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Environmental factors influencing vegetation succession at disturbed sites on broader spatial scales

Ph.D. Thesis

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České Budějovice 2025

This thesis should be cited as:

Vítovcová, K., 2025: Environmental factors influencing vegetation succession at disturbed sites on broader spatial scales. Ph.D. Thesis. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 104 pp.

ANNOTATION

This thesis deals with the course of spontaneous succession and participation of species during revegetation of human-disturbed habitats. The first chapter assesses the colonisation ability and colonisation potential for most of the species of the Czech flora. Focusing on the presence of rare species during succession, their occurrence was surprisingly found to be quite high in disturbed habitats and these sites can serve as refugia for specialists and competitively weak species (Chapter II). Species composition and the course of succession are generally influenced by many abiotic and biotic factors, the importance of which depends on spatial scale. Not only local site factors, but also landscape factors such as climate and land cover substantially influence the general successional pattern (Chapter III). The thesis further focuses in more detail on industrially extracted raised bogs as a representative of human-disturbed sites. During three decades of spontaneous succession, the species composition of vegetation, fungi, and Lepidoptera did not approach the reference state. The successional pathways of all groups were very similar. Each group of organisms was also influenced by similar environmental factors but in a different order of importance (Chapters IV and V). Describing succession and quantification of the role of environmental factors may help to decide where spontaneous restoration is a viable option in the restoration of disturbed sites.

DECLARATION

I hereby declare that I am the author of this dissertation and that I have used only the sources and literature detailed in the list of references.

České Budějovice, 28 Feb. 2025

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Kamila Vítovcová

FINANCIAL SUPPORT

The research of author presented in this thesis was supported by the Czech Science Foundation (GAČR projects 17-09979S; 19-15031S; and 20-06065S). The participation of co-authors from other institutions was supported by their grants and they are mentioned in each paper.

ACKNOWLEDGEMENTS

I wish to thank my family, my supervisor, and all of my colleagues.

LIST OF PAPERS AND AUTHOR’S CONTRIBUTION

The thesis is based on the following papers:

Chapter I: Prach K., Tichý L., Vítovcová K. & Řehounková K. 2017. Participation of the Czech flora in succession at disturbed sites: quantifying a species' colonization ability. Preslia 89: 87-100.

KP and LT conceived the research ideas. KV, KP, LT, and KŘ collected field data. KV and LT performed statistical analyses. KP led the writing of the paper with help of all the other authors. The contribution of KV was 20%.

Chapter II: Řehounková K., Vítovcová K. & Prach K. 2020. Threatened vascular plant species in spontaneously revegetated post-mining sites. Restoration Ecology 28: 679-686.

KŘ and KP conceived the research ideas, KV prepared and processed data. KŘ and KV analysed the data. KŘ led the writing of the paper with the help of KV and KP. The contribution of KV was 30%.

Chapter III: Vítovcová K., Tichý L., Řehounková K. & Prach K. 2021. Which landscape and abiotic site factors influence vegetation succession across seres at a country scale? Journal of Vegetation Science 32: e12950.

KV, KŘ, and KP conceived the research ideas. All authors collected data. KV analysed the data with the help of LT. KV led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The contribution of KV was 60%.

Chapter IV: Vítovcová K., Lipárová J., Manukjanová A., Vašutová M., Vrba P. & Prach K. 2022. Biodiversity restoration of formerly extracted raised bogs: vegetation succession and recovery of other trophic groups. Wetlands Ecology and Management 30: 207-237.

KP, KV, and MV conceived the research ideas. All authors collected field data. KV performed statistical analyses. KV led the writing of the paper with the help of KP and MV. The contribution of KV was 60%.

Chapter V: Vítovcová K., Vašutová M., Lipárová J., Vrba P. & Prach K. 2024. Successional pathways and trophic specialisation of different groups of organisms in formerly extracted raised bogs – Restoration and conservation perspectives. Biological Conservation 296: 110649.

KV, KP, and MV conceived the research ideas. All authors collected the field data, KV processed and analysed the field data. KV led the writing of the paper with the help of KP, and MV. The contribution of KV was 60%.

CO-AUTHOR AGREEMENT

Karel Prach, supervisor of this Ph.D. thesis and co-author of all papers, fully acknowledges the stated contribution of Kamila Vítovcová to these manuscripts.

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Prof. Karel Prach

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1 GENERAL INTRODUCTION

1.1 SUCCESSION AND FACTORS INFLUENCING SPONTANEOUS VEGETATION DEVELOPMENT

The succession theory has been developing more than one century (Clemens 1916, Gleason 1939, Egler 1954, Odum 1969, Connell & Slatyer 1977, Glenn-Lewin et al. 1992, Finegan 1996, Walker & del Moral 2003, Pickett et al. 2011, Walker & Wardle 2014, Arroyo-Rodriguez et al. 2017, Prach & Walker 2020) and is a fundamental concept in ecology. It indicates how species populations, communities, and ecosystems change over time after a disturbance. In general, at human-disturbed sites both primary and secondary successions can occur. Primary succession starts in a lifeless substratum contrary to secondary succession, where some biota is already present. They are not always clearly distinguishable but are states on a continuum (White & Jentsch 2001). The most important factor determining species composition during succession is **age of the site**, i.e. the time since the last disturbance (Johnson et al. 1982). The vegetation pattern is further significantly affected by **landscape factors**, namely by macroclimate, history of human influence, and the present state of the surrounding landscape, including regional species pools. **Local site factors** influencing succession include substratum quality (e.g. Tardif et al. 2019; van Breugel et al. 2019), site moisture (Osbornová et al. 1990), character of disturbances (Johnstone et al. 2016; Tardif et al. 2019), local species pool (Řehounková & Prach 2008), interactions between species (Bardgett & Wardle, 2010), and unpredictable chance factors (Connor & Simberloff, 1976). The importance of all factors highly depends on the spatial scale (Fig. 1, Arroyo-Rodriguez et al., 2017*)*. In some cases, the surrounding landscape may be more important than local site conditions in the course of succession (Salonen & Setälä 1992) or even more important than successional age (Řehounková & Prach 2006). Many environmental factors can hardly be measured exactly across sites and seres, thus, despite the various restrictions this has, some substitute factors and proxies may be used, such as surrounding land cover, mean annual temperature, precipitation, altitude, and latitude. The colonisation of newly created sites by plants is also determined by the characteristics of incoming species and their abundance in the surrounding landscape. Quantification of the role of particular factors driving succession and knowledge of the colonisation ability of particular species may improve the understanding of succession and may help to restore vegetation at disturbed sites and indicate ways in which certain factors may be manipulated to direct succession under ecological restoration (Walker et al. 2007).

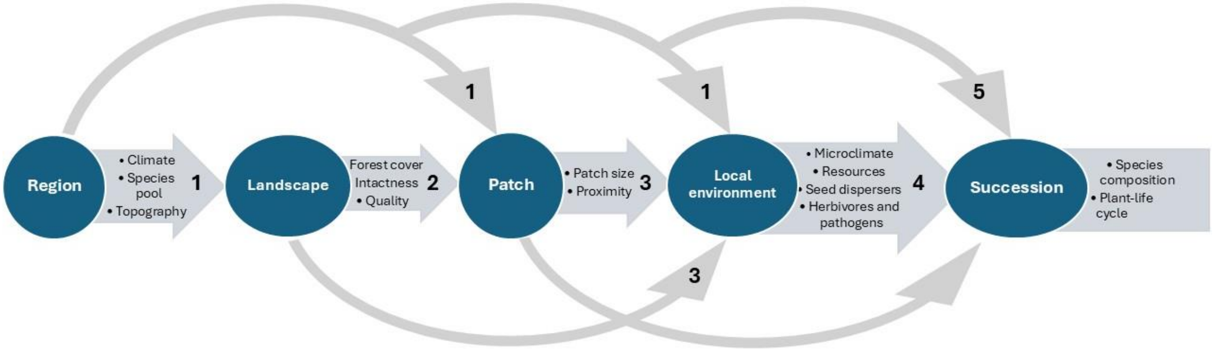

Fig. 1. Spatial scales (proposed by Arroyo-Rodriguez et al. 2017) - *Succession is influenced by factors operating from broad to local spatial scales. Regional climate, topography, and socio-economic conditions (not shown) affect land use, and hence landscape and patch characteristics (1). The landscape context determines patch isolation (2). Both landscape and patch affect the local biotic environment (seed dispersers) and abiotic environment (microclimate and resources) (3). The regional species pool (5) together with local conditions (4) shape succession by affecting plant life cycles and species composition. The model highlights the role of landscape characteristics [forest cover, intactness (i.e. the opposite of fragmentation) and remaining forest quality in terms of diversity and old-growth species] and patch characteristics (patch size, and proximity to neighbouring forest patches) in succession. Taken and adapted from Poorter et al. 2023.*

1.2 LANDSCAPE FACTORS

1.2.1 Climate

Macroclimate is an important landscape factor driving succession (Otto et al. 2006, Prach et al. 2007, Prach & Walker 2020, Janečková et al. 2024) as it can directly affect species establishment. However, it has also an indirect effect through determination of the regional species pool (Settele et al. 1996). The importance of climate as an environmental factor probably depends on spatial scale. It seems that the broader the scale is, the more influential the climate is. Šebelíková et al. (2016), for example, showed that climate factors did not, logically, significantly influence vegetation variability in sandpits within one small region, while Řehounková & Prach (2006) found that precipitation and temperature (besides substratum pH and water table) are crucial in determining the vegetation pattern in spontaneously revegetating sand pits across the Czech Republic.

The climatic factors which can influence the course of succession are especially mean annual temperature, length of vegetation season, and mean annual precipitation. Some of these factors are correlated and are, besides substratum pH, the most important factors differentiating successions at all (Prach & Walker 2020). Climatic conditions can constrain or favour participation of particular species in the course of succession, which was for example documented for woody species in Central Europe (Novák & Prach 2003, Prach & Pyšek 1994), or for the occurrence of ruderals and alien species (Řehounková & Prach 2008). It was also demonstrated that lower numbers of undesirable species were recorded at sites located in wetter and colder regions than in dry, warmer regions (Ballesteros et al. 2021).

1.2.2 History of human landscape modification

Throughout history, humans have consistently improved their ability to extract natural resources, especially by clearing forests, draining wetlands, and mining raw materials. The level of human activity and environmental changes are also related to macroclimate. In warmer lowlands the effect of human impact is stronger than in colder highlands.

Looking at history, starting from the Mesolithic period (i.e. from c. 12,000 BP to 7,000 BP), there has been a significant human impact on the environment (Willis & Bennett 1994), and environmental changes occurred both in the global climate and ecosystems around the world. Because of the increasing forest area, Mesolithic plant populations started to be less mobile, thus affecting local environments around settlements more intensively, for example using intentional burning and spreading of some species. This impact had probably still only a local character (Kuneš et al. 2008). Especially from the Late Neolithic, small-scale agriculture and woodland clearings expanded, and there is strong evidence for extensive landscape alterations by enhanced pasturing and mixed farming. The main vegetation exploitation techniques were selective tree felling (mainly *Quercus*), pollarding (mainly *Corylus* and *Carpinus*), and woodland clearing to establish grazing pastures and small-scale crop farming (Magyari et al. 2012). Later on, during the Bronze Age, humans were growing arable crops in a shifting cultivation system and most of the indigenous large herbivores were gradually replaced by livestock. In Medieval times, degradation of primeval forests continued, including regulation of hydrological conditions by drains and ditches as population density and number of settlements increased. Agricultural activities were still carried out only in a fine-scale mosaic, and without using artificial fertilisers. However, land consolidation and intensification of agriculture and mining practices have eliminated these small and heterogeneous structures. This decline started in the 19th century and has accelerated in the 2nd half of the twentieth century (Poschlod & Braun-Reichert 2017). Recent human activities include eutrophication and emission of large quantities of chemicals and other pollutants into the environment, which has led to vegetation and climate changes (Bazzaz 1996).

1.2.3 Present landscape structure and regional species pool

The process of spontaneous colonisation of disturbed sites is facilitated by the occurrence of (semi)natural vegetation in the immediate vicinity of these sites (Novák & Konvička 2006, Řehounková & Prach 2008, Kopeć et al. 2011). The regional species pool largely depends on the climate as mentioned above and on the history of landscape management in the region (Settele et al. 1996). These external factors make up the 'landscape context' in which succession proceeds. A higher importance of landscape context compared to substrate was reported by del Moral et al. (2005), but most studies concerned only one sere and were not performed at a broad geographical scale.

Under Central European conditions, at least a half of plant species from the surrounding vegetation can be found also in spontaneously developed disturbed sites (Brändle et al. 2003). In case of target species (i.e. grassland, shrubland, woodland, and wetland species), an even higher proportion (70-90%) can colonise disturbed sites from their surroundings (Kabrna et al. 2014, Lencová & Prach 2011). All chapters in this thesis repeatedly address the colonisation ability of species at disturbed sites with special attention to target species.

1.2.4 Undesirable species

In human-altered landscapes, undesirable plants such as ruderals and aliens mostly competitive dominants, may colonise a disturbed site. Generally, a larger number of undesirable plants can be expected if a disturbed site is located in heavily altered landscapes such as those of intensively used agricultural or urban land (Roy et al. 1999, Prach et al. 2001). Moreover, many alien plants are introduced through gardening, which is correlated with human population density (Decker et al 2012). However, it is quite a long-term question whether human-made habitats are vulnerable to colonisation by alien species which may block succession or change the trajectory of successional pathways towards an undesirable state (Walker & del Moral 2003, Yurkonis et al. 2005). In general, alien species can be found more frequently in young successional stages, and their importance in the course of succession gradually decreases in most cases (Rejmánek 1989, Bastl et al. 1997, Řehounková & Prach 2008, Ballestéros et al. 2021). Tischew et al. (2014) found that spontaneous succession facilitates the development of native plant communities with a low proportion of neophytes and invasive species in former lignite coal mines, even if surrounded by a cultural landscape. However, some aliens may become serious invaders during succession at disturbed sites. This is the case of *Robinia pseudoacacia* in some regions of Central Europe, where it may cause problems if there are seed trees of *Robinia* in the close surroundings (Řehounková & Prach 2008, Tischew et al. 2014). The invasion rate is associated with land use, land cover, and human activities, such as those creating transport corridors, agriculture, and recreation (Larson et al. 2001, Pyšek et al. 2010, Sutton et al. 2007). Furthermore, altitude, climate, and substrate can shape the general vegetation pattern and occurrence of aliens. Specifically, neophytes benefit from the density of roads and railways and the extent of agricultural land in the surrounding landscape, confirming that these land uses are relevant invasion supporters (Ballestéros et al. 2021), which is highlighted also in this thesis (Chapter III).

1.3 LOCAL SITE FACTORS

1.3.1 Substratum

The importance of substrate quality on the course of succession was even accepted in the first studies of succession (Clements 1916). Many studies have investigated the influence of various soil factors on the course of succession, especially nutrient content (Tilman 1988, van der Putten et al. 2013), pH (Prach et al. 2007), and soil texture (Ejrnæs et al. 2003). Unfavourable local site conditions (e.g. low pH, lack of nutrients, poor substratum stability, overheating of the surface), especially during early stages of vegetation development, may prevent many plant species from colonising a site (Walker & del Moral 2003, Alday et al. 2011). On the other hand, a lack of nutrients may favour some rare, competitively weak species

(Wassen et al. 2005). Soil nitrogen and its forms were usually considered as one of the most important factors (Tilman 1988, Wilson & Tilman 2002). Also Fridley & Wright (2012) suggested that site edaphic conditions are stronger determinants in community dynamics than climate, but it obviously depends on the spatial scale and variability of factors. The importance of pH in determining the vegetation pattern has been well described too (Ellenberg 1988), but most studies dealt with changes in pH over time of succession (Bazzaz 1996), and only rarely was pH studied as a factor determining the successional pattern across stages and seres (Christensen & Peet 1981, Prach et al. 2007) as was, among others, evaluated in this thesis, mainly in Chapter III.

1.3.2 Site moisture and water regime

Water content is essential to soil development and has a major influence on the rate and trajectories of succession by determining which species germinate, grow and survive. Therefore, wetter sites normally develop more quickly than dry ones of similar age (Walker & del Moral 2003). Moreover, site moisture, similarly to macroclimate, may have an important influence on the local species pool and thus play a crucial role in re-vegetation processes (Prach et al. 2013), especially in the participation of woody species in succession (Prach & Pyšek 1994). Site moisture is generally influenced by local relief, climate (Ellenberg 1988), and soil texture (Walker & del Moral 2003). For example in large-scale studies, site moisture is reported to have a significant role in determining the course of succession in old fields (Prach et al. 2014, Ejrnaes et al. 2003, Otto et al. 2006). It was also the most important local site factor of divergent succession in disused sand pits analysed at a country-scale (Řehounková & Prach 2006). One of the most destructive disturbances influencing soil moisture is large-scale industrial peat harvesting, accompanied by profound changes in water regime. These disturbed peatlands generally recover very slowly, as they are complex systems often susceptible to shifting to an alternative state (Dise 2009; Matthews & Spyreas 2010), and have been paid special attention to in this thesis (Chapters IV and V).

1.3.3 Disturbances initiating succession, and ongoing disturbances

Succession and disturbances are linked processes. Every disturbance caused by nature or humans can be characterised by type, frequency, size, severity, intensity, and timing (Temperton et al. 2004). Frequency of disturbances determines the period between events during which a community can recover. Frequent disturbance events may reduce the occurrence of species whose regeneration time exceeds the time of the disturbance return, and favour more short-lived species. More intensive disturbances tend to influence the whole plant community and resource availability more than less intense ones. In the context of succession, the dynamics initiated by disturbances may or may not generate a community similar in composition or structure to the pre-disturbance conditions and may alter successional trajectories in unpredictable ways (Kreyling et al. 2011). The extent of a disturbance influences the rate and perhaps even the process through which a community recovers. Finally, the timing of a disturbance has an effect on the community from the phenological perspective (time of seeding, dormancy time of dominant species; Meiners et al. 2015). A species' response to disturbance is one of the main functional differentiations of plant species (Grubb 1977; Grime 1979; Westoby 1998). It depends on the species' traits

(Grime 1979; Westoby 1998; Westoby et al. 2002) and the general limitation of the disturbance niche of individual species (Herben et al. 2016). Generally, the persistence of some habitat types (e.g. riparian sites) is deeply dependent on frequent, rather low-intensity disturbance. Without any disturbances, these ecosystems gradually change into other vegetation types (Temperton et al. 2004). Ongoing disturbances, including human-introduced management, can keep an ecosystem in a certain successional stage for long periods (e.g. grazing – Lindborg & Eriksson 2004, flooding dynamics – Moerke & Lamberti 2004, mechanical soil disturbances – Řehounková et al. 2016, prescribed burning – Fulé et al. 2004).

1.3.4 Local species pool and colonisation ability of species

Surrounding vegetation determines ecological succession via the local species pool (Zobel et al. 1998), and especially the early stages of primary succession are often strongly dependent on adjacent donor sites and their species composition (Wood & del Moral 1987).

Colonisation of disturbed sites by vascular plants is substantially influenced by proximity effects and relies on the influx of propagules and the ability of species to establish and persist there (Lõhmus et al. 2014). Even when disturbed sites have similar abiotic environmental conditions, species composition can be different because of the different species composition (different local species pool) of the immediate surroundings (Prach et al. 2015). It was reported that proximity (up to 100 m) to populations of target plant species was decisive for their spontaneous colonisation (del Moral et al. 2005, Řehounková & Prach 2008). However, some species may overcome distances up to several kilometres or more (Kirmer et al. 2008, Brändle et al. 2003, Tischew & Lorenz 2005). For example Ash et al. (1994) observed in their studies of industrial waste heaps that species with very small seeds and specialised soil preferences (e.g. orchids) are able to overcome distances of up to 40 km to reach suitable sites.

Colonisation success is determined by the traits of species, intensity of vectors transporting diaspores, and by the abundance of species in the surrounding landscape (mass effect). Herben et al. (2016), attempting to evaluate species on gradients of disturbance frequency and severity, proposed two indices, one based on expert estimation, not on quantitative data, and one based on vegetation structure parameters. These indices testify of a species' relationship to disturbance but not of a species’ colonisation success. Other similar indices proposed as bioindicators of disturbance and human impact are hemeroby, urbanity and ruderality (Hill et al. 2002). However, disturbances often come as a result of human activity, and are thus correlated with many other factors, especially eutrophication, confounding these indices. In this thesis, new indices are proposed based on real presence in succession series, better reflecting the reality (Chapter I).

1.3.5 Interactions between species

The biotic interactions in vegetation influencing the course of succession are those between living organisms – humans, plants, animals, and microorganisms (Walker & del Moral 2003). They can be specified as interactions between plants and local animals and humans, such as grazing, cutting, pollination, seed and fruit dispersal, etc.; interactions between plants growing in a community, such as competition for water, essential minerals, organic compounds, and light; and interactions between plants and soil micro-organisms, for example mycorrhizal association and decomposition. In the case of secondary succession, soil biota and propagules are present in the soil seed bank, and together with new arrivals these can be the most important biotic determinants at the beginning of a successional pathway (Callaway & Walker 1997) compared to primary succession where only new arrivals play a role. Plants are a core component of terrestrial ecosystems, providing food, substrate, or shelter to fungi and insects. Many plants also depend on mycorrhiza and profit from insect pollination, whereas fungi are important decomposers, plant symbionts, or parasites, and play a key role in nutrient cycling. However, multi-taxa studies of disturbed sites are rare (e.g. Strobl et al. 2020). This has been reflected in this thesis and a multi-taxa approach was used to reveal interactions between the main indicator groups of organisms in extracted peatbogs (Chapters IV and V).

1.3.6 Chance factors

Chance events influence the variability in the process of succession (Gleason 1939). Both stochastic and deterministic processes operate together during succession and thus the composition of colonisers may be less predictable with an increasing role of stochastic factors (Walker & del Moral 2003). However, the starting point of species assembly after disturbance has been proved to be rather stochastic in general (see e.g. Wiegleb & Felinks 2001, Zaplata et al. 2013). For example, based on their study on Mt St Helens, del Moral et al. (2005) concluded that plant succession is determined as much by chance factors and landscape context as by characteristics of the site itself. Especially long-distance dispersal of seeds is largely driven by chance (Kirmer et al. 2008). Higgins et al. (2003), in their study of non-standard long-distance dispersal, emphasised the fact that many seeds utilise both standard and non-standard dispersal vectors, with the latter being responsible for rare long-distance dispersal events. The role of processes related to chance and dispersal decreased with time, while those related to environmental filtering mediated by biotic interactions increased (Baasch et al. 2010). Further unlikely factors in succession may be extreme weather events and unpredictable disturbances such as unusual herbivory, fire, etc.

1.4 SUCCESSIONAL PATHWAYS AND RESTORATION OF NEAR-NATURAL STATES

The question of whether succession runs toward potential natural vegetation or toward a pre-disturbance state has been asked by ecologists for many decades (Walker & del Moral 2003, Prach et al. 2016). However, most successional theories have only focused on the successional trajectory of plants, probably because plants are sedentary and can easily be identified, and have cascading effects on other trophic levels (Connell & Slatyer 1977). The succession trajectory can be unidirectional, but multiple pathways to reach the endpoint are also possible. Some successions, especially those in heavily altered environments, may terminate or be diverted far from their theoretical endpoints. On the other hand, some of the seres certainly have approached their endpoints rather closely after a few decades. Convergence to a particular end state is more probable when initial colonists are few, conditions are stressful, and biodiversity is low (Walker et al. 2010). Divergence is more commonly observed due to priority effects (i.e. the sequence of species arrivals), differences in initial conditions, and initial site heterogeneity (Matthews & Whittaker 1987; Walker et al. 2010). A rich local species pool can contribute to high within-stand diversity, and therefore increase the likelihood of divergence as well (Walker et al. 2010). This thesis partially dealt with recovery of more trophic groups of organisms, and has revealed the successional pathways of heavily disturbed extracted peatbogs (Chapters IV and V).

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3 SUBJECTS AND AIMS OF THE THESIS

In the present thesis, major emphasis is put on the effect of factors influencing succession on different spatial scales: (i) landscape (country) scale – various disturbed sites across the Czech Republic (Chapters I–III) – and (ii) local scale – one meta-population complex of two industrially extracted and two undisturbed raised bogs in the Šumava National Park and Protected Landscape Area (Chapters IV and V).

The first three studies are based on the Database of Successional Seres, comprising of 21 different types of successional seres, currently consisting of four thousand phytosociological relevés from various human-disturbed sites, therefore well justifying a generalisation of the results.

The thesis particularly addresses the following aims: (i) to assess the ability of the Czech flora to colonise disturbed sites, how species participate in different successional stages, and species from which habitats are the most successful during succession (Chapter I); (ii) to define whether and under which conditions spontaneously revegetated post-mining sites may act as important secondary habitats for threatened vascular plant species (Chapter II); (iii) to reveal how much abiotic site factors and land-cover categories influence the course of succession, and if there are any differences between primary and secondary seres (Chapter III); (iv) to characterise recovery, successional pathways, and trophic specialisation of different groups of organisms in formerly extracted raised bogs (Chapters IV and V).

More specifically:

Chapter I aims to assess the ability of the Czech flora to colonise disturbed sites, i.e. to participate in succession, what dominance they can reach and if there are some differences between the successional stages. The other question was what the habitat affiliations of the most successful species at colonising disturbed sites are and how their participation changes over the course of succession. We introduce two indices of species colonisation ability: (i) 'colonisation success index', which reflects the actual realised colonisation of a disturbed site by a species, and (ii) 'colonisation potential index', which is a measure of a species' potential colonisation ability based on its frequency of occurrence in seral stages corrected to its commonness in the country.

Chapter II is concentrated on the potential of post-mining sites to harbour threatened vascular plant species, and attempts to reveal the distribution of different classes of threatened species at post-mining sites and across successional stages. It is the first study evaluating the success of threatened vascular plant species at various spontaneously developing post-mining sites at a broad country scale.

Chapter III analyses the effect of abiotic site factors and land cover categories on the course of succession across a high number of successional series at a country scale and attempts to find some differences between primary and secondary seres. We also assess factors influencing species richness and participation of target species.

Chapter IV aims to assess successional pathways and the recovery of vegetation, fungi, and Lepidoptera communities in formerly extracted raised bogs. The main question is if the succession directs toward the undisturbed reference and if the directions of recovery of the different groups of organisms are comparable. The study evaluates the participation of peatland specialists during succession and attempts to answer the question if these specialists are able to establish spontaneously in disturbed raised bogs.

Chapter V, following the previous one, shows successional trends in disturbed raised bogs, and attempts to evaluate the importance of particular environmental factors influencing the succession of different groups of organisms. The study observes the level of trophic specialisation of fungi and Lepidoptera and attempts to infer implications for the restoration and conservation of extracted raised bogs.

4 CHAPTER I

Participation of the Czech flora in succession at disturbed sites: quantifying species' colonization ability.

Prach et al. 2017). Preslia 89: 87–100. doi: 10.23855/preslia.2017.087

Preslia 89: 87–100, 2017

Participation of the Czech flora in succession at disturbed sites: quantifying species' colonization ability

Účast druhů české flóry v sukcesi – kvantifikace kolonizační schopnosti druhů

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Prach K., Tichý L., Vítovcová K. & Řehounková K. (2017): Participation of the Czech flora in succession at disturbed sites: quantifying species' colonization ability. – Preslia 89: 87–100.

The colonization of newly created sites by plants is determined by the characteristics of the species and their frequency in the surrounding landscape (mass effect). We used species frequencies from the Database of Successional Series of various disturbed sites across the Czech Republic (DaSS, 2817 phytosociological relevés, 1013 species of vascular plants) to calculate two indices of species colonization ability. One index (index of colonization potential – ICP) was corrected using occurrence data in the Czech National Phytosociological Database (CNPD) and the other (index of colonization success – ICS) was used without correction. We also evaluated the participation of species in successional stages of different ages and assessed their maximum cover. Then we asked, species of which habitat types are the most successful in colonizing disturbed sites and how their participation changes over the course of succession. Species characteristic of the following habitat types were statistically over-represented in the successional series compared to in the CNPD: synanthropic habitats; cliffs, screes and walls; acidophilous grassland; dry grassland; and sandy grassland. Species characterizing particular types of habitat exhibited significant trends in their participation in different successional stages: those of dry grassland, heathland, scrub land and forest increased during succession whereas species of synanthropic acidophilous grassland, mesic grassland and wetland decreased. Species with high values of both indices are more likely to spread in landscapes continuously disturbed by human activity. Thus, these indices can help to predict future changes in vegetation in central-European landscapes and be used in ecological restoration projects.

Keywords: colonization ability, Czech Republic, disturbances, succession, vascular plants, habitat types

Introduction

The colonization ability of plants has to date been inferred indirectly from their life history strategies (Noble & Slatyer 1980, Grime 2002) or their ability to disperse (Klotz et al. 2002, Consens et al. 2008). A more exact colonization ability has only been assessed for limited sets of species at particular localities and in certain habitats (e.g. Eriksson 1996, Kirmer et al. 2008), but such results can hardly be applied in different types of vegetation. The colonization ability of species can only be directly evaluated from their

doi: 10.23855/preslia.2017.087

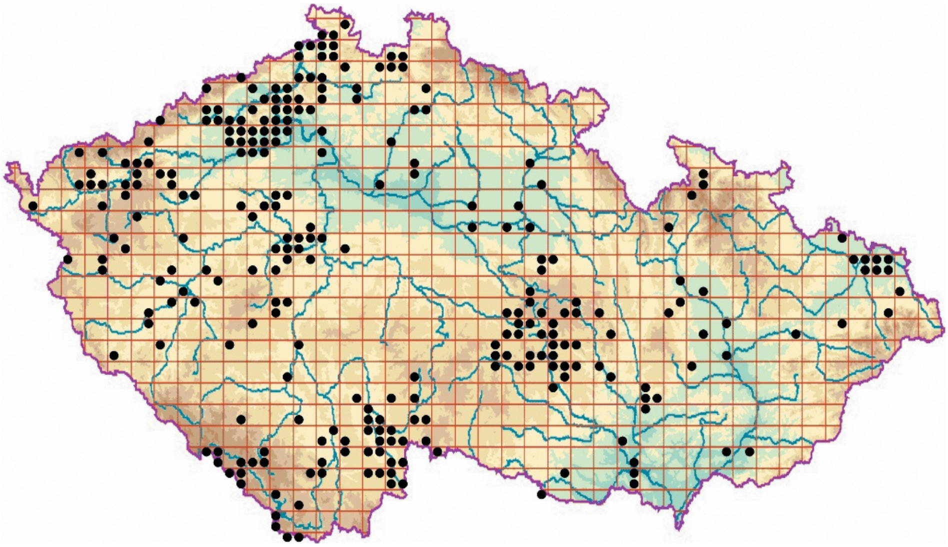

Fig. 1. – Location of the relevés included in the Database of Successional Series (DaSS; based on occupied quadrats).

occurrence at a high number of disturbed sites in areas that differ widely in their environmental conditions.

Therefore, we gathered data on the occurrence of particular species at various seral stages in differently disturbed sites throughout the Czech Republic (Fig. 1). This data set (Database of Successional Series – DaSS; Prach et al. 2014, 2016) includes nearly 3000 phytosociological relevés from seral stages aged 1 to > 150 years, for a high number of successional series (hereafter seres), both primary and secondary, and in terms of the encountered species it includes more than half of the Czech flora (Prach et al. 2014, 2016).This extensive material therefore is sufficiently representative and suitable for evaluating the ability of the Czech flora to colonize disturbed sites, based on real quantitative data.

The composition of species inhabiting a disturbed site generally depends on their ability to survive the disturbance or to colonize disturbed sites (Fenner & Thompson 2005). Since nearly all of the seres we investigated started on bare ground, it can be assumed that colonization from the surroundings was decisive in determining the successional vegetation despite the presence of initial seed banks in some cases of secondary succession. The colonization of disturbed sites depends on the influx of propagules and the ability of species to establish and persist (Lőhmus et al. 2014). Propagule arrival at a site is determined by its intrinsic dispersal characteristics, type and effectiveness of transport vectors (Consens et al. 2008), composition of the local flora (i.e. species pool; Zobel 1997) and the frequency of species occurring in the surroundings, i.e. mass effect (Pärtel et al. 1998). Even though disturbed sites provide species with very different opportunities for becoming established during the process of succession (Walker & del Moral 2003), a general ability to colonize various disturbed sites has not yet been quantified for central-European plants.

By analysing the DaSS database, we aimed to answer the following questions: (i) What is the ability of the Czech flora to colonize disturbed sites, i.e. to participate in succession? (ii) How do species participate in different successional stages and what dominance can they reach? (iii) What are the habitat affiliations of the species that are most successful at colonizing disturbed sites and how does their participation change over the course of succession? To answer these questions, we introduce two indices of species' colonization ability: (i) 'index of colonization success', which reflects the actual realized colonization of a disturbed site by a species, and (ii) 'index of colonization potential', which is a measure of a species' potential colonization ability, based on its frequency of occurrence in seral stages corrected by its commonness in the country (as recorded in the Czech National Phytosociological Database; Chytrý & Rafajová 2003).

Methods

Database of successional series (DaSS)

We sampled 39 different seres including 21 main types of succession (for example, there were four particular seres recorded after coal mining in four different parts of this country.) We also extracted some data from published and unpublished records (see Prach et al. 2014). We considered all seres, which we identified in a sufficient number of representative successional stages in the Czech Republic over the past four decades (1975–2015). The seres included successional stages on various spoil heaps from brown coal, black coal and uranium mining, sand and sand-gravel pits, limestone quarries, acidic rock quarries, basalt quarries, extracted peatlands, road verges, ploughed and then abandoned strips along the state border (the former "iron curtain"), river gravel bars, artificial islands and barriers in fishponds, the bottom of a former water reservoir, sedimentary basins, ruderal urban sites, abandoned fields, bulldozed sites of forests damaged by air pollution, forest clearings and burnt forests. Most of the seres are described in separate studies or summarized in papers (Prach et al. 2013, 2014, 2016). In these references, there are details of the seres, including determination of successional age, which was based on rather precise records provided by mining companies, land owners and our own observations. In some cases, when woody species established immediately at the start of the succession, we used a tree-ring analysis.

The particular seres differed in number of samples, number of sites, location and successional age, but they were all sampled in a comparable way (Prach et al. 2014). All but one of the seres (river gravel bars) were initiated by human activity. All the seres thereafter developed without any additional significant disturbances, so are examples of spontaneous succession (Prach et al. 2001).

In total, 2817 phytosociological relevés are available in DaSS, in which 1013 species of vascular plants are recorded. The abundance or cover of each species was visually estimated by using the values of the semi-quantitative Braun-Blanquet scale transformed to percentages, or by directly estimating percentages in the field (van der Maarel 1979, Kent & Coker 1992). We had to make certain adjustments to the list of species before we could compare the DaSS with the checklist of vascular plants in the Czech Republic, which contains 3601 species, not including cultivars and hybrids (Danihelka et al. 2012). First, we left out all alpine species (43 species), halophytic species (11 species) and aquatic macrophytes (47 species; distinguished according to Ellenberg et al. 1991), except those present in DaSS, because we did not sample any seres in alpine, saline or aquatic habitats. We also excluded extinct and currently missing species (155 species of the categories A1, A2 and A3 in the Red List of the Czech Republic – Grulich 2012). Furthermore, all neophytes evaluated as casuals (834 species) according to the checklist of vascular plants (Danihelka et al. 2012) and the catalogue of alien plants (Pyšek et al. 2012) were excluded because they often occur only temporarily and are not permanent components of the Czech flora. Groups of species and subspecies difficult to distinguish were merged (*Rubus* spp., *Alchemilla* spp., *Taraxacum* spp. and some others), which further reduced the list by excluding 810 species. The resulting list (hereafter termed 'adjusted Czech flora') comprised 1701 species. The final list of species in DaSS, based on this adjusted list, was 958.

Index of colonization success (ICS)

This index estimates the realized colonization success. Generally rare species do not have a very high realized success, even if their potential to colonize newly established sites is high. To define this index, species frequency data (i.e. the numbers of occurrences in 2817 phytosociological relevés in the database; SF) were divided between 21 types of seres. Each sere was then geographically stratified (within a grid of $0.75' \times 1.25'$ or $\approx 1.4 \times 1.3$ km), thus obtaining the total number of grid cells with a sere for each species (i.e. ecologically and geographically stratified species frequency; EGSSF). In this way, the effect of replicated occurrence of species in permanent plots or at closely located sites is completely removed. However, we believe that repeated observations at the same location may also contain some additional information about a species' success. Therefore, we defined the ICS index as a combination of both frequencies:

$$ICS^{*} = \log((SF + EGSSF)/2) + 1$$

The ICS^{*} index was then rescaled and rounded to integer numbers in the range of 1 to 9 (or 2 to 9, if the value 1 was reserved for all species not found in the seral stages):

$$ICS = 1.5 + 8 \times ICS^{*}/ICS^{*}_{max}$$

Index of colonization potential (ICP)

This index estimates the relative ability of species to colonize disturbed sites, i.e. it indicates the relative success of species establishment at disturbed sites in comparison with its relative frequency in all types of Czech vegetation (except alpine, saline and aquatic – see above). Therefore, it takes into account the ratio between relative ecologically and geographically stratified species frequencies (relEGSSF) in the DaSS database and its relative frequency in the geographically stratified data set in the Czech National Phytosociological Database (relCNPD; Chytrý & Rafajová 2003) comprised of 20,467 relevés and 2027 species (Knollová et al. 2005). Relative species frequencies from both data sets were standardized to the same median value. The index was calculated as:

$$ICP = 0.5 + \mathrm{arctg}\,(relEGSSF0/relCNPD) / 10$$

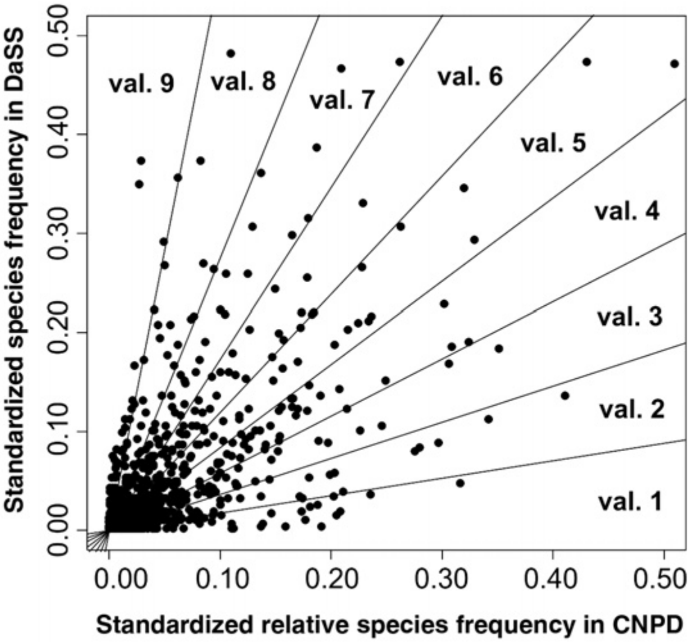

Fig. 2. – The index of colonization potential (ICP) takes into account ratios between relative standardized species frequencies in the DaSS and CNPD databases. The species were divided into nine categories. Both axes were standardized to the same median value of relative frequencies.

The ICP index was then rounded to integer numbers in the range of 1 to 9 (Fig. 2). Each index value was evaluated by means of a bootstrap model. The preciseness of the estimated ICP value was categorized into three levels, i.e. good, sufficient and weak, if the range of the bootstrapped confidence interval ICP index (Q_{95}–Q_5) estimated from 10,000 bootstrapped selections was smaller than 1.5, between 1.5 and 3.0 or higher than 3.0, respectively. We assigned the value X to generally rare species present in less than 20 relevés in the CNPD, i.e. the index was not assessed. Other more frequent species not found in the DaSS were considered as poor colonizers (ICP index value 1).

Species minimum, optimum and maximum stages, and maximum cover attained

The minimum, optimum and maximum stages were assessed for each species occurring in the DaSS using the minimum, median and maximum successional age (expressed as the number of years from the start of succession) in which they occurred. The preciseness of each median was defined by the bootstrap confidence interval of age medians (Q_{95}–Q_5) estimated from 10,000 bootstrapped selections. Values higher than 50 years were included into one category (> 50) as imprecisely estimated when some late successional stages were not properly dated and the seres differed in duration. To reduce possible subjective bias in estimating the cover of species, we transformed all percentage values into values on the Braun-Blanquet scale: r, +, 1–5 (van der Maarel 1979).

Affiliations of colonizing species with particular types of habitat

We compared the relative frequencies of species included in the CNPD and the DaSS with their affiliations to the main habitats occurring in the Czech Republic. We used the database elaborated by Sádlo et al. (2007) based on CNPD and expert knowledge, to affiliate each species to 10 broad habitats in which it frequently occurs: cliffs, screes and walls; springs and mires; other wetlands; meadows and mesic pastures; acidophilous grasslands; dry grasslands; sandy grasslands and rocky outcrops; heathlands and scrub land; forests and synanthropic habitats (for more information about the methods see Sádlo et al. 2007). To reduce the heterogeneity in the data (different alpha- and beta diversity of plots) in both databases, medians of species frequencies in both datasets were standardized to the same value. Therefore, all relative species frequencies in the dataset with successional series (DaSS) were multiplied by the ratio of the medians from both datasets. Modified relative species frequencies from the CNPD and DaSS for species typical of a particular habitat were compared, and their differences tested using a non-parametric Wilcoxon test (R Core Team 2015).

Results

Colonization ability of species

The frequency distribution of both indices in the adjusted Czech flora is presented in Fig. 3. Values of both indices for the adjusted Czech flora are listed in Electronic Appendix 1 together with other characteristics of species occurring in various successional stages. In the adjusted Czech flora, 43% of the species were not recorded as occurring in any of the successional stages studied.

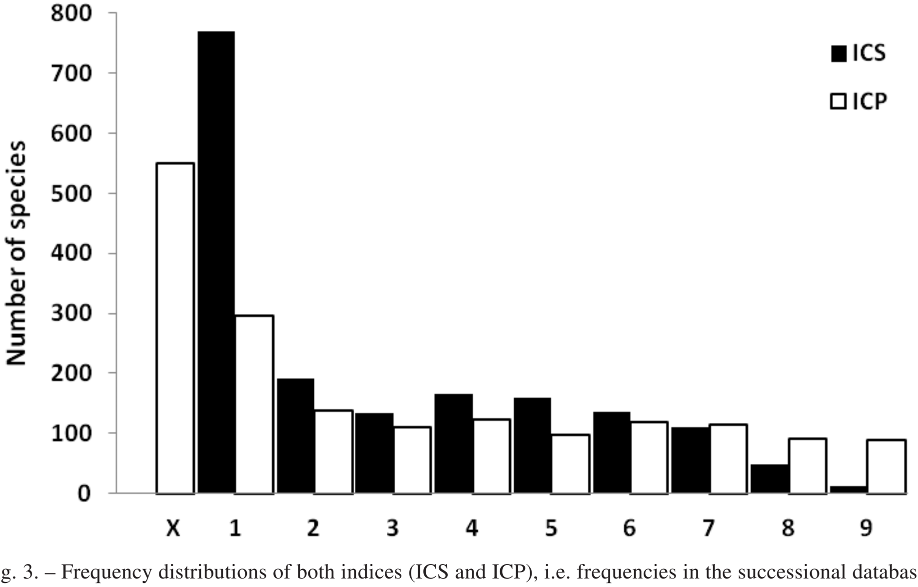

Fig. 3. – Frequency distributions of both indices (ICS and ICP), i.e. frequencies in the successional database and colonization ability, respectively, based on the adjusted Czech flora: X – species occurring in less than 20 relevés in CNPD and not in DaSS; ICP 1 – species more frequent in CNPD but not recorded, or very poorly so in DaSS; ICS 1 – species not recorded in the DaSS.

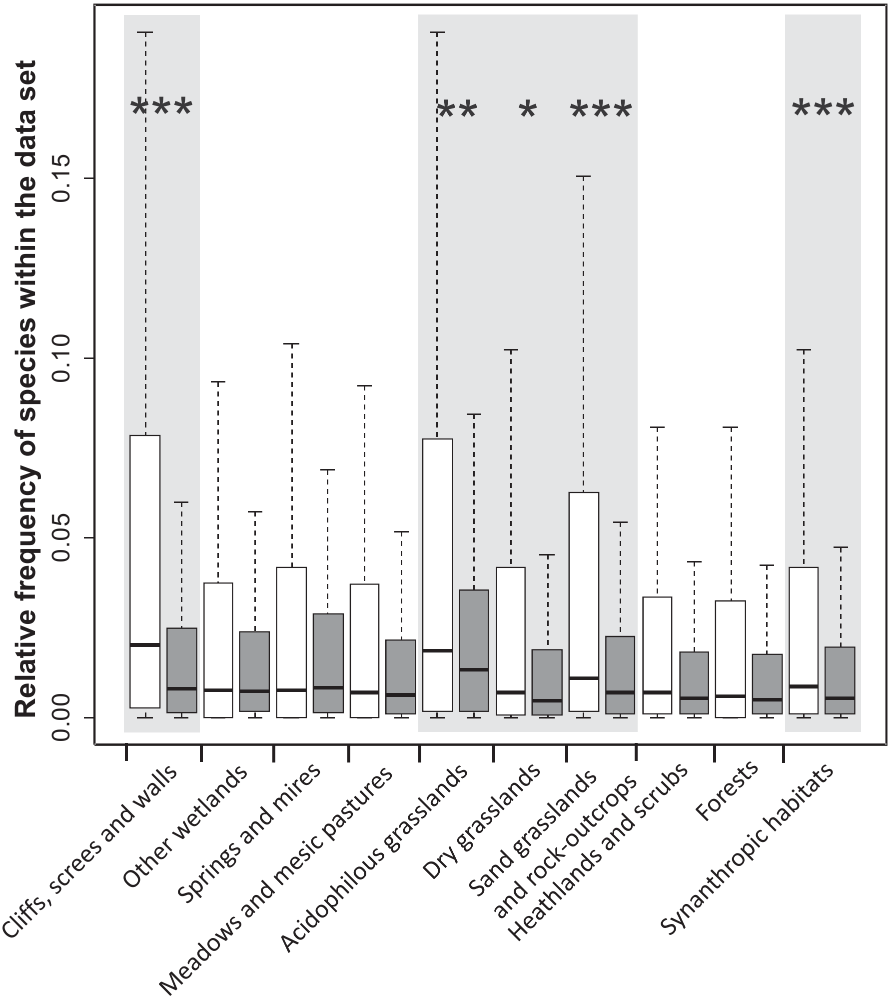

Fig. 4. – Relative frequencies of species in the successional seres (DaSS, white boxplots) and relative frequencies of species in the Czech National Phytosociological Database (CNPD, dark grey boxplots). Both species frequencies were standardized with the database median (see the text). Differences in relative species frequencies in both datasets for each type of habitat were statistically tested using the Wilcoxon test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Habitat types for which the ratio of frequently occurring species in DaSS is significantly higher than in CNPD are highlighted by a light grey background.

The following 12 taxa were the most frequent (highest ICS index 9, in decreasing order) and are therefore the most successful colonizers of seral stages: *Betula pendula*, *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Achillea millefolium* agg., *Taraxacum* spp., *Salix caprea*, *Rosa canina* agg., *Pinus sylvestris*, *Hypericum perforatum*, *Rubus* spp., *Artemisia vulgaris* and *Cirsium arvense.* These species usually occurred also in the highest number of seres (see Electronic Appendix 1).

Among the species with the highest ICP (= 9), i.e. those with a distinctly higher relative occurrence in the successional database DaSS than in the CNPD, several groups of

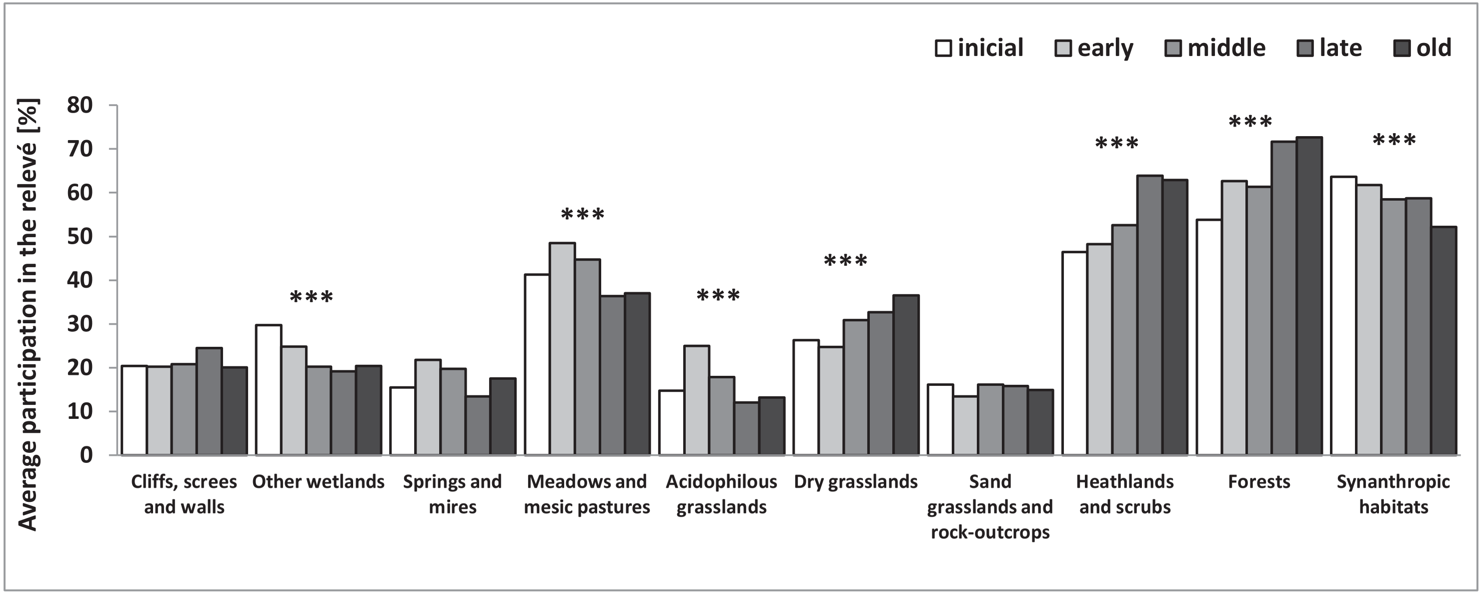

Fig. 5. – Participation of species characterizing different types of habitats in differently aged seral stages (based on numbers of species): initial (1–3 years) – 353 relevés, young (4–10 years) – 660 relevés, middle (11–25 years) – 695 relevés, late (26–40 years) – 518 relevés and old (> 40 years) 591 relevés. The categories roughly corresponded to the general experience that pioneer annuals usually prevail at the initial stages, followed by perennial herbaceous plants, grasses and woody species, later accompanied by species typical of the natural vegetation of the respective geographical region. The sums of values exceed 100% because species can belong to many types of habitats (Sádlo et al. 2007). Trends in the participation of species characterizing different habitats during succession were statistically tested using GLM (family: Gaussian; link: identity) with absolute values of successional age.

species can be distinguished: (i) generally common species that easily colonize seral stages (e.g. *Salix caprea, Rosa canina* agg., *Populus tremula*, *Epilobium angustifolium*), with a high ICS; (b) species, often synanthropic and/or alien neophytes, less common but also colonizing seral stages if they occur in the surroundings (e.g. *Acer negundo*, *Pinus strobus*, *Quercus rubra*, *Lupinus polyphyllus*); (iii) some rare species in both databases, which usually produce a high number of easily dispersed seeds, that are able to establish in seral stages with a higher frequency than expected from their occurrence in CNPD (e.g. *Pyrola minor* and *Epilobium dodonaei*), including some less common neophytes such as *Hordeum jubatum*, *Erucastrum gallicum* and *Senecio vernalis*.

Species common in the CNPD but not (ICS = 1) or only rarely (ICS = 2) occurring in seral stages and therefore exhibiting a low intrinsic colonization ability, include e.g. *Caltha palustris, Cirsium oleraceum*, *Crepis paludosa*, *Filipendula ulmaria*, *Sanguisorba officinalis* and *Abies alba*, typical of wet meadows or occasionally woodlands.

Affiliation of colonizing species with particular habitats

Species typical of cliffs, screes and walls, acidophilous grasslands, dry grasslands, sandy grasslands and rocky outcrops, heathlands and scrub land, and synanthropic vegetation were significantly over-represented in the seral stages compared to CNPD (Fig. 4). There was no significant over-representation of any particular species groups in CNPD compared to the DaSS.

The participation of species characteristic of different types of vegetation in the five successional stages distinguished is shown in Fig. 5. Species typical of dry grasslands and woody vegetation clearly increased during succession, while synanthropic and wetland species markedly decreased. Only species typical of spring and mires, cliffs, screes and walls, and sandy habitats did not exhibit statistically significant trends. Species typical of woody vegetation and synanthropic species were the most common in seral stages, being followed by species typical of mesic and dry grasslands. Species of acidophilous grasslands, sandy grasslands, springs and mires, and rocky-outcrop vegetation were least frequent.

Discussion

Colonization of disturbed sites by the Czech flora

More than half of the species in the Czech flora colonized seral stages at disturbed sites. The seral stages were scattered across the Czech Republic, so our dataset is representative of the whole country and comparable on the basis of the entire Czech flora. Because seral stages of different ages were similarly frequent in our database (Fig. 5 and Prach et al. 2016), we do not expect any bias towards over-representation of species typical of young seral stages, which is usually the case in human-altered landscapes (Walker et al. 2007). It should also be mentioned that late-successional species may also occur in early successional stages (Egler 1954) and thus reduce the importance of some differences in frequencies between differently aged seral stages. We found many rare and a low number of very common species in the seral stages studied. This is in accordance with the usual frequency distribution of species in floras as a whole (Preston 1948, Preston et al. 2002).

The index of colonization success (ICS) is not an intrinsic characteristic of a species, as it is substantially influenced by the rarity or commonness of the species in the surrounding landscape. In other words, the more common a species is in a region, the more likely it is to colonize new sites (Pärtel et al. 1998). This is better reflected in the other suggested index of colonization potential (ICP), which better characterizes the real colonization ability of a species. However, it was not possible to calculate this index for many species due to their low frequency or absence in both databases. It should also be mentioned that the ability to colonize disturbed sites is not only based on propagule quantity and dispersibility, but also largely on the tolerance of species of environmental conditions, so it also includes establishment capacity. The broader this capacity is, the greater the chance of a species becoming established elsewhere (Grime 2002). Moreover, competition codetermines the species composition of seral stages (Walker & del Moral 2003). Considering all these aspects, we expect that the actual frequency of species in seral stages, and thus their ICS, says more about the probabilities with which different species colonize new sites in the contemporary Czech landscape than their ICP. Correlation coefficient between these indices is not high ($r = 0.33$), which justifies using both. Only species with the highest ICS categories also had a high ICP, in the other categories the correlation was low.

Looking at particular species, distortions may occur caused by the fact that some of the seral stages were concentrated in areas where certain otherwise rare species are common and vice versa. They may, therefore, be over- or under-represented to some degree in our successional database compared to the CNPD, resulting in similarly high or low values of both indices, especially the ICP. Thus, differences between regional species pools (Zobel 1997) throughout this country influenced the participation of species in seral stages.

We preferred the metric scale rounded to integer numbers for both indices, which corresponds to the widely used Ellenberg's indicator values (Ellenberg et al. 1991). Both values are obviously influenced by our sampling design, occurrence of seral stages and possibly by various random factors. Decimal values would have been misleading, because decimal digits are not significant due to insufficient internal reliability. Both indices, as well as the median of successional age of species occurrence (which may be called the "successional status of species"), are potentially useful in ecological studies, at least in the context of central Europe. The advantage of our indices is that they are based on real quantitative data, which reduces their subjectivity (Zelený & Schaffers 2012, Herben et al. 2016).

Our indices can be used in ecological restoration, for example, for predicting species composition at a restored site based on the list of local flora. For this, we consider the ICS to be more convenient because it only considers the actual presence of a species in seral stages, i.e. the "realized successional niche". On the other hand, its use should be restricted to the Czech Republic. The ICP can be more convenient for various theoretical ecological studies dealing, for example, with species traits. It may also have a broader application and not only in the area studied. It will be possible to compare our indices with the disturbance indices recently proposed by Herben et al. (2016), who partly address similar issues but from the opposite direction, i.e. going from vegetation to particular species, while our approach goes from particular species to vegetation. Moreover, their approach is not based on real field data. However, our indices, like all other similar indices, must be used and interpreted with some caution. Besides the above-mentioned limitations, certain undisclosed factors could have biased the values. However, such discrepancies should be balanced out by using larger sets of species in particular studies (Diekmann 2003).

Successional age, i.e. the time that has elapsed since the last disturbance, can be seen as a factor to which species respond in a way similar to other environmental conditions. The response of a species to such factors is usually expected to be unimodal, so the extent of the response indicates a species' tolerance, which also applies to successional age (see minimum, maximum and median age values over the course of succession in the Electronic Appendix 1). Tolerance is usually a missing parameter in the cases of indicator values (ter Braak & Gremmen 1987). It should be mentioned that the "tolerance" of species to successional age is summarized here across all the seres, disregarding sere identity. This is justified by our earlier finding (Prach et al. 2014) that sere identity is not a statistically significant factor determining the species composition of seral stages; successions over a large geographical area and across environmental factors form a continuum in space. This validates our decision to consider all the seral stages together and disregard their identity.

Differences between groups of species in their ability to colonize different seral stages

Species characterizing five of the 10 main habitat types (based on Sádlo et al. 2007) are over-represented in the seral stages studied (Fig. 4) and all of them are well interpretable. Species typical of synanthropic vegetation are naturally frequent at human-disturbed sites, which constitute nearly the whole database. Species typical of the vegetation on cliffs, screes and walls are obviously over-represented due to the presence of many stone quarries in our database (Novák & Prach 2003, Trnková et al. 2010). Especially sand and sand-gravel pits, sampled across the whole country (Řehounková & Prach 2006), and some acidic spoil heaps support the presence of species typical of sandy and other acidophilous grasslands. Species typical of dry grasslands are present in many seral stages if they occur in warmer and dry parts of this country, e.g. in limestone and basalt quarries, some abandoned fields (Prach et al. 2016) and on some coal mining spoil heaps (Prach 1987).

Species characteristic of woodlands, scrubland, synanthropic vegetation and mesic grasslands are the most common in the seral stages (Fig. 5), which is in accordance with the prevalence of these vegetation types in the entire Czech landscape (Chytrý & Rafajová 2003). Also, the trends of changing participation during succession of species with different affiliations to different habitats are mostly in accordance with common ecological expectations, both in the literature (Walker & del Moral 2003, Prach et al. 2014) and based on field experience (Fig. 5 and Electronic Appendix 1). During succession, synanthropic species continuously decreased, while species typical of scrub and woodland vegetation increased, which is quite typical of successions in human-altered temperate landscapes (Glenn-Lewin et al. 1992, Walker & del Moral 2003). In the geographical area considered, succession usually proceeds towards potential natural vegetation, which in most cases is some kind of woodland, as documented by Prach et al. (2016). In non-synanthropic heliophilous vegetation in open habitats, only species typical of dry grasslands increased while others decreased or did not exhibit any significant trend. This can be explained by the fact that at very dry sites, woody species develop slowly or not at all, so succession may eventually lead to vegetation resembling steppes (Prach et al. 2016). The decrease in heliophilous wetland species can be explained by gradual silting of some wet depressions due to sedimentary processes, especially at mining sites, and by increasing transpiration and shading accompanying the development of woody species (Bazzaz 1996).

We conclude that species with high values of our two indices are more likely to spread over landscapes continuously disturbed by human activity. The quantification of species occurrence in differently aged successional stages presented here also allows the prediction of which stage in succession particular species may participate, or possibly dominate. Thus, the results presented may help predict future successional patterns in the central-European landscape and might prove useful in various restoration and landscape management projects.

See www.preslia.cz for Electronic Appendix 1

Acknowledgements

This study was supported by the Czech Science Foundation, project no. 17-09979S and project CZ.1.07/2.3.00/20.0289 under the Education for Competitiveness Operational Programme. LT was supported by the PLADIAS Centre of Excellence (Czech Science Foundation; 14-36079G). We thank all our colleagues and students who agreed to include their data into our database, namely Martin Adámek, Alena Bartošová, Marek Bastl, Helena Dvořáková, Darina Hodačová, Alena Jírová, Alexandra Klaudisová, Petra Konvalinková, Petr Koštel, Tomáš Koutecký, Ondřej Mudrák, Jan Novák, Petr Petřík, Petr Pyšek, Jiří Sádlo, Petr Šmilauer, Zdeněk Špringar, Vojtěch Študent, Romana Trnková and Zdeněk Vaněček. We also thank Milan Chytrý for providing the stratified dataset of the Czech National Phytosociological Database. We are indebted to Tomáš Herben, Péter Török, Jitka Klimešová, Petr Pyšek and anonymous reviewers for their valuable comments on earlier versions of the manuscript, Frederick Rooks and Jan W. Jongepier for their linguistic improvements, Tony Dixon for editing English of the accepted manuscript, and Petr Šmilauer for his advice on statistics. We also thank Alena Jírová and Lenka Šebelíková for their help in completing the database.

Souhrn

Využili jsme rozsáhlou databázi fytocenologických snímků z různých narušených míst v České republice (DaSS), pořízených v rozmanitých, různě starých sukcesních stadiích (2817 snímků) a obsahujících 1013 druhů cévnatých rostlin, k vyhodnocení kolonizační schopnosti druhů české flóry. Počet výskytů jednotlivých druhů v této databázi se stal základem výpočtu indexu vycházejícího z prosté frekvence výskytu jednotlivých druhů v sukcesních stadiích (ICS – index kolonizační úspěšnosti v sukcesních stadiích) v rozsahu 1 (žádný výskyt), až 9 (vysoká frekvence v sukcesních stadiích). Protože je ale výskyt druhů v sukcesních stadiích ovlivněn vedle vlastností druhů i jejich hojností v krajině, byl výskyt v sukcesních stadiích korigován frekvencí příslušných druhů v České národní fytocenologické databázi (ČNFD). Takto upravený index (ICP – index kolonizačního potenciálu) vyjadřuje lépe vlastní kolonizační potenciál jednotlivých druhů stanovený opět v rozsahu 1 (nízký) až 9 (vysoký kolonizační potenciál). Hodnotili jsme rovněž výskyt druhů v různě starých sukcesních stadiích s označením prvního a posledního výskytu a mediánu sukcesního stáří. Zároveň je udána i maximální zaznamenaná pokryvnost (v sedmičlenné Braun-Blanquetově stupnici). Tyto základní informace o uplatnění druhů české flóry v sukcesi jsou shrnuty v přiložené tabulce (Electronic Appendix 1). Dále jsme se tázali, jak se liší zastoupení druhů charakterizujících 10 základních typů stanovišť v DaSS a v ČNFD. Statisticky významně byly v sukcesních sériích více než v ČNFD zastoupeny druhy synantropní, druhy skalních štěrbin, sutí a zdí, druhy psamofytní a druhy typické pro acidofilní a suché trávníky. Statisticky významně se měnilo zastoupení následujících cenotických skupin druhů během sukcese: vzrůstalo zastoupení lesních druhů, druhů typických pro keřová společenstva a suché trávníky, naopak klesalo zastoupení synantropních druhů, mokřadních druhů, psamofytních druhů a druhů typických pro mezické trávníky. Předpokládáme, že zde navržené indexy mohou být úspěšně využity v řadě navazujících studií podobně jako Ellenbergovy indikační hodnoty a pomocí nich by

bylo možné s určitou pravděpodobností předpovídat sukcesní změny v člověkem narušovaných krajinách střední Evropy. Indexy (hlavně ICS) mohou být rovněž využity v různých praktických projektech ekologické obnovy.

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Received 22 September 2016
Revision received 2 February 2017
Accepted 22 February 2017

5 CHAPTER II

Threatened vascular plant species in spontaneously revegetated post-mining sites.

Řehounková et al. 2019. Restoration Ecology 28(3). doi: 10.1111/rec.13027

RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Threatened vascular plant species in spontaneously revegetated post-mining sites

Klára Řehounková[1,2], Kamila Vítovcová[1], Karel Prach[1,3]

The occurrence of threatened vascular plant species has been occasionally reported from some disturbed sites. Nevertheless, almost nothing is known about the conservation potential of post-mining habitats for vascular plant species at a landscape scale. We asked how much threatened species occur in the artificial habitats, and if the participation of particular threatened species categories differ over the course of succession. We studied 10 successional series running in 321 post-mining sites across the Czech Republic, Central Europe. In total, 2,597 vegetation samples comprising 935 vascular plant species were analyzed. We found 235 threatened species (14% of the country's threatened flora). The majority of the threatened plants, namely 223, avoided plots overgrown by woody species, in which only 48 species occurred. The importance of spontaneously revegetated habitats for nature conservation differed among successional stages formed by discontinuous vegetation cover (not fully developed and still open, up to approximately 25 years since site abandonment), which harbored especially critically endangered species of open habitats, and continuous vegetation cover (fully developed and closed, over approximately 25 years), which was suitable for specialized threatened species typical of fully established vegetation. A mosaic of various successional stages comprising both categories of vegetation cover should be applied as an effective restoration solution to maintain a variety of habitats for threatened species.

Key words: mining, national Red List, nature conservation, restoration, spontaneous succession, vascular plants

Implications for Practice

- Spontaneously revegetated post-mining sites may act as important secondary habitats for many threatened vascular plant species, especially in basic quarries.
- At least partly open, early successional habitats play a vital role in the survival of critically endangered short-lived species
- Habitats with continuous vegetation cover are prosperous especially for specialized threatened species typical of advanced woodland or grassland vegetation.
- Maximize the conservation potential of post-mining sites through the creation of differently aged sites and consider them as a potential complement to already existing protected natural habitats.

Introduction

From the beginning, conservation efforts have been focused almost exclusively on well-preserved habitats, or their still surviving fragments in heavily altered landscapes (Cairns & Heckman 1996). Gradually, attention has also been paid to degraded, damaged, or completely destroyed habitats, including those after mining, with the aim to restore target ecosystems (SER 2002). The prevailing earlier negative view on post-mining wastelands predetermined strictly technical solutions, that is, reclamation, being usually oriented to future production outcomes (e.g. timber, crop). This view has been gradually transformed, thanks to ongoing research, toward a completely new paradigm which considers post-mining and other disturbed sites as surrogate habitats harboring species retreating from contemporary cultural landscapes (Prach & Hobbs 2008). Research on restoration practices revealed spontaneous succession as a cost-effective method for encouraging the conservation potential of post-mining landscapes (Kirmer et al. 2008; Tomlinson et al. 2008; Bétard 2013; Prach et al. 2014). This approach might provide long-term benefits if sometimes combined with assisted succession (Řehounková et al. 2016).

The intensive human pressure on many natural and semi-natural habitats has increased the threat to many vascular plants. In the Czech Republic, which well represents the conditions in temperate Europe (Chytrý et al. 2017), 1,720 vascular plant species are classified as threatened in the national Red List, accounting for more than half (59%) of the native Czech flora (Danihelka et al. 2012). Moreover, the total number of species of the national threatened flora has increased by

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Author contributions: all authors collected the data; KŘ, KL did the data analyses; KŘ wrote the first version of the manuscript; all authors commented on the first version of the manuscript and wrote the final version.

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doi: 10.1111/rec.13027
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13027/suppinfo

about one-third during the last 40 years (Grulich & Chobot 2017). Among threatened species, there are often species which require low-productivity sites and which generally vanish from eutrophicated, heavily used landscapes (Kirmer et al. 2008). Such species are often found in quarries and other post-mining sites which, to a certain degree, can substitute for naturally disturbed sites. These sites provide habitat to disturbance-dependent species, which are usually characterized as having a poor competitive ability (Gilardelli et al. 2015).

Furthermore, the estimated conservation budget (cost–benefit) at the site is often positive, especially if mining did not disturb a well-preserved site (Prach et al. 2011). The profit often depends on the existence of well-preserved vegetation in close proximity of a disturbed site (Bétard 2013; Prach et al. 2015). A detailed study of basalt quarries revealed the importance of distance to donor vegetation, that is, dry grasslands, for successful colonization of post-mining sites, but this was found to be only up to about 50 m (Novák & Konvička 2006). On the other hand, it is obvious that not all species have a similar chance to successfully disperse into post-mining habitats (Řehounková & Prach 2010; Kasowska & Koszelnik-Leszek 2014), and their establishment and subsequent spread are further modified by habitat environmental barriers (Thornton 1996).

Post-mining sites can share many important features with threatened natural habitats in continental Europe (European Commission 2007). They include nutrient-poor, fine-grained, and often unstable substrates in sand pits, corresponding to sandy grasslands or sand dunes, basic rock, and slopes of various inclinations in limestone or basalt quarries, which are equivalent to calcareous rocky steppes and natural cliffs (Wheater & Cullen 1997), as well as a wide range of wetland and woodland habitats forming a diverse mosaic which may contrast to the simplified structure of recent cultural and productive landscapes (Bétard 2013).

Spontaneous succession in various post-mining sites has been studied many times during the past circa 20 years with the aim to describe general vegetation patterns (e.g. Bradshaw 1997; Schulze & Wiegleb 2000; Kirmer & Mahn 2001; Prach et al. 2014). Nevertheless, the conservation potential of mining sites for vascular plant species remains generally unexplored. Only a limited number of studies recorded the occurrence of threatened vascular plant species, being moreover confined to only one successional series or one type of post-mining site. These include several regional studies dealing with rare basic habitats established in post-mining sites, namely in large spoil heaps (Kirmer et al. 2008) or different types of quarries (Mota et al. 2004; Novák & Konvička 2006; Tropek et al. 2010). Basic quarries are thought to be particularly important for restoration, because the base-rich bedrock allows the development of species-rich natural communities, such as calcareous grasslands, which are among the richest and most threatened habitats in Europe (e.g. Jefferson 1984; Poschlod & Wallis DeVries 2002). Records of threatened vascular plant species occurring in various post-mining sites have been repeatedly reported from studies focused on the population dynamics of some rare species such as orchids (Jacquemyn et al. 2001; Bzdon & Ciosek 2006; Esfeld et al. 2010) or various highly specialized species (Ballesteros et al. 2013), and especially in local botanical inventory surveys (e.g. Lindström 1999; Windgren 2005). However, we are not aware of any systematic evaluation of the occurrence of rare and retreating species in a larger set of mining sites. This is in contrast to comprehensive zoological studies dealing with various groups of arthropods (e.g. Krauss et al. 2009; Tropek et al. 2010; Heneberg et al. 2016), birds (Santoul et al. 2004; Šálek 2012), or amphibians (Vojar et al. 2016), which consider not only species richness, but also the conservation value of the recorded species.

In this article, we concentrated on three main questions: (1) What is the potential of post-mining sites to harbor threatened vascular plant species? (2) Does the distribution of different classes of threatened species vary in post-mining sites? (3) Does the occurrence of threatened species vary across successional stages? Up to now, this is the first study evaluating the success of threatened vascular plant species in various spontaneously developing post-mining sites at a broad country scale. Such results could be profitable for both ecological restoration and nature conservation planning.

Methods

Study Sites

We sampled altogether 10 post-mining successional series which roughly corresponded to those described in Prach et al. (2014). Several of them had been enlarged by a number of new samples (see Table S1, series no. 1, 2, 4, 6, 9, 10) and one new series on uranium spoil heaps (no. 3) was included. The post-mining site database comprised a total of 2,597 samples from sand and gravel-sand pits, extracted peatlands, acidic, basalt, and limestone quarries, different types of spoil heaps from black or brown coal mining, and uranium mining (Table S1, for characteristics and references). We do not have contaminated soils or any other extreme substrates in the studied post-mining sites. The samples were recorded in differently aged stages ranging from 1 to 100 years. The age of the successional stages was identified because the year of each site creation was known. The following successional stages were defined: (1) early, 1–10 years; (2) middle, 11–25 years; (3) late, 26–40 years, and (4) old, more than 40 years. The space-for-time substitution approach largely prevailed in research (seven series) and only rarely (three series: no. 4, 5, and 10) the approach was combined with the permanent plot approach (Pickett 1989).

The studied series occurred over almost the whole Czech Republic (latitude 49°38′–50°06′, longitude 12°16′–18°26′). The series differed in the number of samples, the number of sampled sites, the geographical area in which they occurred, and successional age. These differences resulted from the availability of successional stages in the post-mining sites and their accessibility. Phytosociological relevés of 10–625 m^2 in size were placed in the center of each homogeneous stage. All vascular plants present in each sample plot were recorded and their percentage cover was visually estimated (Kent & Coker 1992).

We also recorded woody species cover in each sampled plot. All of the series occurred in places directly disturbed by mining activities and started on bare ground. Some series were sampled by the authors, while others using the same field methods of phytosociological relevés were extracted from published or unpublished sources (Table S1).

The Czech Red List is based on the taxonomy and nomenclature used in the checklist of vascular plants of the Czech Republic (Danihelka et al. 2012). The species recorded in the sampled sites were classified according to the national Red List of vascular plants (Grulich 2017) in the following way: critically endangered (C1), highly endangered (C2), endangered (C3), and less threatened (C4). All the species classified in the abovementioned categories are considered to be threatened species. The rest of the species were classified as common (co). The threatened categories used in the national Red List correspond to a certain extent to those used by IUCN (2012), that is, the C1 category roughly corresponds to critically endangered, C2 to endangered, C3 to vulnerable, and C4 to near threatened (Grulich 2017). The complete national threatened flora corresponding to the abovementioned categories consists of 1,573 vascular plant species. Of this number, we excluded extinct, recently unknown species, and alpine species, because none of the post-mining sites occurs in the alpine zone. In this way, we obtained an adjusted Czech Red List flora accounting for 1,386 vascular plant species.

Data Analyses

We carried out a detrended correspondence analysis (DCA) of the vegetation samples (phytosociological relevés) comprising the samples to see the general pattern of threatened species in post-mining sites. Prior to the ordinations, we logarithmically transformed the cover data and down-weighted rare species. Canonical correspondence analysis (CCA) was used to test the influence of successional age (years since sites abandonment) and woody species cover on the vegetation pattern (forward selection, 999 permutations). Because some plots were sampled repeatedly, plot identity was used as a covariable. Plot size was also used as a co-variable. Inside each series, centroids represented all samples of each age category. The use of unimodal methods was justified by the length of the gradient (Šmilauer & Lepš 2014), which reached 9.64 SD units. All ordinations were conducted using CANOCO (ter Braak & Šmilauer 2012). Both CCA and DCA showed a similar pattern, therefore only the results of the DCA are shown using the significant environmental variables (tested in CCA) as passive variables.

In Central Europe, it usually takes circa 25 years of succession to reach a closed (semi)-natural vegetation, usually woodland, which subsequently changes little in species composition (Prach 2003). Therefore, we distinguished two types of vegetation cover: discontinuous (not fully developed and still open, less than approximately 25 years since site abandonment) and continuous (fully developed and closed, over approximately 25 years). We tested the effect of successional stage as well as the continuous vegetation cover versus discontinuous vegetation cover on the number of threatened species using a generalized linear mixed model (GLMM) with an assumed Poisson distribution, if relevant, followed by multiple comparisons of means (Tukey test). The locality, plot identity, and type of mining sites were used as random effects. All univariate statistics were conducted in R (R Core Team 2017, the library *lme4* and the library *multcomp*).

Results

Altogether, 935 vascular plant species were identified in the studied series, with 235 (i.e. 25%) classified as threatened. More than one-third of our vegetation samples contained at least one threatened species. See Table S2 for the complete threatened species list identified in the relevés. From this number, 13 species were identified as critically endangered (3% of C1 species in the adjusted national Red List—see above), 37 as highly endangered (11% of C2 species), 99 as endangered (28% of C3 species), and 86 as less threatened (36% of C4 species) (Fig. 1). The relative participation of the particular threatened categories among all species recorded in the mining sites rapidly increased with decreasing conservation status and then slightly decreased in the last category (C1 5%, C2 16%, C3 43%, C4 36%), in sharp contrast to the more balanced distribution in the whole national flora (C1 27%, C2 21%, C3 21%, C4 14%). The overwhelming majority (223) of the threatened species which colonized the spontaneously revegetated post-mining habitats avoided plots overgrown by woody species, with only a limited number of threatened species (48) occurring in woodland sites. However, the same species often repeatedly occurred in woodland sites while different species occurred in the younger stages.

Limestone quarries appeared as the most threatened species-rich post-mining site, containing almost 25% of threatened species out of the recorded vascular plant species. These were followed by basalt quarries representing another basic post-mining site (18% of threatened species) and then by acidic sand and gravel-sand pits (15%) and extracted peatlands (13%). The participation of threatened species was lower in the other post-mining sites, that is, coal and uranium mining spoil heaps, ranging between 1 and 5% (Fig. 2, Table S3).

The ordination diagram (DCA) of species (Fig. 3A), composed of all species, but visualized with only the threatened species which occurred in the sampled plots, revealed a clustering of the threatened species in two opposite edges of the whole spectrum of post-mining sites. The edges are represented by acidic and mostly wet peatlands and sand pits on the left side of the first axis, and by comparably dry and basic limestone and basalt quarries on the right side (Fig. 3B). The central zone remained almost empty of threatened species. The series were arranged along the first ordination axis (DCA: $\lambda = 0.735$). The first axis could be interpreted as corresponding to a composite pH-moisture gradient (Prach et al. 2014). The second ordination axis (DCA: $\lambda = 0.560$) clearly reflected time, that is, the successional age. The correlation coefficient between the successional age of samples and their score on the second ordination axis was $R = 0.656$, $p < 0.001$.

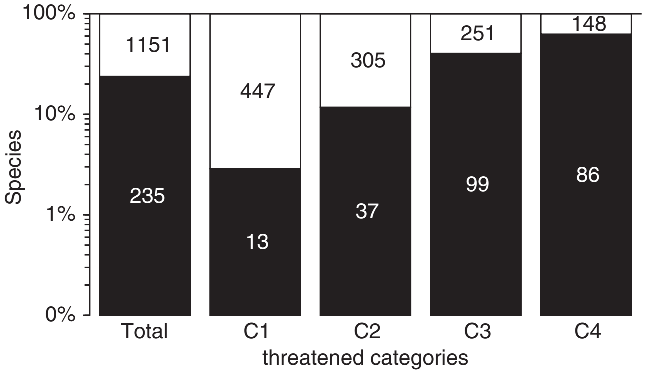

Figure 1. Numbers and proportion of threatened vascular plant species in post-mining sites. Species: present (black column), missing (white column). Categories: C1 critically endangered, C2 highly endangered, C3 endangered, C4 less threatened, Total number of the adjusted national Red List of vascular plant species. The absolute numbers of species for each category are shown in the bars. (Note the logarithmic scale of the vertical axis.)

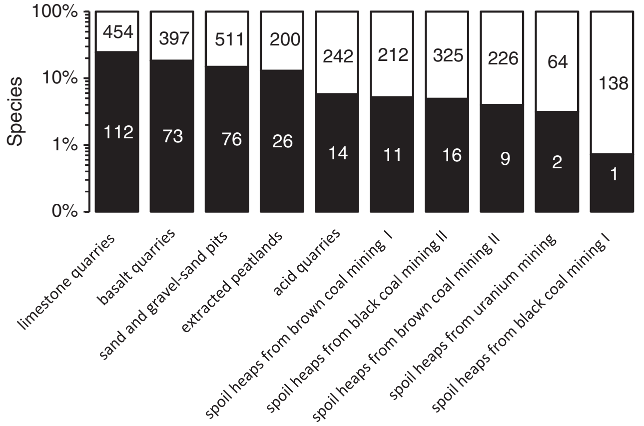

Figure 2. Numbers and proportion of threatened vascular plant species in the studied successional series in various post-mining sites. Threatened species (black), common species (white). The absolute numbers of species in particular series are shown in the bars. (Note the logarithmic scale of the vertical axis.)

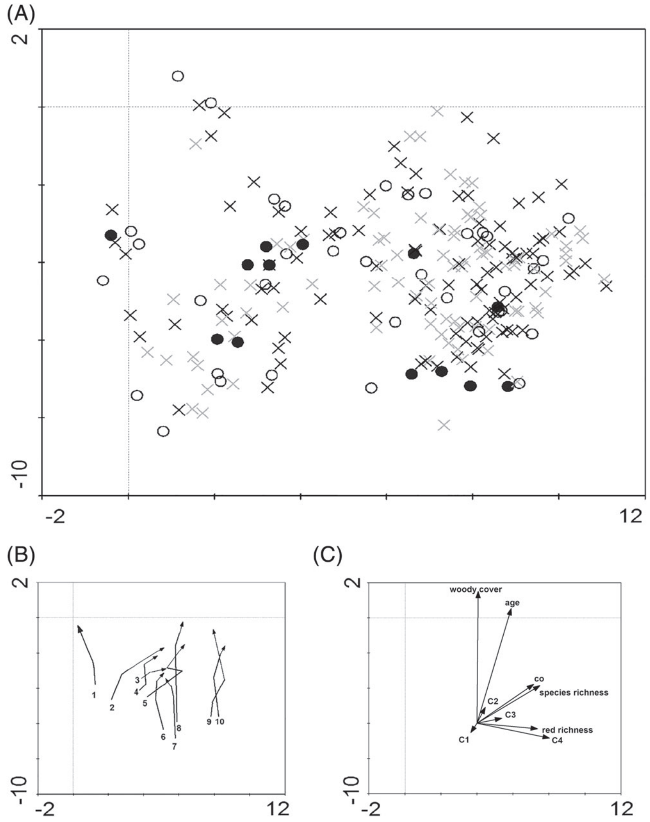

Figure 3. Ordination diagram (DCA) displaying (A) threatened species, (B) series, and (C) environmental variables fitted as passive variables in post-mining sites. Age (years since site abandonment), woody cover—woody species cover in the shrub and tree layers, red richness—number of threatened species, species richness—number of all species, co—common species. Species: C1 critically endangered (full circles), C2 highly endangered (white circles), C3 endangered (black crosses), C4 less threatened (gray crosses). Series: 1. extracted peatlands, 2. sand and sand gravel pits, 3. spoil heaps from uranium mining, 4. acidic quarries, 5. spoil heaps from black coal mining I, 6. spoil heap from brown coal mining II, 7. spoil heap from brown coal mining I, 8. spoil heap from black coal mining II, 9. basalt quarries, 10. limestone quarries. The arrows connect centroids representing the early, middle, late, and old stages of each particular series. Stages: early (1–10 years), middle (11–25 years), late (26–40 years), old (>40 years).

The occurrence of critically endangered species is mostly bound to stages with discontinuous vegetation cover characterized by low tree and shrub cover (Fig. 3C). Sand pits are typical of such post-mining sites, which provide optimal conditions for low competitive, often annual specialists that occurred in both wet and dry habitats. Also, basic limestone and basalt quarries represent open nutrient-poor habitats having often discontinuous vegetation cover where occur less competitive, short-lived species classified as critically endangered. The threatened species classified in other categories than critically endangered can prosper to some extent also in older successional stages dominated by a continuous vegetation cover. The number of common species, reflected in species richness, increased with succession (Fig. 3C).

The CCA ordination ($\lambda_1 = 0.362$, $\lambda_2 = 0.142$) revealed that successional age and woody species cover significantly explained 35.3 and 17.8%, respectively, of the variability of vegetation data ($F_{\text{age}} = 29.748$, $F_{\text{cover}} = 15.080$, $p < 0.001$).

The GLMM analysis revealed a significant effect of successional stage on the participation of threatened species. The younger stages, that is, early and middle stages, which are characterized by discontinuous vegetation cover, differed significantly from more advanced stages, that is, late and old ones having the character of continuous, well-established vegetation cover (Fig. 4). Subsequently, we combined the younger stages with still at least partly open vegetation (discontinuous vegetation cover) and more advanced stages with closed vegetation (continuous vegetation cover).

The category of vegetation cover, that is, discontinuous cover occurring up to approximately 25 years since site abandonment

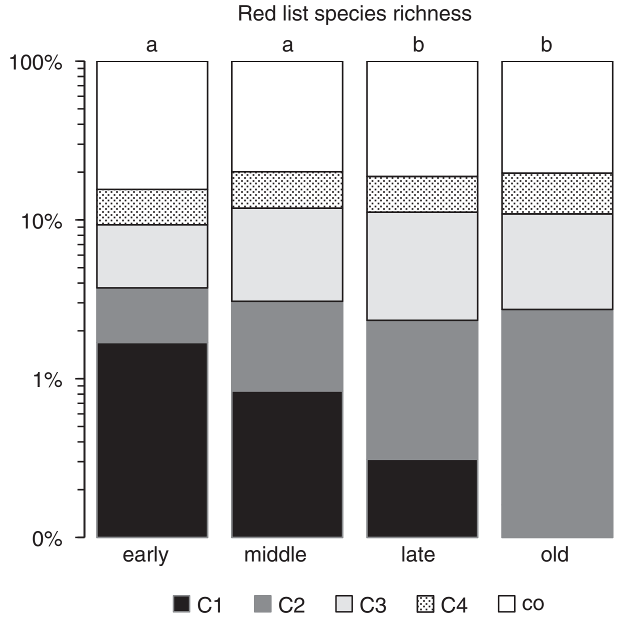

Figure 4. Participation of threatened and common, non-threatened species in particular successional stages in post-mining sites. GLMM analysis was used ($F = 3.668$, $df = 4$; $p < 0.001$). Different letters above the columns indicate significant differences between the successional stages. Species: C1—critically endangered, C2—highly endangered, C3—endangered, C4—less threatened, co—common. Stages: early (1–10 years), middle (11–25 years), late (26–40 years), old (>40 years).

versus continuous cover typical of advanced stages after approximately 25 years of site development, appeared to be significant for the occurrence of threatened species in the majority of the categories when tested by GLMM analyses. Among the threatened categories, critically endangered species occurred almost exclusively in plots with discontinuous vegetation cover while such species almost vanished in plots dominated by continuous vegetation cover ($Z = 1.849$, $p = 0.06$). In the case of the remaining threatened categories, that is, highly endangered and endangered, the participation of threatened species was significantly higher in the successional stages formed by continuous vegetation cover ($Z = 3.11$, $p < 0.01$; $Z = 3.48$, $p < 0.001$). Similarly, species typical of the less threatened category ($Z = 3.19$, $p < 0.01$) and also common species ($Z = 9.71$, $p < 0.001$) exhibited significantly higher participation in successionally advanced stages with continuous vegetation cover.

Discussion

Biodiversity of anthropogenic ecosystems may derive from spontaneous vegetation development (Prach & Walker 2019). In particular, post-mining sites were found to serve as important refugia for many threatened species (Jefferson 1984; Tropek et al. 2010). The average cover of all recorded vascular plant species reached 72% in the sampled plots (herb, shrub, and tree layer). The average cover of recorded threatened species reached 2% in a sample, which should be large enough for many threatened species to successfully survive at the scale of the sampled plot. The recorded number of 235 threatened vascular plant species that participated in spontaneous vegetation succession in the studied post-mining series represented approximately 14% of the national threatened flora (Grulich 2017) and 17% of the adjusted national threatened flora. We intentionally prioritized the national classification scheme which is sufficient if applied at a country scale and corresponds to a certain extent to IUCN criteria (IUCN 2012). Almost 80% of the recorded threatened species classified in the national Red List fulfill also the international criteria of IUCN, being listed in some of the threatened categories of IUCN (Grulich 2017). Simultaneously, we are aware that some of the threatened species, which are rare in the Czech Republic, may be common in other parts of the world. On the other hand, vascular plants are very diverse, e.g. in morphology and biology, and some of the key characteristics may not be available. Thus, it can be very difficult to classify them correctly into the defined IUCN categories (Chobot et al. 2017).

The spontaneously revegetated disturbed sites certainly may not provide long-term benefits for the whole spectrum of threatened species. Spontaneous succession in Central European post-mining sites proceeds rather fast toward woodland with a closed canopy usually established in about 25 years after site abandonment in the majority of habitats (Řehounková et al. 2018). The threatened species specialized for more open habitats retreat rather fast from the aboveground vegetation (Šebelíková et al. 2016). Moreover, the seed bank in the older stages of succession contained an extremely low number of species typical of more open habitats, including threatened specialists (Horáčková et al. 2019). Thus, longer persistence of such threatened species in mining sites with closed vegetation cover seems to be improbable.

It is useful to identify the conservation potential of particular successional stages which would provide optimal conditions for the establishment of species compositions that are analogous to rare natural habitats (Pitz et al. 2018). Participation of threatened categories increased with ongoing succession except for the most valuable critically endangered species, which tended not to establish in habitats with continuous cover. Many of the critically endangered species belonged to a unique group of archaeophytes often specialized to regularly disturbed, nutrient-poor low productive habitats. These findings are similar to those of other multi-taxa studies (e.g. Řehounková et al. 2016), which revealed post-mining sites as refuges for specialists of disturbed habitats. Similar results were documented also in zoological studies dealing mostly with various insect groups, especially threatened wild bees and wasps bound to open sandy habitats (e.g. Heneberg et al. 2013).

The post-mining sites were apparently colonized by threatened species from the surrounding vegetation, such as weed communities adapted to nutrient-poor conditions, dry steppe grasslands, or wetlands (Richardson et al. 2013). Critically endangered species, which are the most valuable from a conservation perspective, occupied sparsely vegetated habitats with still exposed bedrock as documented by Gilardelli et al. (2015). This observation agrees with other biodiversity surveys of various groups of organisms in post-mining sites, which revealed that such biotopes are often highly heterogeneous, containing diverse abiotic conditions, and thus harboring a high number of species (Beneš et al. 2003; Bétard 2013; Pitz et al. 2018). These cannot be achieved in the recent cultural landscape or even in traditionally protected areas where barren land and diverse successional stages are often lacking (Jarošik et al. 2011).

Some studies found that increasing woody species cover (Řehounková et al. 2018; Zakkak et al. 2018) changed specific habitat conditions and gradually decreased the habitat heterogeneity of post-mining sites. This may lead to the complete disappearance of threatened species specialized for at least partly open successional stages (Ursic et al. 1997). Simultaneously, threatened species typical of well-developed late successional stages in either grasslands or woodlands have usually a limited ability to overcome environmental barriers to reach and colonize the disturbed sites (Řehounková & Prach 2010; Gilardelli et al. 2015). Even the longest post-mining series, which approached approximately 100 years since site abandonment, might not be sufficient for the establishment of well-developed late successional vegetation. Prach et al. (2016) estimated a period of about 200 years for the full development of primary successions including post-mining sites.

Vascular plant diversity is usually related to basic rather than acidic substrates (Chytrý et al. 2007). In concordance with this, we identified the highest number of threatened vascular plant species in basic limestone and basalt quarries prevailingly located in well-preserved landscapes with diverse regional species pools. On the other hand, repeated records of threatened vascular plant species with high conservation status, specialized for acidic and shallow or periodically flooded habitats represented by sand and gravel-sand pits or extracted peatlands, imply that even acidic post-mining habitats could have high conservation potential, similarly as natural acidic nutrient-poor flooded habitats characterized by the frequent occurrence of threatened species (Chytrý 2011).

The above-discussed conservation potential of the post-mining sites for vascular plant species strongly depends on the restoration method applied, in that spontaneously revegetated sites harbor a much higher number of these species than technically reclaimed sites (Šebelíková et al. 2016). The finding of as many as one-sixth of all nationally recorded threatened vascular plant species in the studied post-mining sites justifies the importance of spontaneous succession as a cost-effective restoration method for threatened plants in the newly established habitats. Thus, a compromise solution consisting of the gradual abandonment of parts of a post-mining area for nature conservation whenever possible would give rise to a network complementary to already existing protected areas for a large spectrum of threatened species. It seems that such species can find appropriate environmental conditions in the diverse, post-mining habitats. However, we consider only the temporal persistence of these habitats (with the exception of extreme sites where succession might be blocked for a long time, Prach et al. 2014), which vanish due to ongoing successional processes, which in temperate central Europe, leads toward closed woodland (Leuchner & Ellenberg 2017). If a network of temporal habitats in post-mining sites is created, they could serve as stepping stones and enable species to move across the landscape (Heneberg et al. 2013). We know that spontaneously revegetated disturbed sites may not provide long-term benefits for the whole spectrum of threatened species (Řehounková et al. 2016). We expect that they can be sooner or later outcompeted by native or even alien competitors, the latter locally invading the mining sites (Řehounková & Prach 2008). Thus, some kind of management treatment seems to be desirable, at least in certain parts of post-mining sites once the mining activities cease, to keep the mosaic character of habitats in different stages of succession and maintain space-temporal heterogeneity.

Despite increasing awareness that post-mining sites can represent secondary habitats of conservation interests, legislation in many European countries requires fast reclamation of post-mining sites, often with requirements for future economic profit (e.g. timber production, crops). Therefore, an evidence-based restoration approach which allows the evaluation of both the collateral benefits and drawbacks of mining activities in various habitats can help to identify the most effective method from a conservation perspective. Our results suggest that, under certain circumstances, heavily damaged anthropogenic wastelands might have similar conservation potential as rare natural unproductive habitats, such as barren, sandy areas, or rock outcrops (Novák & Konvička 2006). Therefore, we recommend that mining activity should not destroy anything that might be more valuable than mining is able to afterwards create through restoration. The mining activity should respect well-preserved habitats which can serve as a donor site for spontaneous colonization of post-mining sites in the close surroundings (Trnková et al. 2010). Following this general rule, such an approach could help to reconcile the necessary natural resource exploitation with effective restoration of diverse ecosystems of high conservation value (Richardson et al. 2013).

Acknowledgments

This work was supported by grant GACR 17-09979S. We thank all our colleagues and students that agreed to have their data included in our database, namely Petra Konvalinková, Tomáš Koutecký, Jan Novák, Lubomír Tichý, Alena Bartošová, Marek Bastl, Ondřej Mudrák, Táňa Štechová, Jiří Sádlo, Romana Trnková, Tereza Dudíková, and Helena Dvořáková. The authors thank Keith Edwards for language revision.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Summarizing characteristics of particular series—comparison with the study by Prach et al. (2014).

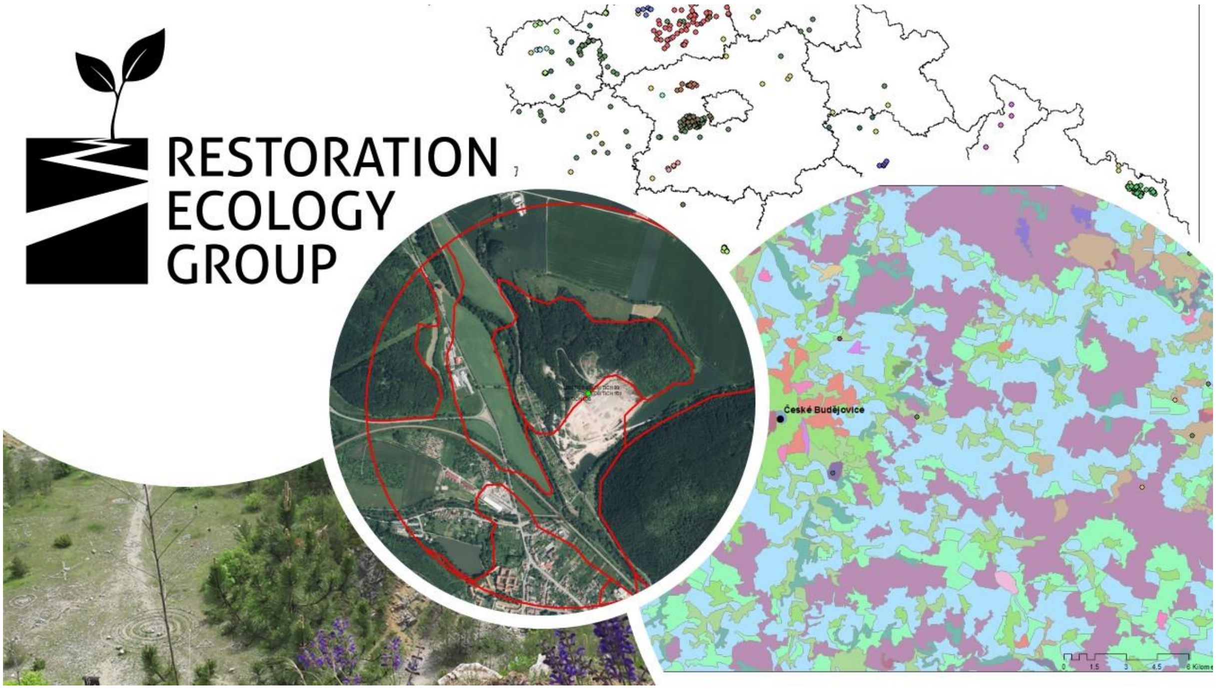
Table S2. Threatened vascular plant species in the post-mining sites.

Table S3. Numbers of vascular plant species recorded in particular series and threatened categories.

Guest Coordinating Editor: Dr Cristina Branquinho

Received: 28 February, 2019; First decision: 9 August, 2019; Revised: 15 July, 2019; Accepted: 28 April, 2019

6 CHAPTER III



Which landscape and abiotic site factors influence vegetation succession across seres at a country scale?

Vítovcová et al. 2020. J. Veg. Sci.:1–10. doi: 10.1111/jvs.12950

Received: 9 September 2019 | Revised: 3 September 2020 | Accepted: 6 September 2020

DOI: 10.1111/jvs.12950

RESEARCH ARTICLE

Journal of Vegetation Science IAVS

Which landscape and abiotic site factors influence vegetation succession across seres at a country scale?

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Funding information
Grantová Agentura České Republiky, Grant/Award Number: 20-06065S

Co-ordinating Editor: Alicia Teresa Rosario Acosta

Abstract

Questions: (1) How much do abiotic site factors and land-cover categories influence the course of succession across successional series at a country scale? (2) Are there any differences in the abiotic site factors and land-cover categories which are responsible for driving primary and secondary seres? (3) Which of the factors influence species richness and participation of target species?

Location: Various disturbed sites in the Czech Republic, Central Europe.

Methods: The Database of Successional Series (DaSS) was compiled of 21 different types of succession, comprising 2,846 phytosociological relevés. The stages ranged from 1 to >150 years in age. Abiotic site factors included macroclimate characteristics and substrate; landscape factors comprised various land-cover categories in a radius of 1 km around each sampled site. Principal Coordinate Analysis of Neighbour Matrices (PCNM) was performed to quantify the effect of abiotic site factors and landscape factors on seral vegetation, also regarding the primary or secondary status of succession. The relationships between number of species, number and proportion of target species and abiotic site and landscape factors were further assessed using generalised linear model analysis.

Results: All considered abiotic and landscape factors were found to have significant effects on the course of succession. The effects of abiotic site factors appeared to be more important than those of the surrounding landscape structure. Species richness was higher on basic substrates. The proportion of target species increased with increasing woodland area in the surrounding and with a wetter and colder climate, and decreased with urbanisation rate of the landscape.

Conclusion: Not only local but landscape factors, such as climate and land cover, should be considered in any study of succession, as they substantially influence the general successional pattern. Quantification of the role of these environmental factors may help to decide where a spontaneous restoration is a viable option for the restoration of disturbed sites. The primary or secondary status of succession is less relevant than has usually been supposed.

KEYWORDS

abiotic factors, landscape context, species richness, succession, target species, vascular plants

1 | INTRODUCTION

Succession is the process of vegetation recovery following a disturbance, which has been studied for more than a century (Clements, 1916; Glenn-Lewin et al., 1992; Walker & del Moral, 2003; Chang & Turner, 2019; Prach & Walker, 2020). Especially the question which environmental factors affect the course of succession have been investigated by many authors (e.g. Řehounková & Prach, 2006; van Breugel et al., 2019; Peña-Angulo et al., 2019; Rohal et al., 2019). However, there is still a lack of studies testing their influence across various successional series (=seres) and at a broader geographical scale (Matthews et al., 2009). Besides our earlier works (e.g. Prach et al., 2014, 2016), we are only aware of a few studies where more than two seres were compared regarding the role of environmental factors on at least a landscape scale (Walker, 1995; Fox et al., 1996; Timoney et al., 1997; Makoto & Wilson, 2019). The lack of such studies does not let us distinguish site-specific and generally valid patterns. In this study, we compared 21 different types of succession running at a country scale with an attempt to partly fill the knowledge gap.

The major factor determining species composition during succession is usually the age of a site, i.e. the time elapsed since the site was created or abandoned (Glenn-Lewin et al., 1992; Peña-Angulo et al., 2019). Of the local site factors influencing succession, we can consider substratum quality (many studies, recently e.g. Tardif et al., 2019; van Breugel et al., 2019), site moisture (Osbornová et al., 1990), the character of disturbances (Johnstone et al., 2016; Tardif et al., 2019), local species pool (Řehounková and Prach, 2008), interactions between species (Bardgett & Wardle, 2010; Turner et al., 2019), and unpredictable chance factors (Connor & Simberloff, 1976). The course of succession is further affected by environmental factors such as macroclimate (Otto et al., 2006; Guil et al., 2009), history of human influence (Benjamin et al., 2005; Cramer et al., 2008), and the present state of the surrounding landscape (Fischer & Lindenmayer, 2007; Prach et al., 2015), especially represented by the regional species pool (Settele et al., 1996). All these factors can hardly be quantified in one study, especially if conducted across many sites and seres. For example, it is extremely difficult or impossible to exactly quantify the species pool or to measure soil moisture for each of the many study sites. Thus, despite the various restrictions this has, some substitute factors may be used, such as surrounding land cover or precipitation.

There are certainly some abiotic factors which can easily be extracted from available sources and then compared between many studied sites located over a large geographical area, such as climatic factors and geological substrate. The surrounding landscape provides propagules to a disturbed site and therefore its evaluation, using for example land-cover categories, has been used to test the effect of landscape structure on species composition and richness of seral vegetation. The effect usually appeared to be highly significant (e.g. Guil et al., 2009; Prach et al., 2015) but different land-cover categories may exhibit different effects on different seres. We considered the above-mentioned factors in this study as explanatory variables of successional changes across all the studied seres to find general trends.

Studies on vegetation succession traditionally emphasise the distinction between primary (no important biological legacy after disturbance) and secondary (soil profiles and diaspores present) seres, expecting differences in the role of environmental factors during the course of succession (Glenn-Lewin et al., 1992; Walker & del Moral, 2003). The affiliation to successional status, i.e. primary versus secondary succession, and its effect on vegetation development could be overestimated (Prach et al., 2001). Moreover, the two principal types of succession are not always clearly distinguishable but form a continuum (White & Jentsch, 2001). Abiotic factors and landscape context seem to determine vegetation succession more than the primary versus secondary status itself (Prach et al., 2001), but a broader comparative study is still missing.

Vegetation ecologists usually describe succession using species composition. Besides the variability of total species composition changing during succession, we also focused on the participation of target species which are appreciated from the perspective of ecological restoration. Most restoration actions at human-disturbed sites are focused on increasing the number and abundance of target species (van Andel & Aronson, 2012) and suppressing and/or preventing the establishment of undesirable, i.e. usually alien and competitive synanthropic species (Török & Helm, 2017).

Quantification of the role of particular factors driving succession at a large scale may not only improve our understanding of succession but also help practitioners in restoring sites or predicting the future vegetation of disturbed sites. In some cases, it may indicate how certain factors can be manipulated to direct the succession (Luken, 1990; Walker et al., 2007).

In this study, we especially asked the following questions:

- Question 1: how much do abiotic site factors and land-cover categories in the surroundings up to 1 km from sites with successional stages influence the course of succession across successional series at a broad spatial, i.e. country, scale?
- Question 2: are there any differences in abiotic site factors and land-cover categories in the surroundings which are responsible for driving primary and secondary seres?
- Question 3: which of the factors influence species richness and participation of target species?

Regarding these questions, we did not have any a priori hypotheses concerning the role of abiotic site factors versus landscape factors because particular studies have provided variable results (Walker & del Moral, 2003). Based on some earlier results (Prach et al., 1997, 2001) we hypothesised that the distinctions between primary and secondary status of succession will not be so relevant as is usually expected by succession theory (Glenn-Lewin et al., 1992). As for the impact of the considered factors on species richness, we expected richer seral vegetation in a warmer climate, i.e. in lowlands, and on basic substrates due the evolutionary history of the central European flora (Chytrý et al., 2003). We also expected higher participation of target species in landscapes less altered by humans (Hobbs et al., 2009).

2 | METHODS

2.1 | Vegetation data

The Database of Successional Series (DaSS; see www.restoration-ecology.eu), i.e. a set of samples from various natural successions ranging from initially colonised sites to late-successional stages, was used. It contained 2,846 phytosociological relevés and the successional stages ranged from 1 to >150 years in age. The relevés included 1,012 species (groups of species and subspecies difficult to distinguish were merged, e.g. *Rubus* spp., *Alchemilla* spp., *Taraxacum* spp., and some other ones). The database consisted of 21 main types of succession and 39 particular seres. Most of the seres have been described in separate studies or summarising papers (for details, see Prach et al., 2013, 2014, 2016, and Appendix S1). The seres differed in number of samples, number of sites, geographic area and successional age, but were sampled comparably. The seres under study included extracted peatlands, corridors of the former Iron Curtain (a fenced continuous strip of land separating part of communist Europe from democratic countries), artificial fishpond islands and barriers, emerged bottoms, sedimentary basins, various spoil heaps after mining, various stone quarries, forest clearings, burnt forests, road verges, ruderal urban sites, sand and gravel-sand pits, river gravel bars and abandoned arable fields (for a distribution of study sites, see Appendix S2). All but one of the seres (river gravel bars) were directly initiated by human disturbance. All the seres developed thereafter without any additional evident disturbances, so they represent spontaneous succession (Prach et al., 2001). Phytosociological relevés were recorded either by the authors or extracted from published or unpublished sources (see Prach et al., 2014, and Appendix S1). Percentage cover was visually estimated (Kent & Cooker, 1992), and the relevés were 10–450 m^2 in size.

Two criteria to distinguish the primary or secondary status of succession were used: the presence of propagules and developed soil at the onset of succession (Glenn-Lewin et al., 1992). Altogether 13 types of succession were classified as primary (mostly at mining sites), six as secondary (abandoned fields, emerged bottoms, forest clearings, burnt forests, ruderal urban sites, and corridors of the former Iron Curtain). In the case of two seres (road verges, artificial fishpond islands and barriers) it was difficult to determine the primary or secondary status unambiguously because substrates with and without propagules and topsoil were present. These two seres were excluded from the analyses regarding primary or secondary status, but were used in the analyses of all seres.

Nomenclature of vascular plants follows Danihelka et al. (2012).

2.2 | Environmental data

The following environmental data were collected for each sampled seral stage in DaSS to indicate the main abiotic site factors: latitude, longitude (either measured directly with a GPS engine or estimated from an orthophoto), mean annual precipitation and mean annual temperature (derived from raster maps produced for the Climate Atlas of Czechia; Tolasz, 2007), and geological substrate (acidic or basic, taken from the Geological Map of the Czech Republic; Cháb et al., 2007). The proportion of main land-cover categories using Land Cover and Land Use inventory (Corine Land Cover 2012, version 18; www.copernicus.eu) was used to indicate the effect of the surroundings. The following broader categories were created by grouping some land-cover categories (see Appendix S3): (a) urban and industrial areas; (b) grasslands; (c) arable land; (d) woodlands; and (e) wetlands. Aquatic categories (streams and water bodies) were omitted because the DaSS contained only terrestrial vegetation. The ArcGIS 10 software (ESRI 2011) was used to estimate the proportion of CORINE categories in a circular 'buffer' zone with a radius of 1,000 m around each sampled site.

2.3 | Data analysis

All recorded species were classified according to their affiliation to the following vegetation units (Ellenberg et al., 1991; Chytrý, 2007–2013): (a) mesic grasslands; (b) dry grasslands and heathlands; (c) woodlands; (d) wetlands; (e) synanthropic, i.e. ruderal or segetal vegetation; and we considered alien species (f) separately. Alien species were determined according to Pyšek et al. (2012). All threatened vascular plants (274 species, according to the national Red List; Grulich, 2012) and all other species except for unthreatened synanthropic species and aliens (475 species) were considered as the target species, which are appreciated to occur in seral stages (van Andel & Aronson, 2012).

For making multivariate analyses of the influence of abiotic site factors and characteristics of the surroundings on seral vegetation, Canoco 5 (Microcomputer Power, Ithaca, NY, US) was used. Logarithmic transformation of the species data and down-weighting of rare species were applied (Šmilauer & Lepš, 2014). Cover of all species in each plot was used as the response variable. Spatial autocorrelation between particular vegetation records was removed by means of Distance-Based Morans Eigenvector Maps analyses (dbMEM; Borcard & Legendre, 2002; Dray et al., 2006), indicated in Canoco 5 software as Principal Coordinate Analysis of Neighbour Matrices (hereafter referred to as PCNM). Only significant spatial axes which explain at least 1% of spatial variability were counted as covariables. False Discovery Rate was used as a parameter for adjusting the significance of the axes. The influence of environmental factors on successional vegetation was calculated by Canonical Correspondence Analysis (CCA) and forward selection analysis followed by a Monte Carlo permutation test (999 permutations), and False Discovery Rate was also used to adjust significance. The unimodal relationship in the species data was justified because Detrended Correspondence Analysis (DCA) revealed the length of the gradient to be 17.2 turnover (*SD*) units (Šmilauer & Lepš, 2014). The environmental variable 'Age' was used as a covariate because seres were of different length and the influence of successional age is not a point of interest in this study. The variables number of species, number of target species, affiliation of species to particular vegetation classes, number of alien species, isolines for a proportion of target species, and centroids for each disturbed habitat were fitted ex-post as passive variables.

Relationships between plant species richness, target species and proportion of target species in all seres together, and particular environmental factors were determined using generalised linear models (GLMs) in the R software (R Development Core Team 2016), using the *glm()* function with an assumed quasi-Poisson distribution because of overdispersion, with a log function and logarithmic transformation of the data. Statistical parameters were tested with the χ^2 test (Lepš & Šmilauer, 2016). The binomial variable 'basic/acidic' was used for testing the influence of the substrate. The numbers of all species, target species and proportion of target species were used as response data. Since the vegetation plots in the database were of different sizes, we used recalculated numbers of species, according to species–area curves, to a single size of 25 m^2, taking into account the species–area relationship (similarly used in e.g. Divíšek & Chytrý, 2018).

3 | RESULTS

3.1 | Factors driving succession across primary and secondary seres

All the considered abiotic factors and characteristics of the surroundings were determined as significant in driving succession, whether primary or secondary, except for the proportion of wetlands in the surroundings in the case of secondary successions. The results of forward selection (CCA ordination analysis) are summarised in Table 1. Generally, the abiotic site factors were more important than the surrounding landscape when we summarised the percentages of the particular factors. In the case of primary successions, the character of the substrate explained the highest amount of variability in vegetation data. On the contrary, in secondary successions the role of the substrate was marginal. The main successional drivers in secondary successions were climatic factors, i.e. mean annual precipitation and mean annual temperature, which were also important factors in primary successions.

TABLE 1 Influence of all considered factors on seral vegetation

Primary succession series	Explaining (%)	*F* statistic
Substrate acidic/basic	1.31	26.3
Wetlands	0.97	19.5
Precipitation	0.49	10.1
Temperature	0.45	9.1
Woodlands	0.37	7.6
Urban and industrial areas	0.29	5.9
Grasslands	0.23	4.8
Arable land	0.14	2.8
Secondary succession series		
Precipitation	2.93	20.9
Temperature	2.14	15.6
Urban and industrial areas	1.87	13.9
Arable land	0.88	6.6
Woodlands	0.45	3.4
Substrate acidic/basic	0.38	2.9
Grasslands	0.25	1.9
Wetlands	n.s.	n.s.

Results of forward selection in CCA. Successional age was used as a covariate; False Discovery Rate was used to adjust significance. The environmental factors are listed in order of decreasing explained variability. Adjusted *P*-level for all factors (except factor Wetlands for secondary successions) is less than 0.001.

Two groups of factors can be clearly distinguished in the ordination diagram, reflecting together climatic conditions and degree of human transformation of the landscape (Figure 1). The first group includes temperature, the proportion of urban and industrial areas and grasslands in the surroundings as indicated by the respective arrows in the diagram. They reflect warm and largely altered landscapes with the highest numbers of alien and synanthropic species. Most spoil heaps and road verges are related to this group of factors. The second group of factors comprises precipitation and proportion of woodlands and wetlands in the surroundings, reflecting wetter and cooler regions which are more forested and less urbanised. Dead forests after air pollution and extracted peatlands, both occurring mostly in montane areas, are most related to this second group of factors. Generally, primary and secondary seres are intermingled in the ordination space, not demonstrating any clear relationship to the considered environmental factors.

3.2 | Effects of factors on species richness

Plant species richness, considering the total number of species and the number of target species, was generally the highest for limestone and basalt quarries, abandoned fields, river gravel bars, and ruderal urban sites in the PCNM ordination analysis (Figure 1b). On the other hand, spoil heaps from uranium mining, one set of spoil heaps from black-coal mining, and sedimentary basins had both the lowest total numbers of species and numbers of target species. The proportion of target species was lower in warmer and drier, and more urbanised landscapes with a higher occurrence of synanthropic and alien species, and higher in forested, wetter and cooler landscapes with more frequent occurrence of wetland species. The highest proportion of target species was recorded for dead forests after air pollution and extracted peatlands located mostly in the mountains. The total species richness, the number of target species, and the number of grassland species were positively related to basic substrate.

In the GLM analysis (Table 2), only one landscape factor, presence of wetlands, exhibited a significant negative effect on the total

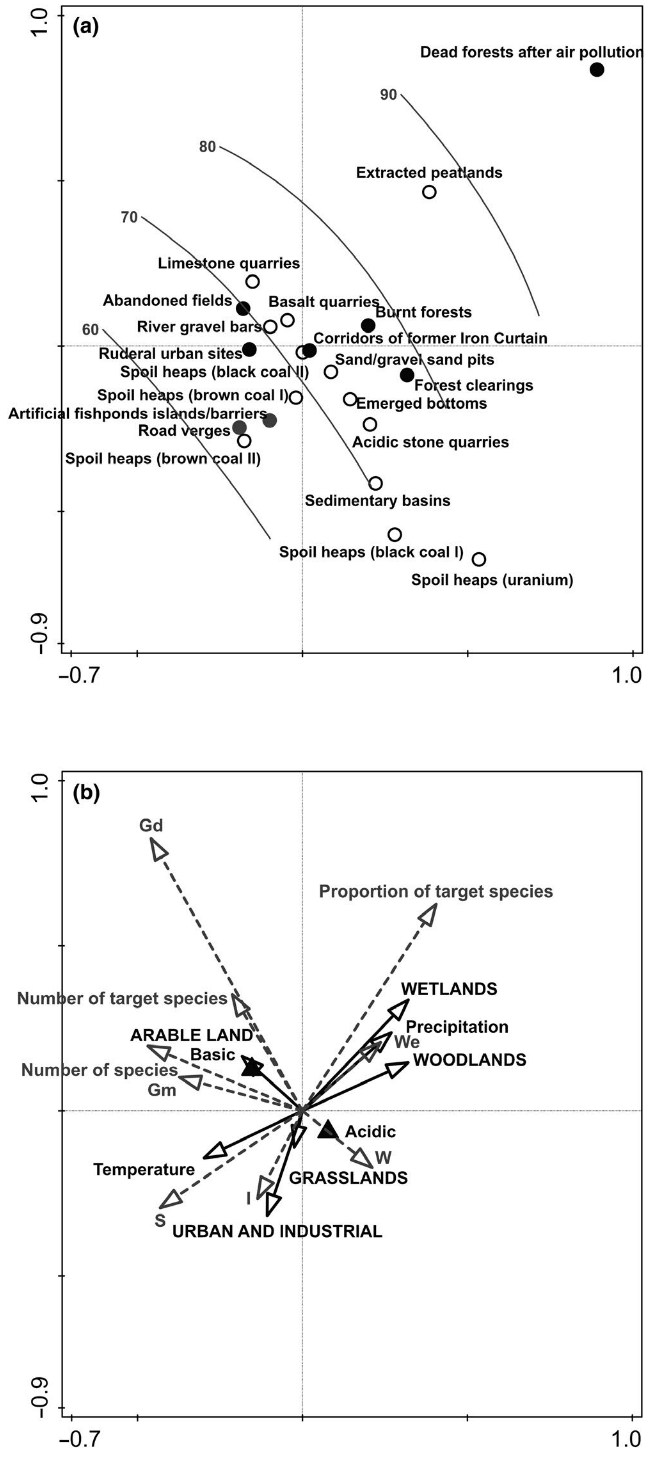

FIGURE 1 Canonical Correspondence Analysis (CCA) ordination diagrams summarising the variation in plant species composition of the seres explained by environmental variables after accounting for spatial effects. Spatial autocorrelation was removed with Principal Coordinate Analysis of Neighbour Matrices (PCNM). Successional age was used as a covariate. (a) Relationships between seres. Open circles indicate primary seres, solid black circles secondary ones, and solid grey circles indicate seres with mixed status. Isolines for the proportion of target species (%) and centroids for each type of seres were supplemented as passive variables. (b) Mutual relationships between community characteristics (grey dashed arrows) and environmental factors (black arrows and triangles, landscape factors with capital letters). All community characteristics, such as 'Number of species', 'Number of target species', 'Proportion of target species' as well as the other arrows showing the affiliation of species to vegetation classes, were supplemented as passive variables. The species were classified according to their affiliation to broad vegetation units with aliens considered separately: W, woodland species; We, wetland species; Gm, mesic grassland species; Gd, dry grassland and heathland species; S, synanthropic species; A, alien species

species richness. On the other hand, basic substrate and marginally also temperature had a significant positive effect on the number of all recorded species. The remaining factors, i.e. proportion of urban and industrial areas, arable land, grasslands and woodlands, exhibited no significant effect on species richness.

The number of target species and their relative proportion were positively correlated to precipitation and relative cover of woodlands in the surroundings, while negatively with temperature and relative area of urban and industrial areas, which is together well interpretable. Basic substratum had a positive effect on the number of target species but a negative effect on their proportion. The occurrence of wetlands was positively correlated with the proportion of target species while exhibiting an insignificant effect on the number of target species. Relative cover of grasslands was negatively correlated with proportion of target species while arable land in the surroundings did not indicate any clear effect on number nor on relative proportion of target species.

4 | DISCUSSION

We considered all available successional series in one country and tested the influence of both site abiotic factors and structure of the surrounding landscape on the course of succession and revealed some general trends (see below) improving our understanding of vegetation succession at broader spatial scales. It would be desirable to have more data on site abiotic factors, such as detailed substratum moisture, chemistry and texture, but such data can only be obtained in a comparable way for a limited number of stages and seres. Vegetation data were intensely collected during the past two decades, and some stages do not exist at present. Thus, it was not possible to measure some important factors mentioned above. Climate and land cover may have changed over time but not substantially for our purpose. Using the special multivariate analysis PCNM, we avoided spatial autocorrelation of the samples, which is the usual obstacle in such kind of data (Borcard & Legendre, 2002).

4.1 | Factors driving succession

In general, abiotic factors, i.e. climate and substrate, exhibited a stronger effect on seral vegetation than the surrounding landscape

TABLE 2 Relationships between species richness and proportion of target species in all successional series together and particular environmental factors

		All species			Target species			Proportion of target species		
	Factor		χ^2	P		χ^2	P		χ^2	P
Abiotic site factors	Precipitation	→	1.528	n.s.	↑	14.86	***	↑	13.139	***
	Temperature	↑	1.828	.	↓	−26.8	***	↓	−14.34	***
	Basic substratum	↑	13.84	***	↑	4.856	***	↓	5.025	***
Landscape factors	Arable land	→	0.194	n.s.	→	−0.903	n.s.	→	1.393	n.s.
	Grasslands	→	1.336	n.s.	→	−0.781	n.s.	↓	−2.51	***
	Urban and industrial areas	→	0.495	n.s.	↓	−13.08	***	↓	−16.27	***
	Wetlands	↓	−10.37	***	→	−1.333	n.s.	↑	9.532	***
	Woodlands	→	−0.821	n.s.	↑	4.055	***	↑	9.873	***

Generalised linear model with quasi-Poisson distribution (used because of overdispersion) and log function was used. Values of all environmental factors were logarithmically transformed; the binomial family was used for testing the factor basic/acidic; the numbers of species per relevé were standardised to a single size of 25 m^2 according to species–area curves. Significance levels: ***, 0.001; **, 0.01; *, 0.05; ., 0.06; n.s., non-significant. Arrows indicate increase (↑), decrease (↓) or no significant trend (→).

structure. However, in some other studies it was clearly shown that abiotic site conditions are less important in determining the structure and dynamics of species composition of particular human-made sites than the composition of the surrounding vegetation (for example in mine tailings – Urbanová et al., 2017; sand and gravel-sand pits – Řehounková & Prach, 2006; coal mining waste dumps – Ninot et al., 2001; stone quarries – Novák & Prach, 2003; abandoned arable fields – Pickett et al., 2001). Since these studies dealt with only one type of succession and a limited number of stages, we consider our findings more robust. The decisive role of climate and substratum for the course of succession was documented by Otto et al. (2006) and Prach et al. (2007). These factors can affect the vegetation directly via species establishment (Bazzaz, 2006) or indirectly by determining the regional species pool (Settele et al., 1996). The importance of climate as an environmental factor probably depends on the scale. It seems that the broader the scale is, the more influential the climate is. Šebelíková et al. (2018) proved that sampling locality (which may be considered representative of the macroclimate if mutually distant) was the most important factor influencing vegetation succession on selected spoil heaps across central Europe. When comparing two studies into vegetation succession in sand pits on two scales, regional versus country, a similar conclusion can be drawn: according to Šebelíková et al. (2016), climate factors did not significantly influence vegetation variability in sandpits within one small region, while Řehounková and Prach (2006) found that precipitation and temperature, besides substratum pH and water table, are crucial in determining the vegetation pattern in spontaneously revegetating sand pits across the whole country. Plant composition at disturbed sites is affected by processes operating on scales ranging from local to regional (Parker, 1997), but the relative influence of them can vary (Matthews et al., 2009). However, soil moisture could not be measured at a large scale in the present study, but it certainly co-determines the course of succession (Osbornová et al., 1990).

The role of landscape structure, especially the surrounding vegetation as a source of propagules, is well studied and its importance for the course of succession has been documented many times (Novák & Prach, 2003; Dovčiak et al., 2005; Novák & Konvička, 2006; Kirmer et al., 2008; Řehounková and Prach, 2008). However, these studies also concerned one sere only and were not performed on such a broad geographical scale as we did. Thus, generalisations were confined to local conditions. Our study revealed that the most important land-cover category in the surroundings of up to 1 km from a disturbed site, which influences the course of both types (primary, secondary) of succession, is the proportion of urban and industrial areas, followed by woodlands. These two land-cover categories are mutually related, as a higher proportion of woodlands indicates lower urbanisation. Both can operate as barriers for the spread of species but also as a source of propagules of different groups of species (Settele et al., 1996). Our results clearly showed that the numbers of synanthropic and even alien species in seral stages increase with the proportion of urban and industrial areas in the surroundings. Besides this, numbers of species of dry grassland and heathlands and mesic grasslands are positively correlated with basic substratum and arable land in the vicinity. This is probably caused by the fact that more agricultural land and basic substrates in the studied country occur in lowlands, where these species have their optimum. Especially for grassland plants, the local community species pool has been reported to be highly dependent on the grassland area in the surroundings (Loos et al., 2014). However, our results showed that the number of grassland species is independent of the proportion of grasslands in the surroundings. It seems important for these species that grasslands are present at all.

It has been generally expected that the primary or secondary status of succession is decisive for its course (Glen-Lewin et al., 1992). However, we revealed only small differences between them. Particularly in the case of secondary seres, substratum pH became less important, probably because the substrate is covered by well-developed soil and the influence of the bedrock is less pronounced. In secondary successions, the proportion of urban and industrial areas in the vicinity had a stronger effect than in primary successions. Secondary seres are usually more nutrient-rich than primary seres (Grime, 2002) and are therefore more colonised by nitrophilous synanthropic species frequently occurring at urban, industrial, and agricultural sites (Chytrý et al., 2017). These species are also often present in the soil seed bank, especially in former arable land (Török et al., 2012). The comparably high role of wetlands present in the surroundings in the case of primary seres can be an artefact, because more wetlands were present in extracted peatlands and at many other post-mining sites, while wetlands are less present in secondary seres such as abandoned fields, clearings and burnt forests. Other factors influencing the course of primary and secondary successions were more or less of comparable importance. Generally, the types of seres did not differ much in the spectrum of factors which played a role in determining their course (cf. Walker & del Moral, 2003).

4.2 | Effects of factors on species richness

Higher species richness may not always be an indicator of higher habitat quality. Especially at disturbed sites non-native species may substantially contribute to the total species number, i.e. even if the overall species richness increases, this fact does not have a positive effect from the perspective of indigenous biodiversity protection (van Andel & Aronson, 2012). For this reason we also focus on target species.

We revealed that basic substrate had the highest positive effect on the species richness of human-disturbed sites. This result was confirmed by both the PCNM and the GLM analysis. Disturbed sites with basic substrates (i.e. limestone and basalt quarries, and in our case also abandoned fields, were often situated in karstic areas) are the species-richest, considering both the total number of species and the number of target species. This corresponds with the general pattern of diversity in Central European vegetation, where areas with basic substrates host higher species numbers than acidic substrates. This is related to the vegetation development in the Pleistocene and early Holocene, selecting larger pools of calcicolous than calcifugous species because for most of the history basic substrates (loess) prevailed (Chytrý et al., 2003). The total number of species was also slightly positively correlated with temperature, which is the generally accepted relationship (Körner, 2003). However, it was not evident for the number and partly for the proportion of target species which occurred more in seral stages located in colder and moister areas. This is probably related to the degree of urbanisation: warmer areas are more urbanised and industrialised. Hence fewer target species typical of natural and semi-natural vegetation occur there (Lososová et al., 2012) and have a smaller chance to colonise disturbed sites. Moreover, large urbanised areas can serve as barriers to target species migration through the landscape. On the other hand, they can serve as source sites for expansive and competitive synanthropic species which may arrest succession for a longer time (Štajerová et al., 2017). This is in agreement with the fact that woodlands in the surroundings were responsible for a higher species richness of target species and especially for their proportion. This corresponds with the lower degree of human transformation of colder and wetter, i.e. more forested landscapes (Chytrý et al., 2017). The proportion of target species exhibited some different trends regarding the factors compared to their number. The proportion was negatively influenced by basic substrates in the GLM analysis or seemed to be neutral in CCA. Based on the latter method, there was no evident relationship between the number and proportion of target species. Obviously, despite their lower number, they were able to attain dominance in seral stages occurring in wetter areas covered more by woodlands and wetlands.

5 | CONCLUSIONS

Our results are generally in accordance with succession theory, but the conclusions are stronger and quantitatively exact because we included a large number of seres and stages, occurring in a large variety of environmental conditions over a broad spatial scale. Therefore, we conclude that (a) the considered abiotic factors, i.e. climate and substratum pH, substantially influence the course of succession, the latter influencing especially primary seres; (b) the abiotic factors as a whole seem to be more important in large-scale studies than the surrounding landscape structure; they start to dominate at least on a national scale; (c) the primary or secondary status of succession is less relevant than has usually been expected; and (d) the total number of species, the number of target species, and especially the proportion of target species are differently influenced by environmental factors.

Considering the main abiotic factors and the surrounding landscape structure helps to determine under which circumstances we can rely on spontaneous succession, i.e. establishment of target species, in restoration projects (Prach et al., 2001) or whether specific technical methods, i.e. sowing or planting of target species, are needed (Allison & Murphy, 2017). Our results indicated that advantage can be taken of spontaneous succession in colder and wetter areas little exploited by humans.

ACKNOWLEDGEMENTS

We thank all our colleagues and students who agreed to include their data into our database, namely Martin Adámek, Alena Bartošová, Marek Bastl, Tereza Dudíková, Helena Dvořáková, Darina Hodačová, Alena Jírová, Alexandra Klaudisová, Petra Konvalinková, Petr Koštel, Tomáš Koutecký, Radek Litvín, Ondřej

Mudrák, Jan Novák, Petr Petřík, Petr Pyšek, Jiří Sádlo, Petr Šmilauer, Zdeněk Špringar, Vojtěch Študent, Romana Trnková and Zdeněk Vaněček. We also thank Jan W. Jongepier for language revision.

AUTHOR CONTRIBUTIONS

KP conceived of the research idea. KV performed statistical analyses and wrote the first version of the manuscript. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The DaSS database is available for re-analyses upon request on the official website: http://www.restoration-ecology.eu/edass/.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1 List of successional seres, location in the Czech Republic, number of samples and sampled sites, age of stages, source and references of the dataset

Appendix S2 Map of the distribution of seral stages in the Czech Republic

Appendix S3 Main grouped CORINE categories and involved subcategories (www.copernicus.eu)

How to cite this article: Vítovcová K, Tichý L, Řehounková K, Prach K. Which landscape and abiotic site factors influence vegetation succession across seres at a country scale?. *J. Veg. Sci.* 2020;00:1–10. https://doi.org/10.1111/jvs.12950

7 CHAPTER IV

RESTORATION
ECOLOGY
GROUP

Biodiversity restoration of formerly extracted raised bogs: vegetation succession and recovery of other trophic groups

Vítovcová et al. 2022. Wetlands Ecol Manage: 30, 207–237. doi:10.1007/s11273-021-09847-z

Wetlands Ecol Manage
https://doi.org/10.1007/s11273-021-09847-z

ORIGINAL PAPER

Biodiversity restoration of formerly extracted raised bogs: vegetation succession and recovery of other trophic groups

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Received: 10 June 2021 / Accepted: 26 October 2021

Abstract Central European raised bogs are unique and fragile ecosystems inhabited by specialists of higher plants, fungi, and insects. Many of these ecosystems have suffered and are still suffering due to peat harvesting and drainage. The respective specialists, so-called tyrphobionts, and their abundance can serve as good indicators of restoration processes after the disturbance. Various taxonomic groups may differ in the response to the processes. This study shows successional trends in two disturbed raised bogs compared to adjoining undisturbed reference raised bogs. During the growing season of 2019 we compared species richness of successional stages with reference sites for the following five groups of organisms: vascular plants, mosses, fungi, butterflies, and moths. After three decades of spontaneous succession, the species composition did not reach the reference site for any taxonomic group. Instead an alternative, near-natural woodland developed. The different groups of organisms exhibited very similar trends in species richness and participation of tyrphobionts. About half of these specialists occurring at the reference sites were able to colonise the disturbed sites, but mostly in low quantity. Water table and pH appeared significant environmental variables. It seems that habitat limitations play a more important role than dispersal limitations in this restoration process. More successful restoration might be possible by substantially increasing the water table in the disturbed raised bogs.

Keywords Raised bogs · Succession · Vascular plants · Bryophytes · Fungi · *Lepidoptera*

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Introduction

The biodiversity of undisturbed raised bogs is especially determined by the long-term persistence and, in Central Europe, by the isolated character of the habitat with relict populations of different biota (Joosten et al. 2017). The microclimate and unique system of microhabitats seem to be essential for survival of some cold-adapted species (Zarzycki et al. 2020). Many of them have persisted at the localities since the last glaciation, having only limited opportunities to shift their regional range of occurrence due to isolation

(Mikkola and Spitzer 1983; Spitzer 1994) and microclimatic specificity of the habitat (Turlure et al. 2010; Weking et al. 2013; Zarzycki et al. 2020). The specialists, so called tyrphobionts (Peus 1928), are the main target species for ecological restoration of disturbed peatlands.

Recent anthropogenic disturbances have had and have prevailingly detrimental effects on these fragile ecosystems. The most destructive is large-scale industrial peat harvesting, accompanied by profound changes in water regime. Possibilities to restore such deeply disturbed bogs are limited (Grootjans et al. 2006). The main obstacles to successful restoration are: (a) altered water regime and unfavourable soil moisture, (b) thin or no layer of remaining peat, (c) lack of source populations of target species, or barriers restricting their spreading to a disturbed site, and (d) inconvenient biotic conditions at a disturbed site, such as a lack of host plants, or species hindering establishment of other ones by competition. An inappropriate water regime and insufficient soil moisture can be improved by an artificial rise of the water table by blocking drainage ditches (Pfadenhauer and Grootjans 1999; Haapalehto et al. 2011). Some of the biotic obstacles can be overcome by artificial sowing or planting of target plant species or introducing some individuals in the case of insects (Neve et al. 1996; Perrow and Davy 2002; etc.). However, this is not realistic in the case of many biota. The other option is to rely on spontaneous colonisation, especially if source populations occur in the close surroundings (Poulin et al. 2005; Konvalinková and Prach 2014; Johansen et al. 2017) but not always and not for every species. Moreover, disturbed peatlands are generally very slowly recovering, complex systems often susceptible to shifting to an alternative state (Dise 2009; Matthews and Spyreas 2010).

Particular groups of organisms in disturbed or undisturbed raised bogs have usually been studied separately for plants (e.g. Konvalinková and Prach 2014); fungi (Zíbarová 2014; Laber 2009) and insects (Spitzer and Danks 2006; Buchholz et al. 2009). Multi-taxa studies are rare and we are not aware of any study dealing with these three trophic groups in the process of raised bog restoration (but see Strobl et al. 2020). In this study, we focus on vascular plants, mosses, fungi, butterflies and moths and the processes of their colonisation of disturbed raised bogs during approx. three decades of succession reconstructed by means of the chronosequence approach (Walker et al. 2010). Vascular plants are the easiest to study and reflect the successional changes and restoration progress well, thus vegetation can be used as the best indicator of restoration processes (Prach et al. 2019). Bryophytes represent the essential component of raised bogs (Clymo and Hayward 1982). Fungi as decomposers, plant symbionts or parasites play a key role in nutrient cycling (Juan-Overejero et al. 2019). Moreover, we studied both diurnal and nocturnal Lepidoptera, hereafter referred to as butterflies and moths, because they appear to be important components of raised bog diversity (Spitzer and Danks 2006) and can serve as an umbrella group of other relict bog insects (New 1997).

To understand the processes of peatland restoration, we need to know how these crucial groups of organisms colonise, co-exist and persist in formerly disturbed raised bogs. As a reference, we considered all these groups of biota in nearby undisturbed raised bogs which are expected to serve as sources for spontaneous colonisation of the disturbed sites. Population densities of specialists, e.g. tyrphobionts, and possibly tyrphotolerants, may reflect the quality of habitats and indicate if the restoration process is going in the desired direction, i.e. towards the reference sites.

We asked the following questions: (1) Does spontaneous succession direct towards the undisturbed reference raised bogs? (2) Are the directions of recovery of formerly extracted raised bogs comparable for several different groups of organisms? and (3) What proportions of tyrphobionts and tyrphotolerant species among the studied groups of organisms, occurring in undisturbed raised bogs, are able to establish spontaneously in the disturbed raised bogs?

Methods

Study sites

The study sites included two disturbed (Soumarský Most and Vlčí Jámy, hereafter SM and VJ) and two undisturbed raised bogs (Malá Niva, Velká Niva, hereafter MN and VN) in the Šumava Mts. in the south-western part of the Czech Republic (48°53′54″–48°55′21″N; 13°46′45″–13°50′27″E; average altitude 750 a.s.l.). This region, with a relatively cold and wet climate, is characterised by a mean annual temperature of about 5.3 °C and a mean annual precipitation of about 900 mm (Tolasz 2007). The formerly extracted and the undisturbed reference raised bogs are located close to each other (see Appendix 1), thus forming a complex where metapopulation dynamics (Hanski 1999) is expected to operate. They clearly represent the same vegetation type belonging to the *Sphagnion medii* alliance of the *Oxycocco-Sphagnetea* class of the continental classification system (Chytrý 2011). The disturbed bogs used to be heavily drained and industrially extracted. Peat extraction activities were gradually terminated in the period from the 1980s to 2004. The remaining peat depth was about 0.5 m or less. The average water table in extracted bogs was located at − 22.9 cm (± 15.3), in natural bogs at -16.1 cm (± 4.1). The average pH in extracted bogs was 3.68 (± 0.24), in natural bogs 3.54 (± 0.07). Detailed values of water table and pH are showed in Appendix 2. All these raised bogs are protected as parts of the Šumava National Park, thus the disturbed raised bogs were not artificially afforested by mining companies, which is a common practice after peat extraction elsewhere in the country.

Data collection

The field survey was conducted during the 2019 vegetation season. The following successional stages were distinguished in each studied disturbed bog (see also Appendix 3): (1) young stage, 10–15 years old, open vegetation with a cover of 10–25%; (2) middle stage, 16–25 years old, vegetation cover about 50%, including young woody species; (3) old stage, 26–35 years old, closed vegetation with no bare peat and woody species cover of > 50%. In the undisturbed reference bogs only one stage was considered. The dating was based on official records of the Šumava National Park Administration and on tree ring analyses. In the undisturbed bogs, the oldest trees were more than 200 years old, and this age was arbitrarily used for the undisturbed bogs.

The various taxonomic groups required different sampling sizes and methods. For *Lepidoptera* sampling, three 1-ha plots corresponding to the successional stages were delimited in both disturbed bogs and one 1-ha plot in both undisturbed bogs. For fungi, vascular plants and bryophytes, four smaller plots (9 × 9 m) were monitored, randomly located inside each 1-ha plot, two in wetter and two in drier places to include variability in site moisture. Vegetation of the raised bogs was sampled using phytosociological relevés with visual estimates of percentage cover of all present vascular plant species and mosses (Kent and Coker 1992). Furthermore, in the smaller plots the total cover of different vegetation layers and cover of bare substrate, litter and deadwood were estimated, and average water table and pH were determined. The water table was measured each month during the vegetation season and pH was measured once per year. Vascular plant nomenclature follows Danihelka et al. (2012), that of mosses Kučera et al. (2012).

Fungal fruit bodies were recorded 6 times per vegetation season (May–November). Basidiomycota were sampled in the 9 × 9 plots, Ascomycota—due to their mostly tiny fruit bodies (ca 1 mm)—in inner plots (3 × 3 m) only. Fruit bodies were identified in the field, or later using the microscope. Nomenclature of fungi follows Mycobank (www.mycobank.org).

Diurnal *Lepidoptera* (super-families *Papilionoidea*, *Hesperioidea* and *Zygaenoidea* plus day-active species from other groups) were sampled under suitable weather conditions (low wind speed, low cloudiness and air temperature > 15 °C) using time-constrained searches between 9:00–16:00, zigzagging the site for 45-person-minutes (Kadlec et al. 2012), netting each observed butterfly or identifying them on the wing if possible, and locating as many species as possible. Each site was sampled five times throughout the season (May–September) to well cover all phenological aspects of species diversity.

Moths were sampled with portable light traps (8 W UV light powered by a 7.2 Ah/12 V lead battery, with a cotton pad soaked with chloroform), 4 traps per each 1-ha plot, i.e. 32 light traps in total. Traps from each 1-ha plot were pooled into one sample. The traps were placed ± 30 m apart from each other and, concurrently, from the edge of the plot. The survey was conducted five times throughout the season (in dry weather, morning air-temperature above 7 °C, wind speed at Beaufort scale ≤ 4). Traps had been activated before dusk and were collected after sunrise, only in the period between the last and first quarter moon when the influence of moonlight was almost negligible. The collected moths were afterwards wrapped in tissue paper and transferred for identification. If the identification required examining genitalia, individuals were dissected. Lepidoptera nomenclature follows Fauna Europaea (Van Swaay et al. 2008).

Species classification

We classified all recorded species into three categories: (a) tyrphobionts—occurring exclusively in bogs, (b) tyrphotolerants—often occurring in bogs, but not strictly confined to them, (c) others—species distributed across different types of habitats (Peus 1928). Affinity of biota to peatland habitats was assessed according to Chytrý (2011) for vascular plants, based on Kučera et al. (2004) and expert assessment for bryophytes, according to Hofmeister and Hošek (2016), Thorman and Rice (2007) as well as expert assessment for fungi, and according to Macek et al. (2015), Mikkola and Spitzer (1983), and Jaroš et al. (2014) in the case of butterflies and moths.

Data analyses

All vegetation samples (9 × 9 m in size) from undisturbed and disturbed peat bogs were analysed with multivariate methods using CANOCO 5 (Microcomputer Power, Ithaca, NY, US). To summarise the similarity (in species composition) between plots we performed principal coordinate analysis (PCoA). We used Bray–Curtis distances and axes with positive eigenvalues. We used canonical correspondence analysis (CCA) to test the influence of measured environmental factors, which was justified by the length of gradient being 5, 8 SD units (Šmilauer and Lepš 2014). We calculated the numbers of tyrphobionts and tyrphotolerants and other species separately for each taxonomic group (vascular plants, bryophytes, fungi, butterflies, moths) and used these metrics as passive variables in the ordination diagram. Environmental factors (average water table, pH) and site characteristics, such as percentage cover of bare substrate, cover of dead wood, litter cover, and cover of particular vegetation layers were also projected passively (Šmilauer and Lepš 2014).

Differences in the numbers of tyrphobionts, tyrphotolerants, and other species within each group of organisms between the three successional stages and reference sites were tested with one-way ANOVA followed by *post-hoc* comparisons using Tukey's HSD method in the R software (R Development Core Team 2020).

Results

During the one-year field survey we recorded in the studied bogs in total 74 species of vascular plants (5 tyrphobionts, 23 tyrphotolerants, 46 other ones), 70 species of bryophytes (9, 19 and 42, respectively), 241 species of fungi (21, 25 and 195), 27 species of butterflies (2, 3 and 22) and 332 species of moths (5, 22 and 305). The following numbers of species had not been able to reach the disturbed sites yet and were recorded in undisturbed peat bogs only: 3 tyrphobionts, 1 tyrphotolerants and no other vascular plants; 2, 3 and 3 bryophytes; 9, 6 and 35 fungi; 1, 0 and 8 butterflies; and 2, 4 and 79 moths, respectively. For complete lists of species, see Appendix 4. In all groups of organisms, 50% of tyrphobionts present in the undisturbed raised bogs were found to be able to establish in disturbed peat bogs. Moreover, 67% of tyrphotolerant species recorded in the undisturbed bogs established in the disturbed raised bogs as well.

Summarised information on vegetation structure and species numbers per succession stage are shown in Table 1. Among the disturbed bogs, the herb layer had the highest cover in the young stages and then significantly decreased. It was much lower in old disturbed stages as compared with the reference bogs. The shrub and tree layer cover continuously increased with time. The tree layer in the old successional stages had a higher cover in comparison to the reference bogs. The cover of mosses varied with successional stage. It increased during the first years, however the highest cover was recorded in the middle successional stages. Nevertheless, the cover of mosses was lower at the disturbed than at the reference sites. The total numbers of tyrphobiont, tyrphotolerant, and other species of the particular groups of biota mostly changed significantly over the successional stages and differed from the undisturbed reference sites. Only tyrphotolerant fungi and tyrphobiont butterflies remained consistent during the succession and at the reference sites.

The most dominant plant species were *Eriophorum vaginatum*, *Juncus effusus*, *Carex rostrata* and *C. canescens* in young successional stages. In the middle stages, the most dominant species were *Betula pendula*, *Carex rostrata*, *Eriophorum vaginatum*, *Juncus effusus*, and *Pinus sylvestris*. The most dominant species in the oldest stages were *Betula pendula*, *B. pubescens*, *Juncus effusus*, *Picea abies*, *Pinus*

Table 1 Vegetation structure (average cover of particular layers) and total numbers of tyrphobiont, tyrphotolerant and other species for particular groups of biota recorded in both disturbed bogs (totals per all plots for each successional stage) and both reference bogs (totals for all plots)

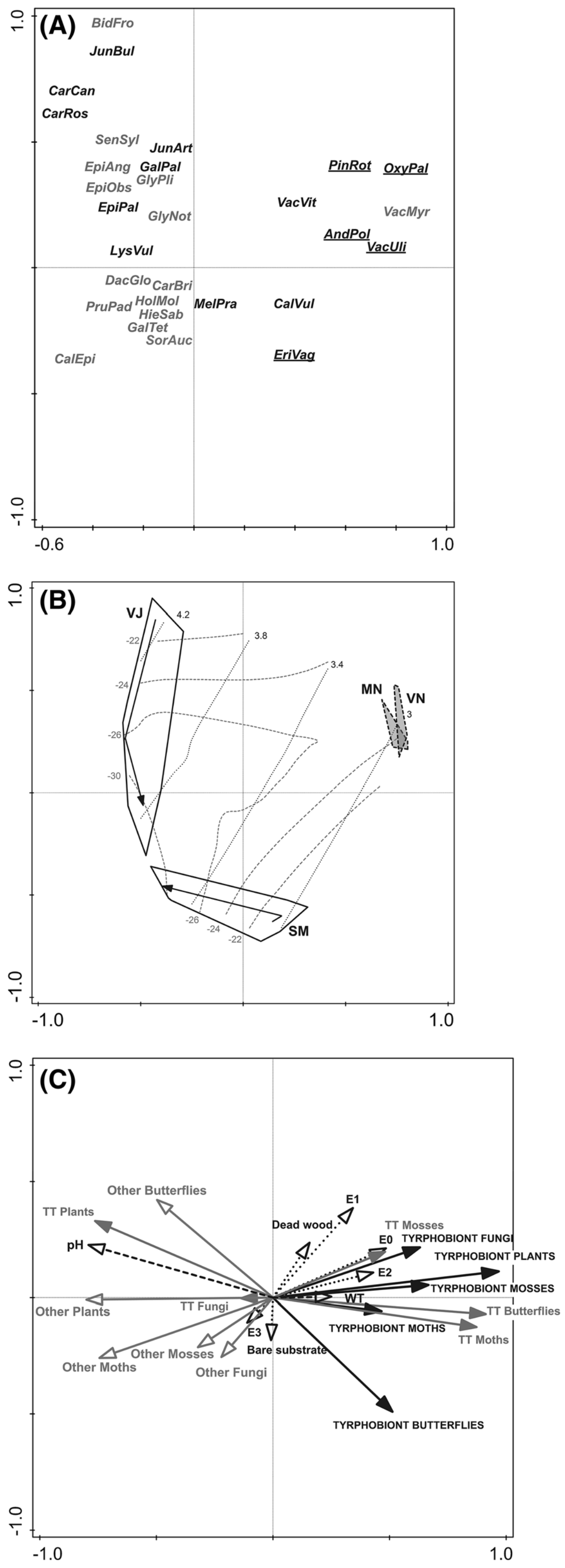
		Disturbed bogs			Undisturbed bogs	F (Df = 3, 28)	p
		Young	Middle	Old			
Vegetation structure (%)	Moss layer	4	32	25	74	11.0	***
	Herb layer	32	41	18	47	4.3	*
	Shrub layer	4	13	14	26	11.7	***
	Tree layer	0	18	33	21	6.0	**
Number of vascular plant species	Tyrphobionts	2	2	0	5	56.4	***
	Tyrphotolerant	13	16	14	3	4.2	*
	Other species	21	22	30	3	10.4	***
Number of moss species	Tyrphobionts	2	4	3	5	8.4	***
	Tyrphotolerant	5	10	9	12	5.7	**
	Other species	11	25	29	12	19.2	***
Number of fungal species	Tyrphobionts	7	7	4	15	10.7	***
	Tyrphotolerant	10	13	13	10	1.1	n.s
	Other species	35	71	102	57	8.7	***
Number of butterfly species	Tyrphobionts	1	1	0	2	2.3	n.s
	Tyrphotolerant	3	2	1	2	14.8	***
	Other species	14	13	9	8	8.0	***
Number of moth species	Tyrphobionts	4	3	4	7	80.0	***
	Tyrphotolerant	9	10	14	15	14.4	***
	Other species	122	130	225	79	196.3	***
Total number of species	Tyrphobionts	17	17	11	34	43.4	***
	Tyrphotolerant	40	51	51	42	4.8	**
	Other species	203	261	395	159	116.8	***

The results of one-way ANOVA (h_0: species numbers change with successional stage) are indicated by F tests and significance levels: *** 0.001; ** 0.01; * 0.05; n.s. > 0.05

sylvestris and *Populus tremula*. In the undisturbed peat bogs, the dominants were *Eriophorum vaginatum*, *Oxycoccus palustris*, *Pinus rotundata*, *Vaccinium myrtillus* and *Vaccinium uliginosum*. Both species composition and structure of vegetation exhibited only low similarity when comparing the disturbed and undisturbed peat bogs (Fig. 1A, Table 1).

Similar trends in species groups changing during succession were revealed by the multivariate method (Fig. 1A). The first two PCoA axes explained 67.9% of variability in the data (eigenvalues for first two axes: 0.431 and 0.248). The PCoA diagrams showed marked differences in plant species composition between disturbed and reference raised bogs. The envelopes (Fig. 1B) connecting the marginal samples of disturbed and undisturbed bogs do not overlap. Moreover, both disturbed bogs exhibited mutually convergent successional trajectories, their oldest stages being closest to each other. Obviously, the spontaneous succession did not direct towards the reference peat bogs at all.

The summarising PCoA diagram (Fig. 1C) revealed that tyrphobiont species of all groups, i.e. vascular plants, bryophytes, fungi, butterflies, and moths, were strongly related to each other and to a higher water table and a lower pH. Tyrphobiont mosses and tyrphobiont fungi are strongly related to the presence of bare substrate and negatively related to tyrphotolerant and other plants. In contrast, the tyrphotolerant and other fungi and tyrphotolerant and other mosses were positively correlated to higher tree and shrub covers and to the presence of dead wood.



◀**Fig. 1** Principal coordinate analysis (PCoA)—ordination of plant species recorded at disturbed and reference sites (**A**); ordination of samples from disturbed and reference sites (**B**); passively projected groups of organisms together with selected habitat characteristics and environmental factors (**C**). The 30 plant species with the highest weight are shown (the abbreviations of species names are composed from the first letters of generic and specific names—see Appendix 4). Tyrphobiont species are underlined, tyrphotolerant species are in bold and other species are grey. Envelopes for disturbed sites (SM, VJ) are indicated by full lines, reference sites (MV, VN) by dashed lines. The arrows connect centroids of successional stages from the young to middle and old stages and show trends of succession. In (C), tyrphobionts are indicated by thick black arrows and capital letters, tyrphotolerant species (TT) by dark-grey arrows and other species (Other) by light grey arrows. Black dotted arrows show some habitat characteristics, such as structure of vegetation (cover of layers E_0–E_3) and proportion of dead litter, bare substrate and dead wood. Black dashed arrows show environmental factors average water table (WT) and pH

Both tyrphobiont and tyrphotolerant butterflies and moths are closely related to tyrphobiont plants. Moreover, tyrphobiont moths had a positive relationship to higher tree and shrub covers, and are thus related to more overgrown, successionally advanced habitats. Both environmental factors, average water table (WT) and pH, appeared to be significant in the separate CCA analysis (explaining 20.1%, p = 0.03, and 5%, p = 0.001, respectively).

There was significant evidence of a decrease in tyrphobionts in the total group of organisms during the succession in the disturbed bogs (SM: F = 4.76, p = 0.015; VJ: F = 6.164, p = 0.006) (Fig. 2). The significantly lowest numbers of tyrphobiont species in the oldest successional stages compared to the reference raised bogs were found in the case of vascular plants, mosses and fungi. In the case of butterflies and moths the differences could not be tested due to the different sampling design. Tyrphotolerant species in each group of organisms or totalled showed more or less the same patterns, with non-significant differences during the succession, and their numbers were similar to the undisturbed peat bogs. The numbers of other species usually increased during succession and were higher at the disturbed than at the reference sites.

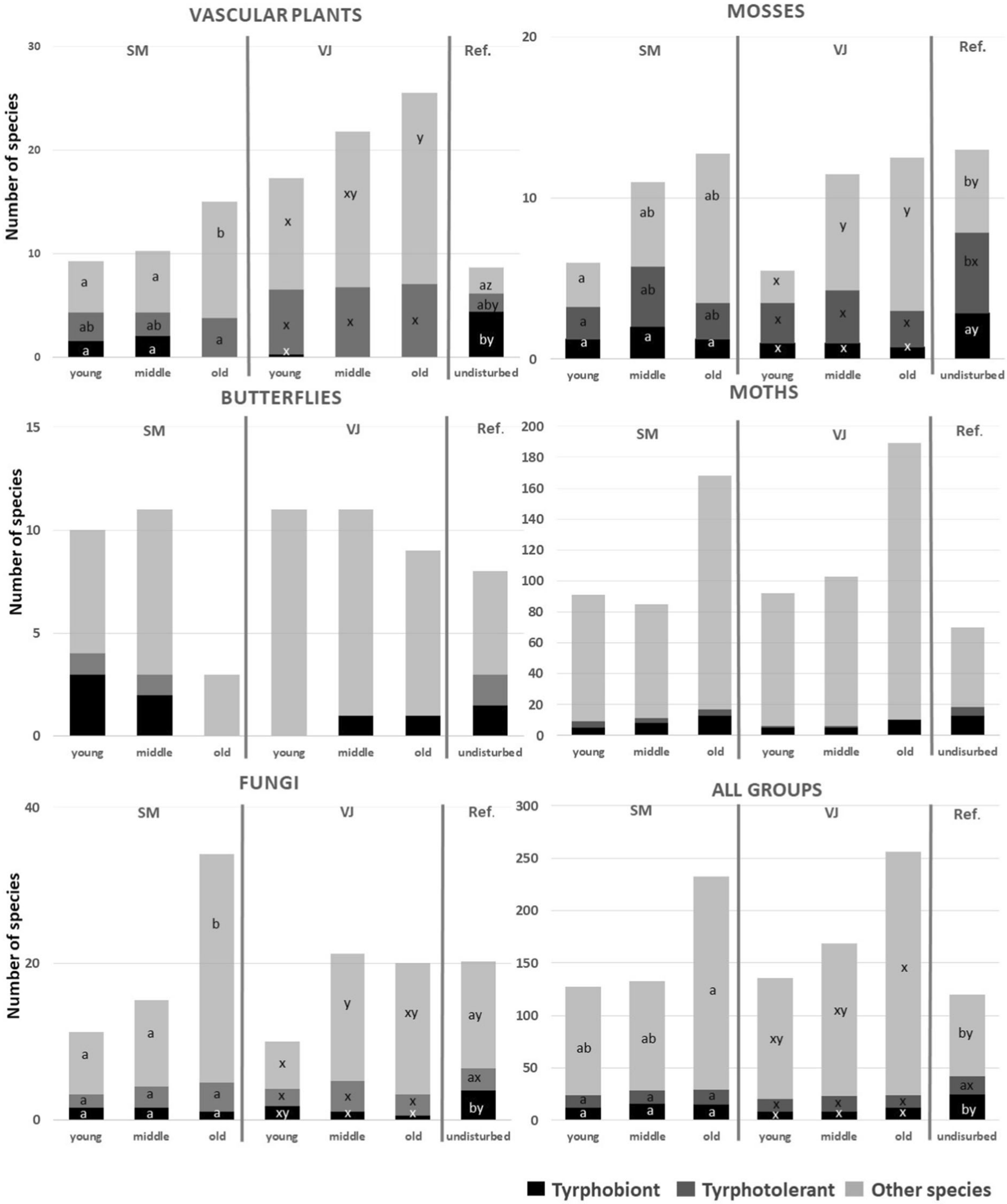


Fig. 2 Numbers of tyrphobiont, tyrphotolerant and other species in particular groups of organisms, and all groups of taxa together (average numbers per 9 × 9 m plot in case of vascular plants, mosses, and fungi; total numbers per 1-ha plot in case of butterflies and moths), related to successional age (young, middle, and old) and compared to undisturbed reference sites. The results of one-way ANOVA followed by *post-hoc* comparisons using Tukey's HSD method are indicated by letters (abc; xyz) in the columns (except butterflies and moths due to the different sampling design)

Discussion

Restoration progress towards a reference species composition can be detected as the increase in species similarity between disturbed and undisturbed reference sites (Matthews and Spyreas 2010). For this, a species inventory is necessary to conduct (Prach et al. 2019). However, other groups of organisms may respond differently to successional changes (van Andel and Aronson 2012), thus a multi-taxa approach is desirable to evaluate any restoration success. We evaluated five different groups of organisms changing during spontaneous succession and revealed that they responded in a similar way to the successional gradient. However, during three decades of spontaneous succession did not proceed towards the reference undisturbed stage which was indicated by all the studied groups. An alternative stage developed despite being composed of native species and exhibiting a natural character, but with a lower participation of target, i.e. tyrphobiont, species. Both disturbed bogs mutually converged in vascular plant composition and the advanced vegetation corresponded to that known from other industrially disturbed raised bogs in the country (Konvalinková and Prach 2014). This is in contrast to our earlier expectations that close proximity of undisturbed bogs and presence of wetter patches supports the colonisation by target species (Prach et al. 2015). The possible constraints causing a deviation of the disturbed bogs from the ideal trajectory can be generally explained by inconvenient abiotic site conditions for peatland species, mostly by a non-functional water regime (Haapalehto et al. 2011; Triisberg et al. 2013; Johansen et al. 2017) and/or a thin remaining peat layer (Salonen 1994). Although the wettest sites were also considered in each investigated stage, they were probably not sufficient to support the respective target species. The absence or low occurrence of tyrphobiont host plants for butterflies, and *Sphagnum* spp. important for some tyrphobiont fungi, besides some mobility constraints, might be the main limiting factor in the colonisation of disturbed bogs by the respective biota (Dennis and Eales 1997; Baguette 2003).

At the disturbed sites, only one tyrphobiont plant species, namely *Eriophorum vaginatum*, was frequent in young and middle stages of succession. Several other studies demonstrate the role of this species as an early coloniser in restored peatlands, being opportunistic and growing well even in newly created peat environments (Tuittila et al. 2007; Johansen et al. 2017). It serves as a host plant for several tyrphobiont moths (Jaroš et al. 2016) as well as for the tyrphotolerant butterfly *Coenonympha tullia*, strongly declining in central Europe (Macek et al. 2015), which we recorded in the successional stages and open parts of both reference sites. Litter of *E. vaginatum* is an important substrate for some fungal species (for example *Lachnum clavisporum*, *L. imbecile*). Both *E. vaginatum* and another typical species of early and middle successional stages, tyrphotolerant *Carex rostrata*, have deep rooting systems and can tolerate a wider range of moisture conditions (Visser et al. 2000). Nevertheless, *E. vaginatum* gradually disappears under the closing canopy of ubiquitous Scots Pine and birches. We can expect that the closing canopy decreases light at the bottom and increases transpiration and thus a moisture deficit (Larcher 2003). These are probably the main reasons, besides the somewhat lower water table at the disturbed sites compared to the reference sites, that not more tyrphobiont plant species established, and consequently, also lower numbers of fungi, butterflies and moths were recorded.

The typical components of raised bog diversity are various *Sphagnum* species (Grootjans et al. 2012), which are also responsible for a restart of peat formation (Breeuwer et al. 2009). We found only rare occurrences of *Sphagnum* species in the youngest plots, mainly *S. cuspidatum* growing in wet depressions, which is its typical habitat (Laine et al. 2018). The middle and the oldest succession stages were colonised by *S. flexuosum* and *S. fallax*, which are capable of fast colonisation of wet depressions (Kučerová et al. 2008). However, they reached a higher coverage only rarely. These species also dominated reference sites, where they occurred with *S. magellanicum.* This species, growing usually in low hummocks of undisturbed bogs, is dependent on an undisturbed water regime (Karofeld et al. 2015), which is probably the reason why it is absent from the disturbed sites.

Polytrichum mosses are capable of fast colonisation of disturbed peat substrate (Bastl et al. 2009). Tyrphobiontic *P. commune* appeared to be abundant in the studied disturbed bogs, especially in the old stages of succession (> 26 years). Moss cover and thickness may facilitate (Groeneveld et al. 2007;

Rocheford et al. 2013) or limit (Gonzáles et al. 2013) establishment of other species. Johansen et al. (2017) described the negative relationship between *Polytrichum* species and the abundance of target species, both mosses and vascular plants, in restored peat bogs, which we expected also in our case. The extensive cover of *Polytrichum* observed in the late successional stages of disturbed bogs may reflect a failure in the full recovery of the hydrological regime and thus contribute to divergence from the successional trend to the target reference sites. *Polytrichum* species can withstand relatively dry or unbalanced moisture conditions better than many other tyrphobiont and tyrphotolerant bryophytes, especially typical *Sphagnum* species (Bayfield 1973).

The occurrence of tyrphobiont and tyrphotolerant fungi differ from each other. Within both groups, there are species with various ecological requirements, therefore the interpretation is not straightforward. Most tyrphobiont fungi are associated with *Sphagnum* (for example *Arrhenia gerardiana*, *Galerina* spp., *Hypholoma* spp., *Tephrocybe palustris*) and are the most abundant in undisturbed reference bogs with a high *Sphagnum* cover. However, some tyrphobionts (*Psilocybe turficola*, *Hypholoma udum, Lachnum* spp.) are able to grow on bare peat or on dense *Eriophorum* tussocks and are therefore abundant in young stages with bare substrate. Tyrphotolerant fungi have broader niches, so they can grow outside bogs and bog forests related to other, non-specialised plants. Their occurrence is more random, most of them growing in plots with various peat bog vegetation (*Juncus* spp., *Carex* spp.) and ectomycorrhizal trees (*Betula, Pinus*).

Caterpillars of both tyrphobiont butterflies recorded at our study sites*,* *Colias palaeno* and *Vaccinia optilete*, strictly feed on the tyrphobiont plant species *Vaccinium uliginosum*. The host plant presence was reflected not only by the occurrence, but also by the abundance of both butterfly species. The two species prefer open patches and are able to only tolerate a low tree canopy cover (Beneš et al. 2002; Macek et al. 2015), and both also decrease with drainage (Noreika et al. 2016). This was confirmed by our records either from young and middle successional stages or from the most open parts of undisturbed sites. The last fact might point out that current populations are only surviving there and use the last suitable parts of that habitat. The same is also count for some tyrphotolerant species, e.g. *Coenonympha tullia*. This strongly declining butterfly (inhabiting also wet meadows and fens) survives only in open, sunny stands of *Eriophorum* spp. with a stable, humid microclimate (Weking et al. 2013; Čelik and Vreš 2018). Its occurrence pattern at our study sites was similar to that of tyrphobiont butterflies. In contrast to butterflies, moth communities are generally richer in species and contain also more raised bog specialists (Jaroš et al. 2014). Generally, moth assemblages contain more species developing on woody plants (Macek et al. 2015), therefore they reached a higher diversity in middle and older successional stages of our study sites. The specialised tyrphobiont and tyrphololerant species *Celaena haworthii*, *Amphipoea lucens* and *Glyphipterix haworthana* are only partly dependent on tyrphobiont plants, such as *Eriophorum* spp. Other specialised species might be rather dependent on a specific microclimate. The strongly tyrphobiont species *Coenophila subrosea*, inhabiting exclusively raised bogs throughout its range, successfully colonised younger successional stages of one disturbed bog (SM). This species uses various host plants, but always depends on a stable hydrological regime of the localities (Fowles et al. 2004). Despite the fact that most species of this group prefer older successional stages, the occurrence of open and humid patches in young successional stages seems to be suitable for the most specialised tyrphobionts, as previously demonstrated by Spitzer et al. (1999).

Conclusions

After three decades of spontaneous succession, the recovery of formerly industrially extracted peatlands does not direct towards the reference, undisturbed sites in contrast to our earlier expectations. Instead, an alternative stage developed, composed of native species. This stage can be accepted as a reasonable alternative which is certainly better than artificial reforestation. The five different species groups exhibited very similar trends in species richness and participation of tyrphobionts, tytphotolerants and other species. Except for diurnal butterflies, the total number of species increased and was higher at the disturbed than at the reference sites. However, other species than tyrphobionts and tyrphotolerants contributed to the increase. Considering all the groups of organisms together, the participation of tyrphobionts and tyrphotolerants during succession remained more or less the same and was much lower than at the reference sites (about half of these species occurring at the reference sites colonised the disturbed sites). We can conclude that more successful restoration of the pre-disturbance stage can probably not be achieved without a substantial rise in the water table across the whole disturbed localities. It seems that habitat limitations play a more important role than dispersal limitations in this type of succession.

Acknowledgements The authors thank the Šumava National Park Administration for permission to access the study sites, Jan Altman for tree ring analysis and for dating our sites, Pavlína Matysková, Sujan Balami and Hedvika Synková for their help in the field, Táňa Štechová for her assistance with moss identification and classification, Markéta Šandová for identifying most Ascomycota fruit bodies, and together with Lucie Zíbarová for comments on the classification of tyrphobiont and tyrphotolerant fungi.

Author contributions All authors contributed to the study conception and design and collected the data. All analyses were performed by KV. The first draft of the manuscript was written by KV, edited by KP and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding The work was funded by the Czech Grant Agency (19-15031S).

Data availability Average water table and pH values are available in Appendix 2. The dataset (P/A data of all species in all successional stages) generated and analysed during the current study is available in Appendix 4 to this manuscript.

Code availability Not applicable.

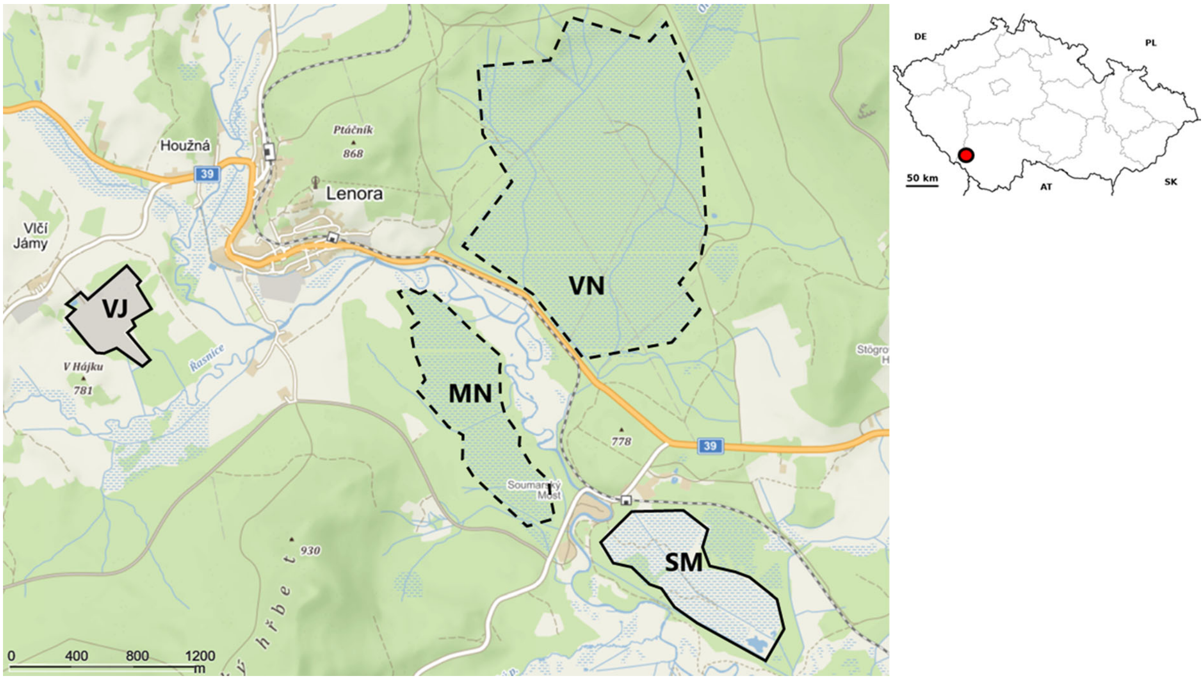
Declarations

Conflict of interest The authors declare that they have no conflict of interest/competing interests.

Ethical approval The matter presented in this manuscript is in compliance with ethical standards. The research work mentioned in this paper does not involve human participants or animals.

Informed consent The consent to participate in this study was obtained by the authors from the authorities concerned.

Appendix 1



Appendix 2

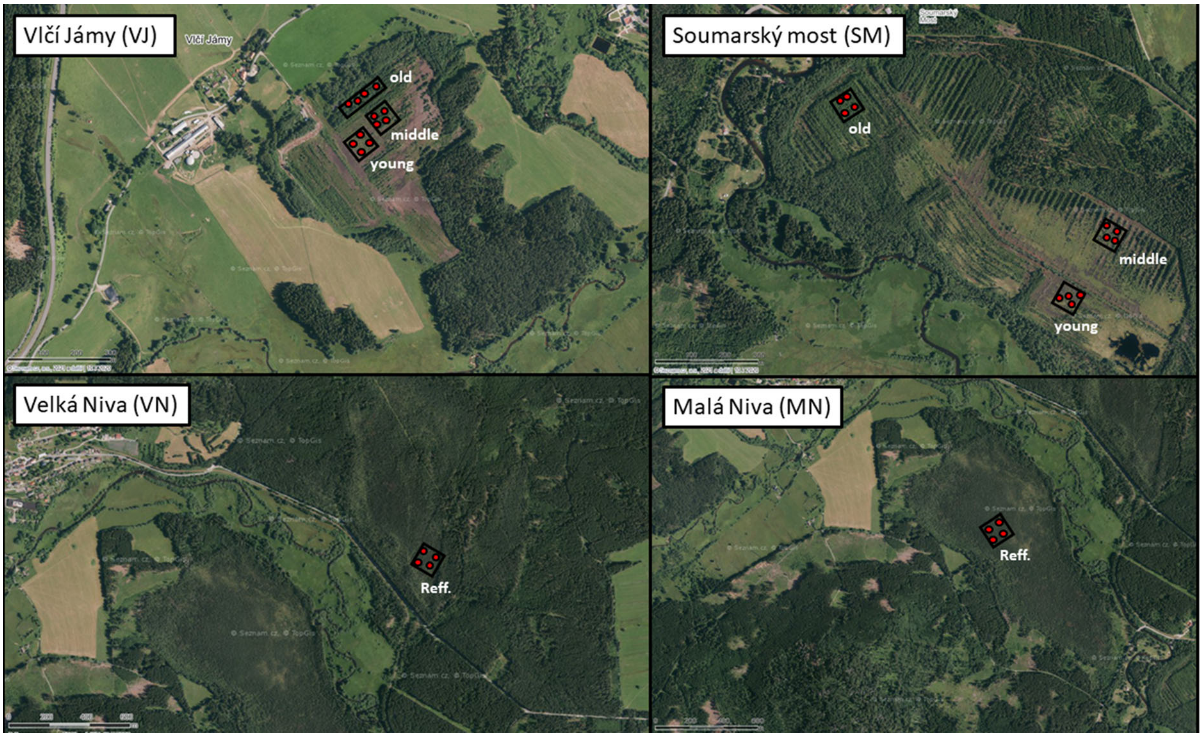
Author: The analytical laboratory in Třeboň, Institute of Botany of the Czech Academy of Sciences.

Date of analysis: January 2020.

Water table—measured each month in 2019 (except January, February and March).

Sample	Disturbed/natural	Locality	pH dest	pH KCl	Average water table cm
S1a	Disturbed	SM	3.41	2.46	− 13.84
S1b	Disturbed	SM	3.38	2.50	− 14.86
S1c	Disturbed	SM	3.52	2.56	− 9.76
S1d	Disturbed	SM	3.39	2.65	− 16.08
S2a	Disturbed	SM	3.59	2.76	− 9.47
S2b	Disturbed	SM	3.47	2.70	− 25.50
S2c	Disturbed	SM	3.41	2.59	− 13.00
S2d	Disturbed	SM	3.50	2.77	− 4.81
S3a	Disturbed	SM	3.62	3.18	− 34.97
S3b	Disturbed	SM	3.68	3.17	− 35.94
S3c	Disturbed	SM	3.58	3.09	− 31.44
S3d	Disturbed	SM	3.61	3.20	− 20.75
J1a	Disturbed	VJ	3.56	3.15	− 21.47
J1b	Disturbed	VJ	4.08	3.33	− 7.19
J1c	Disturbed	VJ	3.88	3.16	− 15.25
J1d	Disturbed	VJ	3.85	3.50	− 10.78
J2a	Disturbed	VJ	4.21	3.53	− 22.00
J2b	Disturbed	VJ	3.66	3.36	− 18.76
J2c	Disturbed	VJ	3.74	3.29	− 25.19
J2d	Disturbed	VJ	3.65	3.31	− 16.38
J3a	Disturbed	VJ	4.21	3.66	− 28.28
J3b	Disturbed	VJ	3.73	3.20	− 50.00
J3c	Disturbed	VJ	3.85	3.29	− 28.56
J3d	Disturbed	VJ	3.85	3.28	− 74.86
Ma	Natural	MN	3.61	2.80	− 21.72
Mb	Natural	MN	3.54	2.84	− 17.53
Mc	Natural	MN	3.54	2.73	− 10.78
Md	Natural	MN	3.53	2.85	− 13.61
Va	Natural	VN	3.59	2.74	− 17.06
Vb	Natural	VN	3.45	2.68	− 21.11
Vc	Natural	VN	3.44	2.67	− 15.86
Vd	Natural	VN	3.63	2.66	− 11.17

Appendix 3



Appendix 4

The presence-absence data of all recorded species. Classification indicates a relationship to raised bogs (*TB* tyrphobiont; *TT* tyrphotolerant; *O* other, no relationships to raised bogs). Young, middle, and old indicate the successional stage of disturbed raised bogs (*SM* Soumarský Most; *VJ* Vlčí Jámy). Undisturbed raised bogs are MN (Malá Niva) a VN (Velká Niva).

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Vascular plants	*Agrostis canina*	TT					*	*		
	Agrostis capillaris	O				*	*	*		
	Agrostis stolonifera	O				*	*	*		
	Andromeda polifolia	TB							*	*
	Anthoxanthum odoratum	O						*		
	Avenella flexuosa	O			*		*	*		
	Betula pendula	O	*	*	*	*	*	*		
	Betula pubescens	TT	*	*	*	*	*	*		
	Bidens frondosa	O				*				
	Calamagrostis epigejos	O				*		*		
	Calamagrostis villosa	O			*			*		
	Calluna vulgaris	TT	*	*	*			*	*	*
	Carex brizoides	O						*		
	Carex canescens	TT				*	*	*		
	Carex echinata	TT						*		
	Carex leporina	O			*		*			
	Carex muricata	O						*		
	Carex rostrata	TT			*	*	*	*		
	Cerastium holosteoides	O				*				
	Cirsium palustre	TT				*	*	*		
	Dactylis glomerata	O						*		
	Deschampsia cespitosa	O					*			
	Dryopteris carthusiana	TT	*	*		*	*	*		
	Dryopteris dilatata	O					*	*		
	Epilobium angustifolium	O				*	*			
	Epilobium obscurum	O				*	*			
	Epilobium palustre	TT				*	*			
	Eriophorum angustifolium	TT		*						
	Eriophorum vaginatum	TB	*	*					*	*
	Frangula alnus	O						*		
	Galeopsis tetrahit/bifida	O						*		
	Galium aparine	O					*			
	Galium palustre	TT				*				
	Galium uliginosum	TT					*			
	Glyceria notata	O				*				
	Hieracium lachenalii	O						*		
	Hieracium sabaudum	O						*		
	Holcus mollis	O						*		
	Hypochaeris radicata	O				*				
	Juncus articulatus	TT				*				
	Juncus bulbosus	TT				*				
	Juncus effusus	O			*	*	*	*		
	Juncus filiformis	TT			*	*	*			
	Larix decidua	O						*		
	Lychnis flos-cuculi	TT					*			

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Lysimachia vulgaris	TT				*	*	*		
	Melampyrum pratense	TT			*				*	
	Molinia caerulea	TT			*		*	*		
	Oxycoccus palustris	TB							*	*
	Peucedanum palustre	TT	*			*	*	*		
	Phalaris arundinacea	O						*		
	Picea abies	O	*	*	*		*	*		*
	Pinus rotundata	TB							*	*
	Pinus sylvestris	O	*	*	*	*	*	*		
	Plantago major	O						*		
	Populus tremula	O			*	*	*	*		
	Potentilla erecta	TT						*		
	Prunus padus	O						*		
	Quercus robur	O					*	*		
	Ranunculus repens	O					*			
	Rubus fruticosus	O				*				
	Rumex acetosella	O				*				
	Salix aurita	O	*		*	*	*	*		
	Salix cinerea	O				*	*	*		
	Senecio sylvaticus	O				*				
	Solidago virgaurea	O					*			
	Sorbus aucuparia	O			*			*		
	Stellaria graminea	O					*			
	Taraxacum species	O				*				
	Urtica dioica	O					*			
	Vaccinium myrtillus	O	*	*	*			*	*	*
	Vaccinium uliginosum	TB	*	*					*	*
	Vaccinium vitis-idaea	TT							*	*
	Viola palustris	TT					*			
Mosses	*Amblystegium serpens*	O						*		
	Atrichum undulatum	O					*			
	Aulacomnium palustre	TT			*		*	*	*	*
	Bazzania trilobata	TT							*	
	Brachytheciastrum velutinum	O		*						
	Brachythecium rutabulum	O		*	*		*	*		
	Brachythecium salebrosum	O					*	*		
	Brachythecium sp.	O		*		*		*		
	Bryum sp.	O				*				
	Calypogeia sp.	O							*	*
	Campylopus flexuosus	TT	*							
	Campylopus introflexus	O	*	*		*	*			
	Campylopus pyriformis	TB	*	*						
	Cephalozia bicuspidata	O		*				*	*	*
	Cephalozia connivens	TT		*					*	*
	Cephalozia loitlesbergeri	TB								*

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Cephalozia lunulifolia	TT		*						*
	Cephalozia sp.	O							*	
	Ceratodon purpureus	O		*		*	*			
	Dicranella cerviculata	TT	*	*		*	*	*		
	Dicranodontium denudatum	TT		*			*			
	Dicranum flagellare	TT							*	
	Dicranum montanum	O			*					*
	Dicranum polysetum	TT			*				*	*
	Dicranum scoparium	O	*	*	*		*	*	*	*
	Eurhynchium angustirete	O			*			*		
	Herzogiella seligeri	O		*	*		*	*		
	Hylocomium splendens	O			*		*			
	Hypnum cupressiforme	O			*			*		
	Hypnum pallescens	O			*					
	Chiloscyphus coadunatus	O		*				*		
	Chiloscyphus profundus	O	*	*	*		*	*		*
	Lepidozia reptans	O					*			*
	Leucobryum glaucum	O		*						
	Mylia anomala	TB							*	*
	Pellia sp.	O					*	*		
	Plagiomnium affine	O			*		*	*		
	Plagiothecium curvifolium	O	*		*		*	*		
	Plagiothecium denticulatum var. denticulatum	O					*	*		
	Plagiothecium laetum	O			*			*		
	Plagiothecium sp.	O								*
	Pleurozium schreberi	O		*	*		*	*	*	*
	Pohlia nutans subsp. nutans	O	*	*	*	*	*	*		*
	Polytrichum commune	TB		*	*	*	*	*		
	Polytrichum formosum	O	*	*				*	*	
	Polytrichum juniperinum	TT	*		*	*	*		*	*
	Polytrichum longisetum	TT	*	*		*	*			
	Polytrichum perigoniale	TT			*					
	Polytrichum strictum	TB		*					*	*
	Ptilidium pulcherrimum	O			*				*	*
	Rhytidiadelphus squarrosus	O			*		*	*		
	Rhytidiadelphus triquetrus	O			*					
	Riccardia latifrons	TT								*
	Sanionia uncinata	O					*			
	Scapania irrigua	O					*			
	Scapania sp.	O					*	*		
	Sciuro-hypnum curtum	O			*					
	Sphagnum angustifolium	TB				*				*
	Sphagnum capillifolium	TT		*						*
	Sphagnum cuspidatum	TB	*	*						
	Sphagnum fallax	TT	*	*	*		*	*	*	*
	Sphagnum fimbriatum	TT			*					
	Sphagnum flexuosum	TT		*					*	*
	Sphagnum fuscum	TB		*						
	Sphagnum girgensohnii	O			*					

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Sphagnum magellanicum agg	TB						*	*	*
	Sphagnum russowii	TT						*		*
	Straminergon stramineum	TT			*			*		
	Tetraphis pellucida	O	*		*			*	*	*
	Thuidium tamariscinum	O						*		
Fungi	*Aphanobasidium pseudotsugae*	O		*						*
	Arrhenia gerardiana	TB								*
	Athelia decipiens	O						*	*	*
	Athelia epiphylla agg	O		*	*			*	*	*
	Botryobasidium subcoronatum	O	*	*	*		*			*
	Clitocybe phyllophila cf	O			*		*			*
	Collybia cirrhata	O	*	*	*		*	*	*	*
	Cortinarius bataillei	TT			*				*	*
	Cortinarius biformis	O								*
	Cortinarius croceus	O		*					*	*
	Cortinarius fulvescens	O							*	*
	Cortinarius chrysolitus	TB								*
	Cortinarius obtusus	O								*
	Cortinarius tubarius	TB								*
	Dacrymyces macnabbii	O							*	*
	Dacrymyces minor	O			*				*	*
	Dacrymyces stillatus	O							*	*
	Dacrymyces tortus	O								*
	Dacryobolus karstenii	TT							*	*
	Entoloma cetratum	O			*				*	*
	Galerina allospora	O	*	*						*
	Galerina atkinsoniana	O			*		*	*		*
	Galerina cerina	O								*
	Galerina farinacea	TB							*	*
	Galerina paludosa	TB		*				*	*	*
	Gorgoniceps viridula cf	O								*
	Hebeloma incarnatulum	TB							*	*
	Hypholoma elongatum	TB	*			*	*			*
	Hypholoma udum	TB	*			*			*	*
	Chroogomphus rutilus	O								*
	Kneiffiella subalutacea	TT								*
	Lactarius rufus	O	*	*					*	*
	Lachnum imbecile	TB	*	*		*				*
	Lachnum virgineum	O		*	*				*	*
	Lasiobolus sp.	O								*
	Lophodermium picae	O								*
	Mollisia sp.	O					*			*
	Monilinia baccarum	TB								*
	Mycena galopus	O			*		*	*	*	*
	Mycena rorida	O							*	*

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Mycena sp.	O								*
	Paxillus involutus	O	*	*						*
	Peniophorella pratermissa	O			*			*		*
	Piloderma sphaerosporum	O								*
	Psathyrella tenuicula	O								*
	Rhodocollybia prolixa var. distorta	O			*					*
	Russula emetica	O		*					*	*
	Russula paludosa	TT							*	*
	Lyophyllum palustre	TB		*				*		*
	Trechispora farinacea	O	*						*	*
	Trichaptum fuscoviolaceum	O							*	*
	Tubulicrinis accedens	O	*	*						*
	Tubulicrinis borealis cf	O								*
	Tubulicrinis glebulosus	TT							*	*
	Tubulicrinis sp.	O								*
	Tubulicrinis subulatus	O							*	*
	Xylodon sp.	O							*	*
	Amanita fulva	TT			*				*	
	Amphinema byssoides	O					*	*		
	Helotiales	O	*							
	Athelia binucleospora	O							*	
	Athelia bombacina cf	O			*					
	Auriscalpium vulgare	O						*		
	Baeospora myosura	O						*		
	Bertia moriformis	O			*					
	Bisporella citrina	O						*		
	Botryobasidium aureum	O				*				
	Botryobasidium conspersum	O		*						
	Brevicellicium exile cf	O							*	
	Calocera viscosa	O					*			
	Calycellina leucella	O		*	*		*	*		
	Cistella lagenipila	O				*				
	Ampulloclitocybe clavipes	O			*					
	Clitocybe metachroa	O					*			
	Collybia cookei	O	*							
	Collybia tuberosa	O		*	*					
	Coprinopsis sp.	O					*			
	Coprinopsis stercoreus	O							*	
	Cortinarius caperatus	O							*	
	Cortinarius comptulus cf	O			*					
	Cortinarius fasciatus	O							*	
	Cortinarius flexipes var. flabellus	TT							*	
	Cortinarius fulvescentoides	O							*	
	Cortinarius sect. Telamonia	O					*			
	Cortinarius semisanguineus	O			*					
	Cortinarius tenuifulvescens	O							*	
	Cortinarius umbrinolens	O						*		
	Cyclaneusma minus	O	*		*			*		

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Cystoderma amiantinum	O			*		*			
	Cystoderma jasonis	O					*	*		
	Dacrymyces estonicus	O							*	
	Dacrymyces lacrymalis	O			*					
	Dacrymyces microsporus	O		*						
	Dasyscyphella pulverulenta	O			*					
	Diatrypella favacea	O			*			*		
	Entoloma elodes	TB							*	
	Entoloma sericeum	O							*	
	Entoloma sp. 1	O						*		
	Entoloma sp. 2	O			*					
	Entoloma vinaceum	O	*							
	Eutypa sp.	O				*				
	Exidia recisa	O						*		
	Exidiopsis sp.	O	*							
	Exobasidium oxycocci	TB							*	
	Exobasidium vaccinii	TT							*	
	Exobasidium vaccinii—uliginosi	TB		*					*	
	Flammulaster sp.	O			*					
	Galerina calyptrata	O	*							
	Galerina hybrida	TB							*	
	Galerina hypnorum	O	*		*		*			
	Galerina hypnorum aff	O	*	*				*	*	
	Galerina pumila	O			*					
	Galerina stordalii	TT						*		
	Galerina vittiformis	O					*			
	Gloiocephala caricis	TT					*	*		
	Gymnopilus fulgens	TB				*				
	Gymnopus androsaceus	O		*			*			
	Gymnopus aquosus	TT					*			
	Gymnopus ocior	O		*	*		*	*		
	Gymnopus putilus	O		*						
	Gymnopus terginus	O		*	*					
	Hebeloma birrum	O						*		
	Hebeloma leucosarx	O			*					
	Hebeloma mesophaeum	O						*		
	Hebeloma velutipes	O					*			
	Hemimycena mauretanica	O					*			
	Heyderia pusilla	O					*	*		
	Hyaloscypha aurivella cf	O							*	
	Hyaloscypha fuckelii var. alniseda	O	*	*						
	Hyaloscypha herbarum	O	*							
	Hyaloscypha leuconica	TT		*						
	Hyaloscypha paludosa	O					*			
	Hyaloscypha sp. 1	O			*					
	Hyaloscypha sp. 2	O	*							

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Hymenoscyphus caudatus cf	O			*					
	Hymenoscyphus sp. 1	O				*	*	*		
	Hymenoscyphus sp. 2	O					*	*		
	Hymenoscyphus vitellinus	O					*			
	Basidioradulum radula	O			*					
	Hyphoderma setigerum	O			*					
	Hyphodontia pallidula	O						*		
	Hypholoma fasciculare	O						*		
	Hypholoma polytrichi	O			*					
	Hypomyces luteovirens	O						*		
	Cheilymenia stercorea	O							*	
	Inocybe napipes	O			*					
	Inocybe subcarpta	O		*						
	Irpex lacteus	O			*			*		
	Jaapia argillacea	O				*	*			
	Laccaria proxima	O	*	*	*	*	*	*		
	Lactarius helvus	TT		*	*		*	*	*	
	Lactarius necator	O			*					
	Lactarius tabidus	TT	*	*	*					
	Lactarius vietus	O			*					
	Lachnum apalum	O				*	*			
	Lachnum ciliaris	O					*	*		
	Lachnum clavisporum	TB				*				
	Lachnum diminutum	TT		*		*	*	*		
	Lachnum elongatisporum	O						*		
	Lachnum pygmaeum	O						*		
	Lachnum schoenoplecti	TT					*			
	Lachnum tenue	TT	*	*	*		*			
	Laxitextum bicolor	O			*					
	Leccinum bruneogriseolum	O			*					
	Leccinum variicolor	TT	*		*		*	*		
	Leotia lubrica	O			*					
	Lophodermium melaleucum	TT	*							
	Lophodermium pinastri	O					*			
	Marasmius limosus	TT				*				
	Melzericium udicola cf	O					*			
	Merismodes confusa	O			*		*	*		
	Merulius tremellosus	O			*					
	Mollisia aquosa cf	O	*							
	Mollisia discolor cf	O		*	*			*		
	Mollisia humidicola cf	O				*				
	Mollisia palustris agg	TT	*			*	*	*		
	Mollisia pastinaceae	O					*			
	Mollisia ramealis	O						*		
	Mollisia sp. 1	O			*			*		
	Mollisia sp. 3	O			*		*	*		
	Mycena cinerella	O			*		*	*		

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Mycena epipterygia	O	*		*			*		
	Mycena metata	O			*	*	*	*		
	Mycena sanguinolenta	O			*					
	Mycena silvae-nigrae	O								
	Mycena vitilis	O						*		
	Nimbomollisia eriophori	TB				*				
	Omphalina sp.	O		*						
	Orbilia coccinella	O			*					
	Paullicortium pearsonii cf	O					*			
	Peniophora cinerea	O			*					
	Peniophorella pubera	O			*					
	Pezizella subtilis	O		*						
	Phanerochaete sanguinea	O			*			*		
	Phanerochaete sp.	O			*					
	Phellinus lundellii	TB			*					
	Phialina lachnobrachya	O					*			
	Phlebia sp.	O			*					
	Piptoporus betulinus	O			*					
	Plicaturopsis crispa	O			*					
	Polyporus ciliatus	O			*					
	Psathyrella fibrillosa	O			*					
	Psilocybe inquilina	O					*			
	Psilocybe phyllogena	O			*		*			
	Psilocybe turficola	TB				*	*			
	Radulomyces sp.	O			*					
	Repetobasidium macrosporum	O					*			
	Collybia butyracea var. asema	O			*					
	Rickenella fibula	O					*			
	Russula amara	O						*		
	Russula amoena	O						*		
	Russula betularum	TT	*	*	*		*	*		
	Russula clavipes	O			*			*		
	Russula fragilis	O			*			*		
	Russula ochroleuca	O			*			*		
	Russula sphagnicola	TB		*				*		
	Rutstroemia calopus	O					*			
	Scleroderma citrinum	O		*						
	Schizopora sp.	O			*					
	Sistotrema gloeocystidiatum cf	O				*				
	Sistotrema porulosum	O			*		*			
	Skeletocutis amorfa cf	O							*	
	Stictis sp.	O				*				
	Strobilurus tenacellus	O						*		
	Stropharia semiglobata	O					*			
	Suillus bovinus	TT	*	*						

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
	Suillus variegatus	TT			*			*	*	
	Tapesia fusca	O					*	*		
	Tapesia fusca aff	O			*	*	*			
	Thelephora terrestris	O				*				
	Tomentella sp.	O					*			
	Tomentella ellisii	O		*		*	*			
	Tomentellopsis sp.	O			*			*	*	
	Tomentellopsis submollis	O		*						
	Trechispora antipus cf	O	*							
	Trechispora mollusca	O						*		
	Trechispora subsphaerospora	O							*	
	Trechispora vaga	O							*	
	Tricholoma fulvum	O			*			*		
	Tulasnella violea	O						*		
	Typhula caricina	TT				*	*	*		
Butterflies	*Anthocharis cardamines*	O								*
	Aphantopus hyperantus	O				*	*	*		
	Aporia crataegi	O	*	*						
	Araschnia levana	O				*		*		*
	Argynnis aglaja	O	*						*	
	Brenthis ino	O		*						
	Callophrys rubi	TT	*							*
	Carterocephalus palaemon	O						*		
	Celastrina argiolus	O	*				*			
	Coenonympha tullia	TT	*	*						
	Colias palaeno	TB	*	*					*	*
	Ematurga atomaria	TT	*	*			*	*	*	*
	Gonepteryx rhamni	O				*	*	*		
	Inachis io	O					*			
	Melitaea athalia	O			*				*	*
	Nymphalis antiopa	O		*		*	*			
	Ochlodes sylvanus	O			*	*	*	*		
	Papilio machaon	O				*				
	Pararge aegeria	O						*		
	Pieris brassicae	O		*						
	Pieris napi	O		*	*	*	*	*		*
	Pieris rapae	O	*	*		*	*	*	*	*
	Polygonia c-album	O				*				
	Thymelicus sylvestris	O		*			*		*	
	Vacciniina optilete	TB							*	
	Vanessa atalanta	O	*			*				
	Vanessa cardui	O	*	*		*	*			*
Moths	*Acleris aspersana*	O						*		
	Acleris hastiana	O						*		
	Acleris logiana	O					*			
	Acleris maccana	TT							*	*
	Acleris notana	O			*					

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Acleris rufanaa	O		*							
Acleris variegana	O	*			*		*			
Acompsia cinerella	O						*			
Acronicta auricoma	O	*	*	*		*	*			
Acronicta leporina	O				*		*			
Acronicta megacephala	O			*			*			
Acronicta menyanthidis	TB	*	*	*				*	*	
Acronicta rumicis	O		*			*	*			
Adoxophyes orana	O			*		*				
Aethalura punctulata	O	*	*	*		*	*	*		
Aethes cnicana	O				*	*	*			
Agonopterix arenella	O		*				*			
Agonopterix ciliella	O		*	*	*	*	*		*	
Agonopterix liturosa	O	*	*	*	*			*		
Agonopterix propinquella	O						*			
Agriphila tristella	O	*		*	*	*	*		*	
Agrotis exclamationis	O				*					
Agrotis ipsilon	O		*			*				
Achyla flavicornis	O								*	
Alcis repandata	O			*		*	*	*	*	
Amphipoea lucens	TB	*	*	*	*	*		*		
Amphipyra pyramidea	O	*								
Amphipyra tragopoginis	O	*	*		*	*		*	*	
Anania coronata	O						*			
Anania hortulata	O			*			*	*		
Anaplectoides prasina	O			*			*			
Ancylis badiana	O			*						
Ancylis laetana	O						*			
Ancylis myrtillana	TT							*	*	
Ancylis uncella	O	*	*	*	*	*	*			
Angerona prunaria	TT			*					*	
Apamea crenata	O			*						
Apamea monoglypha	O	*			*					
Apamea rubrirena	O			*	*		*			
Apamea sublustris	O						*			
Aplocera praeformata	O			*						
Apomyelois bistriatella	O			*	*					
Apotomis betuletana	O	*		*		*	*			
Apotomis capreana	O						*			
Apotomis turbidana	O			*						
Arctia caja	O	*			*	*	*			
Argyresthia albistria	O	*								
Argyresthia glabratella	O			*			*		*	
Arichanna melanaria	TB			*				*	*	
Aroga velocella	O	*								
Assara terebrella	O	*	*		*					
Bactra lancealana	TT			*	*	*	*			

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Bisigna procerella	O							*		
Biston betularia	O		*				*			
Biston strataria	O	*								
Blastobasis glandulella	O							*		
Blepharita satura	O	*	*	*	*	*	*	*		
Bryotropha galbanella	O								*	
Bryotropha senectella	O	*					*			
Bupalus piniaria	O			*		*		*	*	
Cabera exanthemata	O			*		*	*			
Cabera pusaria	O			*		*	*			
Calliteara pudibunda	O			*	*	*	*		*	
Caloptilia betulicola	O			*						
Caloptilia stigmatella	O			*						
Calospilos sylvata	O			*			*			
Campaea margaritaria	O			*	*		*			
Camptogramma bilineata	O	*	*		*	*	*			
Capua vulgana	O		*	*		*	*			
Carpatolechia proximella	O			*						
Catocala fraxini	O		*	*						
Catoptria falsella	O			*	*					
Catoptria margaritella	TT	*	*	*	*	*	*	*	*	
Cedestis gysseleniella	O	*		*			*		*	
Celaena haworthii	TB	*		*					*	
Celaena leucostigma	O	*			*					
Celypha lacunana	O	*					*			
Celypha rufana	O	*								
Cepphis advenaria	O			*			*	*	*	
Cerastis rubricosa	O								*	
Clepsis rurinana	O			*			*			
Clostera curtula	O						*			
Clostera pigra	O	*			*	*	*			
Cnephasia asseclana	O						*			
Cnephasia stephensiana	O						*			
Coenophila subrosea	TB	*	*					*	*	
Cochylis nana	O						*			
Coleophora alcyonipennella	O	*	*							
Coleophora alticolella	O				*	*	*			
Coleophora caespititiella	O						*			
Coleophora glaucicolella	O				*					
Coleophora mayrella	O						*			
Coleophora milvipennis	O			*			*			
Coleophora otidipennella	O			*			*			
Coleophora sylvaticella	O						*			
Coleophora tamesis	O				*					
Coleophora vacciniella	TT								*	
Coleophora vitisella	O							*		

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Colocasia coryli	O		*	*		*	*			
Colostygia pectinataria	O			*	*	*	*			
Conistra vaccinii	O	*			*					
Cosmia trapezina	O	*		*			*			
Cossus cossus	O						*			
Crambus lathoniellus	O	*	*	*	*	*	*			
Crambus pascuella	O	*	*		*	*	*			
Crocallis elinguaria	O							*		
Cryphia algae	O		*							
Cybosia mesomella	O	*	*	*	*	*	*	*		
Cyclophora albipunctata	O	*	*	*	*	*	*			
Cyclophora linearia	O					*				
Deileptenia ribeata	O			*			*			
Deltote uncula	O						*			
Denisia stipella	O			*		*	*			
Depressaria pimpinellae	O	*								
Diacrisia sannio	O	*	*	*	*	*	*	*	*	
Diachrysia chrysitis	O						*			
Diaphora mendica	O	*	*							
Diarsia brunnea	O			*			*		*	
Diarsia mendica	O			*			*			
Diarsia rubi	O	*					*			
Discoloxia blomeri	O						*			
Diurnea fagella	O			*		*				
Drepana falcataria	O	*		*			*			
Eana incanana	O			*						
Ecliptopera silaceata	O			*			*			
Ectropis crepuscularia	O			*		*	*	*	*	
Eilema complana	O	*	*					*		
Eilema depressa	O	*	*	*	*	*	*	*	*	
Eilema lurideola	O		*	*		*	*			
Eilema lutarella	O	*	*							
Eilema sororcula	O	*					*		*	
Elachista canapennella	O	*	*	*	*		*		*	
Elachista apicipunctella	O			*						
Elachista maculicerusella	O					*				
Elophila nymphaeata	O				*					
Elophos vittaria	O							*		
Enargia paleacea	O	*		*						
Endromis versicolora	O				*					
Ennomos autumnaria	O				*		*			
Ennomos fuscantaria	O				*					
Epermenia chaerophyllella	O				*					
Epiblema hepaticana	O						*			
Epinotia ramella	O		*		*		*			

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Epinotia tedella	O			*			*			
Epinotia trigonella	O					*	*			
Epione repandaria	O						*		*	
Epione vespertaria	O						*			
Epirrhoe alternata	O			*	*	*	*	*		
Epirrhoe rivata	O						*			
Eucosma campoliliana	O						*			
Eucosma cana	O		*			*	*			
Eudonia lacustrata	O	*	*	*	*	*	*			
Eudonia murana	O			*				*	*	
Eudonia pallida	O					*	*			
Eudonia truncicolella	O	*	*	*	*	*	*	*	*	
Eugnorisma depuncta	O					*	*			
Eulia ministrana	O			*		*	*	*		
Eulithis populata	O		*	*		*	*	*	*	
Eulithis pyraliata	O						*			
Eulithis testata	TT		*		*	*		*	*	
Eupithecia absinthiata	O						*			
Eupithecia exiguata	O						*	*		
Eupithecia satyrata	O				*					
Eupithecia selinata	O			*						
Eupithecia tantillaria	O		*			*				
Eupithecia tripunctaria	O						*			
Eupithecia vulgata	O		*	*			*	*		
Eurois occulta	TT		*	*	*		*	*	*	
Euspilapteryx auroguttella	O	*	*	*	*		*	*	*	
Exaeretia ciniflonella	TT		*	*			*			
Falcaria lacertinaria	O			*	*					
Geometra papilionaria	O		*	*		*	*		*	
Gortyna flavago	O					*				
Habrosyne pyritoides	O			*	*					
Hada plebeja	O								*	
Helcystogramma rufescens	O						*			
Hellinsia osteodactylus	O						*			
Herminia grisealis	O			*						
Hoplodrina blanda	O	*		*			*			
Hoplodrina octogenaria	O			*	*	*	*			
Hydrelia sylvata	O			*			*			
Hydriomena furcata	O							*		
Hydriomena impluviata	O			*		*	*			
Hyloicus pinastri	O	*	*	*		*	*	*	*	
Hypatopa binotella	O		*	*			*	*		

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Hypena crassalis	TT							*	*	
Hypena proboscidalis	O			*			*			
Hypenodes humidalis	TT		*	*		*		*	*	
Hypomecis punctinalis	O			*	*	*	*			
Hypomecis roboraria	O			*		*	*	*	*	
Chiasmia clathrata	O				*					
Chionodes nebulosella	TB							*	*	
Chloroclysta citrata	O			*			*		*	
Chloroclysta siterata	O			*			*			
Chloroclysta truncata	O		*							
Chortodes pygmina	O			*	*	*	*		*	
Chrysoteuchia culmella	O						*			
Idaea aversata	O						*		*	
Idaea biselata	O						*			
Ipimorpha retusa	O			*	*					
Itame brunneata	TT			*				*	*	
Lacanobia thalassina	O			*		*	*	*		
Lampropteryx suffumata	O			*						
Laothoe populi	O	*	*	*	*		*	*		
Lathronympha strigana	O	*	*		*		*			
Leucodonta bicoloria	O			*						
Limnaecia phragmitella	O				*					
Lithomoia solidaginis	TT		*	*			*	*	*	
Lithophane consocia	O					*	*	*	*	
Lithophane socia	O			*			*			
Lithosia quadra	O	*	*	*			*	*	*	
Lomapilis marginata	O	*		*	*		*			
Lomographa bimaculata	O						*			
Lomographa temerata	O			*						
Luperina testacea	O		*							
Lycia hirtaria	O	*	*	*			*	*	*	
Lycophotia porphyrea	TT	*	*	*			*	*	*	
Lygephila pastinum	O					*				
Lymantria monacha	O							*		
Lypusa maurella	O			*						
Macaria alternata	O			*		*	*			
Macaria liturata	O			*						
Macaria notata	O			*		*	*			
Macrothylacia rubi	O	*	*			*	*			
Matilella fusca	O	*		*	*					
Melanchra pisi	O	*			*	*				
Mesapamea secalis	O		*							
Mompha propinquella	O							*		
Montescardia tessulatellus	O								*	
Mythimna conigera	O	*								
Mythimna ferrago	O			*						

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Mythimna impura	O	*	*	*	*	*	*		*	
Mythimna pudorina	O	*								
Nematopogon robertella	O			*						
Nematopogon schwarziellus	O			*						
Neofaculta ericetella	TT	*								
Neofaculta infernella	TT			*		*	*			
Noctua comes	O					*				
Noctua pronuba	O		*				*			
Notodonta ziczac	O				*	*				
Odontopera bidentata	O		*	*			*	*	*	
Odontosia carmelita	O		*	*			*			
Ochropacha duplaris	O			*		*	*			
Ochropleura plecta	O	*			*					
Oligia versicolor	O			*						
Oncocera semirubella	O		*				*			
Ortholepis betulae	O			*		*	*			
Orthonama vittata	O				*					
Orthosia gothica	O		*	*	*	*	*		*	
Orthosia incerta	O	*		*		*	*			
Orthotaenia undulana	O			*			*			
Pandemis cerasana	O			*			*			
Pandemis heparana	O								*	
Paradarisa consonaria	O		*	*						
Paramesia gnomana	O			*			*			
Parectopa ononidis	O	*	*						*	
Parornix betulae	O	*	*	*	*	*	*			
Pediasia truncatellus	TB							*	*	
Pennithera firmata	O	*	*	*	*	*	*	*	*	
Peribatodes secundaria	O		*							
Perizoma parallelolineata	O								*	
Perizoma affinitata	O						*	*		
Perizoma albulata	O	*				*				
Perizoma alchemillata	O			*			*			
Phalera bucephala	O			*			*			
Pharmacis fusconebulosa	O							*		
Pheosia gnoma	O	*		*		*	*			
Pheosia tremula	O			*	*	*				
Phiaris micana	TT						*	*		
Phiaris palustrana	TT			*	*		*			
Phragmatobia fuliginosa	O				*					
Plagodis pulveraria	O			*				*	*	
Plemyria rubiginata	O			*			*			
Pleuroptya ruralis	O	*	*	*	*	*	*	*		
Pleurota bicostella	TT			*			*	*		
Plutella xylostella	O	*	*	*	*	*	*	*	*	
Polia bombycina	O	*	*	*	*	*	*			
Polia hepatica	O	*	*		*	*	*			

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Protodeltote pygarga	O			*			*			
Protolampra sobrina	TT	*	*					*		
Pterostoma palpina	O	*					*			
Ptilodon capucina	O			*		*	*		*	
Pyrausta despicata	O	*	*		*	*				
Rhopobota naevana	O								*	
Rivula sericealis	O			*			*			
Rusina ferruginea	O	*	*	*	*	*	*	*	*	
Saturnia pavonia	TT	*								
Scoliopteryx libatrix	O						*			
Scoparia ambigualis	O			*		*	*	*	*	
Scoparia pyralella	O						*			
Scopula floslactata	O			*						
Scopula immorata	O	*		*	*					
Scopula immutata	O					*				
Scotopteryx chenopodiata	O			*			*			
Scrobipalpa acuminatella	O				*	*	*			
Selenia dentaria	O			*		*	*	*	*	
Selenia lunularia	O			*						
Selenia tetralunaria	O			*	*					
Smerinthus ocellata	O	*				*				
Sphinx ligustri	O	*			*					
Spilosoma lubricipeda	O						*			
Spilosoma lutea	O			*			*			
Stenoptilia pterodactyla	O					*				
Syndemis musculana	O						*		*	
Syngrapha interrogationis	TT			*						
Teleiopsis diffinis	O				*					
Tethea or	O			*			*			
Tetheella fluctuosa	O			*			*			
Thera obeliscata	O	*	*		*					
Tholera cespitis	O					*				
Tholera decimalis	O	*	*		*	*	*	*		
Thumatha senex	O	*	*		*	*	*			
Thyatira batis	O	*	*	*					*	
Timandra comae	O			*			*	*		
Tinea trinotella	O						*			
Trichopteryx carpinata	O			*		*	*			
Udea olivalis	O						*			
Udea prunalis	O			*			*			
Xanthia icteritia	O	*	*	*	*	*				
Xanthia togata	O	*								
Xanthorhoe biriviata	O			*						
Xanthorhoe designata	O					*				
Xanthorhoe fluctuata	O			*	*					
Xanthorhoe incursata	O							*	*	
Xanthorhoe montanata	O			*			*			

Group	Species	Classification	Disturbed						Undisturbed	
			SM			VJ			MN	VN
			Young	Middle	Old	Young	Middle	Old		
Xanthorhoe spadicearia	O		*	*			*			
Xestia baja	O	*	*	*	*	*	*	*		
Xestia c-nigrum	O				*	*				
Xestia rhomboidea	O			*						
Xestia sexstrigata	O				*		*			
Xestia xanthographa	O					*				
Xylena vetusta	O	*	*		*	*	*		*	

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8 CHAPTER V

Successional pathways and trophic specialisation of different groups of organisms in formerly extracted raised bogs – Restoration and conservation perspectives

Vítovcová et al. 2024. Biological Conservation: 296, 110649. doi: 10.1016/j.biocon.2024.110649

Biological Conservation 296 (2024) 110649

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Successional pathways and trophic specialisation of different groups of organisms in formerly extracted raised bogs – Restoration and conservation perspectives

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ARTICLE INFO

Keywords:
Bryophytes
Fungi
Lepidoptera
Raised bogs
Succession
Vascular plants

ABSTRACT

Central European raised bogs are valuable habitats inhabited by highly adapted peatland specialists, so-called tyrphobionts and tyrphotolerants. Many of them have been destroyed by drainage and peat extraction. After such strong disturbance, the entire biota is deeply influenced, and recovery to a pre-disturbance state may be limited.

This study shows successional trends in the recovery of vegetation, fungi, and Lepidoptera in two disturbed raised bogs comparing with reference. After three decades of spontaneous development, the species composition did not match the reference natural bogs in any of the studied taxonomic groups; however, all groups responded in a very similar way to the disturbance. Alternative communities with low peatland specialists developed. Each taxonomic group was influenced by similar environmental factors, mostly by remaining peat, water table, and successional age, while successional age and pH were the most important factors for peatland specialists. If all species were considered, we found an increasing pattern in trophic specialisation during the succession. As successional age is one of the most important factor, restoration measures should be taken as soon as possible, otherwise the site will not be inhabited by peatland specialists. Generally, peatland specialists should be focused more on in restoration projects, but also dominant plant species are important because they are associated with most fungal and Lepidoptera species. Restoration will be more successful if a thicker layer of peat is left after peat extraction, and water table has returned to pre-draining conditions.

1. Introduction

Peatlands are regarded to be the most efficient terrestrial carbon storage on Earth (Andersen et al., 2017; Wyatt et al., 2021), thus their conservation and restoration are of eminent interest. Peatlands are widespread ecosystems especially in the boreal zone of Europe and North America, but cover a limited area in central Europe. A distinct type is represented by ombrotrophic raised bogs (Joosten et al., 2017), which form rather isolated habitats. The natural value of untouched raised bogs is well accepted. Besides having an island character, they have also persisted for a long time supporting the occurrence of relict populations of various biota (Dierssen, 2001). Many raised bogs have remained at their sites since the last glaciation, with very limited opportunities to change due to the island character and specific site conditions (Mikkola and Spitzer, 1983; Spitzer, 1994). The specific microrelief and microclimate appear to play a key role, especially in the survival of some cold-adapted species (Zarzycki et al., 2022). We use the old but still useful classification of species here, according to their link to the peatland habitat (Peus, 1928): strict specialists, so-called tyrphobionts; tyrphotolerants; and other species. Population densities of the peatland specialists, in our case tyrphobionts and tyrphotolerants, may indicate the quality of the habitats or show the trajectory of the restoration process towards reference sites.

Large-scale industrial peat harvesting is the most destructive anthropogenic disturbance accompanied by deep changes in water regime and by a decrease or complete retreat of the peat layer. Methods of restoring such deeply altered raised bogs are limited (Grootjans et al., 2006) but still exist. Limitations of successful raised bog restoration include (a) insufficient soil moisture, (b) thin or absent layer of remaining peat, (c) absence of source populations of target species in the

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https://doi.org/10.1016/j.biocon.2024.110649
Received 22 February 2024; Received in revised form 13 May 2024; Accepted 19 May 2024

surrounding, or barriers to their colonisation, and (d) unsuitable biotic conditions, such as a lack of host plants, or strong competition. Restoration measures include raising the water table by blocking drainage ditches (Pfadenhauer and Grootjans, 1999; Haapalehto et al., 2011), additional sowing or planting of target plant species, and introducing individuals in the case of animals (Neve et al., 1996; Perrow and Davy, 2002; etc.). The other, easiest way is to rely on spontaneous succession, particularly when there are source populations in the close surroundings (Poulin et al., 2005; Konvalinková and Prach, 2014; Johansen et al., 2017). Using spontaneous succession in peatland restoration after human-induced disturbances has been repeatedly demonstrated to be an efficient option, but not always (Konvalinková and Prach, 2010; Woziwoda and Kopec, 2014; González et al., 2014; Räsänen et al., 2023). It may fail even if source populations occur nearby, because species largely differ in their colonisation ability. Instead of recovery of pre-disturbance vegetation, an alternative state often develops by spontaneous succession (Dise, 2009; Matthews and Spyreas, 2010; Pospíšilová et al., 2023).

Vascular plants are most frequently used as indicators of restoration success of disturbed ecosystems because they are the easiest to study and reflect the changes well (van Andel and Aronson, 2012). Nevertheless, it is important to monitor other groups which may be sensitive to environmental factors in a different way. Hence, in addition to vascular plants we selected bryophytes, fungi, diurnal butterflies, and moths, all of which are considered good indicators of peatland quality (Vítovcová et al., 2022). Particular groups of organisms in raised bogs have usually been studied separately for plants (e.g. Campbell et al., 2003; Konvalinková and Prach, 2014), fungi (Laber, 2009), and insects (Spitzer and Danks, 2006; Buchholz et al., 2009). Multi-taxa studies of disturbed raised bogs are rare (Strobl et al., 2020). In this study, we focus on five groups of organisms and their participation during approximately three decades of succession described by the space-for-time substitution, i.e. by the chronosequence approach (Walker et al., 2010). Plants are a core component of terrestrial ecosystems, and provide food, substrate or shelter to fungi and insects. On the other hand, many plants depend on mycorrhiza and profit from insect pollination. Fungi are decomposers, plant symbionts, or parasites, and play a key role in nutrient cycling (Juan-Ovejero et al., 2020). Diurnal and nocturnal Lepidoptera may represent an umbrella group of other relict bog insects, being an integral component of bog diversity (New, 1997). Raised bogs are included into the priority habitats listed in Annex I of the European Union Habitat Directive (https://inspire.ec.europa.eu/document/HabDir).

The trophic relationships especially between plants and fungi are considered essential for the functioning of peatlands in carbon sequestration (Artz et al., 2007), while trophic relationships between plants and Lepidoptera are especially important from the biodiversity point of view (Spitzer and Danks, 2006). However, there are very few studies investigating relationships between different taxonomic groups changing during this type of succession (Räsänen et al., 2023), and we are not aware of any study conducted in peatlands dealing with more than two taxonomic, i.e. also functional, groups and relationships between them. Such studies are rare also in other habitat types (Emery et al., 2015). Generally, changing trophic relationships between different groups of organisms during succession has not been frequently investigated except for aquatic and soil environments. One of the reasons is that quantification of the strength of trophic relationships is difficult and often unknown for many species (Neutel et al., 2007). It is generally expected that trophic specialisation increases during succession (Walker and del Moral, 2003), and specialists are more sensitive to environmental changes than generalists, thus being better indicators of the state of an ecosystem (Fridley et al., 2007). The degree of trophic specialisation can serve as a good indicator of the recovery towards the reference state, thus we also included this into the study. Trophic relationships can be viewed as one of the important components of biodiversity (Minayeva et al., 2017).

Effective peatland restoration and an appropriate design of restoration measures require a good understanding of the processes of how basic groups of organisms colonise, co-exist, interact, and persist in previously disturbed raised bogs. Undisturbed raised bogs (without evident anthropogenic disturbance) in the surrounding, which are expected to serve as sources for spontaneous colonisation, were used as reference. We asked the following questions:

(a) Do different groups of organisms follow comparable successional pathways?
(b) Are the same environmental factors significant for their development?
(c) Does the trophic specialisation of fungi and Lepidoptera on plants increase during succession?
(d) What are the implications of the study for restoration and conservation of the habitats?

2. Methods

2.1. Study sites

The study sites included two disturbed Soumarský Most (85 ha), and Vlčí Jámy (49 ha) and two reference raised bogs Malá Niva (147 ha), and Velká Niva (120 ha) in the Šumava Mts in the south-western part of the Czech Republic (48.53054–48.55021 N; 13.46045–13.50027E); average altitude 750 a.s.l.; mean annual temperature ca 5.3 °C, mean annual precipitation ca 900 mm (Tolasz, 2007). The formerly extracted and the reference raised bogs are located close to each other in a radius of 5 km and were of the same vegetation type (Sphagnion medii alliance of the Oxycocco-Sphagnetea class of the continental classification; Chytrý, 2011) before the disturbance. The disturbed bogs were heavily drained by channels and pipes and peat was industrially extracted. Industrial peat extraction started in 1977 and were gradually terminated in the period from the 1980s to 2004. The remaining peat depth was about 0.5 m or less. The average water table in extracted bogs was located at −22.9 (± 15.3) cm, in natural bogs at −16.1 (± 4.1) cm. The average pH in extracted bogs was 3.68 (± 0.24), in natural bogs 3.54 (± 0.07). All these raised bogs are protected as parts of the Šumava National Park or Šumava Protected Landscape Area, therefore the disturbed raised bogs were not artificially afforested by mining companies to Scots pine plantations which is the usual approach prevailing to date (Pospíšilová et al., 2023). For a detailed description of the study sites, see Vítovcová et al. (2022).

2.2. Data collection

The field survey was conducted in 2019–2021. The following successional stages were distinguished in each studied disturbed bog: (1) young stage, 10–15 years old, open vegetation with a cover of 10–25%; (2) middle stage, 16–25 years old, vegetation cover about 50%, including young woody species; (3) old stage, 26–35 years old, closed vegetation with no bare peat, woody species cover ca 50%. In the reference bogs, only one stage was distinguished. Dating of the successional stages was based on official records of the Šumava National Park Administration and on tree ring analyses. In the reference bogs, the oldest trees were >200 years old and we took the 200 years as a formal age of reference in some analyses. We used the following sampling sizes and methods for the various taxonomic groups: 1) for Lepidoptera sampling, three 1-ha plots corresponding to the successional stages were monitored in both disturbed bogs, and one 1-ha plot was monitored in both reference bogs; 2) for fungi, vascular plants and bryophytes, four smaller plots (9 × 9 m) were monitored, randomly located inside each 1-ha plot but permanently fixed.

Vegetation of the raised bogs was sampled using phytosociological relevés with visual estimates of percentage cover of all present vascular plant species and bryophytes (Kent and Coker, 1992). Furthermore, the total cover of different vegetation layers was estimated, and average water table, thickness of remaining peat (hereafter remaining peat), and pH were determined in each 9x9m plots. The water table was measured each month during the three vegetation seasons (2019–2021) using a bore holes buried in the peat in each of 9x9m plots. The depth of remaining peat was measured once using a soil probe as well as pH which was assessed from the water samples in the chemical laboratory (Institute of Botany, Czech Academy of Science) once in November 2020. Vascular plant nomenclature follows Danihelka et al. (2012), that of bryophytes Kučera et al. (2012). Fungal fruitbodies were recorded depending on weather conditions up to 8 times per vegetation season (April to November). Basidiomycota were sampled in the 9 × 9 plots, Ascomycota – due to their mostly tiny fruitbodies (ca 1 mm) – in inner plots (3 × 3 m) only. Fruitbodies were identified in the field, later using the microscope, or using molecular identification based on ITS rDNA. Nomenclature of fungi follows Mycobank (www.mycobank.org). Diurnal *Lepidoptera* (super-families *Papilionoidea*, *Hesperioidea*, and *Zygaenoidea* plus day-active species from other groups) were sampled under suitable weather conditions (low wind speed, low cloudiness and air temperature about 15 °C using time-constrained searches between 9:00 and 16:00, zigzagging the site for 45 person-minutes (Kadlec et al., 2012), netting each observed butterfly or identifying them on the wing if possible, and locating as many species as possible. Each site was sampled five times throughout the season (May–September) to cover all phenological aspects of species diversity. Moths were sampled with portable light traps (8 W UV-light powered by a 7.2 Ah/12 V lead battery, with a cotton pad soaked with chloroform), 4 traps per 1-ha plot, i.e. 32 light traps in total. Traps from each 1-ha plot were pooled into one sample. The traps were placed ±30 m apart from each other and, concurrently, from the edge of the plot. The survey was also conducted five times throughout each season (in dry weather, morning air-temperature above 7 °C, wind speed at Beaufort scale B 4). Traps were activated before dusk and were collected after sunrise, only in the period between the last and first quarter moon when the influence of moonlight was almost negligible. After, the collected moths were transferred for identification. If the identification required the examination of genitalia, individuals were dissected. Lepidoptera nomenclature follows Fauna Europaea (Van Swaay et al., 2008).

2.3. Species classification

We classified all recorded species into three categories: (a) tyrphobionts occurring exclusively in bogs, (b) tyrphotolerants often occurring in bogs, but not strictly confined to them, (c) other species distributed over various types of habitats (Peus, 1928). Affinity of biota to peatland habitats was assessed according to Chytrý (2011) for vascular plants, based on Kučera et al. (2012) and expert assessment for bryophytes, according to Hofmeister and Hošek (2016), Thormann and Rice (2007) as well as expert assessment for fungi, and according to Macek et al. (2015), Mikkola and Spitzer (1983), and Jaroš et al. (2014) in the case of butterflies and moths. Moreover, we classified all recorded fungal species according to their degree of trophic specialisation to plants into three classes: (0) not specifically associated with plants; (1) associated with a wide range of plants; (2) strictly associated with a plant family, genus or species (Knudsen and Vesterholt, 2018; Ellis, 1985; www.mykologie.net; see Supplementary Table 1). Determination of the plants most used by fungi was assessed based on field observation, i.e. by records on substrate or presence of ectomycorrhizal hosts. All recorded Lepidoptera species were classified as follows: (0) not specifically associated with plants (feeding on lichens, fungi or other non-plant material); (1) polyphagous, associated with a wide range of plants (from >3 families); (2) oligo- or monophagous, feeding on <4 genera from a single family or on <3 genera from different families (Potocký et al., 2018; Laštůvka et al., 2018; Šumpich et al., 2022; see Supplementary Table 1). For determining the trophic use of present plant species we considered only oligo- and monophagous Lepidoptera species, information on host plants in Central Europe was obtained from Macek et al. (2007, 2008, 2012), Laštůvka et al. (2018), and Šumpich et al. (2022).

2.4. Data analysis

The presence of all recorded species of the studied organisms was unified to one scale per sample, which had three levels of abundance: *level 1* – rare species, for plants and bryophytes, 0.02 and 0.1% cover corresponding to the degrees of r and + in traditional vegetation records; one find for fungi; one individual for diurnal butterflies; 1 to 5 individuals for moths; *level 2* – uncommon species, 1 to 5% cover for plants and bryophytes; 2 to 5 finds for fungi; 2 to 5 individuals for diurnal butterflies; 5 to 20 individuals for moths; *level 3* – common species, >5% cover for plants and bryophytes; >5 finds for fungi; >5 individuals for diurnal butterflies; >20 individuals for moths. One fungal find means 1 fruitbody, or 1 substrate with fruitbodies in case fruitbodies could not be counted (tiny fruitbodies of small Ascomycota or resupinate fruitbodies).

The numbers of samples in the two disturbed and two reference bogs (three successional stages per disturbed bog and one stage per reference one) for particular groups were as follows: 32 samples for plants, bryophytes, and fungi; 8 samples for diurnal butterflies and moths. To quantify the heterogeneity of all the data sets together, as well as for particular datasets, we calculated gradient lengths with Detrended Correspondence Analysis (DCA) using the CANOCO 5 software (Microcomputer Power, Ithaca, NY, US).

The environmental factors (successional age, average water table, pH, remaining peat) and site characteristics (cover of particular vegetation layers) were added as passive variables. Moreover, the numbers of tyrphobionts, tyrphotolerants, and other species for each taxonomic group were used as passive variables in the ordination diagram.

The resulting separate DCA ordinations of particular datasets were compared with the Procrustean analysis, which attempts to match different ordination patterns through rotation and dilatation, and describes the degree of concordance between two ordinations. The concordance values, which increase with the dissimilarity of ordinations, were used to create a distance matrix of all ordinations (Šmilauer and Lepš, 2014).

To find out which factors influenced the species composition of particular groups of organisms, we performed Canonical Correspondence analysis (CCA), followed by Forward Selection with 999 permutations, and the Bonferroni correction with significance level $p < 0.05$.

The average number of fungal and Lepidoptera species with trophic specialisation degree (0,1,2) per sample was calculated, also taking into account peatland specialists (tyrphobionts and tyrphotolerants). The homogeneity of variances was verified by means of Bartlett's test. According to these results, either the Analysis of Variance or nonparametric Kruskal-Wallis test were used, both followed by post-hoc comparisons (Tukey's HSD method, respectively non-parametric post hoc comparisons implemented directly in the package *pgirmess*) in the R software (R Development Core Team, 2023) to reveal trends in succession.

3. Results

3.1. Successional pathways

During the field survey we recorded in the studied bogs a total of 74 vascular plant species (5 tyrphobionts, 23 tyrphotolerants), 69 bryophyte species (9, 19), 335 fungal species (17, 34), 33 butterfly species (2,2), and 471 moth species (9, 31). For complete species lists, see Supplementary Table 1.

The DCA diagrams (Fig. 1) show that tyrphobiont species in all groups, i.e. vascular plants, bryophytes, fungi, butterflies, and moths, were strongly related to each other, to a higher water table, and to a lower pH, thus exhibiting very similar patterns in the ordination diagrams. The ordinations also revealed marked differences in species

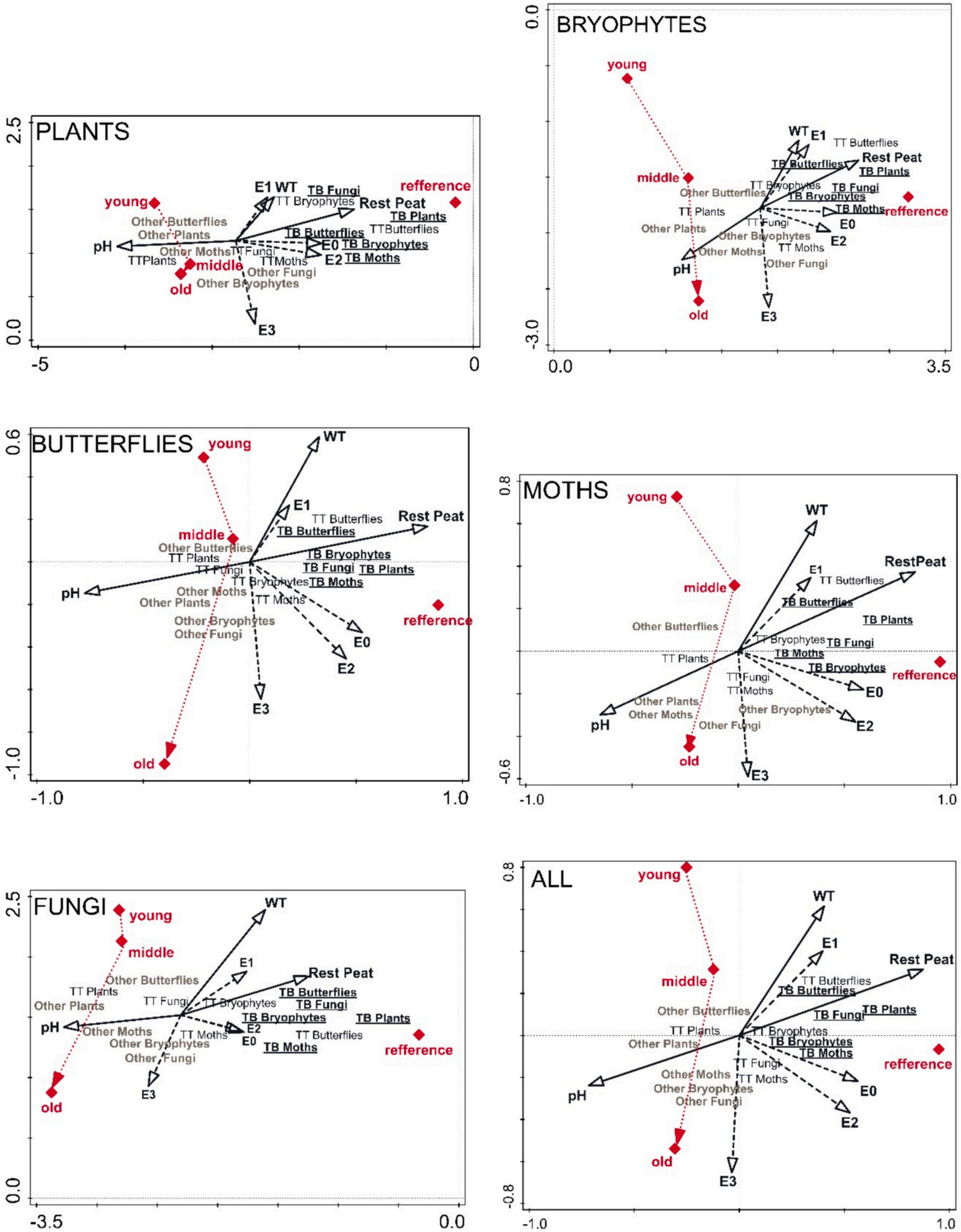

Fig. 1. DCAs of each taxonomic group and all recorded species together. The red dotted arrows connect centroids of the young, middle, and old successional stages, and show the main course of successional changes. Black arrows indicate the environmental factors (WT – water table; Rest Peat – the remaining peat layer after the extraction), dashed arrows show the vegetation structure (E3 – tree cover; E2 – shrub layer; E1 – herb layer; E0 – moss layer). All factors were passively projected. Centroids of particular groups of organisms and their position are indicated by abbreviations TB – tyrphobionts, TT – tyrphotolerants, and Others. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

composition between disturbed and reference raised bogs, and all groups of organisms exhibited deflected successional trajectories to the reference. The oldest successional stages tended to be more covered by woody species and were drier compared to the younger stages as well as the references. Obviously, the spontaneous succession of all groups of organisms did not direct towards the reference peat bogs at all. The gradient lengths in particular datasets were as follows: plants – 4.9; bryophytes – 3.8; fungi – 4.6; butterflies – 2.2; moths – 2.3 SD units. The merged dataset reached a gradient of 2.7 SD units. Tyrphobiont and tyrphotolerant species of all particular groups of organisms correlated with more open sites with a higher water table and a thicker remaining peat layer. On the contrary, the other species usually correlated with drier conditions, higher presence of trees (closed canopy), and higher pH.

Comparing all DCAs using the Procrustean analysis revealed that analyses based on moth and butterfly species datasets are the most similar, while the ordinations of both Lepidoptera groups are the least similar to the vascular plant ordination (Table 1). However, all cases showed high correlations between the first axes of the ordinations.

3.2. Environmental factors influencing particular taxonomic groups

Environmental factors significantly influencing the species composition of the whole dataset were remaining peat layer, average water table (WT), successional age, pH, and tree cover. In the separate CCA analyses, different factors appeared to be significant with different importance (Table 2). The most important factor in the case of plants as well as day butterflies was the remaining peat layer. On the other hand, water table was not a significant factor for these two groups at all. The species composition of bryophytes was influenced by all considered factors, except for tree cover. In the case of fungi, the most important factors were successional age, then water table and pH, but thickness of the remaining peat layer did not play a role. All presented factors influenced the species composition of moths, the most important factor being the remaining peat layer. The same was found when all taxonomic groups were considered together.

When we considered peatland specialists only, all groups of organisms were significantly influenced by successional age and pH, in the case of plants also by remaining peat layer, and in the case of moths by tree cover. Except for vascular plants, all groups of peatland specialists were significantly influenced by fewer factors than if all species were considered, however with higher explained variation. Butterfly peatland specialists cannot be evaluated due to the small number of species.

3.3. Trophic specialisation and most used plants

If all species of the respective taxonomic groups were considered, we found some successional patterns regarding to trophic specialisation, especially in the case of fungi. The average numbers of trophic specialists (degrees 1 and 2) increased during succession. In terms of Lepidoptera species, comparing the old stages and reference bogs, trophic specialisation was lower in all degrees in the reference. The successional trend was not evident if only peatland specialists were taken into account, but the average number of trophic specialists was the highest in the reference (Fig. 2).

Table 1

Results of Procrustean analysis; the percentage of discrepancy between the DCA ordinations, and correlations between their first two axes are indicated.

	Plants	Bryophytes	Fungi	Moths
Bryophytes	54% 0.88; 0.45	–	–	–
Fungi	39% 0.98; 0.45	44% 0.91; 0.63	–	–
Moths	56% 0.96; 0.34	39% 0.96; 0.86	51% 0.97; 0.72	–
Butterflies	56% 0.96; 0.64	43% 0.94; 0.86	53% 0.93; 0.66	16% 0.98; 0.95

Table 2

Results of particular CCAs followed by forward selection (999 permutations, Bonferroni correction); all significant factors are listed for each group of organisms ($p < 0.05$) with decreasing contribution.

	All species		Peatland specialists	
Group	% explained variation (adjusted)	Significant factors	% explained variation (adjusted)	Significant factors
Vascular plants	29.4%	Remaining peat; Successional age; pH	35.6%	Successional age; pH; Remaining peat
Bryophytes	20.3%	WT; pH; Remaining peat; Successional age	33.4%	Successional age; pH
Fungi	13.6%	Successional age, WT, pH	29.1%	Successional age; pH
Moths	60.6%	Remaining peat; WT, Tree cover; Successional age; pH	84.7%	Successional age; pH; Tree cover
Butterflies	61.6%	Remaining peat; Successional age; pH	cannot be evaluated	cannot be evaluated
All groups	32.5%	Remaining peat; WT; Successional age; pH; Tree cover	41.0%	Successional age; pH

The plant species most used by fungi and Lepidoptera were usually the dominant woody species and partly overlapped for the two groups (Table 3). Moreover, the number of species associated with woody plants increased with successional stage. Fungal species appreciated more bryophytes and *Cyperaceae* as compared to Lepidoptera species, which prefer *Populus* and prominently flowering plants such as *Calluna*, *Cirsium*, and the grass *Molinia*.

4. Discussion

All five groups of organisms showed very similar successional trajectories and all can be used to indicate successional or restoration processes, although plants are easiest to study (Walker and del Moral, 2003). Successional age was the most important explanatory factor for all groups if peatland specialists were taken into account, while other environmental factors were important in a different order for the respective groups if all species were considered. The expected increase in trophic specialisation during succession (Neutel et al., 2007) was evident in successional stages only if we considered all species. In the case of peatland specialists, no apparent successional trends in trophic specialisation were found, but the average number of trophic specialists was higher in the reference, which underlines their importance in restoration efforts.

4.1. Successional trajectories

The direction of succession in all five groups of organisms appeared to be very similar though not directing towards the reference as had earlier been expected (Konvalinková and Prach, 2014) but later already shown in another study (Vítovcová et al., 2022). The trajectory can be considered as deflected succession (Walker and del Moral, 2003). Although not directing towards the reference, the resulting successional stages developed after more than three decades by spontaneous development can be seen as an acceptable alternative stage (Gann et al., 2019) being composed of native species only. Nevertheless, the main nature conservation goal of restoring peatland will probably not be

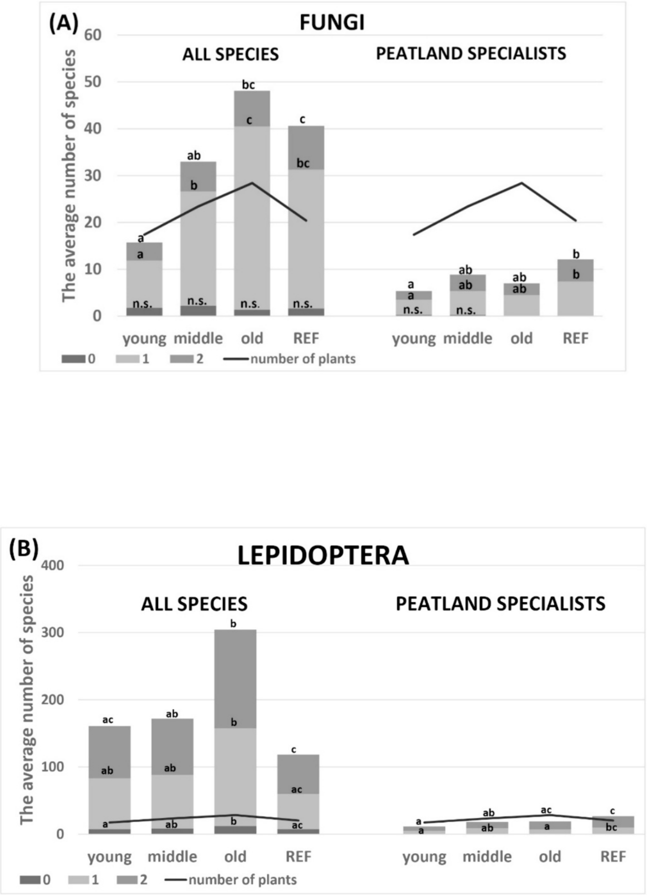

Fig. 2. Average numbers of species of (A) all fungi and fungal peatland specialists, and (B) all Lepidoptera species and Lepidoptera peatland specialists of particular trophic degrees (0, 1, 2) for successional stages and the reference. Black lines indicated the average number of plants per sample. Results of the Analysis of variance or the Kruskal-Wallis test followed by nonparametric post-hoc comparisons are indicated by letters (a, b, c) in the columns and show differences between successional stages and references in terms of the number of species in the respective trophic groups.

reached unless restoration measures are adopted. The main limiting factor responsible for the deflected trajectory seems to be the low water table probably supported by intensive transpiration of gradually closing woodland canopy (Kashian et al., 2023). If a peatland should be restored, a substantial rise of the water table is needed, and perhaps a reduction of tree density as well (Limpens et al., 2014). Similar conclusions, i.e. that abandoned mined peatlands do not return readily to a functional peat-forming system typically dominated by *Sphagnum* species, were presented by e.g. Poulin et al. (1999). *Sphagnum* species are the best indicators of peatland recovery (González et al., 2014) and were present in the studied successional stages only rarely (see Supplementary Table 1 and Vítovcová et al., 2022).

Comparison of the ordinations revealed the lowest similarity between both groups of Lepidoptera and plants, and the highest between both Lepidoptera groups. The latter is not surprising because of the same broad taxonomic affiliation and similar role in ecosystems (Summerville et al., 2004; Rákosy and Schmitt, 2011). The second highest similarity was evident between fungi and plants, both vascular and bryophytes. This is also expectable, as fungi are more closely confined to plants by their trophic relationships, while Lepidoptera are also influenced by overall vegetation structure, namely canopy cover and vertical structure (Vanreusel and van Dyck, 2007), which both influence, among others, their ability to penetrate into a habitat (Tyler, 2020). There was comparably low similarity between the ordinations of vascular plants and bryophytes, but the participation of these groups in peatland succession is often antagonistic (Purre et al., 2021). It must be stressed that the results of ordination do not express functional relationships between various groups of organisms. Their similar patterns can be influenced by some "third party" factors, i.e. particular environmental factors and successional age. Regarding the generally high similarity between the successional trajectories of the monitored organisms, it can be stated that in the future it may in some cases (e.g. lack of financial resources for detailed monitoring) be sufficient to surveyed only plants to show a successional trajectory.

4.2. Role of environmental factors

The results of the study indicate that the occurrence of vascular plants, bryophytes, fungi, and Lepidoptera species in formerly extracted raised bogs depends on similar factors, however with different importance. The most important factors were remaining peat layer, average water table (WT), successional age, pH, and tree cover. Räsänen et al. (2023) showed that spontaneous recovery of peatlands in general is determined by two main factors, remaining peat layer and water table. These two factors were significantly important for most of organisms also in our study. The removal of the upper peat layer is usually followed by a decrease in the thickness of the remaining peat due to decomposition if the water table is low (Lennartz and Liu, 2019). Interestingly, the water table was not the significant factor for vascular plants. It should be stressed that for plants the capillary pressure of the surface peat or volumetric water content may be a more important than water table itself (Price, 1997). Nevertheless, the decisive role of the water table in formerly extracted raised bogs has been shown by numerous studies (e.g. Lavoie et al., 2005; González et al., 2014; Konvalinková and Prach, 2014). In our case, the effect of the water table is probably overshadowed by the remaining peat layer factor, because sites with a thicker peat layer had a higher water table as well.

Compared to vascular plants, bryophytes react to changing environmental conditions faster and with strong fluctuations (Herben, 1987). Moreover, they have a different phenology and are much more abundant in moist conditions (Al-Mufti et al., 1977). The species composition of bryophytes was influenced by all considered factors, except for tree cover. Bryophytes, especially *Sphagnum*, take up water and nutrients with their entire body surface, therefore depend on a high water table in the substrate, precipitation, or high humidity (van Breemen, 1995). However in our case, the main successional changes in bryophyte species composition direct towards drier habitats with a higher pH, i.e. conditions completely different to those prevailing in preserved raised bogs. Under drier conditions, various species of true mosses (Bryopsida) such as *Pleurozium schreberi* are present, due to their relatively wide habitat amplitude and association with forest habitats (Hedwall et al., 2017).

In the case of fungi, the most important factor was successional age. The successional stage reflects the state of vegetation development as well as habitat development longevity and continuity. Therefore, the dependence of fungi on the time in which they can reach and establish at the site is expectable. The strength of the fungi-plant association varies between fungal groups and studied habitats (see discussion below). Generally, fungi forming fruitbodies are more strictly associated with vegetation than moulds and yeasts, which can be obtained with environmental sequencing methods (Vašutová et al., 2023). The occurrence of a fungal species is further influenced by a number of other factors which are difficult to study in the field, e.g. dispersal limitation, stochasticity, competition with other fungal species, and relationships with other groups of organisms.

All presented factors influenced the species composition of moths and butterflies, but remaining peat layer was the most important factor. Also plant species composition depends on a sufficient remaining peat layer. Thus, the Lepidoptera communities are connected to the vegetation, either as food plants or as nectar sources and the remaining peat

Table 3

Plants (first ten taxa) most used by (A) fungi and (B) Lepidoptera species, with numbers of species recorded to be associated with particular genera in permanent plots of the appropriate successional stages and the reference. Dashes mean that the plant species was not present. It should be noted that the Lepidoptera were sampled in larger plots (1 ha) compared to fungi (9 × 9 m).

Plants	Young		Middle		Old		Reference	
	Associated species	Average plant cover (%)	Associated species	Average plant cover (%)	Associated species	Average plant cover (%)	Associated species	Average plant cover (%)
A) Associated Fungi								
Pinus	15	1	35	5	40	5	68	20
Betula	8	1	33	10	84	20	–	–
Picea	0	0.1	19	1	28	10	16	1
Sphagnum	2	1	6	5	5	10	12	20
Juncus	10	3	8	3	7	3	–	–
Eriophorum	9	5	8	10	–	–	6	5
Carex	5	1	9	1	3	0.1	–	–
Vaccinium	1	0.1	4	1	0	0.02	9	10
Polytrichum	2	1	4	5	5	20	1	3
Salix	0	0.02	0	0.1	5	0.1	–	–
B) Associated Lepidoptera								
Betula	20	0.1	26	3	37	5	–	–
Populus	14	0.02	16	0.02	29	1	–	–
Salix	11	0.02	16	0.1	31	0.1	–	–
Picea	8	0.02	11	0.1	15	3	7	0.1
Pinus	7	0.1	10	1	12	1	10	5
Vaccinium	3	0.02	7	1	9	0.1	18	10
Calluna	5	0.1	5	0.1	9	0.1	7	1
Juncus	5	3	3	3	6	1	–	–
Cirsium	2	0.02	4	0.1	4	0.02	–	–
Molinia	0	0.02	5	0.1	5	1	–	–

layer influences them indirectly. Moreover, the Lepidoptera communities are significantly influenced by successional age, which is connected with habitat structure. Especially some open patches without trees, i.e. early successional stages, are necessary for some butterflies. On the other hand, in the case of moths, tree cover is an important factor, due to the associations of many species with woody species as food plants (Spitzer et al., 2003).

When we considered only peatland specialists, all groups of organisms were significantly influenced by successional age, probably due to the deflected successional trajectory towards the alternative drier state which hosts a rather different species pool with fewer peatland specialists. Other key factors are pH, remaining peat layer, and in the case of moths, tree cover as well. Most peatland specialists were significantly influenced by a fewer number of factors than all species, but they were considered to be more sensitive to them (Konvalinková and Prach, 2014). Regarding the importance of successional age, restoration should be carried out as soon as possible, otherwise the restored site will be colonised by alternative communities, not by peatland specialists.

4.3. Trophic specialisation

Our findings, despite some inconclusive results, are not contradictory to the expectations that trophic relationships increase during the course of succession (Temperton et al., 2004). This fact is probably connected to changes from prevailing generalists to specialists during succession (Ballesteros et al., 2023). Specialists are generally thought to be more competitive in natural communities, whereas generalists benefit from a certain degree of habitat destruction (Ramiadantsoa et al., 2018). Specialists are endangered by habitat loss and fragmentation, especially if they possess limited dispersal abilities (Büchi and Vuilleumier, 2014) and this endangerment can be multiplied by trophic association with other organisms.

Comparing fungi and Lepidoptera, fungi have a less strict association with plants – there are not so many species strictly associated to a genus, so we shifted their trophic specialisation scale (see Methods). Even so, there were about half the proportion specialists among fungi than in Lepidoptera. Generally, it was difficult to evaluate trophic associations of Ascomycota possessing tiny fruitbodies due to a lack of data. Moreover, the known associations have often exceptions, therefore they were classified in a lower category (1- associated with a wide range of plants). For example, a huge bulk of species associated with conifers exceptionally also use deciduous trees and vice versa. Most recorded fungal trophic specialists are also habitat specialists associated as saprotrophs or parasites with *Sphagnum* or as parasites with ericoid shrubs. Some other ones are associated with Pinaceae (*Pinus, Picea*, or both, or even other genera), Poaceae, or Cyperaceae, the first family also including ectomycorrhizal associations. It should be noted that the presence of a plant species is a necessary condition for the occurrence of trophic specialists, but not a guarantee.

In Lepidoptera, any generalisations of trophic specialisation in succession are also complicated because of the broader delimitation of suitable habitats, and appropriate studies are rare. For example, Slancarova et al. (2016) found no differences in trophic specialisation of Mediterranean butterfly communities between various successional stages. These mobile organisms require different resources during their lifetime, such as host plants, nectar supply, mate location sites, shelter for adults, etc. (Dennis et al., 2006). Even more, host plant ranges may shift regionally (e.g. Singer et al., 2002; Dennis et al., 2008). Nevertheless, peatland specialist Lepidoptera typically require a specific microclimate, especially humidity, and microtopography of the sites, rather than particular host plant species (Mikkola and Spitzer, 1983). However, these specialists often feed on a limited spectrum of tyrphobiont plants (e.g. *Vaccinium uliginosum*, *V. oxycoccos*, *Eriophorum* spp.), so a higher participation of trophic specialists at reference sites is easily explicable.

As for most used plants, fungi have preferences similar to Lepidoptera, except for associations with *Salix* and *Populus*. This is caused by their ability to form arbuscular mycorrhizae. Subsequently, they have a much lower diversity of ectomycorrhizal fungi. Moreover, the differences in size of sampled plots (four 9 × 9 m plots versus one 100 × 100 m plot) could have played a role. The number of species associated with selected plants increased with successional stage in the case of woody plants only (see Table 3), probably because increasing coverage and a prolonged time for establishing fungal species due to the long lifespan of woody species. To sum up, if communities of plant-associated organisms are to be successfully recovered, it is worth focusing on plant dominants.

The most used plants for *Lepidoptera* are, first of all, deciduous trees and shrubs followed by Pinaceae trees. This is mainly due to the species-rich guild of moths feeding on woody plant species, which reach a high cover at both disturbed (middle and old stages) and reference sites. Low *Vaccinium* and *Erica* shrubs also host plenty of species, partly tyrphobionts (Spitzer et al., 2003), but also species of other oligotrophic habitats in various successional stages. Generally, the high representation of common forest species in older stages of disturbed sites (and rare records of tyrphobionts) confirms the development towards an alternative state, where both vegetation and microclimatic conditions required by peat bog specialists are still missing. For successful restoration of the target communities, it is important to restore the dominant plant species composition because it provides the highest diversity of associated fungi and Lepidoptera species.

5. Conclusions

During three decades of spontaneous succession in formerly extracted raised bogs, the species composition of vegetation, fungi, and Lepidoptera did not reach the reference state. The successional pathways of all groups were very similar, it can be stated that in some justified cases (e.g. lack of financial resources) only plants may be surveyed to show a successional trajectory. Each group of organisms was also influenced by similar environmental factors but in a different order of importance. Apart from the water table, they were significantly influenced by thickness of the peat layer remaining after extraction, pH, successional age, and exceptionally by tree cover. Peatland specialists were influenced by fewer environmental factors, mainly by successional age and pH. An increase of trophic specialisation during succession was evident. Nevertheless, if taking into account peatland specialists only, no successional trend was recorded, and trophic specialisation was higher in the reference state. Restoration should be carried out as soon as possible, otherwise the restored site will be colonised by alternative communities instead of peatland specialists. More successful restoration can be achieved only if the water table substantially increases, a thicker peat layer is left, and the dominant plant species composition is fully restored because it provides the highest diversity of associated fungi and Lepidoptera species.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110649.

CRediT authorship contribution statement

Kamila Vítovcová: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Martina Vašutová:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Jana Lipárová:** Writing – review & editing, Methodology, Investigation. **Pavel Vrba:** Writing – review & editing, Methodology, Investigation. **Karel Prach:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors have no conflict of interest to declare.

Data availability statement

The dataset (presence and covers of all species in all successional stages) generated and analysed during the current study is available in the Supplementary material (Table 1) included in this manuscript.

Acknowledgement

The work was funded by the Czech Grant Agency (19-15031S). The authors thank the Šumava National Park Administration for permission to access the study sites. The authors express thanks to Alžběta Manukjanová, Pavlína Petrásková, Sujan Balami, Aleš Jirsa, Hedvika Synková, and Markéta Šandová for their help in the field and identification of fungal species, and Karel Jaroš for help with the identification of Lepidoptera species. The authors also thank for the language revisions to Jan Willem Jongepier.

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9 GENERAL CONCLUSIONS

Besides contributing to successional theory, the new findings from the meta-analysis across large datasets can have practical implications for projects of ecological restoration of disturbed habitats. The presented thesis is innovative in quantitatively comparing a large number of successional series together, helps to understand the processes and trajectories of vegetation development, and identifies key environmental factors influencing succession. We can conclude that species with higher values of the two proposed colonisation indices are more likely to spread over landscapes continuously disturbed by human activity. The quantification of species occurrence in differently aged successional stages also allows a prediction of the stage in succession which particular species may participate or possibly dominate in. Thus, the results presented may help predict future successional patterns in the Central European landscape and might prove useful in various restoration and landscape management projects. Related to the colonisation ability of species at disturbed sites, our findings can be implemented in e.g. projects using native regional seed mixtures or wherever fast re-vegetation is needed, e.g. urban sites and road verges (**Chapter I**). Our results suggest that, under certain circumstances, heavily damaged anthropogenic wastelands have similar conservation potential as rare natural unproductive habitats, such as barren, sandy areas or rock outcrops. Nevertheless, we recommend that mining activity should not destroy anything that might be more valuable than mining is able to create through restoration afterward (**Chapter II**). We conclude that abiotic factors, particularly climate and substratum pH, substantially influence the course of succession. These factors seem to be more important than the surrounding landscape structure, and the latter especially influences primary series. Surprisingly, the primary or secondary status of succession is less relevant than has usually been expected. Quantification of the role of these environmental factors may help to decide where spontaneous restoration is a viable option for the restoration of disturbed sites. We can determine which site is threatened by an invasion of alien species or undesirable expansive species, or on the other hand, which site deserves protection or special interest due to its high conservation value (**Chapter III**).

Concerning succession in formerly extracted raised bogs, during three decades of spontaneous development, the species composition of vegetation, fungi, and Lepidoptera did not reach the reference state, nor did it direct towards it. The successional pathways of all groups were very similar. Therefore, in some justified cases (e.g. lack of financial resources), only plants may be surveyed to show a successional trajectory. Each group of organisms was also influenced by similar environmental factors but in a different order of importance. Apart from the water table, they were significantly influenced by thickness of the peat layer remaining after extraction, pH, successional age, and exceptionally by tree cover. An increase in trophic specialisation during succession was evident. Based on the results, we can conclude that restoration, especially consisting of an artificial rise in the water table, should be carried out as soon as possible, otherwise the restored site will be colonised by alternative communities instead of peatland specialists. More successful restoration can be achieved only if the water table is close to the surface, a thicker peat layer has remained, and the dominant plant species composition, since it provides a suitable environment for associated fungi and Lepidoptera species (**Chapters IV and V**).

The prevailing earlier negative view on post-mining or other human-disturbed wastelands predetermined strictly technical solutions, i.e. reclamation, being usually oriented at future production outcomes (e.g. timber, crop). Thanks to ongoing research, this view has gradually changed toward a completely new paradigm considering these sites as surrogate habitats harbouring species retreating from contemporary cultural landscapes.

10 CURRICULUM VITAE

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EMPLOYMENT

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Scientometry

Number of citations = 472, h-index = 11 (Web of Science 21-2-2025)

PROJECTS

Team member in ongoing projects:

25-18351S (GAČR) Role of alien species in vegetation succession – from local to global scales, 2025–2027, investigator: K. Prach

Sigma PoC 01-01 (TAČR) Validation and optimisation of technology for collecting regional grass and herb seeds from species-rich grasslands, 2025–2026, investigator: K. Řehounková

SS07010037 (TAČR) Restoration of springs - retention of water in the landscape directly at the source, 2024–2026, investigator: K. Prach

SS07020238 (TAČR) Biodiverse green roofs supporting natural plant and insect communities, 2024-2026, co–investigator: K. Řehounková

24-10844S (GAČR) How do communities of different organisms respond to insularity in a fragmented mire habitat?, 2024–2026, co-investigator: K. Prach

101081177 (HORIZON-RIA) Effects of rewilding in forests and agricultural lands on carbon sequestration and diversity (WILDCARD), 2023–2027, coordinator: Universita Delgi Studi di Udine, project partner: PřF JU (K. Prach)

101103653 (EC Erasmus+) Team-up knowledge on ecological restoration to maximize benefits for nature and people (TEAM#UP), 2023–2027, coordinator: Hochschule Anhalt, project partner: PřF JU (K. Řehounková)

Team member in finished projects:

3211100009 (EEA and Norway grants) Regional seed mixtures as an effective tool for protecting the diversity of grassland habitats, 2022–2024, investigator: Český svaz ochránců přírody, project partner: PřF JU (K. Řehounková)

20-06065S (Czech Science Foundation) Patterns of vegetation succession at broad geographical scales: The time is ripe for comparative studies and meta-analyses, 2020–2023, investigator: K. Prach

2021-2-BE02-KA210-VET-000049240 (EC Erasmus+) TRAIN#ER-TRAIniNg Ecological Restoration, 2022, investigator: SERE, project partner: PřF JU (K. Řehounková)

20-08900S (Czech Science Foundation) Restoration of species rich grasslands: Do we miss intraspecific variability in our understanding to community assembly?, 2020–2022, investigator: O. Mudrák, co-investigator: K. Prach

19-15031S (Czech Science Foundation) Restoring biodiversity of disturbed peatlands as a basis for restoration of their future ecosystem functions and services, 2019–2021, investigator: Karel Prach

17-09979S (Czech Science Foundation) Factors determining vegetation succession at the country scale, 2017–2019, investigator: K. Řehounková

7AMB17DE017 (MŠMT) Establishment of species-rich field margins and wildflower strips in rural and urban areas - optimization of methods for biodiversity enhancement, 2017–2018, investigator: K. Prach

P505-11-0256 (Czech Science Foundation) Vegetation succession over broad environmental gradients – meta-analyses of data for theoretical and practical outputs, 2011–2014, investigator: K. Prach

OPVVV - PAPAVER Centre for human and plant studies in Europe and Northern Africa in the postglacial period, 2013–2015, investigator: J. Beneš

CONFERENCES

2024: Vítovcová K.: Ekologická obnova květnatých luk a nové technologie pro získávání regionálních směsí osiv. Konference Ekologie travního porostu IX, Technická univerzita Liberec, Czech Republic (Invited speaker).

2023: Vítovcová K., Řehounková K. & Tichý L.: Regional seed mixtures – efficiency of seed biomass harvesting. 10th World Conference on Ecological Restoration, Australia, Darwin (Oral presentation)

2021:
Vítovcová K. & Prach K.: Biodiversity restoration of formerly mined raised bogs – vegetation succession and recovery of other trophic groups. 12th European Conference on Ecological Restoration, Alicante, Spain (Oral presentation-online)

Vítovcová K. et al.: Obnova těžených rašelinišť - sukcese vegetace a dalších trofických skupin. 3th Conference Research Actualities in Bohemian Forest, Srní, Czech Republic (Oral presentation).

2019: Vítovcová et al.: Databáze sukcesních sérií – teoretické a praktické výstupy. Konference České botanické společnosti, Praha, Czech Republic (Oral presentation).

2016: Vítovcová K.: Colonization of disturbed sites by central European flora – new indicator values suggested. 10th European Conference on Ecological Restoration, Freising, Germany (Poster)

2014:
Lencová K.: How much do alien species participate in contemporary human-made habitats? With special attention to archaeophytes. 9th European Conference on Ecological Restoration, Oulu, Finsko (Oral presentation)

Jírová A. and Lencová K.: Obnova travinných ekosystémů na orné půdě. Konference České botanické společnosti, Praha, Czech Republic (Oral presentation)

2012: 8th European Conference on Ecological Restoration (ECER 2012), České Budějovice (member of the organization committee)

INTERNSHIPS

Anhalt University of Applied Sciences, Bernburg, Germany; working group led by Dr. Anita Kirmer and Prof. Dr. Sabine Tischew; 16 days: June 2017.

Western Norway University of Applied Sciences, Erasmus+, working group led by Knut Rydgren, 7 days: August 2023.

TEACHING ACTIVITIES

KBE/022 Ekologie/Ecology – practice, 2016.

KBO/137 Základní kurz z botaniky, fykologie a mykologie - cvičení/ Basic course in botany, phycology and mycology – practice, 2017.

KBO/447 Ekologie obnovy II – ekologická obnova/ Restoration ecology II – ecological restoration – field excursion 2017.

KBO/429 Zimní kurz ekologických měření/ Winter course in ecological measurements, 2022 and 2025.

KBE/410 Seminář z ekologie a ŽP/ Ecology and Environmental Protection seminar – practice on restoration ecology, 2024.

STUDENTS' SUPERVISION AND CONSULTANCY

Ongoing thesis

2024 GONCHAROVA Viktoriya Společenstva hub na obnovovaných lesních prameništích v CHKO a NP Šumava

2024 KAFKŮ Sáva Abiotické faktory prostředí ovlivňující uchycování vybraných druhů rašeliníků na těženém rašeliništi (MUNI Brno).

Defended theses

2024 ŠPRDLÍKOVÁ Anna Regionální semenná směs pro obnovu druhově bohatých lučních porostů

2023 VÁVROVÁ Adéla Vliv revitalizace na společenstva hub na obnovovaném rašeliništi Vlčí Jámy

2019 SLABA Michal Predikace druhového složení těžeben na základě biotopového mapování okolní krajiny: využití charakteristických druhů vyšších rostlin

Awards

Winning project in international competition Quarry Life Award (2012) – member of the team.