al.*, 2020).

Scientist, therefore, attempts to derive fine-scale (~1-100 m) microclimatic grids through interpolation of in-situ measurements, e.g. (Fridley, 2009; Ashcroft & Gollan, 2012; Greiser *et al.*, 2018; Macek *et al.*, 2019; Haesen *et al.*, 2021) or through mechanistic modelling based on physical principles (Davis *et al.*, 2017; Kearney *et al.*, 2020; Maclean, 2020). However, fine-scale microclimatic grids are still relatively scarce, often local, and not standardized. To overcome missing microclimatic grids, ecologists often use topographic variables derived from high resolution (~ 1-10 m) digital elevation models (DEMs), assuming a causal relationship between topography and microclimate (Leempoel *et al.*, 2015; Muscarella *et al.*, 2020). Such topographic variables have been used, for example, to estimate species vulnerability to climate change (Torresan *et al.*, 2012), assess invasive species potential (Kopeć *et al.*, 2020) or model microhabitat suitability for endemic species (Moreno *et al.*, 2011).

Studies using topographic variables as proxies for microclimate differ in type and number of variables used, but most of them focus on variables with the largest expected relationship to solar energy income and heat flux near the ground (Dobrowski, 2011; Moeslund *et al.*, 2013). Local insolation can be approximated by simple variables like slope and aspect or more advanced indices like heat load index and potential solar radiation (McCune & Keon, 2002; Böhner & Antonić, 2009; Reger *et al.*, 2011). But recent advances in digital terrain analyses offer a large number of terrain variables (see e.g. (Hengl & Reuter, 2009; Wilson, 2018)) with proved, but less direct and intuitive, relationship to microclimate (Dobrowski *et al.*, 2009; Leempoel *et al.*, 2015; Macek *et al.*, 2019). For instance, indices describing water flow and accumulation (e.g. topographic wetness index) are successfully used as a proxy for cool air pooling (Fridley, 2009; Ashcroft & Gollan, 2012; Meineri & Hylander, 2017). Indices describing relative topographic position, various landforms or topographic heterogeneity can be used as a proxy for wind exposition or other differences to mezo- and macroclimate (Frey *et al.*, 2016; Zellweger *et al.*, 2019a; Haesen *et al.*, 2021).

Vegetation cover modifies solar radiation, affects air mixing near the ground and cools the air by evapotranspiration (Geiger *et al.*, 2009; von Arx *et al.*, 2012; Zellweger *et al.*, 2019a). Therefore, the effect of microclimate on understory sessile organisms can be largely colinear with the effect of vegetation structure. To capture the effect of vegetation on microclimate, researchers used, for example, canopy height models (Jucker *et al.*, 2018; Kašpar *et al.*, 2021) or canopy structure derived from hemispherical photographs (Hennon *et al.*, 2010; Rose *et al.*, 2020) or LiDAR point clouds (Moeser *et al.*, 2014; Davis *et al.*, 2019; Stickley & Fraterrigo, 2021). None of these methods is exclusively preferred, but remote sensing approaches are increasingly preferred because they provide spatially continuous data (Bode *et al.*, 2014; Zellweger *et al.*, 2019b; Kašpar *et al.*, 2021).

Bryophytes are small, immobile and thus very sensitive to the local microclimate (Stewart & Mallik, 2006; Giaccone *et al.*, 2019; Tinya *et al.*, 2021). Bryophytes sensitivity to microclimate is further elevated by their poikilohydric life strategy (Merinero *et al.*, 2020). They lack lignified water-conducting systems, the ability to suck water with roots and do not have the storage organs (Carleton & Dunham, 2003; Proctor *et al.*, 2007b). Therefore, their strategy to cope with short-term climatic variability and climatic extremes lies in their biochemical or morphological adaptations leading to desiccation tolerance and fast rehydration (Smirnoff, 1992; Oliver *et al.*, 2004; Proctor *et al.*, 2007a). In forests, bryophytes are further strongly affected by upper vegetation layers, e.g. through vegetation shading and microclimate buffering (Márialigeti *et al.*, 2009; Bartels & Chen, 2013; Chollet *et al.*, 2013; Kumar *et al.*, 2018). In situ measured temperature extremes and soil moisture significantly affected bryophytes assemblages in tundra (Kemppinen *et al.*, 2019) as well boreal (Dahlberg *et al.*, 2020) and temperate forest (Ódor *et al.*, 2013; Kopecký *et al.*, 2021).

Here, we asked whether topographic variables derived from a high-resolution LiDAR-based DEM and forest vegetation structure can substitute in-situ measured microclimate as a driver of forest bryophyte species richness and community composition. To answer this question, we partitioned variability in bryophyte species richness and composition explained by microclimate, topography, and vegetation structure. Furthermore, we determined the most important microclimatic variables whose effect is independent of the effect of topography and vegetation structure.

2. Methods

2.1. Study area

Our study took place in a sandstone region with diverse bryophyte flora - National Park Bohemian Switzerland, Czech Republic (**Fig. 1**). This region has rugged topography, which results in sharp microclimatic gradients over short distances (Beer, 2007; Wild *et al.*, 2013). The elevation in the study area ranges from 125 to 620 m a.s.l. In the middle of the area, the mean annual precipitation is 765 mm, and the mean annual temperature at 2 m height is 8.3 °C (weather station Tokáň, data 2011-2019).

The bedrock is formed mostly of Upper Cretaceous quartz sandstones, and the soils are therefore acidic, nutrient-poor Cambisols and Podsols. Shallow Leptosols occur on steep slopes, deeper soils derived from loess occur on the plateaus, and organic-rich soils occur at the valley bottoms (Němeček *et al.*, 2011). Coniferous forests cover the entire region. Norway spruce (*Picea abies*) with an admixture of European beech (*Fagus sylvatica*) dominates the lower slopes and valley bottoms, while Scots pine (*Pinus sylvestris*) dominates the upper slopes and plateaus.

The area has been protected as a national park since 2000. In the core zone, forest management is prohibited (except for invasive species eradication). The area is a hotspot of bryophyte diversity, hosting approximately 300 bryophyte species (one-third of the national species pool), with 71 species listed on the national red list (Kučera *et al.*, 2003; Härtel *et al.*, 2007).

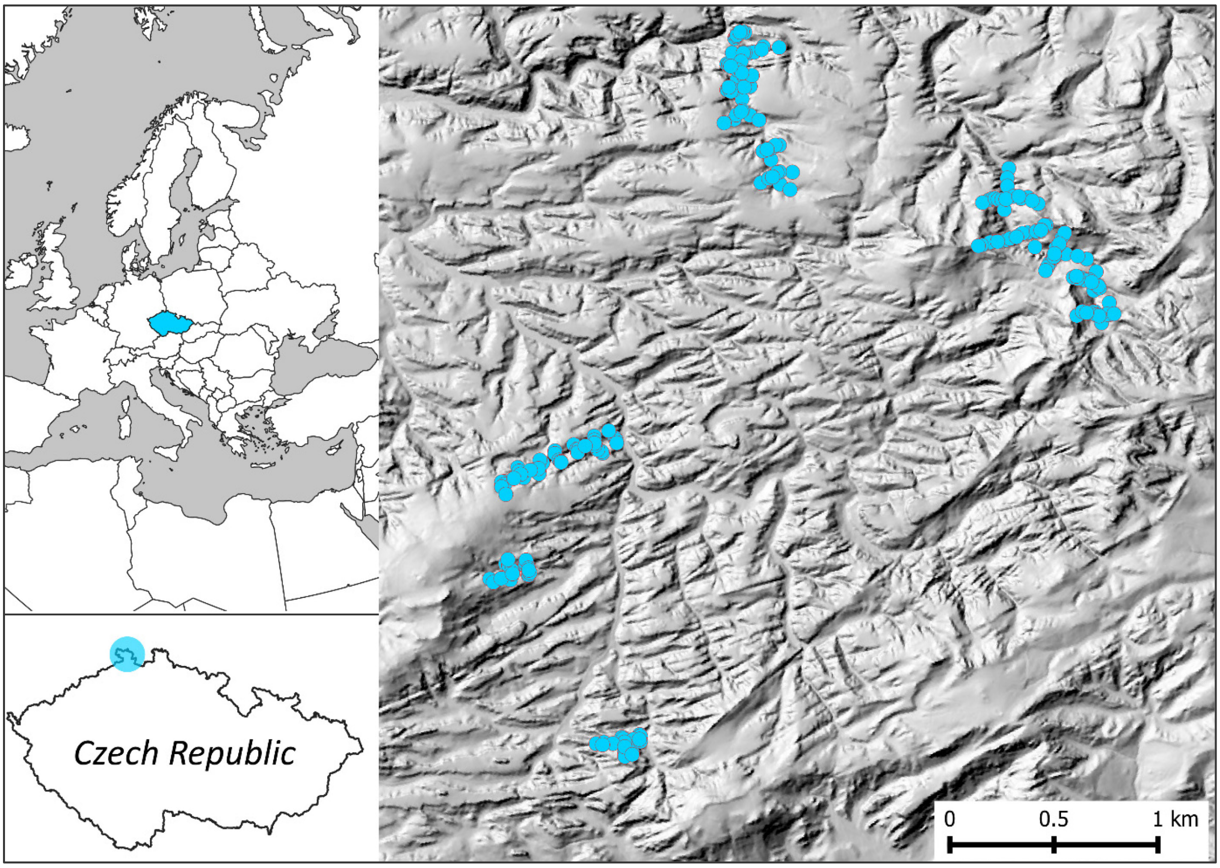


Figure 1 Study plots locations within central Europe. A total of 218 study plots (blue dots) were established across five valleys in the topographically diverse sandstone region in the National Park Bohemian Switzerland, Czech Republic. Each plot was equipped with microclimatic data logger defining the central point for the vegetation and vegetation structure surveys.

2.2. Field data collection

We established 218 study plots located in the five valleys representative of the core area of the National Park Bohemian Switzerland (**Fig. 1**). Each study plot was centred to the microclimatic datalogger recording air and soil temperature and soil moisture. We established study plots every 50 m along the streamline at the bottom of each valley. At every second plot along the streamline, we started vertical transects running up to both sides of the valley, with plots established every 10 vertical metres up to the surrounding plateau (**Fig. 2**). Depending on valley length, we established three to eight transects at each valley. As a result, there were 8 – 74 study plots in each valley.

Geographic coordinates of the microclimatic dataloggers were measured with a differential GNSS Trimble GeoExplorer 2008 GeoXH equipped with an external Zephyr antenna. The field measurements were post-processed using differential corrections from the nearest geodetically fixed stations of the national CZEPOS network to achieve high position accuracy. To assess the vegetation structure of each plot, we acquired hemispherical images with Canon 40D and Sigma 4.5 mm fisheye lenses placed at the height of 0.6 m directly above each microclimatic datalogger.

We identified all bryophyte species in a 1 m^2 plot around the microclimatic datalogger and estimated cover of herbs, and shrubs (1 m^2), and trees (25 m^2). Across all plots, we recorded 66 bryophyte species (see complete species list in Appendix A). Species richness ranged from one to twelve species per plot.

In the centre of each plot, we measured air temperature at 15 cm, surface temperature directly at the soil surface and soil temperatures at a depth of 8 cm and soil moisture in the upper 15 cm of the soil using TMS microclimate loggers, version 1 (Wild *et al.*, 2019b). Temperature sensors used in the TMS loggers have an accuracy of ± 0.5 °C and a resolution of 0.0625 °C. The air temperature sensor was shielded by a standardized white one-layer radiation shield. All microclimatic variables were recorded every 30 minutes from 1 May 2010 to 30 April 2012.

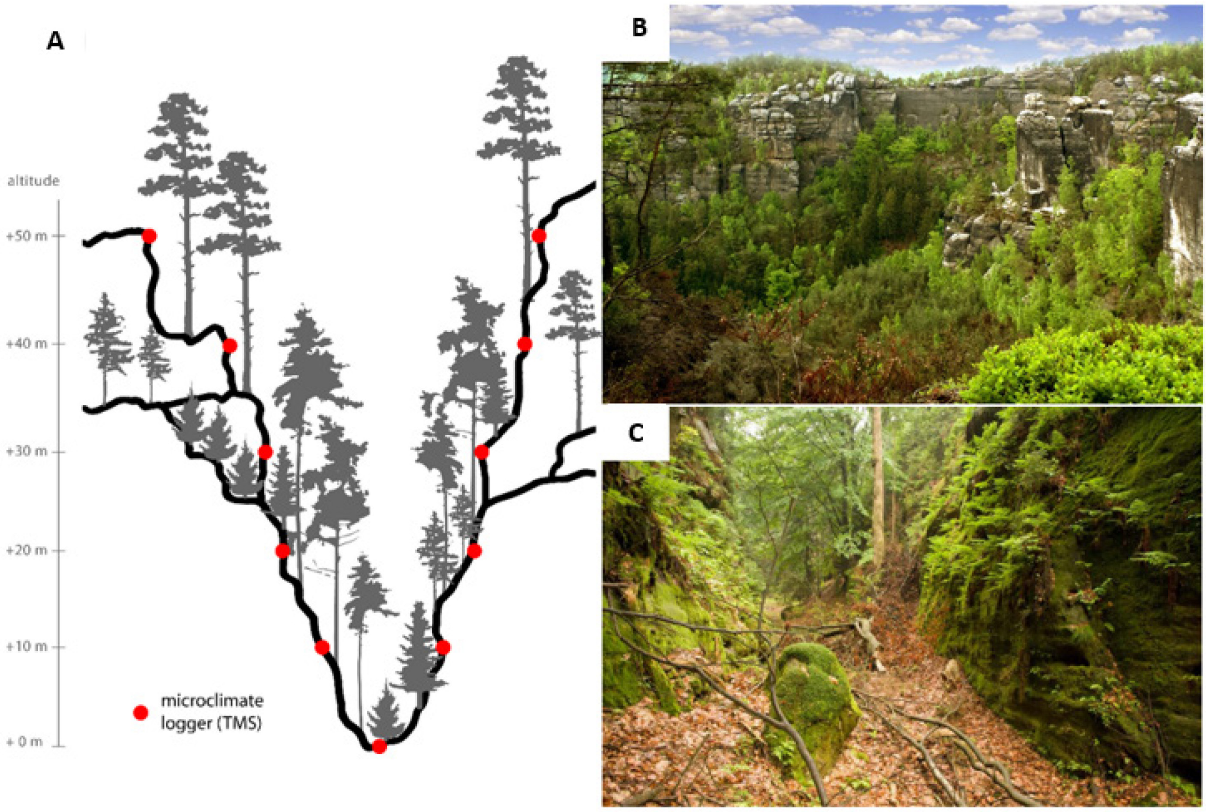


Figure 2 Illustration of the sampling design. (**A**) Schematic representation of vertical transects crossing the valley with eleven study plots. In the centre of each study plot, we measured microclimate with the TMS logger (red dots), (**B**) photograph showing the rugged topography of the study area and (**C**) photograph showing the bottom of the sandstone valley rich in bryophytes.

2.3. Microclimate data processing

Before the analyses, microclimatic data were screened for anomalous records. Specifically, in several cases, soil moisture accidentally dropped and then returned to normal values after a few hours. We detected several multiplicated records or missing records. We also identified several cases when logger erroneously recorded temperatures reaching +100 or -100 °C. Such anomalous records were manually deleted. In total, this data preprocessing resulted in 10% of missing data in the whole dataset.

To fill these gaps, we used geographically weighted Principal Component Analysis (also called Empirical Orthogonal Functions), which estimated missing data values on a single logger from the relationship to all other simultaneously measuring loggers (Tonini *et al.*, 2016). This gap-filling method performs well with microclimatic data (Henn *et al.*, 2013; Tonini *et al.*, 2016), and we implemented it with the (Tonini, 2016) R script.

From the preprocessed microclimate measurements, we calculated 11 microclimatic variables potentially relevant for bryophytes (**Table 1**). As temperature extremes are more ecologically relevant than means (Körner & Hiltbrunner, 2018), we calculated maximum and minimum air temperatures as the 95th and 5th percentiles from all air temperature measurements (Ashcroft & Gollan, 2012; Macek *et al.*, 2019). As a measure of available energy, we calculated growing degree days as the sum of degree days above 5 °C (Scherrer & Körner, 2011; Dahlberg *et al.*, 2020). As a measure of physiological stress, we also calculated freezing degree days as the sum of degree days below 0 °C (Choler, 2018; Giaccone *et al.*, 2019; Löffler & Pape, 2020).

To capture the long-term soil moisture regime, we computed the mean soil volumetric water content (VWC) for each plot. We transformed the raw TMS soil moisture signal to volumetric water content using the calibration curves developed for the first version of the TMS loggers from the soil samples collected directly on our study plots (Vlček, 2010). As a measure of temporal moisture dynamics, we calculated the rate of VWC loss after rain. Specifically, we first selected the ten most distinct rain events followed by at least seven days without rain. Then, we calculated VWC loss as an average of the differences between VWC at the peak and VWC seven days after the peak. Drought stress is an important factor for bryophytes because it limits their metabolic activity and reproduction (Proctor, 2004; Oishi, 2019). Therefore, we also calculated the number of days with a mean daily VWC below 18 % as a proxy for the drought stress at each plot. A threshold of 18% represents the 10th percentile of the lowest daily mean VWC in the whole dataset.

To express the effects of the snow cover on bryophyte assemblages (Niittynen & Luoto, 2018), we calculated the number of days with snow cover from the temperature time series measured on each plot (Dickerson-Lange *et al.*, 2015; Teubner *et al.*, 2015). As a day with snow cover specific for our study area, we counted each day with mean surface temperature below 0.3°C and daily surface temperature range smaller than 2°C. As measures of site microclimatic variability, we used the coefficients of variation calculated from 2-year air temperature, soil temperature and soil moisture data.

Table 1. Overview of eleven microclimatic variables potentially relevant for bryophytes. For each plot, they were calculated from two years of microclimatic measurements.

Variable	**Abbreviation**	**Units**	**mean**	**min; max**
Maximum air temperature (95th percentile)	airT.max	°C	19.57	15.6; 24.9
Minimum air temperature (5th percentile)	airT.min	°C	-2.96	-5.0; -0.8
Coefficient of variation of air temperature	airT.CV	-	1.05	0.93; 1.15
Coefficient of variation of soil temperature	soilT.CV	-	0.69	0.48; 0.96
Growing degree days above 5°C	airT.GDD	°C·d	3087.71	2416.4; 3984
Freezing degree days below 0°C	airT.FDD	°C·d	321.33	103.4; 494.5
Mean volumetric water content in the soil	VWC.mean	%	30.03	7.8; 63.9
Relative soil moisture loss after the rain	VWC.loss	-	0.2	0.01; 0.76
Drought stress (no. of days with daily mean VWC below 18 %)	VWC.drought	days	155.4	0; 713
Coefficient of variation of soil VWC	VWC.CV	-	0.33	0.07; 0.96
Number of days with snow cover	snow	days	82.14	0; 190

2.4. Terrain analysis

To calculate ecologically relevant topographic variables, we used a high-resolution (1 m) digital terrain model (DTM) derived from LiDAR (Trommler & Csaplovics, 2005) processed with SAGA GIS 5.0.0 (Conrad *et al.*, 2015).

First, we filled the depressions in the DTM (Wang & Liu, 2006). Next, from the filled DTM, we derived a raster of flow accumulation using the top-down approach, with a multiple flow direction method, no threshold for linear flow and flow dispersion of 1.1 (Freeman, 1991). Finally, we used the flow accumulation and local slope (Zevenbergen & Thorne, 1987) to calculate the *SAGA wetness index*, using a suction factor t = 10 (Böhner & Selige, 2006).

We also used the flow accumulation raster to derive a channel network with an initial threshold of 10 000 m^2 and a minimum segment length of 10 m. We combined this channel network with the original DTM to derive a *vertical distance to the channel network* (Böhner & Antonić, 2009)

As a measure of terrain heterogeneity, we calculated the *vector terrain ruggedness index* in two circle search radii of 1 m and 10 m, with default Gaussian weighting (Sappington *et al.*, 2007). To approximate the erosion/accumulation potential for each plot, we calculated the *mass balance index* with 15° as the slope threshold, 0.01 as the curvature threshold and 15 m as the threshold for the vertical distance to the channel network (Möller *et al.*, 2008).

As a measure of the concavity/convexity of the terrain around each microclimatic logger, we calculated the *convergence index* expressing how many surrounding cells point toward the focal cell (Kiss, 2004). We calculated the *convergence index* with a search radius of 50 m and used inverse distance weighting to give more weight to the cells closer to the focal cell.

As a measure of the potential exposure to the wind, we calculated the *wind exposition index* with a search distance of 6 km, angular step size of 15° and acceleration of 1.5 (Böhner & Antonić, 2009). To express plot position relative to the surrounding terrain, we calculated the *topographic position index* as the difference between plot elevation and the mean elevation of the surrounding terrain within a radius of 30 m (Guisan *et al.*, 1999).

Potential insolation for the period from 28 February to 28 November was calculated for each plot using the central latitude of our study area, and calculation was performed every four days and every four hours within each day, starting at 8 AM and ending at 8 PM. We used the default settings in SAGA GIS version 5.0.0 for other parameters (Böhner & Antonić, 2009). Because temperature maxima are on northern hemisphere higher on south-western slopes than on south-eastern slopes, we also calculated the *diurnal anisotropic heating* with the maximum heat surplus set to 202.5° (Böhner & Antonić, 2009).

2.5. Vegetation structure

We characterized vegetation structure from the three data sources: i) hemispherical photography; ii) LiDAR digital surface and terrain models; and iii) vegetation sampling. i.) Hemispherical photographs were preprocessed by supervised thresholding of sky/canopy pixels using the local maxima of edge value in Sidelook 1.1.01 (Nobis & Hunziker, 2005). Calculations of canopy openness, direct, diffuse, and total solar radiation were subsequently performed in WinSCanopy

2014a (Regent Instruments Canada, Inc.). ii.) To include the effects of the forest canopy height, we constructed a canopy height model as the difference between the digital terrain and surface models. We extracted the mean canopy height in one-, two-, five- and ten-metre buffers around the study plot centre. iii.) Finally, we used a percentage cover of three vegetation layers estimated in situ in 1 m^2 study plots for herbs and shrubs and 25 m^2 for trees.

2.6. Data analysis

To assess the ability of topographic and vegetation structural variables to replace in situ measured microclimatic data, we partitioned the variation explained in bryophyte species richness and community composition (Borcard *et al.*, 1992; Økland, 2003). First, to address collinearity (**Fig. A4** in Appendix A) and reduce the number of predictor variables, we extracted sample scores from principal component analyses (PCA) calculated separately for microclimate, topography and vegetation structure, using the R package *vegan* 2.5-5 (Oksanen *et al.*, 2019). For further analyses, we used the sample scores from the first six PCA ordination axes, which accounted for 94 % variability in microclimate, 91% in topography, and 94% in vegetation structure (Appendix A).

2.6.1. Community composition

To calculate the variation in species composition explained by environmental variables, we used distance-based redundancy analysis (db-RDA), (McArdle & Anderson, 2001). To assess the statistical significance of db-RDA, we used permutation tests based on 9999 random permutations restricted within five blocks defined by five sampled valleys because the plots were spatially clustered within the valleys (**Fig. 1**).

As a measure of compositional dissimilarity between plots, we used the Simpson index (Simpson, 1943) as re-expressed by (Koleff *et al.*, 2003). We used the Simpson index because it is a measure of species turnover independent from the differences in species richness between plots (Lennon *et al.*, 2001).

To distinguish the colinear and unique effect of microclimate, topography, and vegetation structure on bryophytes compositional dissimilarity, we performed variation partitioning (Borcard *et al.*, 1992; Økland, 2003). Doing so, we compared seven db-RDA models explaining compositional dissimilarity by: i) microclimate and topography and vegetation structure; ii) microclimate and topography; iii) microclimate and vegetation structure; iv) topography and vegetation structure; v) microclimate; vi) topography; vii) vegetation structure (Legendre *et al.*, 2009).

To determine the most important microclimatic variables whose unique effects had not been covered by the topography or vegetation structure, we also calculated a partial db-RDA model for each microclimatic variable. Each calculated model contained a single microclimatic variable as an explanatory variable and the scores from the PCA of topographic (6 axes) and vegetation structure (6 axes) variables as covariables.

2.6.2. Species richness

To calculate the deviance in species richness explained by environmental variables, we used generalized additive models (GAMs) fitted with the R package *mgcv* 1.8-28 (Wood, 2011). As a measure of species richness, we used the total number of species recorded per plot. Because of the relatively low species richness per plot and its right-skewed distribution (min = 1, median = 4, max = 12 species) with the majority of plots having several species but few plots having a higher number of species (**Fig. A2** in Appendix A), we used a Poisson distribution with a log link function and smooth terms fitted by thin plate regression splines without null space penalization and smoothing parameter estimation using restricted maximum likelihood (Wood, 2011).

To quantify the shared and unique effects of predictor groups (microclimate, topography, and vegetation structure) on bryophyte species richness, we partitioned the deviance explained in GAMs (Hjort *et al.*, 2012). This approach is conceptually similar to a variation partitioning performed with multivariate data. Specifically, we related species richness to microclimate and topography and vegetation structure (full GAM) and series of partial GAMS with different combinations of variable groups: i) microclimate and topography; ii) microclimate and vegetation structure; iii) topography and vegetation structure; iv) microclimate; v) topography and vi) vegetation structure. However, each GAM can estimate different smoothing parameters, depending on the structure of the model. Therefore, we extracted smoothing parameters from the full GAM and used the same smoothing parameters in all partial GAMs (i – vi). It prevented estimation of smoothing parameters de novo in each partial GAM, which would otherwise influence deviance partitioning. To assess the statistical significance, we compared each GAM against the null model (i.e. GAM with only intercept) using a chi-square test. To estimate the significance of the unique effects of microclimate, topography, and vegetation structure, we again used the chi-square tests, but here we compared partial models (i-iii) with the full GAM.

To determine the effects of individual microclimatic variables independent from the topography and vegetation structure on species richness, we built a series of GAMs, each predicting species richness with a different microclimatic variable (**Table 1**). In each GAM, we used scores from PCA axes of topography and vegetation structure as covariables. We assessed the statistical significance of the effects of each microclimatic variable with the Wald-type test (Wood, 2013).

3. Results

Bryophyte community composition and species richness were significantly driven by microclimate, topography, and vegetation structure, both when tested jointly in a single model or in three separate models (**Table 2A**). In all cases, microclimate was the most important predictor. When tested separately, the effect of vegetation structure on species richness was higher than the effect of topography, and community composition was predicted better by topography than vegetation structure. In contrast, while tested jointly, the additional effect of topography and vegetation structure was not significant.

Table 2. Effect size and significance of predictor groups (microclimate, topography, and vegetation structure) on species richness and community composition. Each predictor group was in the analyses represented by the scores from the first six PCA axes derived from the original eleven variables. R^2 represents explained variation, and D^2 represents explained deviation. Significant ($p < 0.05$) effects are highlighted in bold. (**A**) Effect of the variable group while tested separately without interaction with the other two groups. (**B**) The results of variation partitioning, showing the only additional (unique) effect of the predictor group not covered by predictors from the other two groups.

A Effects of variable groups on bryophytes assemblages while tested separately

	Community composition		Species richness	
	R^2	p-value	D^2	p-value
microclimate	**0.115**	**<0.001**	**0.207**	**<0.001**
topography	**0.076**	**<0.001**	**0.063**	**0.039**
vegetation structure	**0.059**	**0.004**	**0.144**	**<0.001**
full model (microclimate, topography, vegetation)	**0.180**	**0.010**	**0.292**	**0.010**

B Additional effects of variable groups on bryophytes assemblages while tested together

	Community composition		Species richness	
	R^2	p-value	D^2	p-value
microclimate	**0.056**	**<0.001**	**0.144**	**0.021**
topography	0.024	0.521	0.019	0.612
vegetation structure	0.039	0.147	0.055	0.969

The effects of the three predictor groups (microclimate, topography, and vegetation structure) were not independent, and their overlap differed for species richness and community composition (**Fig. 3**).

Topography covered almost half of the variability in species composition explained by the microclimate. In contrast, the effect of the vegetation structure was nearly independent of both microclimatic and topographic effects. Over half of the microclimatic effects on community composition was not explained by topography and vegetation structure. The microclimate was the only predictor group with significant unique effects on community composition while filtered for topography and vegetation structure.

For species richness, topography covered only one-third of the microclimatic effect. Topography thus performed as a worse predictor of species richness than community composition. Moreover, the microclimatic effect on species richness had a larger overlap with the vegetation structure than with the topography. Approximately three-quarters of the microclimatic effect on species richness were not explained by topography and the vegetation structure (**Table 2**).

The importance of the individual microclimatic variables was comparable between models of species richness and community composition (**Table 3**). The two variables with the largest unique effect were the growing degree days and maximum air temperature, both for community composition and species richness. Interestingly, mean soil moisture explained a significant part of the variation in species composition but not in species richness (**Table 3**).

Table 3. Unique effects of microclimatic variables on bryophyte community composition and species richness independent from topography and vegetation structure. **Community composition:** R^2 is the variation in community composition explained by each microclimatic variable after controlling for the effects of topography and vegetation structure. **Species richness:** D^2 is the deviance in species richness explained by each microclimatic variable after controlling for the effects of topography and vegetation structure. Microclimatic variables are sorted according to the decreasing explained variation in community composition. Significant ($p < 0.05$) effects are highlighted in bold.

	Community composition		Species richness	
	R^2	p-value	D^2	p-value
Growing degree days above 5°C	**0.025**	**< 0.001**	**0.061**	**0.031**
Maximum air temperature (95th perc. of air temperature)	**0.023**	**< 0.001**	**0.058**	**0.039**
Mean soil volumetric water content	**0.017**	**0.002**	0.017	0.280
Minimum air temperature (5th perc. of air temperature)	**0.013**	**0.032**	**0.04**	**0.034**
Coefficient of variation of air temperature	**0.012**	**0.023**	0.024	0.068
Freezing degree days below 0°C	0.012	0.062	**0.044**	**0.032**
Relative soil moisture loss within 7 days after the rain	0.009	0.068	0.004	0.343
Coefficient of variation of soil temperature	0.006	0.312	0.024	0.068
No. of days with daily VWC below 18 %	0.005	0.316	0.006	0.245
Coefficient of variation of soil VWC	0.005	0.318	0.005	0.274
Number of days with snow cover	0.003	0.642	0.004	0.838

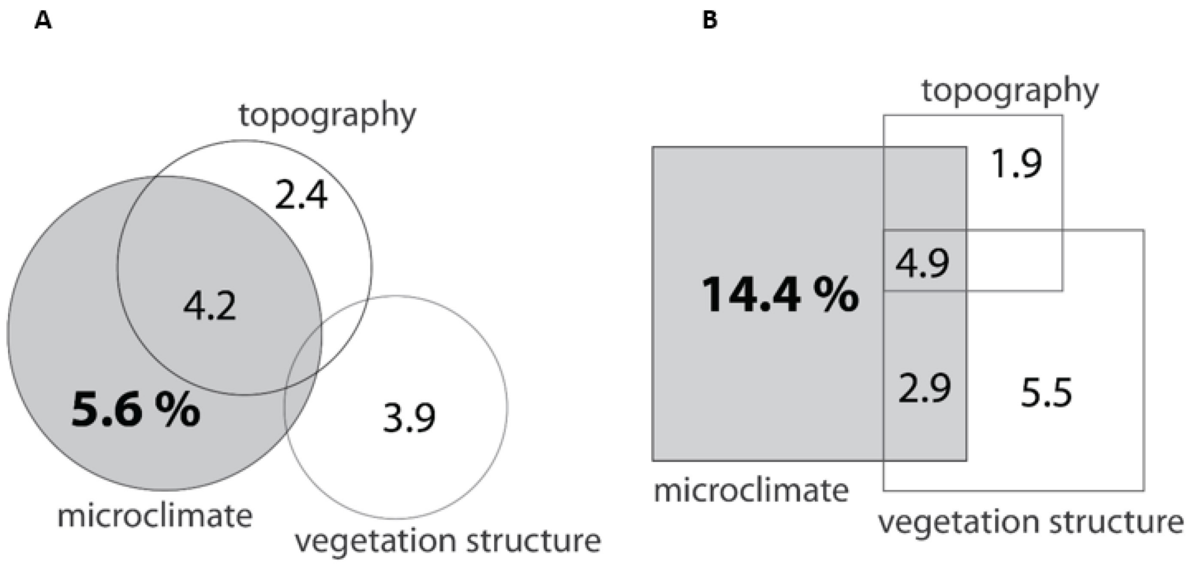


Figure 3 Variation partitioning showing shared and independent effects of microclimate, topography, and vegetation structure on forest bryophyte (**A**) community composition and (**B**) species richness. Values represent the total percentage of explained variation (composition) and deviance (richness). The microclimate (coloured in grey) explained most variation, and its effect only partly overlapped with the effect of topography and vegetation structure. Statistically significant effects ($p<0.05$) are highlighted in bold font, and effects below one percent are not shown.

4. Discussion

We found that bryophyte assemblages were related to microclimate, topography, and vegetation structure (**Table 2A**) when the effects of these variables were tested separately. But when we partitioned the explained variation among the microclimate, topography, and vegetation structure, only microclimate explained significant variation independent from the topography and vegetation structure (**Table 2B**). It is consistent with studies showing that bryophytes assemblages are shaped by microclimate (Ódor *et al.*, 2013; Kemppinen *et al.*, 2019; Oishi, 2019; Táborská *et al.*, 2020; Tinya *et al.*, 2021).

Our results, therefore, support previous studies showing that LiDAR-derived topographical variables like topographic position and wetness indices are the significant drivers of forest bryophyte assemblages (Camathias *et al.*, 2013; Bartels *et al.*, 2018). Similarly, our results agree with previous studies showing that vegetation structure affects forest bryophytes assemblages (Tinya *et al.*, 2009; Węgrzyn *et al.*, 2021). However, in contrast to these studies, we included in-situ measured microclimate and found that neither land-surface topography nor vegetation structure alone explained additional part of variation not explained by microclimate. Moreover, microclimate explained a significant part of variation not explained by topography and vegetation structure. These findings have important implications for studies using topography and vegetation structure as proxies for microclimatic effects on species assemblages.

This finding stresses the importance of forest microclimate and clearly shows that the microclimate cannot be fully substituted by topography and vegetation structure. Our results are therefore highly relevant for community ecology and species distribution modelling at fine spatial scales, which often substitute microclimate with land-surface topographic and vegetation structural proxies. Our study showed limits of such an approach and suggests that ecologists should preferably use in-situ microclimate measurements.

Interestingly, we also found a difference between the relative importance of topography and vegetation structure for bryophytes richness and community composition (**Table 2A**). While species richness was affected more strongly by vegetation structure, community composition was coupled more tightly with topography. Vegetation structure in our study also included cover of the herb layer which could also mirror microvariability of suitable habitats for bryophytes on the study plots, e. g. disturbance patches, presence of small rocks and dead wood or litter characteristics, which are important for bryophytes species richness (Ódor *et al.*, 2006; Chen *et al.*, 2017). In contrast, community composition can be driven by species turnover along environmental gradients from extreme conditions on exposed slopes to mild conditions on valley bottoms, which was better captured by topography than vegetation structure. This environmental filtering thus likely affects the selection of species that can tolerate local conditions but does not necessarily imply changes in species richness (Hájková & Hájek, 2004).

Based on the previous findings that microclimate is strongly driven by land-surface topography (Bennie *et al.*, 2008; Geiger *et al.*, 2009; Ashcroft & Gollan, 2012; Davis *et al.*, 2019; Macek *et al.*, 2019), we expected higher overlap between the effects of microclimate and topography. But in contrast to our expectations, we did not detect any significant additional effect of topography neither vegetation structure on bryophyte assemblages after accounting for the effect of microclimate. This can be partly explained by the relatively uniform and dense vegetation cover in our study system because variation in canopy cover higher than 75 % has a negligible effect on understorey temperatures (Macek *et al.*, 2019; Zellweger *et al.*, 2019a).

The high importance of microclimate relative to the effects of topography and vegetation structure could also be related to the temporal component of the microclimate (Letten *et al.*, 2013; Zellweger *et al.*, 2019a). The microclimate dynamics reflect seasonality, diurnal cycles, and weather patterns, which are all ecologically relevant (Grimmond *et al.*, 2000; Song *et al.*, 2015; Wehr *et al.*, 2016; Wu *et al.*, 2016), but they are not well captured by the temporally static patterns of land-surface topography and vegetation structure (Dyer, 2002; Villegas *et al.*, 2010; Kemppinen *et al.*, 2018). Moreover, moisture availability, which is an important environmental factor for bryophytes (Jonsgard & Birks, 1993; Raabe *et al.*, 2010; Tyler *et al.*, 2018; Schmitz *et al.*, 2020), also reflects the variation caused by differences in water storage capacity and soil water flow on various soil and bedrock types, but these processes are only partly captured by land-surface topography (Beaudette *et al.*, 2013; Jarecke *et al.*, 2021; Riihimäki *et al.*, 2021).

Maximum air temperature and growing degree days were the most important microclimatic predictors of bryophyte assemblages. Their high relevance agrees with previous findings (Dahlberg *et al.*, 2014, 2020; Greiser *et al.*, 2020). In addition to the air temperature, soil moisture affected community composition, but not bryophyte richness in our study area. The importance of soil moisture for bryophyte assemblages also agrees with other studies (Carleton & Dunham, 2003; Kemppinen *et al.*, 2019; Kopecký *et al.*, 2021) and further stresses the significance of soil moisture for bryophyte species composition.

We did not detect any significant effect of snow cover on bryophyte assemblages, in contrast to some previous studies (Niittynen & Luoto, 2018; Górski *et al.*, 2020). The important role of snow as a driver of bryophyte species assemblages was however reported mostly from the cold Arctic and alpine regions. The snow conditions in these regions sharply differ from those in our study region, where snow cover persists on average only for 40 days and is deeper than 15 cm for only a few days in a year (based on our unpublished data). Our results thus suggest that snow cover may not be a limiting factor for bryophyte assemblages in temperate forests.

The relationship between species assemblages and microclimate could also be affected by the scale at which they are studied. Forest microclimate can change substantially at the scale of metre (Grimmond *et al.*, 2000; Pincebourde & Salle, 2020; Kašpar *et al.*, 2021). Bryophytes growing only a few metres from the microclimatic logger may experience very distinct microclimatic conditions from bryophytes near the logger. If this within-plot heterogeneity is not considered, then the effects of microclimate on vegetation may be underestimated in analyses. This may be a serious problem, particularly in topographically heterogeneous landscapes. Therefore, we focused on bryophytes growing immediately around our TMS microclimate loggers, but we acknowledge that this deliberate focus on relatively small plots likely contributed to unexplained variation (Palmer & Dixon, 1990). On such a small scale, biotic factors could overrule the environmental factors (Wisz *et al.*, 2013); small study plots could be dominated by a few or even a single species, growing as dense turf (Bates, 1998). In our case, *Sphagnum* or *Leucobryum* cushions sometimes occupied the entire plot. Bryophytes massively producing viable propagules could also supply closely surrounding populations (Vitt & Belland, 1997; Frahm, 2008; Hutsemekers *et al.*, 2008), and this mass effect can further reduce the importance of local microclimate. Higher stochasticity in species compositional data is therefore an inevitable consequence of a small plot size supporting only a limited number of individuals.

Besides biotic factors decreasing explainable variation by environmental conditions, potential links between remotely sensed environmental data like topography and canopy height models and in situ collected vegetation data could also be affected by uncertainties in the spatial location of sampling plots, especially under a dense canopy in complex terrain (Sigrist *et al.*, 1999; Piedallu & Gégout, 2005). If so, this could eventually favour the in situ measured microclimatic variables over the remotely sensed variables. To minimize this possibility, we used differential GNSS, applied data postprocessing and checked each measured coordinate against high-resolution terrain topography. Therefore, we are confident that location uncertainties did not bias our results.

5. Conclusion

Our results showed that in situ measured microclimate explained more variation in bryophyte assemblages than land-surface topography and vegetation structure. Microclimatic effects only partly overlapped with the effects of topography and vegetation structure. In situ measured growing degree days, maximum air temperature, and mean soil moisture were the most important factors, largely independent of topography or vegetation structure. Our study showed that terrain topography, even when derived from a high-resolution LiDAR DEM and computed with advanced geoprocessing algorithms, cannot fully substitute the effect of in situ measured microclimate on forest bryophytes.

Acknowledgements

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Appendices

Appendix A is available online: https://doi.org/10.1016/j.scitotenv.2022.153377

PAPER 2

Graphical abstract generated with DALL.E GPT 4.o based on manuscript text abstract.

Temperature-driven variability in vapor pressure deficit controls bryophyte community composition within a temperate forest landscape

Anna Růžičková, Matěj Man, Martin Macek, Jan Wild & Martin Kopecký

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Abstract

Atmospheric vapour pressure deficit (VPD) is a key driver of plant ecophysiology and global vegetation productivity. However, VPD variability across forested landscapes, its drivers, and its potential role in bryophyte community assembly remain largely unexplored. To address this, we investigated how forest understory VPD varies across the forested landscape, identified the factors driving this variability, and examined whether VPD variability influences bryophyte community composition.

We recorded bryophyte species composition and concurrently measured understory air temperature and relative humidity at 38 permanent vegetation plots in the temperate forests of Bohemian Switzerland National Park, Central Europe. From the microclimate time series, we calculated actual and saturated water vapour pressures and integrated them into the maximum daily VPD. We then quantified the spatial variability of these microclimatic variables across the landscape. Finally, we partitioned VPD variability into components driven by actual and saturated vapour pressures and used multivariate analyses to assess the effects of VPD on bryophyte community composition.

Forest understory VPD exhibited significant spatial variability among the plots. This variability in atmospheric VPD was primarily driven by temperature-controlled differences in saturated vapour pressure, while actual vapour pressure remained relatively constant across the landscape.

Bryophyte community composition was structured by atmospheric VPD. Widespread mesic bryophytes were also present in plots with high atmospheric VPD, but hygrophilous, boreal, and atlantic species, which occur azonally, were restricted to plots with low atmospheric VPD. Sites with low atmospheric VPD represent species-rich microclimatic refugia, harbouring regionally rare bryophyte species near their distributional range limits.

Atmospheric VPD shapes the composition and richness of bryophyte assemblages in temperate forest understories. Even in landscapes with rugged terrain, spatial variability in atmospheric VPD was closely tied to variability in saturated vapour pressure, and thus to maximum air temperature. Maximum air temperature and VPD are therefore tightly linked at ecologically relevant scales. Many ecological processes and distributional patterns traditionally associated with maximum air temperature may actually be driven by the more physiologically relevant atmospheric VPD.

1. Introduction

Atmospheric vapour pressure deficit (VPD) is one of the most important drivers of plant functioning in terrestrial ecosystems (Grossiord et al., 2020).For plants, higher VPD results in increased evaporative stress, which reduces photosynthesis in the short term and can lead to drought-induced mortality in the long term (McDowell et al., 2008; Zhang et al., 2017; Fu et al., 2022). Unprecedentedly high VPD is already limiting global vegetation productivity (Yuan et al., 2019; López et al., 2021; Lu et al., 2022) and triggering large-scale forest diebacks at continental levels (Breshears et al., 2013; Eamus et al., 2013; Williams et al., 2013).

In contrast to the well-established knowledge about the effects of VPD on plant physiology and global vegetation functioning, the role of atmospheric VPD in plant community assembly across landscape scales remains largely unknown (Novick et al., 2024). However, such knowledge is crucial for improving predictions of climate change impacts on vegetation and for identifying microclimatic refugia (Fenton & Frego, 2005; Ashcroft et al., 2009; Schmalholz & Hylander, 2011; Stark & Fridley, 2022).

Atmospheric vapour pressure deficit (VPD), defined as the difference between vapour pressure in fully saturated air (P_{sat}) and actual vapour pressure (P_{air}), quantifies the desiccating power of the air relevant to plants (Anderson, 1936). While saturated vapour pressure is determined solely by air temperature, actual vapour pressure reflects the amount of water vapour in the air, influenced by several factors such as atmospheric circulation, precipitation, soil evaporation, open water, and plant transpiration (Campbell & Norman, 1998). Therefore, spatial variability in VPD reflects the interaction between patterns in saturated and actual vapour pressure **(Fig. 1)**.

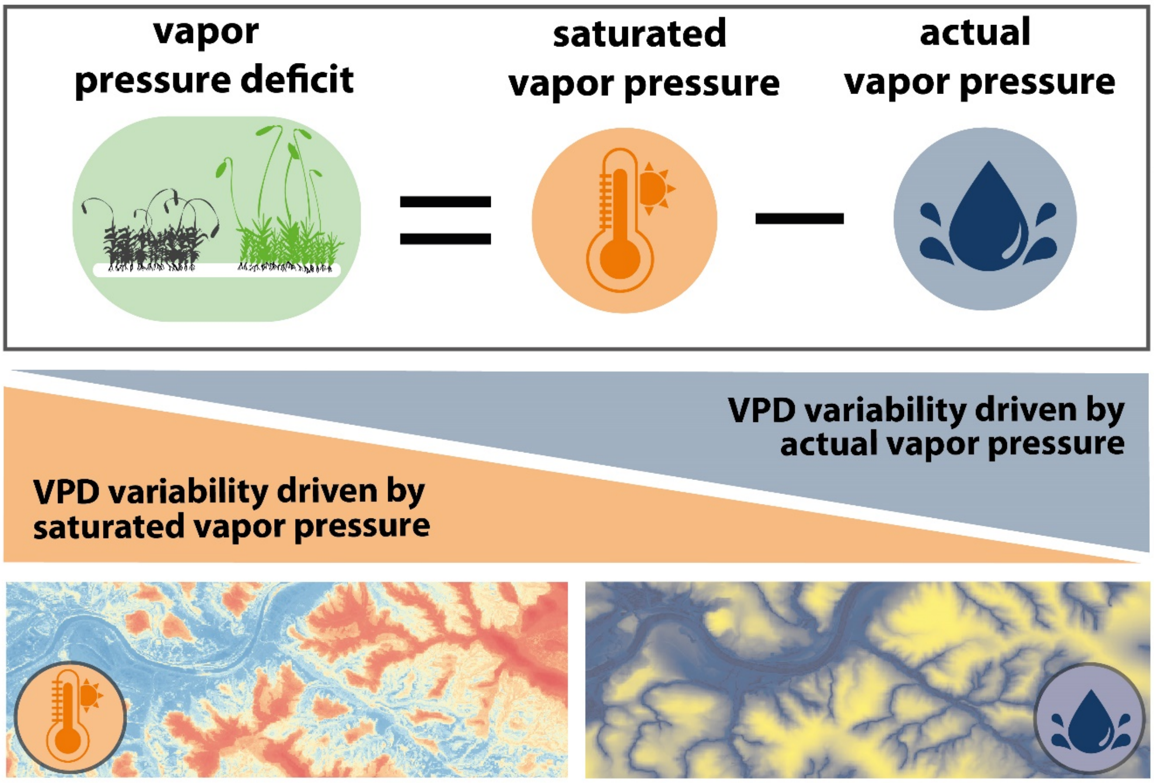

Figure 1 Atmospheric vapor pressure deficit (VPD) is the difference between saturated and actual vapor pressure. While spatial variation in saturated vapor pressure is driven solely by variation in air temperature, actual vapor pressure is determined by the complex interplay of synoptic weather conditions, evaporation, and transpiration. However, the relative importance of these two contrasting drivers of VPD spatial variability across the landscape remains largely unknown.

Understanding the drivers of VPD variability across landscapes is especially important in the context of ongoing climate change. Climatologists project a temperature increase of up to 4.4°C by 2100 (Calvin et al., 2023), which would lead to more than a 40% increase in VPD if atmospheric water vapour content remains constant (Will et al., 2013). This increase is likely to alter patterns of VPD variability across landscapes, potentially affecting species distributions and reshuffling plant community composition. However, we still know very little about the processes controlling VPD variability across landscapes or the links between VPD variability and plant community assembly.

Among plants, the bryophytes, in particular, are highly sensitive to evaporative water loss due to their lack of roots, internal lignified water-conducting systems, water storage tissues, and active stomata, combined with their large surface area relative to biomass (Shaw & Goffinet, 2000; Rice et al., 2001). Unlike tracheophytes bryophytes transport water mainly passively through external capillary spaces between their small body parts (Schofield, 1981; Glime, 2017a). Therefore, bryophyte internal water content is directly influenced by the water content in their surrounding environment (Vanderpoorten & Goffinet, 2009). To cope with this limitation, bryophytes have evolved varying levels of desiccation tolerance (Proctor, 2000), which differ widely among species (Proctor *et al.*, 2007b). Consequently, bryophytes and their assemblages are potentially highly sensitive to the evaporative stress represented by atmospheric VPD (Gehrig-Downie et al., 2011; Karger et al., 2012; Kraichak, 2014). Studies from boreal and tropical regions indicate that VPD can significantly influence bryophyte species composition, richness, and growth (Frego & Carleton, 1995a; Sporn *et al.*, 2009, 2010; Kraichak, 2014). However, surprisingly little is known about the effects of VPD on bryophyte assemblages in temperate forests (Fenton & Frego, 2005).

To fill this knowledge gap, we explored VPD variability across a temperate forest landscape, identified the factors driving this variability, and tested whether VPD influences the diversity and community composition of temperate forest bryophytes.

2. Methods

2.1. Study area

We recorded bryophytes and measured microclimate in the Bohemian Switzerland National Park in the Czech Republic (**Fig. 2**). Rugged terrain of this sandstone landscape creates fine-scale mosaic of contrasting habitats with steep microclimatic gradients over short distances (Wild *et al.*, 2013). The elevation within the national park ranges from 125 to 619 m (mean 340 m). According to the data from the Tokáň weather station (**Fig. 2**), the mean annual air temperature during 2011-2019 period was 8.3 °C, and the mean annual precipitation was 765 mm.

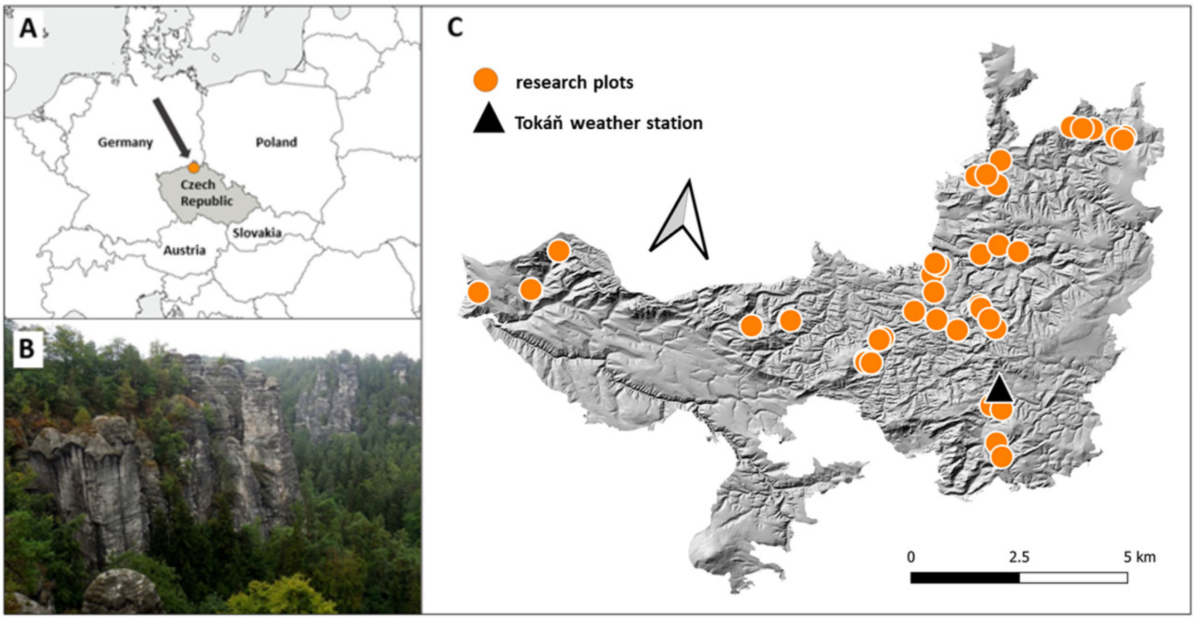

Figure 2 We measured microclimate and simultaneously recoded bryophyte species composition at 38 permanent research plots within the Bohemian Switzerland National Park in Central Europe (**A**). This forested area has a rugged terrain with steep environmental gradients (**B**). The location of the 38 research plots and the Tokáň weather station within the area of the national park (**C**).

Most of the Bohemian Switzerland is covered with coniferous forests. Historically planted Norway spruce (*Picea abies*) predominates in the valleys and on the plateaus, while patches of semi-natural forests on the upper slopes and rocky ridges are dominated either by Scots pine *(Pinus sylvestris*) or by European beech (*Fagus sylvatica*) on more mesic sites. The nutrient poor and strongly acidic soils result in relatively low diversity of vascular plants, which contrasts with the rich bryophyte flora (Härtel *et al.*, 2007). With more than 300 bryophyte species, the Bohemian Switzerland is a hotspot of bryophyte diversity in Central Europe (Marková, 2008).

The bryophyte flora of Bohemian Switzerland is composed of several locally widespread species such as *Tetraphis pellucida, Bazzania trilobata,* and *Dicranum scoparium*. These dominant floristic elements are enriched by azonal occurrences of (sub)alpine or (sub)montane species (e.g., *Hygrobiella laxifolia, Geocalyx graveolens, Anastrophyllum michauxii*), boreal species (e.g., *Dicranum majus, Rhytidiadelphus subpinnatus*), and (sub)atlantic species (e.g., *Tetrodontium brownianum, Plagiothecium undulatum*) (Härtel *et al.*, 2007; Marková, 2008).

2.2. Field data collection

We recorded bryophyte species composition and measured microclimate conditions on 38 permanent research plots (**Fig. 2**). On all plots, we used HOBO U23 ProV2 (Onset, USA) microclimatic dataloggers to simultaneously measure air temperature and relative humidity at a height of 1.5 m every 30 minutes from 1st June to 31st August 2022. Each HOBO U23 ProV2 datalogger has a temperature sensor with a resolution of 0.02 °C and an accuracy of ± 0.21 °C, and a relative humidity sensor with a resolution of 0.05% and an accuracy of ± 2.5%. All dataloggers were installed in white radiation shields with good ventilation hanging on the north side of the tree nearest to the research plot centre. In the middle of the growing season, an experienced bryologist (A. Růžičková) recorded the presence of all bryophyte species (up to a height of 1.5 m on rock and tree trunks) in each 3.14 m² research plot. Species nomenclature follows the Czech national checklist (Kučera *et al.*, 2012).

2.3. Microclimate data processing

First, we checked the microclimatic time series using visual inspection and standard procedures implemented in the *myClim* R package (Man *et al.*, 2023a). Using the checked air temperature and relative humidity data, we then calculated the saturation water vapor pressure (P_{sat}) following the updated Buck formula (Buck, 1981, 1996):

$$P_{sat} = (1.003 + 4.18 \times 10^{-6} \times 101\ kPa) \times 0.61115 \times e^{((23.036 - t/333.7) * (t/(279.82\ +\ t)))}$$

where *t* is air temperature [°C]. Next, we calculated the actual water vapor pressure (P_{air}) using Tetens's formula (Tetens, 1930):

$$P_{air} = P_{sat} \times \left(\frac{rh}{100}\right)$$

Finally, we calculated atmospheric VPD as the difference between P_{sat} and P_{air} (Jones, 2013). From the resulting time series, we extracted the daily maximum VPD, P_{sat} and P_{air} values at the time of the daily maximum VPD for each plot. We then calculated the average daily maximum VPD across entire study period as a measure of evaporative stress for the bryophyte communities and the average daily values of P_{sat} and P_{air} at the time of the daily maximum VPD for each plot (**Table 1**).

Table 1 Summary statistics of microclimatic variables measured in 38 forest research plots during summer (June-August 2022). Vapor pressure deficit is the average daily maxima, while saturated and actual vapor pressure are averages of daily values of these variables at the time of maximum daily VPD for entire study period.

	Abbreviation	Units	Mean across all plots	Range of plot values
Saturated vapor pressure	P_{sat}	kPa	4.00	2.61–5.02
Actual vapor pressure	P_{air}	kPa	1.90	1.75-2.08
Vapor pressure deficit	VPD	kPa	2.09	0.62–3.17

2.4. Data analysis

2.4.1. VPD spatial variability

As a measure of spatial variability in VPD, P_{sat} and P_{air}, we calculated standard deviation (SD) of the daily maximum VPD and corresponding P_{sat} and P_{air} values separately for each day during the study period. To quantify contribution of P_{sat} and P_{air} to the spatial variability of VPD, we performed variation partitioning (Legendre, 2008) based on a multiple linear regression model with the average daily maximum VPD as the response variable and the corresponding average daily P_{sat} and P_{air} values as the predictors. Finally, we averaged the daily standard deviations of maximum VPD and corresponding P_{sat} and P_{air} values over the entire study period as an overall measure of spatial variability for each microclimatic variable.

2.4.2. Bryophyte Communities

We explored the relationship between atmospheric VPD and bryophyte communities through three steps. First, we quantified VPD link to species richness, then, we explored VPD relationship to main gradients in community composition and finally, we tested VPD effects on species composition. To quantify the relationship between the number of bryophyte species recorded in the plot (richness) and VPD, we used generalized additive model (GAM) with Poisson distribution, log link function and smooth terms fitted by thin plate regression splines without null space penalization and smoothing parameter estimation using restricted maximum likelihood fitted with the R package *mgcv* 1.9.1 (Wood, 2011).

To explore the main gradients in the bryophyte community composition and to visualize the occurrence of individual species, we used Non-metric Multidimensional Scaling (NMDS) based on the Sørensen dissimilarity. We calculated two-dimensional NMDS with the weak treatment of ties, maximum of 500 random starts and 999 iterations in each NMDS run using *metaMDS* function from the *vegan* R package version 2.6-4 (Oksanen *et al.*, 2022). To maximize variance along the first ordination axis, we centred and rotated the resulting two-dimensional configuration with Principal Component Analysis. Finally, we used weighted averages of species scores to visualize centroids of individual species distribution in the NMDS ordination space. To explore whether main compositional gradients correlate with microclimate variables, we passively projected gradients in VPD, P_{sat} and P_{air} into the NMDS ordination space and tested the significance of the fit with 999 random permutations using the *envfit* function from *vegan* R package (Oksanen *et al.*, 2022).

2.4.3. Effect of VPD on bryophyte community composition

To express differences in bryophyte species composition between plots, we calculated pairwise Sørensen and Simpson dissimilarity indices with *vegan* R package version 2.6-4 (Oksanen *et al.*, 2022). While the Sørensen index expresses differences in species composition including differences in species richness, the Simpson index expresses species turnover independent from the species richness differences (Lennon *et al.*, 2001). To calculate the variation in species composition explained by the variability of the average daily maximum VPD, we used Distance-based Redundancy Analysis (db-RDA) (McArdle & Anderson, 2001). We built two db-RDA models, one for each species composition matrix (Sørensen and Simpson) as the predictor. As the predictors, we used the average daily maximum VPD. To assess the statistical significance of db-RDA models, we used a permutation test with 999 random permutations (Legendre *et al.*, 2011).

3. Results

3.1. VPD variability

VPD in the forest understory was highly variable in both time and space. The VPD values measured every 30 minutes ranged from 0 kPa to 8.83 kPa (mean 0.85 kPa). The daily VPD maxima had the same range among the plots, with an overall mean of 2.09 kPa during the study period, ranging from 0.62 to 3.17 kPa among the plots (**Table 1**).

Saturated vapor pressure P_{sat} was the dominant driver of VPD variability across the landscape (**Fig. 3**). The spatial variability of P_{sat} (average daily SD = 0.55 kPa) was more than three times higher than the spatial variability of actual vapor pressure P_{air} (SD = 0.14 kPa). While P_{sat} explained 96% of VPD variability, P_{air} explained only 4% of VPD variability.

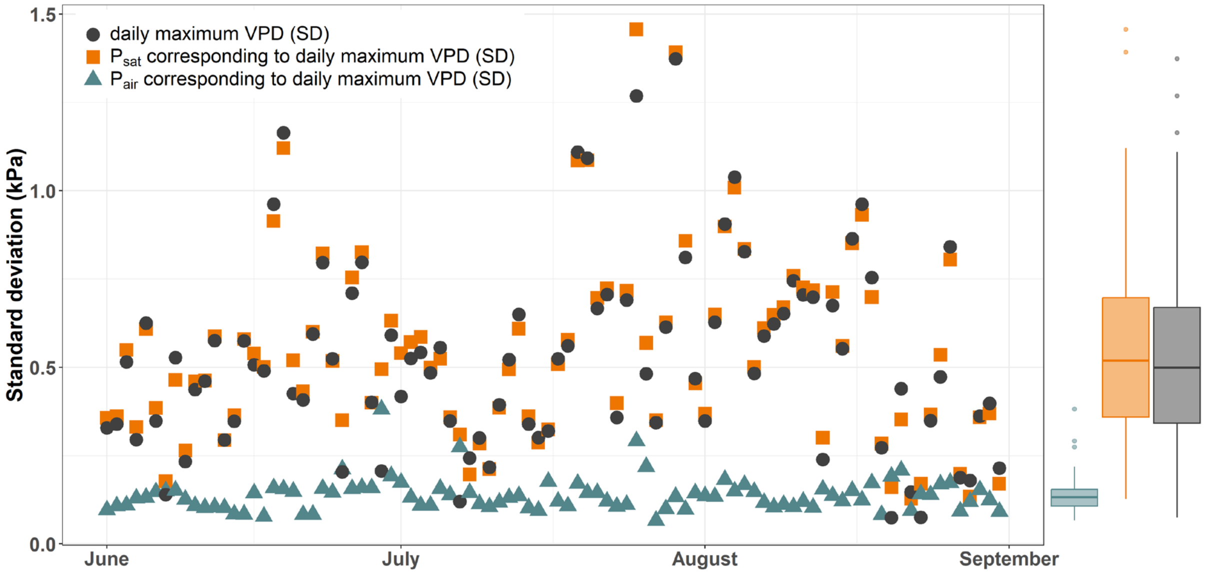

Figure 3 Spatial variability of VPD (black circles) is tightly coupled with the spatial variability in saturated vapor pressure (P_{sat}, orange squares) but not with actual vapour pressure (P_{air}, blue triangles). Each datapoint shows standard deviation of daily value across all 38 study sites. Marginal boxplots summarize spatial variability (daily standard deviations) during growing season (June to August 2022).

3.2. Bryophyte communities

In total, we recorded 39 species of bryophytes (14 liverworts and 25 mosses, **Fig. 4**). The average number of species per plot was 8, with a minimum of 1 and a maximum of 21 species. The most frequent species were *Dicranum scoparium, Leucobryum juniperoideum,* and *Hypnum cupressiforme*. The number of bryophyte species was higher in plots with low VPD and declined with increasing VPD (GAM: explained deviance D^2 = 30 %, p--value = 0.002). The main gradients in bryophyte community composition reflected gradients in atmospheric VPD (**Fig. 4A**). The gradients in VPD and P_{sat} were significantly related to the main gradients in bryophyte community composition (VPD: R^2 = 0.37, p-value = 0.001; P_{sat}: R^2 = 0.34, p-value = 0.001), whereas the gradient in P_{air} was not significantly related to the main gradients in community composition (R^2 = 0.09, p-value = 0.17).

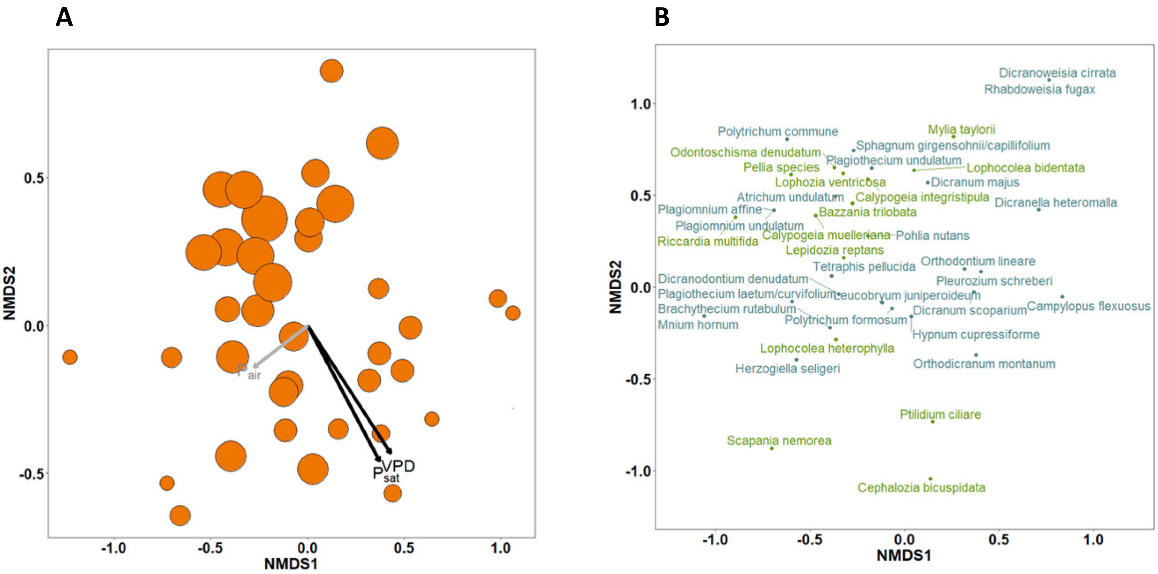

Figure 4 (A) Nonmetric multidimensional scaling of the bryophyte species composition in 38 forest plots with passively projected vectors showing the gradient of the increasing average daily maximum VPD and corresponding saturated (P_{sat}) and actual (P_{air}) vapor pressure. While the fit of VPD and P_{sat} was statistically highly significant (both p-value = 0.001), the fit of P_{air} was not (p-value = 0.17) and the vector is therefore plotted in grey. Points show the positions of the plots, and the point size represents the number of species per plot. **(B)** The diagram shows centroids of species occurrences (weighted averages) of all recorded moss (blue) and liverwort (green) species shown in the NMDS ordination space. Small liverworts (e.g. *Riccardia multifida, Lophozia ventricosa)* and more hygrophilous bryophytes (e.g. *Polytrichum commune*, *Sphagnum girgensohnii/capillifolium, Bazzania trilobata*, *Mylia taylorii*), as well as boreal (e.g. *Dicranum majus*) and atlantic (e.g. *Plagiothecium undulatum*) species occurred on plots with lower atmospheric VPD (**Fig. 4A**). In contrast, mesic species like *Hypnum cupressiforme*, *Polytrichum formosum*, *Dicranum scoparium* and *Brachythecium rutabulum* occurred also in plots with higher atmospheric VPD.

3.3. Effect of VPD on bryophyte community composition

Atmospheric VPD was a significant driver of the community composition of forest bryophytes. The average daily maximum VPD explained 10.95% of the variation in community composition as expressed by the Sørensen index (p-value = 0.001) and 13.52% of the variation as expressed by the Simpson index (p-value = 0.004).

4. Discussion

4.1. VPD variability across the landscape

There was significant spatial variability in atmospheric VPD across the studied forests, and this variability influenced bryophyte community composition. However, because this landscape-scale variation was primarily driven by temperature-controlled P_{sat}, the effects of VPD may be masked by temperature. Microclimatic variation across the landscape, which is crucial for community ecology, is largely shaped by terrain (Dobrowski, 2011). Rugged topography strongly influences maximum temperatures in the forest understory (Macek *et al.*, 2019), and consequently, spatial variability in P_{sat}. In contrast, spatial variability in absolute air humidity is predominantly governed by processes operating at larger scales, such as atmospheric circulation (Campbell & Norman, 1998). Thus, spatial variability in absolute air humidity over the landscape is much smaller than temperature-driven variation in saturated vapour pressure (Wörlen *et al.*, 1999).

Our findings have important implications for both theoretical and applied ecology. First, the variation in VPD across the landscape was controlled by air temperature. As a result, these two microclimatic variables are tightly linked at biologically relevant scales, making it difficult to disentangle their effects on species assemblages and ecological processes using observational data. Our previous research highlighted the significance of maximum temperature for bryophyte and vascular plant species distribution and community composition (Macek *et al.*, 2019; Man *et al.*, 2022). In light of our new findings, we hypothesise that the apparent importance of maximum air temperature does not arise from its direct effects on plant ecophysiology, but rather from its strong influence on VPD variability across the landscape. This hypothesis requires further testing, ideally with extensive data collected across multiple spatial scales.

Second, our results suggest that local microclimatic air temperature measurements can be combined with relative humidity data from nearby weather stations to provide reasonably accurate local estimates of atmospheric VPD. This practical application of our findings could be highly useful, given the increasing availability of microclimatic temperature measurements worldwide (Lembrechts *et al.*, 2020). However, we emphasise that the general applicability of this approach should be further tested in a variety of environmental settings.

4.2. VPD effects on bryophytes

The way in which plants cope with high VPD differs significantly between bryophytes and tracheophytes (Alpert, 2000). Vascular plants have developed an internal lignified transport system, primarily driven by transpiration pull, to distribute water absorbed by their roots from the soil throughout their bodies. Their hydration status is regulated internally via stomata (Shaw & Goffinet, 2000). Although the ability to close stomata helps prevent water loss during short periods of drought, prolonged periods of low soil moisture or high VPD can lead to mortality due to hydraulic failure, which damages plant tissues and may result in plant death (Schönbeck *et al.*, 2022).

In contrast, most bryophytes tolerate desiccation by becoming metabolically inactive in the absence of water (Proctor, 2000). When conditions improve, they quickly reactivate physiological processes such as respiration, photosynthesis, the cell cycle, and normal cytoskeleton function. However, this reactivation is energy-intensive, requiring processes such as the production of specific repair proteins (Oliver & Bewley, 1984; Zeng, 2002) and the maintenance of the integrity and normal function of cell organelles and membranes (Platt *et al.*, 1994). To survive repeated desiccation, bryophytes must maintain a positive carbon balance, making prolonged periods without evaporative stress crucial for their growth and long-term survival (Proctor *et al.*, 2007b).

The osmotic potential of bryophyte cells at full turgor is rarely more negative than -2 MPa. An osmotic potential of -1.36 MPa is in equilibrium with air at 20°C and 99% relative humidity (RH), corresponding to a VPD of less than 0.03 kPa. However, at the same temperature, when RH drops to 90%, the water potential decreases to -14 MPa (Proctor, 2000). Since water moves from areas of higher potential to lower potential, bryophytes inevitably lose water when exposed to air with non-zero VPD (Hinshiri & Proctor, 1971; Busby *et al.*, 1978).

In our study area, conditions with a VPD below 0.03 kPa occurred only 9% of the time. This means that full turgor and normal cell function in bryophytes can only be ensured when liquid water is present near their cells. Under a VPD of 1.22 kPa, this external water completely evaporates within approximately 45–50 minutes (León-Vargas *et al.*, 2006). Once external water is depleted, cells quickly lose turgor, metabolic activity slows, and efficient carbon fixation ceases. In our study area, the average daily maximum VPD during the summer was 2.39 kPa, indicating that forest bryophytes in this region experience significant evaporative stress due to atmospheric VPD.

The large variability in VPD across the landscape creates a fine-scale mosaic of sites with widely differing VPD, resulting in varying levels of evaporative stress for bryophytes. We found that this environmental gradient acts as a filter for bryophyte community assembly. Regionally rare species occurred preferentially in sites with low VPD. These species—typically found in montane, boreal, or atlantic regions—are reaching their distributional limits within our study area (Hill & Preston, 1998). Sites with low VPD thus serve as microclimatic refugia within an otherwise unsuitable landscape matrix. In contrast, widespread mesic bryophytes were able to grow in both low- and high-VPD sites. Therefore, sites with low atmospheric VPD represent hotspots of bryophyte diversity within the landscape, hosting both rare, azonally occurring species and more widespread mesic bryophytes.

Atmospheric VPD increases exponentially with rising temperatures. As climate warming continues, areas with low VPD are likely to shrink, placing their bryophyte diversity at greater risk (Pardow & Lakatos, 2013). Furthermore, the temperature control of spatial patterns in atmospheric VPD suggests that increasingly frequent canopy disturbances will raise understory temperatures and, consequently, VPD near the ground (Wolf *et al.*, 2021). Our results indicate that such changes will alter bryophyte communities in the region, favouring widespread mesic bryophytes at the expense of regionally rare species at their distributional margins.

4.3. Atmospheric VPD or maximum temperature?

The close coupling between VPD and maximum temperature across the landscape highlights both the necessity and the challenge of disentangling the influences of VPD and temperature on plant communities. While temperature affects essential life functions in bryophytes, such as photosynthesis, respiration (Dilks & Proctor, 1975) and growth (Furness & Grime, 1982), bryophytes are adapted to thrive across a wide range of temperatures—from as low as -30°C (Dilks & Proctor, 1975) to over 40°C in a desiccated state (Hearnshaw & Proctor, 1982). The optimal growth temperature for most bryophytes ranges from 12 to 25°C (Vanderpoorten & Goffinet, 2009). However, many bryophyte species are capable of growing at temperatures around 5°C (Dilks & Proctor, 1975), and some can even photosynthesise at temperatures well below 0°C (Pihakaski & Pihakaski, 1979; Lösch *et al.*, 1983). Consequently, temperature alone is rarely a direct limiting factor for bryophyte distribution and community composition in temperate regions.

Several studies on vascular plants have attempted to differentiate the independent effects of VPD from other microclimatic factors influencing plant functioning e.g., (Eamus *et al.*, 2013; Zhang *et al.*, 2017; Amitrano *et al.*, 2021; Jiao *et al.*, 2022; Lu *et al.*, 2022), consistently underscoring the critical role of VPD (Schönbeck *et al.*, 2022; Novick *et al.*, 2024). Unfortunately, no recent physiological studies have addressed the independent effects of VPD on bryophytes, despite strong indications that VPD is a key factor (Busby *et al.*, 1978; Sonnleitner *et al.*, 2009). Most studies have instead focused on bryophyte desiccation (Morales-Sánchez *et al.*, 2022). While desiccation is a response to the external lack of water, the ultimate driver of this physiological process is the drying power of the air, as reflected by atmospheric VPD. Therefore, we propose that a deeper focus on atmospheric VPD as a primary driver of bryophyte desiccation could yield valuable insights into bryophyte ecology and conservation. Understanding the specific role of VPD could help refine our knowledge of bryophyte responses to environmental stress, providing critical information for their long-term conservation under changing climatic conditions.

5. Conclusion

Atmospheric VPD plays a critical role in controlling the composition and richness of bryophyte assemblages in temperate forest understories. Even in landscapes with extremely rugged terrain, spatial variability in atmospheric VPD was primarily driven by temperature-controlled saturated vapour pressure. Maximum air temperature and VPD are closely coupled at biologically relevant scales, making it challenging to disentangle their individual effects. Both ecological and physiological studies indicate that bryophytes in temperate zones are not directly limited by temperature (Dilks & Proctor, 1975; Furness & Grime, 1982), but rather by water availability in their environment, particularly atmospheric water demand (Busby *et al.*, 1978; Dilks & Proctor, 1979). Since atmospheric water demand is directly reflected by VPD (Grossiord *et al.*, 2020; López *et al.*, 2021), the key limiting factor for bryophytes is atmospheric VPD rather than temperature. As a result, many ecological processes and distributional patterns previously attributed to maximum air temperature are more likely driven by atmospheric VPD.

Acknowledgements

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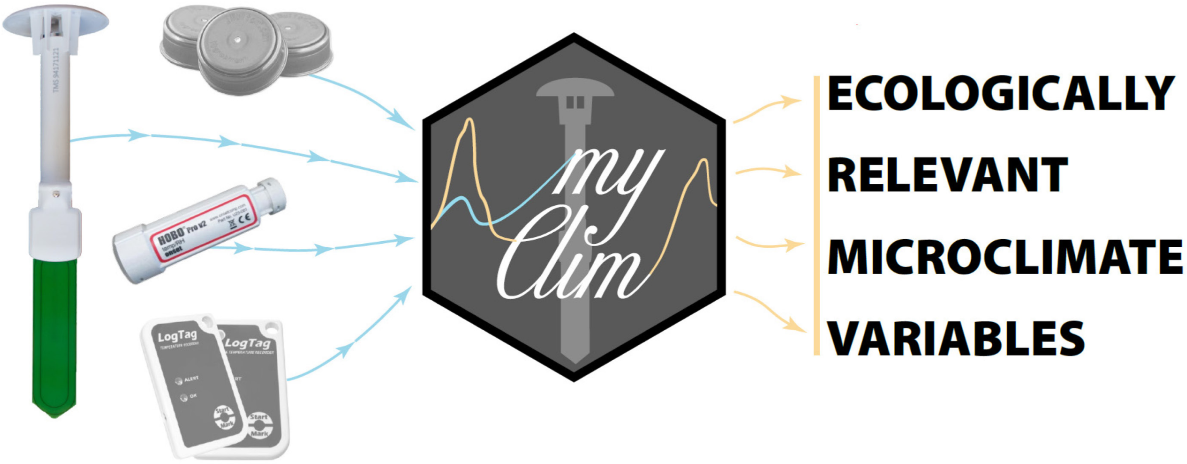
PAPER 3



Graphical abstract from paper 3. Author: Matěj Man

myClim: Microclimate data handling and standardised analyses in R

Matěj Man, Vojtěch Kalčík, Martin Macek, Josef Brůna, Lucia Hederová, Jan Wild & Martin Kopecký

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Abstract

Microclimates have been recognised as one of the key drivers in global change biology. Durable microclimate loggers, detailed in-situ measurements and sophisticated modelling tools are increasingly available, but a lack of standardised workflows for microclimate data handling hinders synthesis across the studies and thus progress in the global change biology. To overcome these limitations, we developed an R package myClim for microclimate data-processing, storage, and analyses. The myClim package supports complete workflow for microclimate data-handling, including reading raw logger data files, their pre-processing and cleaning, time-series' aggregation, calculation of ecologically relevant microclimatic variables, data export and storage.

The myClim package stores data in a size-efficient, hierarchical structure which respects the hierarchy of field microclimate measurement (locality > loggers > sensors). For imported microclimatic data, myClim provides an informative summary and automatically detects and corrects common issues like duplicated and wrongly-ordered measurements. The myClim package also provides advanced functions for microclimate data aggregation to various timescales (e.g., days, months, years, or growing seasons) as well as tools for sensor calibration, data conversion, and joining of multiple microclimatic time-series.

The myClim package provides advanced functions for standardised calculation of ecologically relevant microclimatic variables like freezing and growing degree days, snow cover period, soil volumetric water content, and atmospheric vapour pressure deficit. Calculated microclimatic variables are stored efficiently in myClim data format and can be easily exported to long or wide tables for further analyses and visualisations.

Adopting myClim can facilitate large-scale syntheses, boost data sharing, and increase the comparability and reproducibility of microclimatic studies. The stable version of myClim is available on CRAN (https://cran.r-project.org/web/packages/myClim) and the development version is available on GitHub (https://github.com/ibot-geoecology/myClim).

1. Introduction

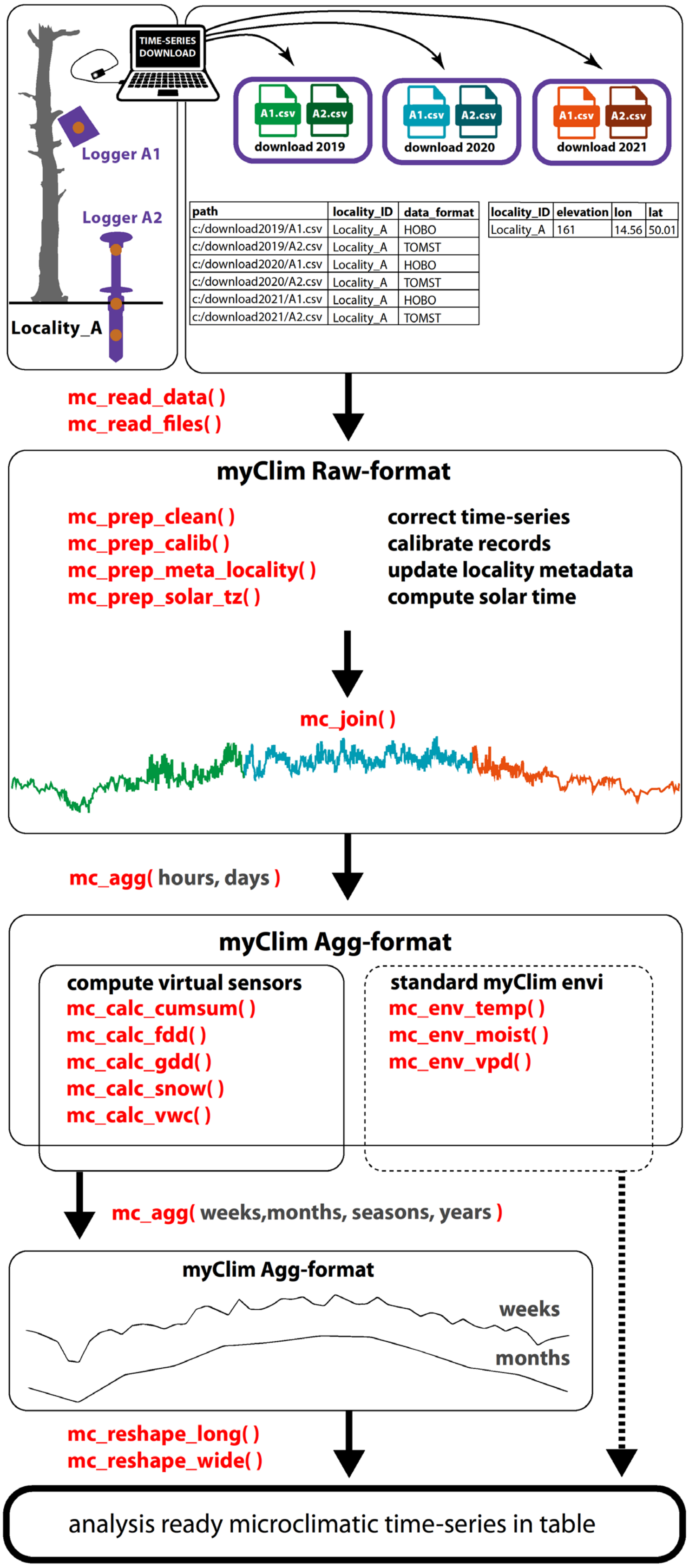
Interacting effects of climate, topography, and vegetation create a fine-scaled and temporary dynamic mosaic of microclimates, substantially different from free-air conditions recorded by standard weather stations and predicted by global climatic models (Geiger *et al.*, 2009; Slavich *et al.*, 2014). Local microclimate, and not regional macroclimate, directly affect organisms and key ecological processes (Nadeau *et al.*, 2017; Körner, 2021). While the microclimate is always local, it also affects biodiversity and ecosystem processes on larger scales (Zellweger *et al.*, 2020; Nadeau *et al.*, 2022). Microclimate thus became a central theme in global change biology and ecology (Potter *et al.*, 2013; De Frenne *et al.*, 2021).

To measure a microclimate in the field, researchers used different nonspecialized industrial loggers (Whiteman *et al.*, 2000; Hubbart *et al.*, 2005; Lundquist & Lott, 2008) and, increasingly, also new microclimatic loggers specially designed for ecological applications (Wild *et al.*, 2019b). The wide variability of employed microclimatic loggers and their different field installation sparked studies exploring effects introduced by different logger types, radiation shields and various other adjustments like waterproofing (Roznik & Alford, 2012; Holden *et al.*, 2013; Terando *et al.*, 2017; Navarro-Serrano *et al.*, 2019; Maclean *et al.*, 2021). The rapidly-increasing number of microclimatic studies (e.g., Finocchiaro et al., 2023; Greiser et al., 2020; Macek et al., 2019) and the establishment of local microclimate monitoring networks (e.g., Aalto et al., 2022; Dickerson-Lange et al., 2015; Lundquist et al., 2016) facilitate the creation of global microclimate database SoilTemp, aggregating data from thousands of localities (Lembrechts *et al.*, 2020).

However, recent development in microclimate monitoring was not accompanied by the development of standardised methods and procedures for microclimate data handling and -processing (Bramer *et al.*, 2018). Microclimatic studies thus often use different workflows, data treatments and storage formats even for the variables measured with the same sensors. Similarly, the algorithms used to calculate microclimatic variables from field measurements often differ between studies. The lack of common processing tools, standard algorithms, and data format hampers comparability across the studies and data integration over the larger scales needed in global change biology.

To overcome these limitations, we developed the *myClim* R package for microclimate data processing, storage, and analysis. Here, we describe *myClim* structure, logic, and functionality (**Table 1**) and provide code examples in an electronic appendix **S2**. The *myClim* package implements the complete microclimatic workflow from the import of the raw microclimatic time-series to the calculation of ecologically relevant variables in a fully-reproducible and standardised way using open-source code (**Fig. 1**). Therefore, the *myClim* R package will be useful to a wide audience and facilitate further advances in microclimate science.

1.1. *myClim* workflow



path	locality_ID	data_format
c:/download2019/A1.csv	Locality_A	HOBO
c:/download2019/A2.csv	Locality_A	TOMST
c:/download2020/A1.csv	Locality_A	HOBO
c:/download2020/A2.csv	Locality_A	TOMST
c:/download2021/A1.csv	Locality_A	HOBO
c:/download2021/A2.csv	Locality_A	TOMST

locality_ID	elevation	lon	lat
Locality_A	161	14.56	50.01

Figure 1 Workflow of microclimatic time-series processing with the *myClim* R package.

1.2. *myClim* data structure

Microclimatic data imported into myClim are stored in custom R classes and predefined lists with a hierarchical structure. This allows a combination of many loggers and localities, speeds up data manipulation and calculations, and reduces memory demand for data storage. For example, after import to myClim, microclimatic data originating from 2000 TOMST TMS loggers (four sensors per logger, recording every 15 minutes, distributed in 2000 CSV files) with a total size of 15 GB on the drive occupy only 5 GB in RAM and can be saved as the myClim R object to an RDS file of only 0.9 GB. This is a substantial reduction compared to the 25 GB RAM needed to load the same data to R as data tables and to the 1.2 GB needed to save those data tables as an RDS file.

The myClim objects have three hierarchical levels: locality, logger, and sensor (**Fig. 2**). Each hierarchical level can hold metadata (**Fig. 2**). Besides metadata, loggers can be associated with the output of the mc_clean function. Sensors can hold calibration, i.e., the correction factor and slope from the mc_prep_calib_load function and states, e.g., for the path to the original files or data quality flags. Each myClim locality can contain an unlimited number of loggers, and each logger can have multiple sensors measuring different physical variables at different heights.

The myClim objects exist either in Raw- or Agg-format, see electronic Appendix S1. The main difference between the formats is at the logger level. With original data in Raw-format, the level of logger is present and can be used for joining multiple downloads from the same logger. With analysis-ready data in Agg-format, the level of logger is missing, and time-series are associated directly with localities. Agg-format thus allows for easily linking microclimatic time-series with other locality-specific data, like species' occurrence data, topography, soil, macroclimate, or habitat type. The myClim functions work with both Raw- and Agg-formats.

Time-series with different timesteps (e.g., there are two loggers simultaneously recording on the same locality, but they are not synchronised; the first one is recording every 15 minutes, the second one is recording every hour) are allowed only in the Raw-format, but not in Agg-format. Therefore, the only way how to get heterogeneous time-series to Agg-format is their aggregation to the same timestep.

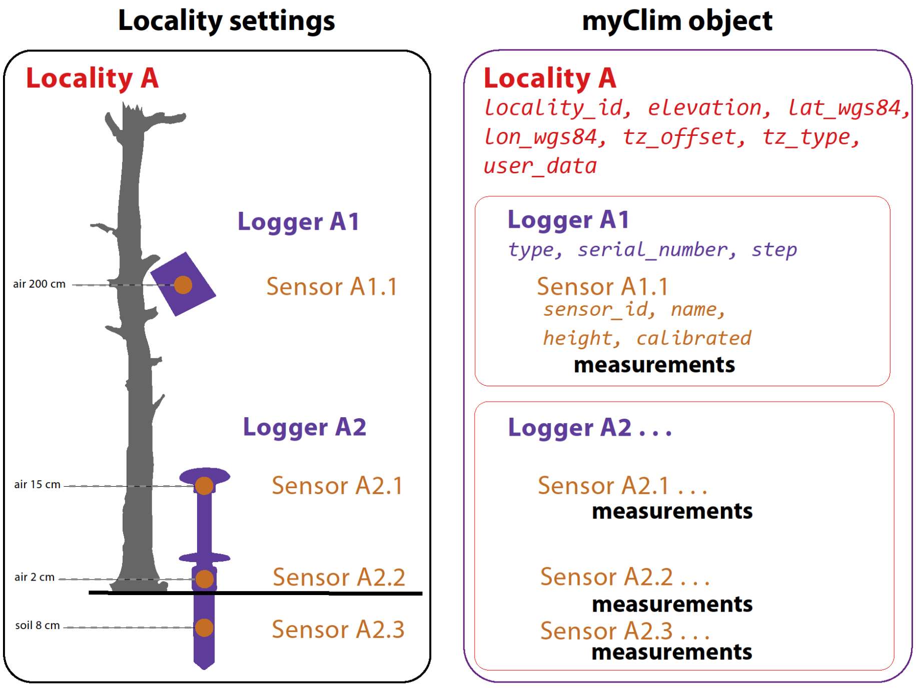


Figure 2 Schema of the *myClim* object in *Raw-format* with associated metadata. The locality (red) is the highest hierarchical level. On the locality, there can be one or more loggers (purple), and each logger can host one or more sensors (brown). Each hierarchical level of the *myClim* object can host its own metadata (*italic*). Microclimatic measurements are attached to the sensor, and time-series are attached to the logger (*Raw-format*) or locality (*Agg-format*).

1.3. Reading the microclimatic data

The *myClim* functions read directly the native files downloaded from various microclimatic loggers (e.g., TOMST TMS loggers and Onset HOBO loggers), but it is also possible to import other climatic time-series. Moreover, the *myClim* routine for data import can be customised to support other logger types like iButton, Lascar, or Logtag. During the data import, *myClim* runs by default automatic time-series cleaning and correction routine (see below *mc_prep_clean*), but the cleaning can be turned off and called up separately.

The myClim package can read either individual data files or all data files from a specified directory (and all its subdirectories) with the *mc_read_files* function. This function reads time-series directly from files without any metadata. The time-series are therefore organised in localities named according to the serial number of the logger (when available in the file header or provided as a part of the file name) or by the corresponding data file name.

To import both microclimatic time-series and associated metadata, we developed the *mc_read_data* function, which reads two tables joined by locality id 1) a table with a path to the data files, locality id, and type of microclimatic logger and 2) a table with metadata for each locality (e.g., geographic coordinates, elevation, time offset to UTC, **Fig. 1**). The locality metadata of the *myClim* object can also be added later or updated with the *mc_prep_meta_locality* function, which can accept either a named list for updating a single metadata slot or a data frame with defined columns for multiple updates.

1.4. Pre-processing

1.4.1. Time

The myClim package works with UTC as well as non-UTC time data, but the *myClim* functions assume that the data are in UTC. Therefore, to work properly in non-UTC time, the temporal offset (in minutes) between the local or solar time and the UTC must be specified in the metadata of each locality. The raw time-series in the *myClim* objects stay in UTC, and the offsets are applied during data aggregation. After the aggregation with local or solar time offsets, the aggregated time-series is no longer in UTC but inherits the solar or local time.

Using the local or solar time could be important in ecological analysis on large spatial scales because of the photoperiod shift around the globe. Therefore, we developed a *mc_prep_solar_tz* function, which, for each microclimatic measurement, calculates the time offset to UTC from geographic coordinates of each locality provided in the metadata. With this function, local solar time can be easily calculated from WGS84 longitude coordinates:

```
lon <- list(17.03887,13.54010,18.39900)# list of longitudes
names(lon) <- c('91171058','91171062','91171063') # locality names
data_clean <- mc_prep_meta(data_clean, lon, "lon_wgs84") # update metadata
data_tz <- mc_prep_solar_tz(data_clean) # calculate solar time
```

Raw time-series downloaded from microclimatic loggers can contain duplicated measurements, measurements in the wrong order, or missing measurements (Aalto *et al.*, 2022; Man *et al.*, 2022). Moreover, the logger's internal clock can drift, or the logger can be accidentally set to recording in unrounded time, e.g., when recording starts at 13:07 instead of 13:00. To fix these problems, we developed the *mc_prep_clean* function, which keeps only the first duplicated measurements, reorders wrongly-ordered measurements, and rounds up time-series to the closest nice break (13:07 -> 13:00). Note that the *mc_prep_clean* function corrects only these problems. It cannot fix other issues like wrong measurements, low contact of soil moisture sensor with the soil, overheating of air temperature sensor due to missing sun shield, or detect loggers dislocated by animals.

By default, the *mc_prep_clean* function prints the summary table of time-series cleaning in the console: the number of loggers, date range, and the list of detected steps in seconds and minutes. This summary table from data-cleaning is directly associated with the *myClim* objects and can be displayed later using the *mc_info_clean* function. Usually, data-cleaning with *mc_prep_clean* function is performed automatically already when reading data with *mc_read_data* and *mc_read_files* functions (default parameter clean = TRUE). Nevertheless, this default parameter can be changed to FALSE, and the data cleaning can be done separately with *mc_prep_clean* function. Below is an example of the output from the *mc_prep_clean* function called during data reading.

```
data <- mc_read_files("c:/TMS/", dataformat_name = "TOMST", clean = TRUE)
> 5 loggers
> datetime range: 2019-09-16 - 2021-07-09
> detected steps: 900s = 15min
```

locality id	serial number	start date	end date	step seconds	count duplicities	count missing	count disordered	rounded
91171058	91171058	2020-11-22 14:45:00	2021-07-09 09:45:00	900	0	0	0	TRUE
91171062	91171062	2020-10-12 12:00:00	2021-05-20 14:15:00	900	0	0	0	FALSE
91171063	91171063	2020-09-28 10:45:00	2021-04-28 12:15:00	900	0	0	0	FALSE
91191256	91191256	2020-08-24 00:00:00	2021-06-03 07:15:00	900	95	9845	2	FALSE
94199122	94199122	2019-09-16 14:30:00	2020-12-08 10:15:00	900	182	1143	8	FALSE

1.4.2. *Sensor calibration*

The low-cost sensors used in many microclimatic loggers have limited accuracy and measured values may be subject to systematic errors (Hubbart *et al.*, 2005; Navarro-Serrano *et al.*, 2019; Maclean *et al.*, 2021). Therefore, we recommend the calibration of individual sensors before their deployment. The *myClim* package offers calibration functionality for correction of the measured values with sensor-specific correction factors, compensating for a constant error (using *correction factor*) or for a linearly increasing/decreasing error with measured value (using *correction slope* different from zero). The` function *mc_prep_calib_load* first assigns correction factors and slopes to sensors in the *myClim* object and stores them as sensor metadata. Then, the *mc_prep_calib* function replaces the original values with corrected values calculated according to the formula (Eq. 1).

$$\text{Corrected Value} = \text{Original Value} \cdot (1 + \text{correction slope}) + \text{correction factor} \tag{1}$$

1.4.3. *Informative summaries*

The functions *mc_info_count*, *mc_info, mc_info_clean,* and *mc_info_meta* provide a general overview of the microclimatic time-series stored in the *myClim* objects. The *mc_info_count* function returns the numbers of localities, loggers, and sensors in the *myClim* object. The *mc_info* function returns the data frame with a summary per sensor (e.g., measurement timestep, first and last measurement date, minimum and maximum value, number of valid measurements, and missing values). The *mc_info_clean* returns the data frame with the time-series pre-processing log (e.g., the number of duplicated timesteps, number of measurements in the wrong order, or missing measurements). The *mc_info_meta* returns the data-frame with locality metadata (e.g., locality ID, coordinates, and elevation).

1.5. Plotting

To facilitate data exploration, we designed two basic plotting functions. The *mc_plot_raster* function shows overall patterns across multiple localities (**Fig. 3**). In contrast, the *mc_plot_lines* function shows individual lines for the time series of the sensors in one locality (**Fig. 4**). Users can plot one or several sensors with the same physical units (e.g., temperatures measured at different heights) or plot sensors with two different physical units using the primary and secondary y-axis (e.g., soil temperature and moisture). The *myClim* plots are returned in the R environment as *ggplot* objects, which allows their further graphical adjustment with *ggplot* (Wickham, 2009).

1.6. Processing

The function *mc_filter* subsets sensors and localities from the *myClim* object. The subsetting of localities is also possible with square brackets (e.g., `tms[1]; tms[c("loc1", "loc2")]`). The *mc_prep_merge* function combines several *myClim* objects together. The *mc_prep_merge* function combines all localities from all input objects and all sensors on identical localities.

The *mc_prep_fillNA* function fills small gaps (missing values) in microclimatic time-series with simple linear interpolation between the first and last recorded values. It is particularly beneficial in cases where there are only a few missing measurements, such as those resulting from a brief sensor malfunction (the default maximum length of the filled gap is set to five missing measurements).

The metadata in the *myClim* object can be updated with *mc_prep_meta_locality* and *mc_prep_meta_sensor* functions. Using these functions, the user can rename locality, sensor, or both. Sensor height provided in the metadata is used by *myClim* during joining time-series from multiple downloads and, therefore, it is important to be set correctly. Some loggers have predefined sensor heights according to common practise, e.g., the TOMST TMS with four sensors (temperature sensors: soil 8 cm, air 2 cm, air 15 cm; moisture sensor: soil 0-15cm). Predefined sensor heights can be updated with the *mc_prep_meta_sensor* function.

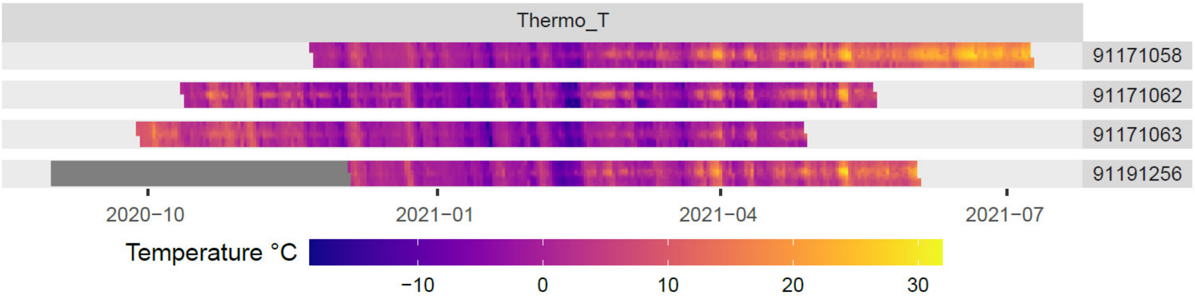


Figure 3 An example of *mc_plot_raster* output depicting raw time-series of air temperature from TOMST Thermologgers. The measurements performed every 15 minutes at two metres above the ground are displayed as faceted raster heatmaps with date on the x-axis and time of the day on the y-axis. The data were imported with *mc_read_files* without metadata; therefore, logger ID was used as a locality name. The logger 91191256 is potentially problematic since there are many missing values (shown in dark grey).

1.7. Joining time-series

The local microclimate is increasingly measured over longer periods. Such long-term measurements require repeated downloads of the logger on the locality. The resulting consecutive time-series need to be merged before the analysis. However, these time-series may contain overlapping sections, gaps, or irrelevant measurements (e.g., measurements obtained before the field installation). Therefore, joining microclimatic time-series cannot be fully automated and requires manual control.

The *mc_join* function combines multiple time-series from the identical sensor type and with the same sensor height at each locality into a single, time-alligned time-series using a semi-automated process. Duplicate time-series fragments with identical measured values are automatically removed. In cases where overlapping parts of time-series are not identical, *myClim* interactively asks the user to decide which of the conflicting time-series should be used. If present, the temporal gaps between individual time-series are automatically filled with NA's.

1.8. Aggregating time-series

Pre-processed, microclimatic data can be aggregated over user-defined timesteps with the *mc_agg* function, which simultaneously applies several numerical operations to single or multiple sensors (see code example below). The function has several predefined numerical operations (e.g., mean, range and percentile), but the user can also apply custom functions. Besides standard timesteps (e.g., hour, day, week, month, and year), aggregation can also be carried out over user-defined periods using *custom_start* and *custom_end* parameters. The custom period works within an annual cycle. Thus, the user can aggregate microclimatic time-series covering several years and gathers aggregated data for several growing seasons, winter seasons or hydrological years in one step.

```
# data30 = the myClim object with raw 30 min measurements
mean_day <- mc_agg(data30, period = "day", fun = "mean") # daily mean
mean_week <- mc_agg(data30, period = "week", fun = "mean") # weekly mean
mean_month <- mc_agg(data30, period = "month", fun = "mean") # monthly mean
```

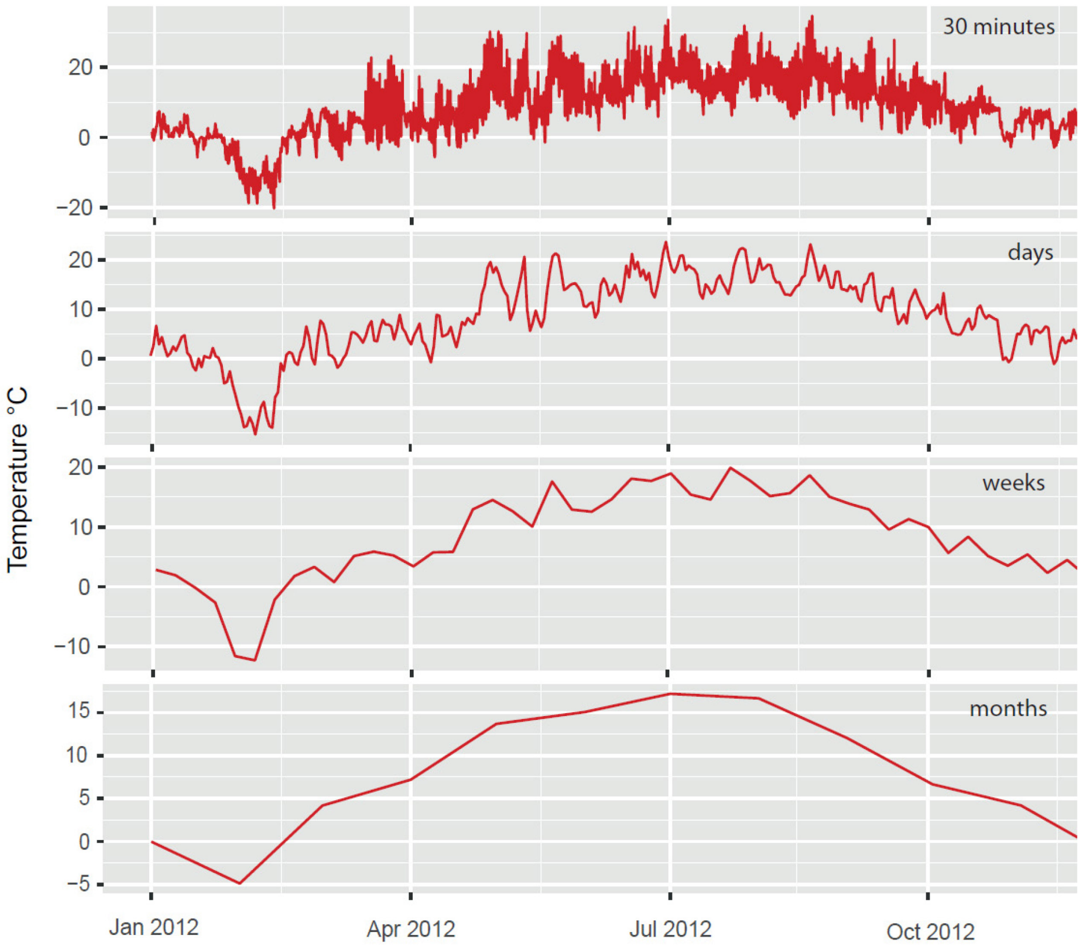


Figure 4 An example of a time-series representing temperature measurements performed every 30 minutes aggregated by the *mc_agg* function to hour, day, week, and month mean values and subsequently plotted with the *mc_plot_lines* function.

1.9. Microclimatic variables

The *myClim* package provides functions for the calculation of microclimatic variables from temperature, soil moisture, and air humidity time-series. All these functions add a new 'virtual' sensor representing a newly-calculated variable to the *myClim* object with the same timestep as the input time-series.

1.9.1. mc_calc_cumsum

Cumulative sum of the values on selected sensor since the beginning of the time-series. In units of the input sensor.

1.9.2. mc_calc_gdd

Growing Degree Days (GDD, units °C · day) provides the contribution of each measurement to growing degree days as a positive difference between the actual temperature and the base temperature (default 5°C), divided by a fraction of a day represented by the measurement timestep. Values are returned as a virtual sensor with the same timestep as in the input time-series. This allows the user to also consider shorter growing events than whole days, which would be otherwise ignored if GDD were calculated from the daily mean temperatures.

If the user prefers to calculate GDD from daily time-series, it is possible first to aggregate data into daily timestep with *mc_agg(period = "day")* and then run *mc_calc_gdd* on this aggregated time-series. To obtain the summed GDD values over longer periods (e.g., months, growing seasons, years), the user can employ the sum function for aggregation or *mc_calc_cumsum*.

1.9.3. *mc_calc_fdd*

Freezing Degree Days (FDD, units °C · day) provides the contribution of each measurement to freezing degree days as an absolute value of negative differences between the actual temperature and the base temperature (default 0°C), divided by a fraction of a day represented by the timestep measurement.

1.9.4. *mc_calc_snow*

Snow cover detection [TRUE/FALSE] from temperature time-series (**Fig. 5**). All records within the user-defined period (the default is one day) are considered as snow-covered when the maximum temperature remains below a specified threshold value (default 0.5°C) and the temperature range does not exceed a defined threshold (default 2°C) on a selected temperature sensor. This function relies on the physical attributes of snow, decoupling temperatures under the snow from the variation in diurnal air temperature, and limiting the maximal temperature to the freezing point (Dickerson-Lange *et al.*, 2015; Teubner *et al.*, 2015). The default upper limit for temperature was set slightly above the freezing point of the water to account for measurement inaccuracy (~ 0.5°C for TOMST TMS loggers) and the effect of conductive heat flux from the soil that affects the sensor in contact with the ground.

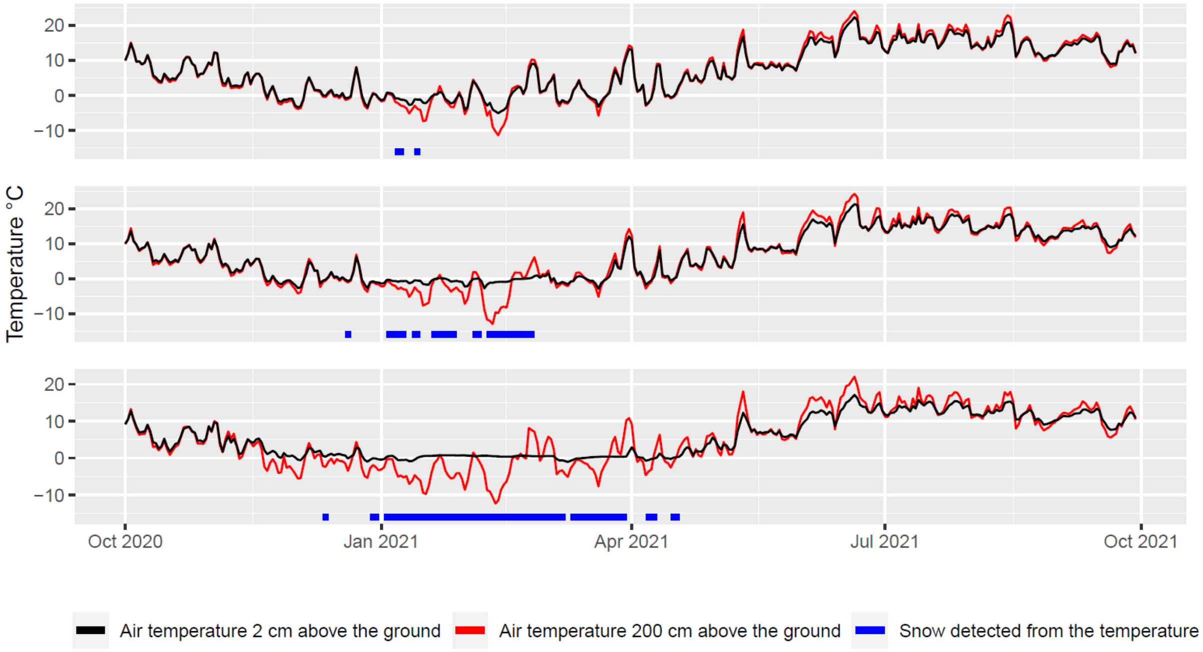


Figure 5 An example of the snow cover detection using *mc_calc_snow* function from near ground (+2 cm) air temperatures measured at three different localities in the Czech Republic.

1.9.5. *mc_calc_vwc*

This function calculates the Volumetric Water Content [m^3/ m^3] from the raw moisture signal recorded by a TMS logger using a calibration function with user-specified empirical coefficients (Wild *et al.*, 2019b). The TMS raw moisture signal is slightly affected by soil temperature (Wild *et al.*, 2019b), and this temperature dependency is corrected by the *mc_calc_vwc* function, using the temperature of the TMS soil temperature sensor.

The relationship between the TMS raw moisture signal and the volume of water frozen in the soil is currently unknown (Wild *et al.*, 2019b) and therefore all values of volumetric water content in frozen soil (soil temperature < 0°C) are replaced by NA's. This default and strongly-recommended replacement, can be switched off by the user.

Coefficients of the calibration function used in the transformation from raw TMS units to volumetric water content can differ between soils according to their physical and chemical properties (e.g., bulk density, soil texture, organic matter content), and users are advised to use site-specific coefficients. When these site-specific coefficients are not available*,* the *myClim* user can choose coefficients for eight different soil types from Wild et al. (2019) or the universal coefficients from Kopecký et al. (2021).

1.9.6. mc_calc_vpd

The Vapour Pressure Deficit [kPa] calculation is based on air temperature and relative air humidity measurements, following the Magnus equation (adapted by Jones, 2013). This equation (Eq. 2) also accounts for the effect of air pressure, which is calculated from site elevation specified directly as a function parameter, or in the *myClim* object locality metadata*.*

(2)

$$VPD = f \cdot a \cdot e^{\left(\frac{b \cdot T}{c+T}\right)} \cdot \left(1 - \frac{RH}{100}\right)$$

Where *T* is the air temperature in degrees (°C), *RH* is the relative humidity in %, *a = 0.61121*, *b = 18.678 - (T / 234.5)*, c = 257.14, *f* is the enhancement factor, which corrects for vapour pressure in moist air compared to pure water vapour: $f = 1.00072 + \left(10e - 7 \cdot P \cdot (0.032 + 5.9 \cdot 10e - 6 \cdot T^2)\right)$, and *P* is air pressure, which is estimated from an elevation: $P = 101300 \cdot e^{\left(-\frac{elevation}{8200}\right)}$.

1.10. *myClim* set of microclimatic variables

To provide a standardised set of ecologically relevant microclimatic variables, we combine several *myClim* functions into three user-friendly wrapper functions - *mc_env_temp*, *mc_env_moist* and *mc_env_vpd*. In contrast to other *myClim* functions that return *myClim* objects, these wrapper functions return analysis-ready tables with a standardised set of environmental variables derived from time-series of air/soil temperatures, soil moisture, and relative air humidity (**Table 2**).

The *mc_env* functions work only with time-series with steps equal to or shorter than one day. The *mc_env* automatically uses all available sensors in the *myClim* object and returns all possible variables based on sensor type and height/depth measurement (**Table 2**).

The *mc_env_temp function* first aggregates time-series to a daily period and then aggregates to the final period specified by a user (e.g., month, year, growing season). Because freezing and growing degree days are always aggregated with the sum function, these two variables are not first aggregated to the daily timesteps.

The *mc_env_moist function* needs time-series of volumetric water content (VWC) measurements as input. Therefore, the moisture measurements of the raw soil must be first converted to VWC. For TMS loggers, this can be done with the *mc_calc_vwc* function, which converts the raw TMS moisture signal into VWC and creates a new virtual VWC sensor. Since the daily oscillation of soil moisture is small, *mc_env_moist* works on the original VWC time-series and does not perform prior daily aggregation as *mc_env_temp* and *mc_env_vpd* functions.

1.11. Data export

After calculations and aggregations, results in the *myClim* format can easily be exported to the standard R data frame format, either with the functions *mc_reshape_wide* or *mc_reshape_long*. In both functions, the user can either reshape all data in the *myClim* object or select only specific localities and sensors. The first column of the wide table specifies the date and time; the accompanying columns are unique combinations of sensors and localities. To export multiple sensors from different localities, we recommend using a long format having only five columns (locality id, logger serial number, sensor name, date with time and value).

Finally, *mc_save* and *mc_load* functions save/load the *myClim* objects. We strongly recommend using these functions for long-term data backup, as the *myClim* objects saved and loaded with these functions will be compatible with future versions of the *myClim* package.

2. Discussion and future outlook

The *myClim* package supports various data sources, including the most common microclimate dataloggers as well as the import of simple data tables from weather stations, climate reanalyses (Kalnay *et al.*, 1996; Muñoz-Sabater *et al.*, 2021) and mechanistic microclimate models (Kearney & Porter, 2017; Maclean *et al.*, 2019). The *myClim* package thus provides a unified framework that enhances data compatibility across studies and stimulates comparisons among the outputs of climate and microclimate models and in-situ measurements. The handling of microclimate data has traditionally involved several processing steps using various packages and approaches. The level of data quality checking and cleaning was, therefore, heavily dependent on the skills and experience of an individual researcher. Adopting *myClim* will standardise microclimatic data workflow across studies, thus facilitate large-scale syntheses, boosting data sharing, and increase the comparability and reproducibility of microclimatic studies.

Adopting *myClim* will also facilitate data sharing within the global microclimatic community, for example, through the SoilTemp database (Lembrechts *et al.*, 2020). The *myClim* package can already be connected to TubeDB, an open-source database designed to handle climate station data (Wöllauer *et al.*, 2021). In the future, we plan to provide also *myClim* functions for automatic data reshaping to the SoilTemp database format and possibly also for direct data download from the SoilTemp.

The development of *myClim* is an ongoing effort, and we will further expand its functionality. Nevertheless, we also welcome active user contributions, preferably through opening new issues or submitting pull requests on GitHub (https://github.com/ibot-geoecology/myClim). Our future plans include the implementation of semi-automatic data quality control mechanisms for the detection of compromised records, such as those from TMS loggers pulled out from the soil, records not originating from the field, or suspicious outliers from local microclimatic logger networks.

3. Conclusion

Here, we described the *myClim* R package for microclimate data processing, storage, and analyses. The *myClim* package provides a complete workflow for microclimate data handling, including a reading of raw data files from microclimatic loggers, their pre-processing and cleaning, time-series aggregation, calculation of ecologically relevant microclimatic variables, and flexible data export options. The *myClim* R package thus implements the complete microclimatic workflow from the import of the raw microclimatic time-series to the calculation of ecologically relevant variables in a standardised and fully reproducible manner using open-source code. Such technical advance is crucial for much-needed global data syntheses and will facilitate wider incorporation of microclimate into global change biology and ecology.

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Data availability statement

The stable version of *myClim* package, documentation, tutorial, and example data are available on CRAN (https://cran.r-project.org/web/packages/myClim). The development version and source code can be assessed at GitHub (https://github.com/ibot-geoecology/myClim) and version 1.0.8 of the package used for this manuscript is archived on Zenodo (Man *et al.*, 2023b).

PAPER 4

Graphical abstract generated with DALL.E GPT 4.o based on manuscript text abstract.

DaLiBor – Database of Lichens and Bryophytes of the Czech Republic

Matěj Man, Jiří Malíček, Vojtěch Kalčík, Petr Novotný, Karel Chobot & Jan Wild

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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 analyzing 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).

1. 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; 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, 2021), WFO (Borsch *et al.*, 2020), continental e.g., EVA (Chytrý *et al.*, 2016) and national scales e.g., Pladias (Wild *et al.*, 2019a).

The effort expended in gathering bryophyte, lichen, and fungal occurrences lags far behind that for vascular plants, with several exceptions (CLU, 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; LGBI, 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, licenses, 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 (NCA, 2021) with ca 350 000/81 000 records, followed by the Czech National Phytosociological Database (Chytrý & Rafajová, 2003) with ca 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 Commons Licence, which enables further analysis, validation, and enhancement of records and the development of new applications based on 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.

2. Methods

2.1. 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 Pladias (Wild *et al.*, 2019a; 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.

2.2. 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.

2.3. Imports and standardisation

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 (NCA, 2021), Database of Czech Forest Classification System (Zouhar, 2012), and Czech National Phytosociological Database (Chytrý & Rafajová, 2003). 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 the author, locality, and substrate. Usually, the records were not physically revised (in herbaria). For bryophytes, the validation is still in process.

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 (NCA CR) [NDOP, AOPK]; Database of Czech Forest Classification System; Czech National Phytosociological Database). Bryophyte records from large databases are supplemented with the personal databases of several researchers (Jan Kučera, Milan Marek, Pavel Dřevojan, Petra Hájková (Hájková *et al.*, 2018), Ivana Marková). Lichen records supplementing the above-named large databases originate from literature excerptions, unpublished field inventories and ecological studies, a few public herbaria [PL, digitalised specimens from PRA and PRC], and the personal database of Jiří Malíček (**Table 1**). During the initial import of bryophytes and lichens records from existing resources, we discovered and reported many records with wrong identification, or wrong co-ordinates. With the large data providers, we negotiated the protocols for further DaLiBor updates. Based on the protocols, we reported incomplete or unreliable records which we had identified to the data providers. Upon gathering the records in one database, we obtained numerous duplicated records which need to be manually assessed. To support duplicity eradication, we automatically tagged the records with the identical species' name, geographic co-ordinates (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 resource, the name of author, locality, and substrate). We usually did not revise the records physically (in herbaria). For bryophytes, the validation is still in process.

Table 1 Number of DaLiBor records per original source. DaLiBor integrated several existing institutional and personal databases together with literature excerption. Referring to the 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

2.4. 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 ca 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).

Substrate classification was the part of data enhancement, similarly to the extraction of environmental factors based on record co-ordinates. For all records, we extracted elevation from a fine-scale digital terrain model, precipitation, and air temperature from interpolated historical weather station data (For technical details on elevation and meteorological data used here see Supplementary **Tables S2, S3**). We compared average air temperature, precipitation, and elevation extracted with DaLiBor records co-ordinates to the average values reported from Climatic atlas and Statistical yearbook of the Czech Republic (Tolasz, 2007; Rojíček, 2020). We did it separately for the bryophytes and lichens *Substrate1* category to show the potential links among the substrate and environmental preferences. Besides comparing the average values, we also visualised the difference in environmental gradient coverage by plotting the density of temperature, precipitation, and elevation of DaLiBor records together with the density of one million randomly generated background occurrences in the Czech Republic. At the landscape scale, we explored habitat type preferences of bryophytes and lichens according to Chytrý et al. (2010). We used habitat mapping layer updated to 2019 provided by NCA CR (Härtel *et al.*, 2009). From co-ordinates intersection, we found 23% of bryophytes and 15% of lichens records fell in the areas with no habitat class, which we excluded from habitat preference exploration. Analysis was performed in R 4.0.3 (R Core Team, 2016).

2.5. 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 (ca 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.

2.6. 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 (ca 6 × 6 km) were analysed.

2.7. 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.

3. Results

3.1. 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 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**).

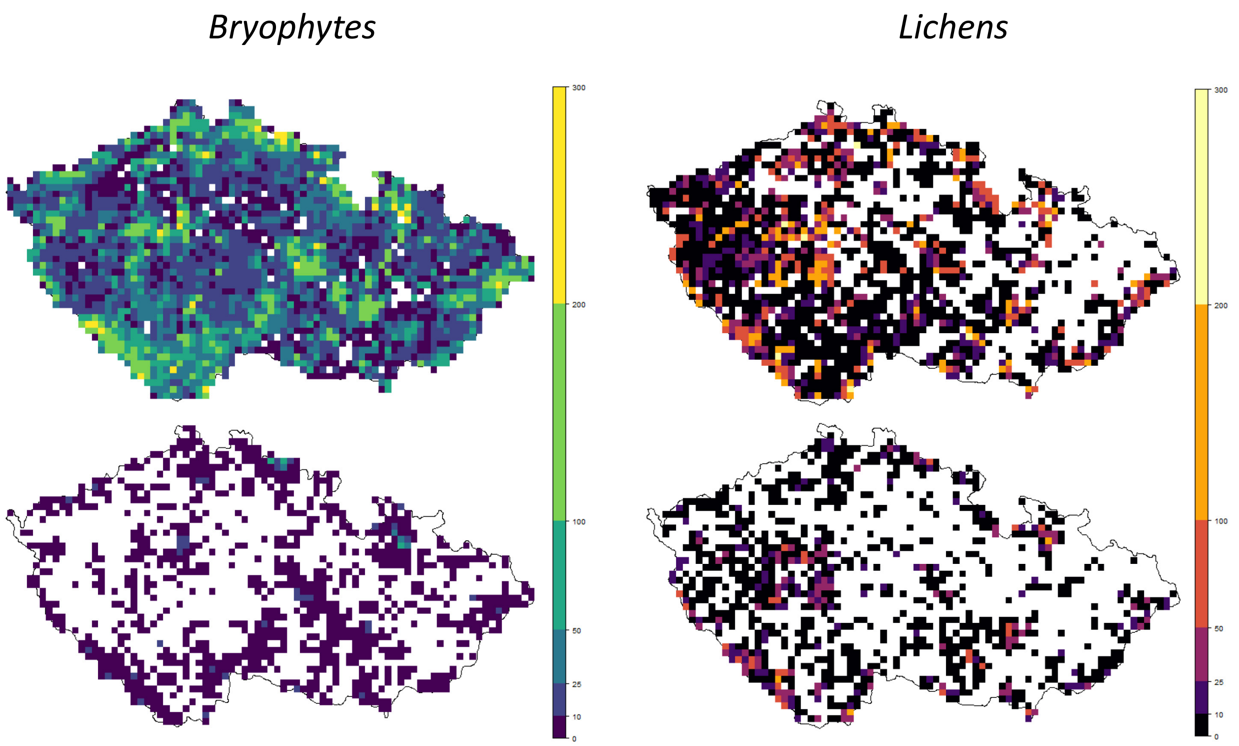


Figure 1. Maps showing the number of species of bryophytes (left) and lichens (right) recorded in quartered KFME mapping grids (ca 6 × 6 km) in the Czech Republic. Red-listed (bottom; red list evaluation CR, EN, RE, VU) and common species (top; all other than Red-listed) are presented separately.

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 physode*s (288) and *Cetraria islandica* (277). According to the total number of records, *Hypogymnia physodes* was the most common species (**Table 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.

A	**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

B	**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

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**)

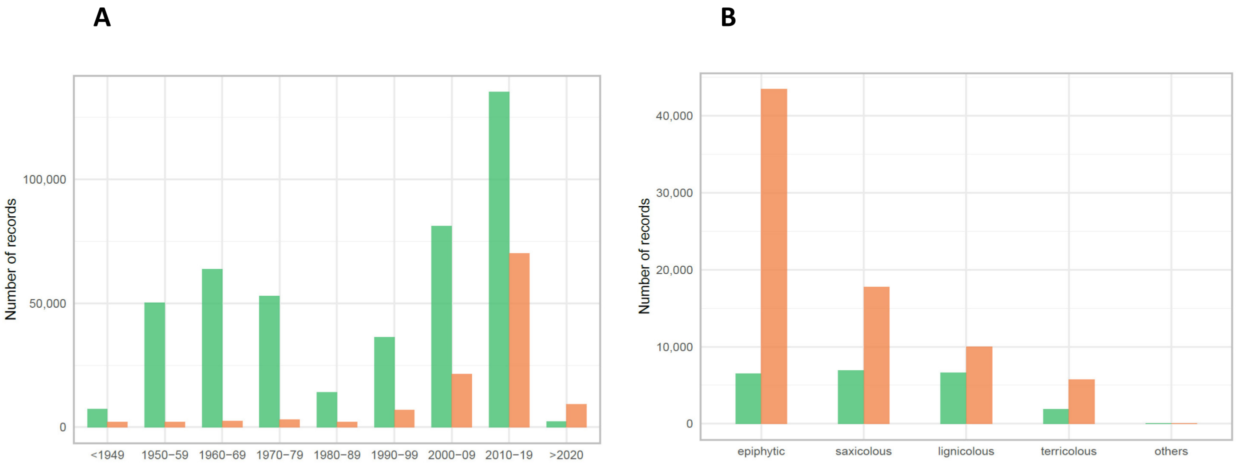
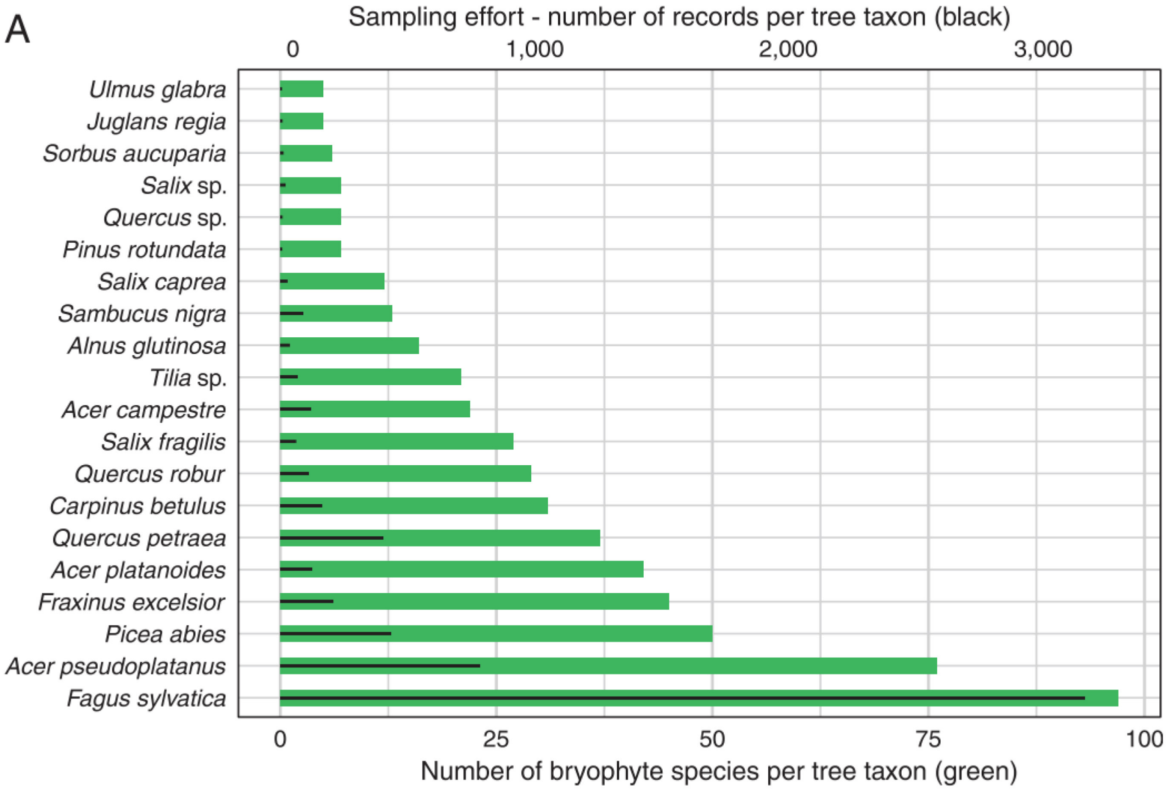


Figure 2 Analysis of the number records in DaLiBor for bryophytes (green) and lichens (orange). Number of records per decade (**A**); number of records for specific substrates (**B**).

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**).



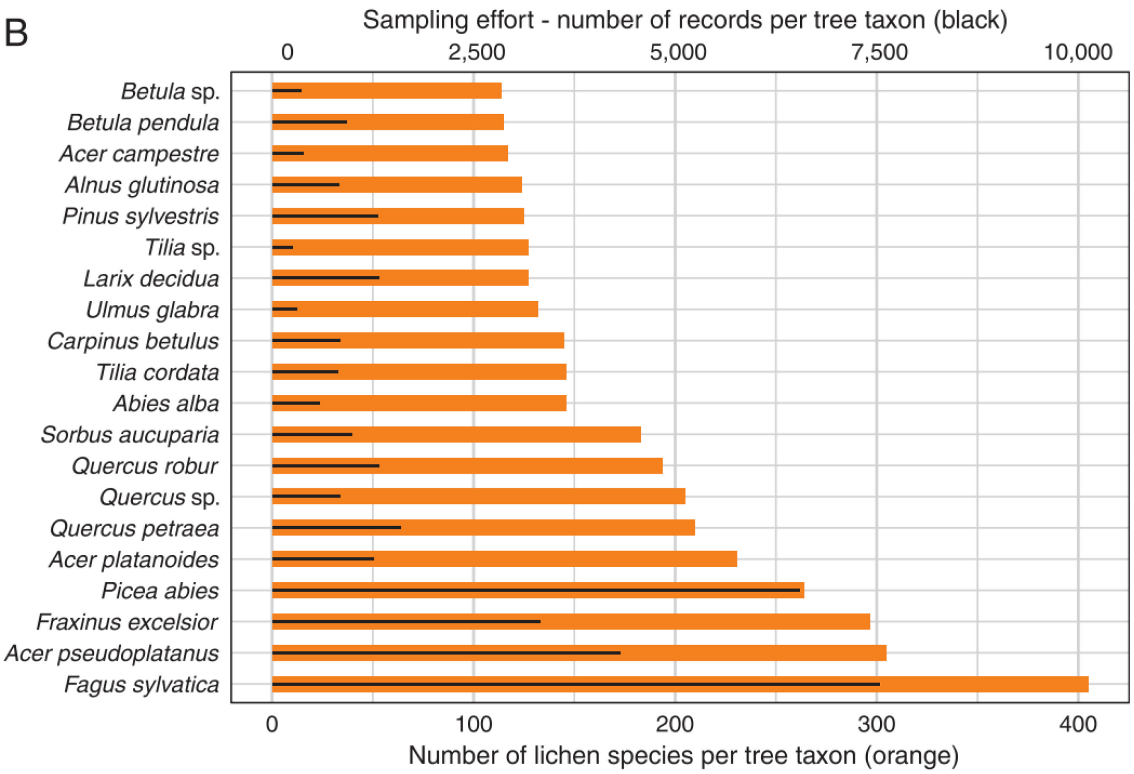


Figure 3 The top 20 trees hosting the highest diversity of bryophytes (**A**) and lichens (**B**). Sum of bryophytes/lichens per species of tree (x axis at the bottom) is shown together with the number of records for a specific tree (x axis at the top)

3.2. 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 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**).

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%)

3.3. 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**).

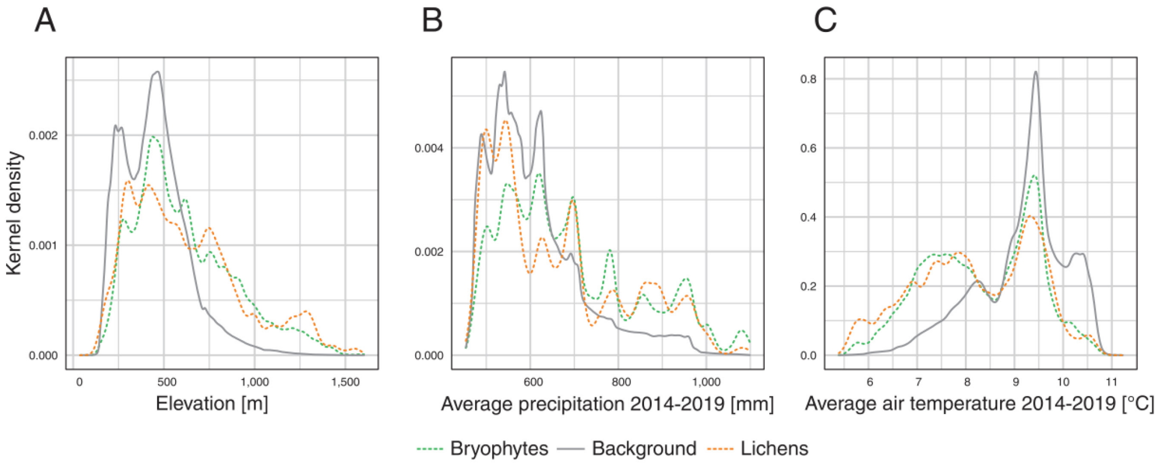


Figure 4 Density of bryophytes and lichens at different altitudes (**A**), areas with different average precipitation (2014–2019) (**B**) and average temperatures (2014–2019) (**C**) compared to background average for these conditions in the Czech Republic. Background density is based on a random area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

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 the 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**).

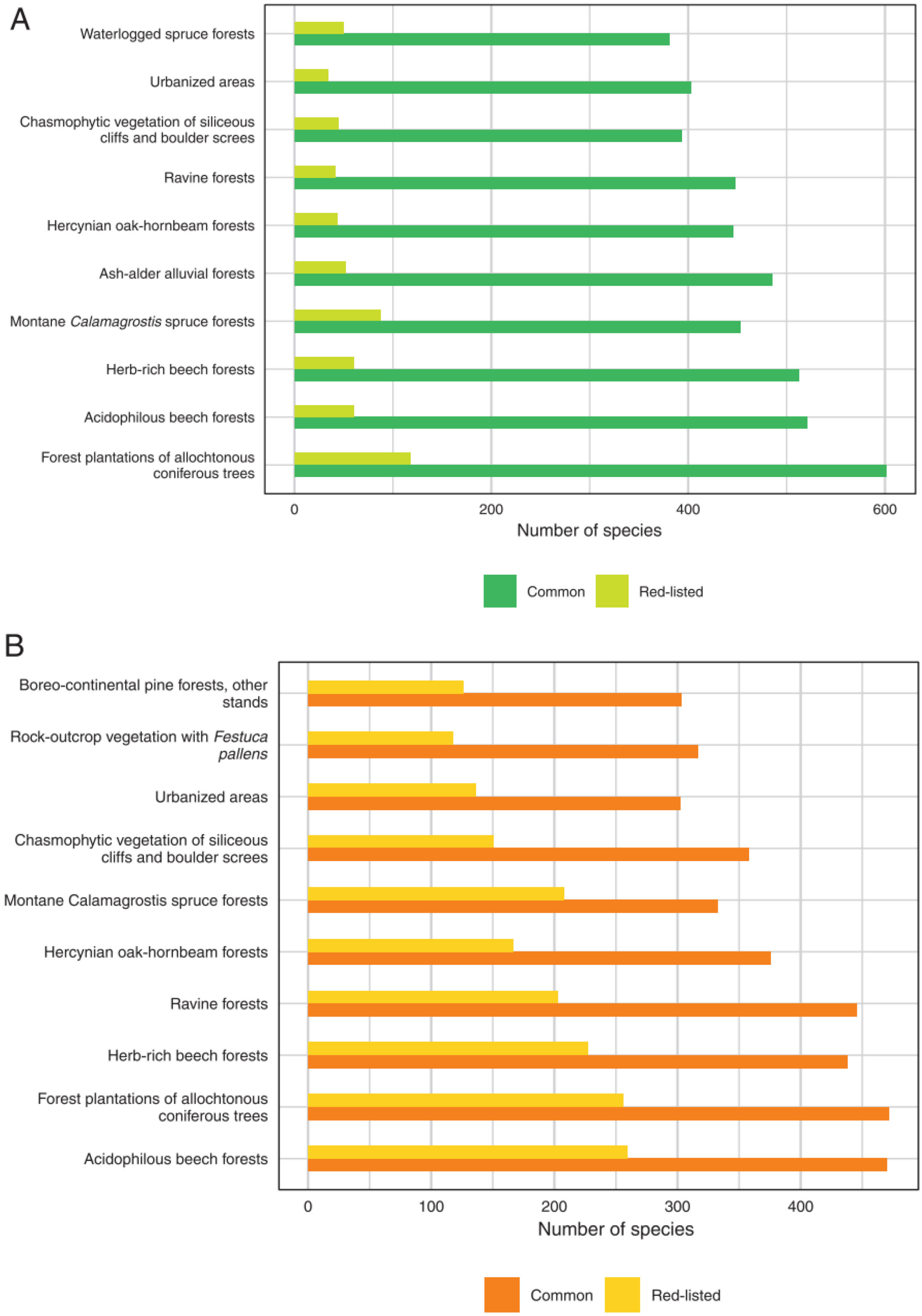


Figure 5 Number of species in DaLiBor recorded in the ten richest habitats. Number of common and Red- listed species of bryophytes (**A**), number of common and Red-listed species of lichens (**B**). There were 23% of bryophyte and 15% of lichen records reported from an area with no information on the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

3.4. 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 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.

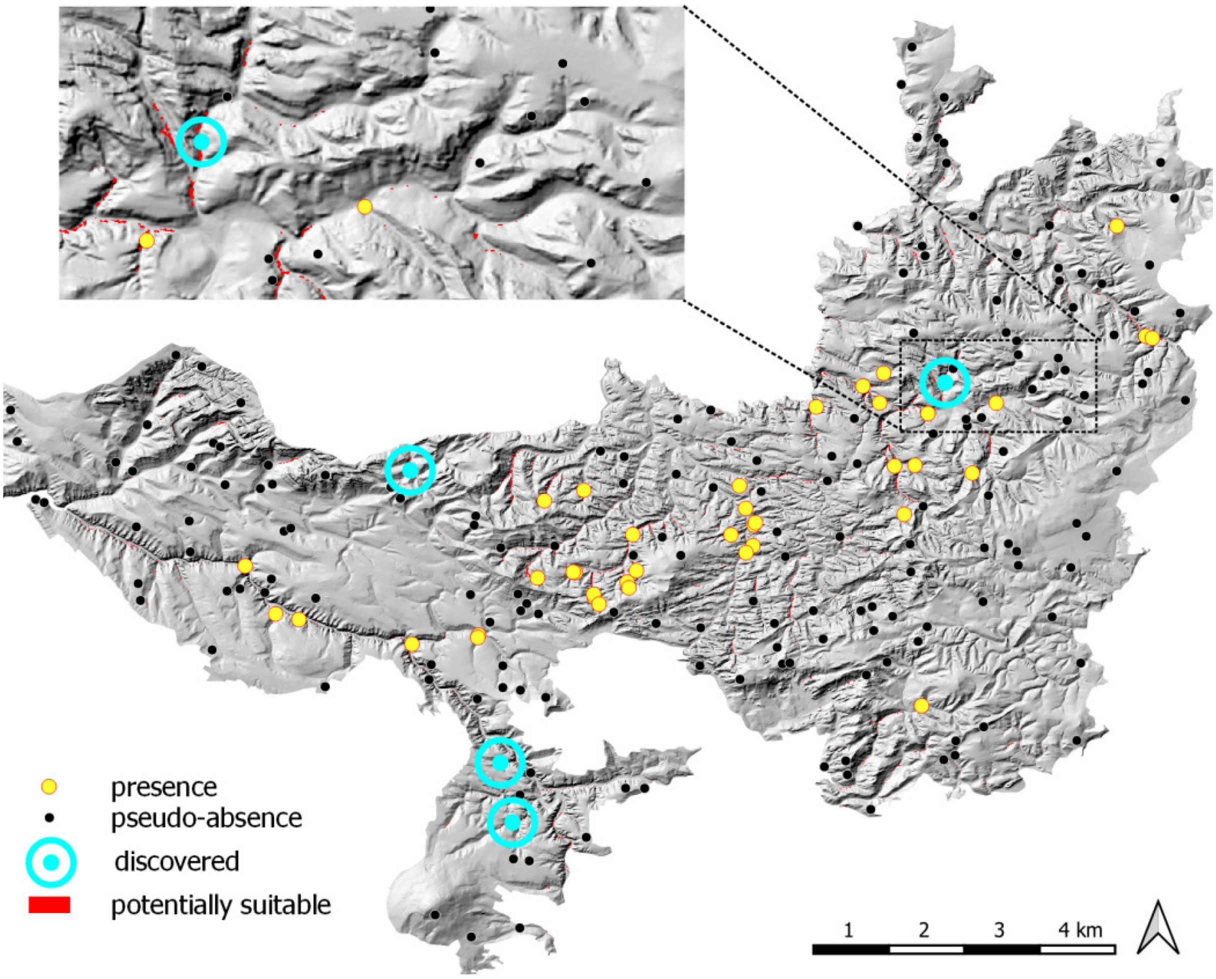


Figure 6 The map of potential habitat suitability for *Dicranum majus* in the National Park Bohemian Switzerland. Known (used for model training) presence is yellow, random pseudoabsence points for model calibration black. Newly-discovered localities during field validation are highlighted in blue. Potentially 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.

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

3.5. 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 (ca 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.

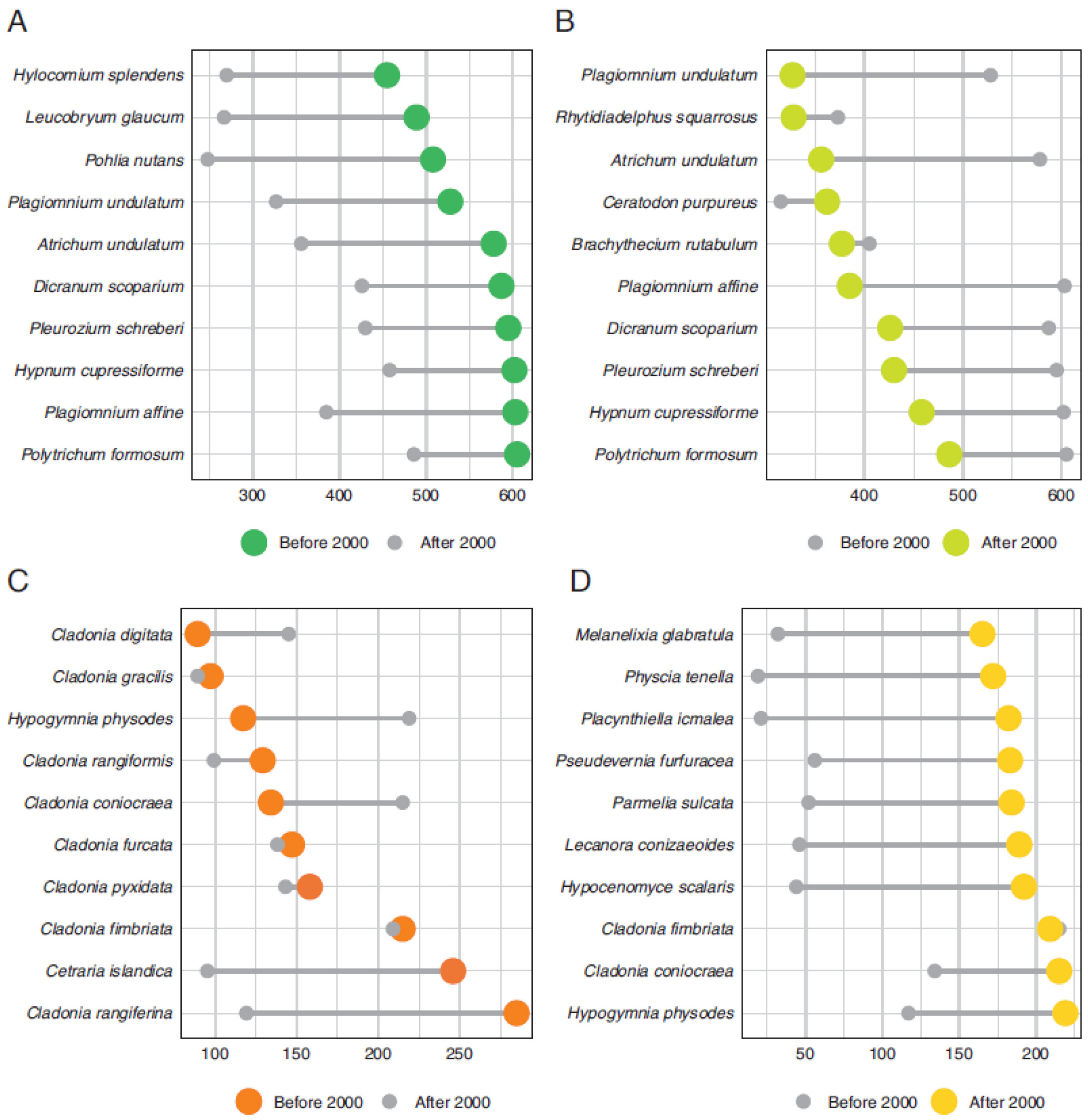


Figure 7 The 10 most abundant bryophytes (green) and lichens (orange, yellow) recorded in the quadrants in the Czech Republic (697) before 2000 (**A**, **C**) and after 2000 (**B**, **D**). Horizontal lines together with smaller points represent the increase/decrease of the species before/after 2000.

3.6. 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 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).

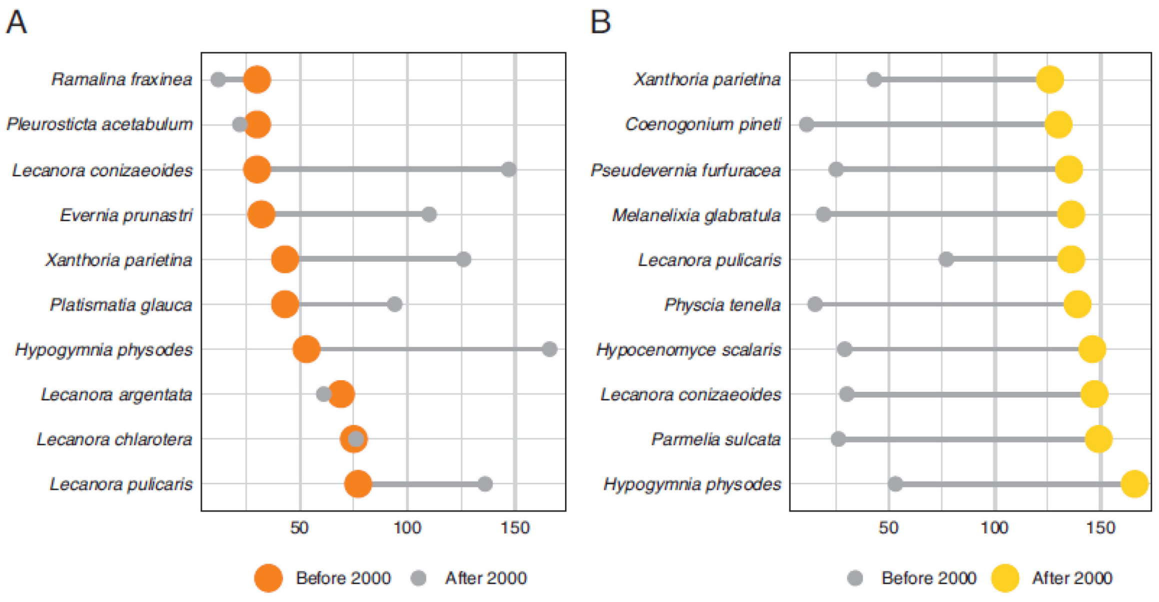


Figure 8 The 10 most abundant species of epiphytic lichens recorded in the quadrants before 2000 (**A**) and after 2000 (**B**) in the Czech Republic. Horizontal lines together with smaller points represent the increase/decrease of the species before/after 2000.

4. Discussion

A national database of bryophytes and lichens (DaLiBor) recorded up to July 2021, including ca 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 into 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.

4.1. 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 a 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.

4.2. 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 limited options 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 the 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.

4.3. 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 competition (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 elevations (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 harbor 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)

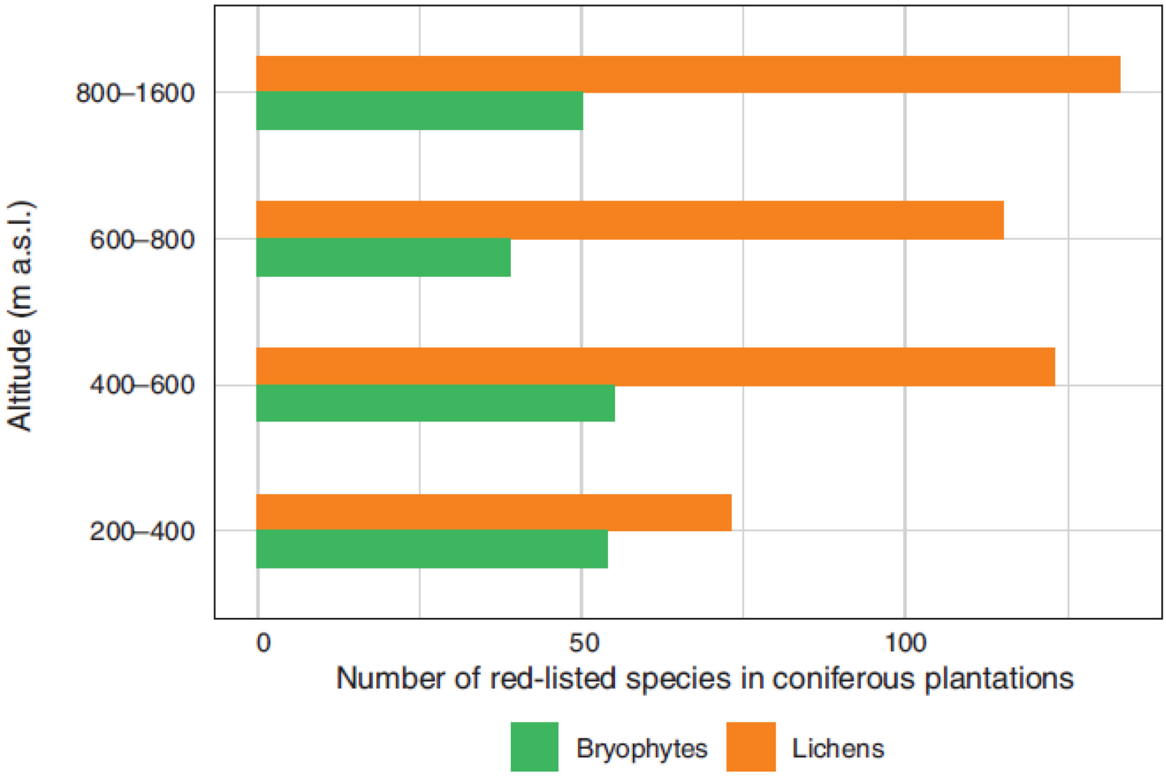


Figure 9 The number of Red-listed bryophyte and lichen species recorded in “Forest plantations of allochthonous coniferous trees” see **Fig. 5**. The number of species in coniferous plantations (dominated by spruce trees) is further sorted into 4 bins based on altitude. Especially for lichens, the highest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

4.4. 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 (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 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 modeling 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.

4.5. 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 artifact 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). The 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.

4.6. 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 France (Ertz *et al.*, 2021), Italy (Nimis & Martellos, 2021), the Netherlands (NDFF Distribution Atlas, 2015), 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 color, according to their credibility and recent/historical records can be distinguished on maps using the moveable timescale.

5. Conclusion

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

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Supplementary materials

Supplementary materials are available online: https://preslia.cz/doi/preslia.2022.579.html

Table S1 – DaLiBor Substrate2 sub-categories.

Table S2 – Environmental factors used for species' distribution modelling.

Table S3 – Meteorological data used in the gradient analysis.

Figure S1 – Increase/decrease in DaLiBor species after the year 2000.

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