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A checklist of vascular plant, bryophyte and macrofungal mire specialists in the Czech Republic

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Abstract: Species can be classified as specialists or non-specialists for a habitat depending on their niche optimum. Habitat specialists exhibit a distinct conservation, functional and indication value and respond specifically to habitat fragmentation and deterioration. This is particularly important in highly vulnerable habitats, such as mires. In this study, we compiled a list of specialists of vascular plants, bryophytes and macrofungi associated with fens (minerotrophic mires) or bogs (ombrotrophic mires) for the Czech Republic. For fen specialists, the association with individual types of fens (calcareous fens, rich fens, poor fens) was further assessed. Taxa were classified into the two main categories reflecting the strength of their specialization: strict (obligate) and partial (facultative) specialists. Altogether 124 vascular plants, 100 bryophytes and 50 macrofungi were classified as either strict or partial specialists for fens or bogs. Out of them, 83 and 26 taxa are strict specialists for fens or bogs, respectively. Using occurrence records of strict specialists obtained from the distribution databases and other datasets, we reconstructed the former distribution of mire habitats in quadrants of grid flora mapping. Comparison of the reconstructed distribution with the current distribution of mire habitats showed their overall large decline. Significant conservation attention should be directed towards the vast majority of strict specialists of both fens and bogs, as well as selected partial specialists.

Keywords: bogs, ecological specialization, fens, floristic databases, peatlands, mire decline, rare species

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Introduction

Species differ in the width of their realized ecological niches (Hutchinson 1957), being either widespread non-specialist species (henceforth "non-specialists") or specialist species (henceforth "specialists") constrained to specific environments. The niches of some specialists are so narrow with respect to some ecological factors, or so specifically arranged along multiple gradients, that such species are largely associated with habitats to which they have tightly adapted during evolution (Di Cecco & Hurlbert 2022). If such a habitat disappears or deteriorates (i.e. its environmental conditions shift or become less specific), these species will become extinct – locally, regionally or globally. And vice versa, occurrences of specialists indicate specific types of habitats or ecosystems (henceforth "habitats").

Mire habitats in central Europe share a unique combination of environmental factors – especially high moisture and low availability of macronutrients – and an island-like distribution (Horsák et al. 2012, Mendez-Castro et al. 2021) making them important refugia of threatened biodiversity with a high proportion of narrow-niched specialists (Essl et al. 2012, Horsáková et al. 2018) accompanied by less specialized species having their optima in different habitats. Recently, rather than focusing on the overall species richness in mire ecology, the emphasis is put on the differentiation between mire specialists and non-specialists. This is relevant, for example, in studies focused on tracing the ongoing habitat changes, in which the overall species richness often increases, while that of conservationally important specialists decreases (Bergamini et al. 2009, Kapfer et al. 2011). Increase of non-specialists in the mire communities often signalizes the initial site deterioration as a consequence of decreasing environmental distinctiveness (Horsáková et al. 2018, Hájek et al. 2020) and the initiation of undesirable successional changes towards vegetation of tall herbs, mono-dominant stands of tall graminoids, wet meadows, shrubs or forests (Koch & Jurasinski 2015, Hájková et al. 2022, Kucharzyk et al. 2025).

Although the distinguishing between the mire specialists and non-specialists is not a new approach (compare Peus 1928), it was rarely applied in central Europe (Bergamini et al. 2009, Horsák et al. 2012, Navrátilová et al. 2022, Vítovcová et al. 2022) or in other regions (Pérez-Haase & Ninot 2017). The group of non-specialists is also denoted as "matrix-derived species", "generalists" or simply "other species", depending on the context of the study. For simplicity, we refer to all species that are not associated with mire habitats as non-specialists, although they may act as specialists in other habitats (e.g. grasslands). The lack of studies distinguishing specialists and non-specialists might be simply rooted in the absence of comprehensive species lists defining habitat specialists for regional scales, such as central Europe or the Czech Republic. The above-cited regional studies dealing with communities of vascular plants and bryophytes coped with this problem by defining the specialist species de novo or by adopting and modifying lists from studies on a European scale (Mucina et al. 2016, Horsáková et al. 2018, Chytrý et al. 2020; see below). Since the lists of specialists newly defined in regional studies frequently include only species present in the analysed dataset (i.e. species present in a series of vegetation plots or other sampling records), their application in studies with a different geographical scope is limited and often deserves a significant update.

At the European scale, the expert-based elaborated list of mire specialists was included in the study of Horsáková et al. (2018). Similarly, the lists of diagnostic taxa for European vegetation classes (Mucina et al. 2016) or EUNIS habitats (Chytrý et al. 2020) may serve as an overview of vascular plants and bryophytes associated with mire habitats. Transferability of these lists to the smaller geographic scales, such as the Czech Republic, is, however, limited due to several reasons. First, species may exhibit broader niches when a broader area is considered (Dítě et al. 2018, Hájek et al. 2022). Second, the continental-scale lists of habitat specialists may lack rare taxa and merge potential habitat specialists into aggregates more frequently. Third, the previous continental-scale lists of mire taxa do not distinguish between strict (obligate) and partial (facultative) specialists unlike analogous lists from other habitats (Heinken et al. 2022, Dítě et al. 2023). Fourth, some lists may be assembled for too specific purpose. For example, Allan et al. (2024) assembled specialists for temperate-boreal peatlands focused on restoration of carbon sequestration, but excluded some fen indicators such as *Scorpidium cossonii* and *S. scorpioides* (cf. Rybníček 1966, Kooijman & Westhoff 1995, Bergamini et al. 2009). As a consequence of these constraints of continental-scale checklists, regional expert-based lists of specialists are being assembled (e.g. Hammerich et al. 2022). For the Czech Republic, a comprehensive critical list of strict and partial mire specialists covering the entire territory and different mire habitats is missing. The lists of diagnostic species of individual vegetation units (Chytrý 2011) do not report all specialized taxa, as they are based on analysis of vegetation plots and thus constrained by the completeness, rarity pattern, and taxonomic resolution of the underlying dataset. Sádlo et al. (2007) compiled vascular plant species pools for habitats, but did not distinguish between specialists and non-specialists. The absence of a list of specialists also applies to macrofungi, i.e. fungi forming macroscopically visible fruiting bodies. Thormann & Rice (2007) compiled a comprehensive yet uncritical overview of fungi occurring in mires and other peatlands without distinguishing mire habitat specialists. Hofmeister & Hošek (2016) published indicator species for natural habitats of the Czech Republic, but they did not distinguish species with different diagnostic value. Moreover, this work was compiled more than a decade ago and therefore does not reflect the most recent findings.

Having habitat specialists critically assembled opens the possibility to track recent and even former distributions of habitats. Although the quantification of a decline in the habitat's area over the last 50 years belongs among the criteria for classification into IUCN Red list categories (Keith et al. 2013, Chytrý et al. 2019), such data are largely unavailable. With robust historical taxa occurrence databases available for regions like the Czech Republic (Chytrý et al. 2021), the list of indicator specialists remains the link in the reconstruction puzzle.

In this study, we (i) compile a critical list of strict and partial specialists of vascular plants, bryophytes and macrofungi for mire habitats in the Czech Republic, (ii) apply the list to reconstruct the former distribution of mire habitats, and (iii) compare the resulting reconstruction with the current distribution to estimate the overall decline of mire habitats.

Material and methods

Target habitats

With respect to the hydrology and site chemistry that affect species compositions, mires are traditionally divided into two main types: fens (minerotrophic mires) and bogs (ombrotrophic mires), with fens being further subdivided according to the mineral richness gradient; see Malmer (1986), Hájek et al. (2006), Chytrý (2011) and Joosten et al. (2017) for details. Preserved fens in the Czech Republic are non-forested, while bogs might be covered by a sparse tree layer of *Pinus uncinata* subsp. *uliginosa* or, less frequently, *Pinus sylvestris* (*Ledo palustris-Pinetum uncinatae* and *Sphagno-Pinetum sylvestris* associations; Chytrý 2011).

Apart from categorizing specialists separately for fens and bogs, we assembled the lists of specialists for the following, easily distinguished fen habitats: (i) Calcareous fens ("calcareous fens" and "extremely-rich fens" sensu Hájek et al. 2006). These fens are characterized by high pH and calcium content, occurring on organic peat intermixed with carbonates, or mineral sediments such as calcareous tufa, or lacustrine chalk. Vegetation is characterized by the presence of calcicole vascular plants and a complete absence of *Sphagnum* species. (ii) Rich fens ("rich fens" and "moderately rich fens" sensu Hájek et al. 2006). These fens developed under intermediate pH and calcium concentrations, allowing for the occurrence of calcium-tolerant *Sphagnum* species. However, *Sphagnum* species do not entirely dominate the habitat, enabling a wide array of other mosses and vascular plants to co-occur, including calcicole and various wetland and grassland species. (iii) Poor fens. Acidic fens developed under low pH and low calcium concentration, usually heavily dominated by late-successional *Sphagnum* species together with other acidophilous bryophytes. Calcicole species are missing and species richness is lower than in the previous types.

A crosswalk of the target mire habitat types to syntaxa, main ecological types and habitats according to the national habitat classification of the Czech Republic and EUNIS classification is summarized in Table 1.

List of specialists

As a baseline, the candidate list of specialist species was assembled based on: (i) diagnostic and characteristic (constant) vascular plant and bryophyte species for mire habitats revealed in continental-scale syntaxonomical overviews and vegetation studies (Mucina et al. 2016, Peterka et al. 2017, Jiroušek et al. 2022) or habitat typologies (Chytrý et al. 2020); (ii) diagnostic and characteristic (constant) vascular plant and bryophyte species for individual mire habitats following Habitat Catalogue of the Czech Republic (Chytrý et al. 2010), indicator macrofungal species for the similarly defined mire habitats (Hofmeister & Hošek 2016); (iii) the list of vascular plants that differentiate Bohemian calcareous fens against other habitats (Sádlo 2000); (iv) other ecological studies defining vascular plant, bryophyte or macrofungi specialists for mires in central Europe (Peterka et al. 2022, Vítovcová et al. 2022) or at the continental scale (Horsáková et al. 2018).

The candidate list of mire specialists was expanded to include rare, scattered, and newly recognized taxa, using an extensive review of national floras (Hejný et al. 1988, 1990, 1992, Slavík et al. 1995, 1997, 2000, 2004, Štěpánková et al. 2010, 2024) and other

Table 1. Crosswalk of target types of mires to vegetation units (according to the Vegetation of the Czech Republic; Chytrý 2011), typology of fens in central Europe (Hájek et al. 2006), national habitat classification (according to Habitat Catalogue of the Czech Republic; Chytrý et al. 2010) and EUNIS habitat classification (Chytrý et al. 2020).

Type of mire habitat (this study)	Vegetation of the Czech Republic (Chytrý 2011)	Typology of central-European fens (Hájek et al. 2006)	Habitat Catalogue of the Czech Republic (Chytrý et al. 2010)	EUNIS habitat classification (Chytrý et al. 2020)
1. fens	*Scheuchzerio palustris-Caricetea nigrae* (except *Sphagnion cuspidati*)	fens		
1a. calcareous fens	*Caricion davallianae*	calcareous fens, extremely-rich fens	R2.1 Calcareous fens (+ R1.1 Meadow springs with tufa formation)	Q41 Alkaline, calcareous, carbonate-rich small-sedge spring fen, Q43 Tall sedge base-rich fen
1b. rich fens	*Sphagno warnstorfii-Tomentypnion nitentis*, *Caricion canescenti-nigrae*	rich fens, moderately-rich fens	R2.2 Acidic moss-rich fens	Q24 Intermediate fen and soft-water spring mire, Q42 Extremely rich moss–sedge fen, Q44 Calcareous quaking mire
1c. poor fens	*Sphagno-Caricion canescentis*	poor fens	R2.3 Transitional mires	Q22 Poor fen, Q25 Non-calcareous quaking mire (partly)
2. bogs (including bog hollows)	*Oxycocco-Sphagnetea*, *Sphagnion cuspidati* (*Scheuchzerio-Caricetea nigrae*)	bogs	R3 Raised bogs	Q11 Raised bog, Q21 Oceanic valley mire, Q25 Non-calcareous quaking mire (partly)

literature (Dierßen 2001 and papers listed in Supplementary Data S1), and following discussions with the experts listed in Acknowledgements. Because the degree of specialization was primarily assessed at taxonomic ranks of species and subspecies, but in some cases also at the level of aggregates, we refer below to a list of mire specialist taxa rather than mire specialist species. Hybrids were not considered, except for *Drosera ×obovata* (*D. anglica* × *D. rotundifolia*), *Pinus ×ascendens* nothosubsp. *skalickyi* (*P. mugo* × *P. uncinata* subsp. *uliginosa*) and *Schoenus ×scheuchzeri* (*S. ferrugineus* × *S. nigricans*). They may occur at sites or in individual vegetation plots where both parents are missing (Klika 1945, Slavík et al. 1997, Kaplan et al. 2023). Their inclusion hence prevents the loss of information for such sites in the phase of the subsequent list application.

Concurrently with the initial compilation of the list, categories of specialist taxa were defined. Based on the concepts introduced by Heinken et al. (2022) and Dítě et al. (2023) and our extensive field experience from various mire habitats, two categories of specialists were adopted: strict specialists and partial specialists (Table 2). At the first hierarchical level, we evaluate whether taxa are associated with fens or bogs compared to other habitats (mainly wet meadows, tall-sedge beds and marshes, springs, alder carrs, peatland forests, or montane spruce forests). Within the group of fen specialist taxa, their

Table 2. Categories of specialization defined by association with either fens or bogs, and in the case of fen specialists, by association with specific types of fen habitats in the Czech Republic. Names of categories of specialization are followed by numerical values in brackets, these values are used in Table 3 and Supplementary Table S3.

Category of specialization	Description
Strict specialist (2)	The taxon occurs exclusively or almost exclusively in either fens or bogs. It may grow in other habitats, but only exceptionally or in extremely rare habitats, such as seepages and wet rocks in glacial cirques, oligotrophic quarry pools, etc. Strict fen specialist does not occur with any significant frequency in bogs or other wetlands; conversely, a strict bog specialist does not occur with any significant frequency in fens. The occurrence of a strict specialist indicates with high probability the current or past presence of either fens or bogs at the site. In the case of strict specialists of fen types (calcareous fens, rich fens or poor fens), the taxon occurs exclusively or almost exclusively in the given fen type. It may grow in other mire habitats, but only extremely rarely; when it occurs in other fen habitat, the stands then often represent transitional vegetation types or communities occurring in the close contact with the habitat where the taxon occurs at its optimum. The occurrence of a strict specialist indicates with high probability the current or past occurrence of a particular fen habitat.
Partial specialist (1)	The taxon occurs predominantly in either fens or bogs; it may occur in other habitats (springs, intermittently wet and wet meadows, reed beds, the littoral zones of oligotrophic waters) as well, but with lower or equal frequency. Taxa that have equally important ecological optima in both fens and bogs are assessed as partial specialists for both habitats. In the case of partial specialists of fen types, the taxon occurs predominantly in the given type of fen. However, it may occur with lower or equal frequency in other fen types, bogs, or in other wetlands. Strict specialists of fens can be partial specialists of more fen types if they occur in given types with an equal frequency.
Uncertain case of strict or partial specialist (2?, 1?)	The affinity to the given habitat cannot be unequivocally evaluated, because (i) the taxon has already become extinct at all sites, or at their majority, or (ii) its ecology is not sufficiently known. However, an association with the given habitat is probable. In some cases, the historical occurrence of the taxon in the Czech Republic is uncertain.
Non-specialist (0)	The taxon occurs in either fens (or given type of fen) or bogs with lower frequency than in any other habitat. Non-specialist for fen and bog habitats may be, however, specialists for other habitats (e.g. for some type of grasslands, forests, or aquatic habitats).
Non-specialist with regional affinity to mire habitats (0 reg.)	The taxon occurs in bogs, fens (or given type of fen) only in a specific region. This association is not necessarily determined by an ecological relationship with mires, but rather by the absence of any other at least partly suitable habitats in the region.

associations with particular fen types (i.e. calcareous fens, rich fens and poor fens) were further assessed (for details see Table 2).

During subsequent discussions and re-evaluations of individual taxa, the categories of specialists were further revised. Specifically, it became necessary to also consider taxa that are currently extinct or nearly extinct in the Czech Republic, or exhibit regional differences in their association with mire habitats. Besides strict specialists, partial specialists and non-specialists, we hence established the following categories: (i) uncertain cases of strict or partial specialists and (ii) non-specialists with regional affinity to mires. Delimitation of all the types is summarized in Table 2.

The updated list of potential specialists with preliminary set categories of specialism was again critically assessed by the authors of this study. Particular attention was paid to discrepancies among individual assessments; the underlying reasons for these differences were examined, and the assessments were subsequently discussed and harmonized to ensure internal consistency. Regional or taxonomic experts (see Acknowledgements) were contacted for their opinion on unresolved issues.

Nomenclature and delimitation of aggregates

The taxonomic concepts and nomenclature of vascular plants are line with Kaplan et al. (2019), except for *Dactylorhiza maculata* agg. treated according to Taraška et al. (2023). The nomenclature of bryophytes mostly follows Kučera et al. (2012), with recently recognized peatmosses *Sphagnum divinum* and *S. medium* (*S. magellanicum* agg.) named in accordance with Hassel et al. (2018). The names of macrofungi follow Zíbarová et al. (2024); the names of taxa not listed in this work were standardized using the MycoBank database (Robert et al. 2013; accessed 30 January 2026).

In several cases, the degree of specialization was also assessed at the level of species complexes (aggregates) besides included taxa. We assume that knowledge of the category of specialization may be beneficial even for aggregates, because field identification is often performed only at this level, especially in vegetation research or during some other botanical surveys (e.g. habitat mapping). If an aggregate contains specialist and non-specialist taxa, both categories are included in the list (Table 3). Aggregates not defined in the sources referenced above are delimited as follows: *Campylium stellatum* agg. (*C. protensum*, *C. stellatum*), *Cephaloziella elachista* agg. (*C. elachista*, *C. spinigera*), *Scorpidium revolvens* agg. (*S. cossonii*, *S. revolvens*), *Sphagnum auriculatum* agg. (*S. auriculatum*, *S. inundatum*), *Sphagnum magellanicum* agg. (*Sphagnum divinum*, *S. medium*), *Sphagnum palustre* agg. (*S. centrale*, *S. palustre*), and *Sphagnum recurvum* agg. (*S. angustifolium*, *S. fallax*, *S. flexuosum*), *Arrhenia gerardiana* agg. (*A. bigelowii*, *A. gerardiana*).

Salix repens and *S. rosmarinifolia* were evaluated in the list of specialists only at the aggregate level, as a proper assessment of their ecology is complicated by morphologically transitional forms and by the prevalence of hybrids among specimens originally assigned as *S. repens* (R. Vašut, personal communication). By analogy, the complex of *Campylium protensum* and *C. stellatum* (*C. stellatum* agg.) comprises several genetic entities within the territory of the Czech Republic showing considerable ecological and morphological variability (J. Kučera, personal communication).

Characterization of vascular plant specialists using Ellenberg-type indicator values

Ellenberg-type indicator values (EIVs) of vascular plants occurring in the Czech Republic (Chytrý et al. 2018) were used to characterize ecological demands of specialist taxa within the context of the Czech flora. We showed key environmental gradients determining mire occurrence: high water level or site moisture, low availability of nutrients and generally sufficient supply of light (Malmer 1986, Hájek et al. 2006, Joosten et al. 2017). To visualize species' ecological niches, EIVs for moisture, nutrients and light were plotted in pairwise scatter diagrams, with each combination of these three variables. Analyses were visualized separately for bogs and fens to account for their differing ecological conditions and specialist-species composition. Diagrams were created using the scatterplot3d package (Ligges & Mächler 2003) in R version 4.3.2 (R Core Team 2023).

Table 3. List of specialists for mire habitats in the Czech Republic. Numerical values refer to the categories of specialization for a habitat, for explanatory notes see Table 2. Taxa are marked in bold except for aggregates with listed subordinate taxa, non-specialists and uncertain cases of specialists. Taxa are arranged in alphabetical order, except for those belonging to aggregates. Delimitation of aggregates is indicated by a right chevron (>) before the taxon name.

Taxon	Main mire habitat types		Habitat types of fens		
	fens	bogs	calcareous	rich	poor
Vascular plants:					
Agrostis canina	1	0	0	1	1
Anacamptis palustris	1	0	1	0	0
Andromeda polifolia	0	2	0	0	0
Angelica palustris	1?	0	1?	0	0
Betula humilis	2?	0	1?	1?	1?
Betula nana	0	2	0	0	0
Blysmus compressus	2	0	2	0	0
Calamagrostis purpurea	1	0	0	1	1
Calamagrostis stricta	2	0	1	1	0
Calamagrostis varia	1	0	1	0	0
Carex appropinquata	1	0	1	1	0
Carex buxbaumii	1	0	1	1	0
Carex canescens	1	0	0	1	1
Carex chordorrhiza	2	0	0	1	1
Carex davalliana	2	0	1	1	0
Carex diandra	2	0	0	1	1
Carex dioica	2	0	0	2	0
Carex distans	1	0	1	0	0
Carex echinata	1	0	0	1	1
Carex flava agg.	1	0	1	1	1
> *Carex flava*	1	0	1	1	0
> *Carex demissa*	1	0	0	1	1
> *Carex lepidocarpa*	2	0	2	0	0
> *Carex oederi*	1	0	1	0	0
Carex hartmanii	1	0	0	1	0
Carex hostiana	2	0	2	0	0
Carex lasiocarpa	2	0	1	1	1
Carex limosa	1	1	0	1	1
Carex magellanica	1	1	0	0	1
Carex nigra	1	0	0	1	1
Carex panicea	1	0	1	1	1
Carex pauciflora	0	2	0	0	0
Carex pulicaris	2	0	1	1	0
Carex rostrata	1	0	1	1	1
Cladium mariscus	2	0	2	0	0
Comarum palustre	1	0	0	1	1
Dactylorhiza bohemica	2	0	0	2	0
Dactylorhiza carpatica	2	0	2	0	0
Dactylorhiza curvifolia	2?	0	1?	1?	1?
Dactylorhiza incarnata	1	0	1	0	0
Dactylorhiza incarnata* subsp. *incarnata	1	0	1	0	0
Dactylorhiza incarnata* subsp. *pulchella	1	0	0	1	1?
Dactylorhiza maculata* subsp. *averyanovii	1	1	0	0	1
Dactylorhiza maculata* subsp. *maculata	2	0	1	1	1
Dactylorhiza maculata* subsp. *sudetica	1	0	0	1	1
Dactylorhiza maculata* subsp. *transsilvanica	1	0	0	1	0
Dactylorhiza majalis	1	0	1	1	0

Taxon	Main mire habitat types fens	bogs	Habitat types of fens calcareous	rich	poor
Dactylorhiza traunsteineri	1	0	0	1	1
Dactylorhiza traunsteineri* subsp. *traunsteineri	2	0	0	1	1
Dactylorhiza traunsteineri* subsp. *turfosa	1	0	0	0	1
Drosera anglica	1	1	1?	1	0
Drosera intermedia	2	0	0	1	1
Drosera rotundifolia	1	1	0	1	1
Drosera ×obovata	1	1	0	0	1
Dryopteris cristata	1	0	0	1	1
Eleocharis quinqueflora	2	0	2	0	0
Empetrum nigrum agg.	0	1	0	0	0
> *Empetrum hermaphroditum*	0	0	0	0	0
> *Empetrum nigrum*	0	2	0	0	0
Epilobium palustre	1	0	0	1	1
Epipactis palustris	1	0	1	1	0
Equisetum variegatum	1	0	1	1	0
Erica tetralix	0	2	0	0	0
Eriophorum angustifolium	2	0	1	1	1
Eriophorum gracile	2	0	0	1	1
Eriophorum latifolium	2	0	1	1	0
Eriophorum vaginatum	1	1	0	0	1
Gentianella amarella* subsp. *lingulata	2	0	2	0	0
Gymnadenia densiflora	1	0	1	0	0
Gymnadenia odoratissima	1?	0	1?	0	0
Hammarbya paludosa	2	0	0	1	1
Herminium monorchis	1	0	1	0	0
Hydrocotyle vulgaris	1	0	0	1	1
Juncus alpinoarticulatus	2	0	1	1	0
Juncus filiformis	1	0	0	0	1
Juncus subnodulosus	2	0	2	0	0
Ligularia sibirica	1	0	1	1	0
Liparis loeselii	2	0	1	1	0
Luzula sudetica	1	0	0	1	1
Lycopodiella inundata	1	1	0	1	1
Lysimachia thyrsiflora	1	0	0	1	1
Menyanthes trifoliata	1	0	1	1	1
Narthecium ossifragum	1?	0	0	1?	1?
Nasturtium microphyllum	1?	0	1?	0	0
Parnassia palustris	2	0	1	1	0
Pedicularis palustris	2	0	1	1	1
Pedicularis palustris* subsp. *palustris	2	0	1	1	1
Pedicularis palustris* subsp. *opsiantha	2	0	0	2	0
Pedicularis sceptrum-carolinum	2?	0	0	2?	0
Pedicularis sylvatica	1	0	0	1	1
Pinguicula vulgaris	1	0	1	1	0
Pinguicula vulgaris* subsp. *bohemica	2	0	1	1	0
Pinguicula vulgaris* subsp. *vulgaris	1	0	1	1	0
Pinus ×ascendens* nothosubsp. *skalickyi	0	1	0	0	0
Pinus uncinata* subsp. *uliginosa	0	2	0	0	0
Polygala amarella	1	0	1	0	0
Primula farinosa	2	0	2	0	0
Rhododendron tomentosum	0	1	0	0	0
Rhynchospora alba	1	1	0	1	1
Rhynchospora fusca	2	0	0	1	1
Rubus chamaemorus	0	2	0	0	0

Taxon	Main mire habitat types		Habitat types of fens		
	fens	bogs	calcareous	rich	poor
Sagina nodosa	1	0	1	1	0
Salix myrsinifolia	1	0	0	1	1
Salix myrtilloides	2	0	0	1	1
Salix pentandra	1	0	0	1	1
***Salix repens* agg.**	1	0	1	1	1
Salix starkeana	2?	0	1?	1?	0
Saxifraga hirculus	2?	0	1?	1?	0
Sedum villosum	2	0	0	2	0
Sesleria uliginosa	1	0	1	0	0
Scheuchzeria palustris	0	2	0	0	0
Schoenus ferrugineus	2	0	2	0	0
Schoenus nigricans	2	0	2	0	0
Schoenus ×scheuchzeri	2	0	2	0	0
Spiranthes aestivalis	2?	0	2?	0	0
Swertia perennis	1	0	0	1	0
Tephroseris palustris	1?	0	0?	1?	1?
Thelypteris palustris	1	0	1	1	1
Tofieldia calyculata	2	0	2	0	0
Triglochin palustris	2	0	1	1	0
Trichophorum alpinum	2	0	0	2	0
Trichophorum cespitosum	0	2	0	0	0
Utricularia intermedia agg.	2	0	0	1	1
> *Utricularia intermedia*	2	0	0	1	1
> *Utricularia ochroleuca*	2	0	0	1	1
Utricularia minor agg.	1	0	1	1	1
> *Utricularia bremii*	1	0	0	1	1
> *Utricularia minor*	1	0	1	1	1
Vaccinium oxycoccos agg.	1	1	0	1	1
> *Vaccinium microcarpum*	0	2	0	0	0
> *Vaccinium oxycoccos*	1	1	0	1	1
Vaccinium uliginosum	0	1	0	0	0
Valeriana dioica	1	0	1	1	0
Valeriana simplicifolia	1	0	1	1	0
Viola epipsila	1?	0	1?	1?	0
Viola palustris	1	0	0	1	1
Viola uliginosa	1?	0	1?	1?	0
Willemetia stipitata	1	0	0	1	1
Bryophytes:					
Aneura pinguis	1	0	1	1	0
Aulacomnium palustre	1	1	0	1	1
Brachythecium mildeanum	1	0	0	1	0
Breidleria pratensis	1	0	0	1	0
Bryum longisetum	2?	0	0	1?	1?
Bryum pseudotriquetrum	1	0	1	1	0
Calliergon giganteum	2	0	1	1	0
Calliergon richardsonii	2?	0	0	2?	0
Calypogeia neesiana	0	1	0	0	1
Calypogeia sphagnicola	1	1	0	0	1
Campyliadelphus elodes	2	0	2	0	0
***Campylium stellatum* agg.**	1	0	1	1	0
Cephalozia connivens	1	1	0	1	1
Cephalozia loitlesbergeri	0	2	0	0	0
Cephalozia macrostachya	1	1	0	0	1

Taxon	Main mire habitat types		Habitat types of fens		
	fens	bogs	calcareous	rich	poor
Cephalozia pleniceps	1	0	0	1	0
***Cephaloziella elachista* agg.**	1?	1	0	0	1?
Chiloscyphus pallescens	1	0	0	1	1
Cinclidium stygium	2?	0	0	2?	0
Cladopodiella fluitans	0	2	0	0	0
Cladopodiella francisci	0	1	0	0	0
Dicranum bonjeanii	1	0	0	1	0
Dicranum undulatum	0	1	0	0	0
Drepanocladus lycopodioides	2	0	2	0	0
Drepanocladus polygamus	2	0	1	1	0
Drepanocladus sendtneri	1	0	1	0	0
Drepanocladus trifarius	2	0	0	2	0
Fissidens adianthoides	2	0	1	1	0
Fissidens osmundoides	1	0	1	1	0
Gymnocolea inflata	1	1	0	0	1
Hamatocaulis vernicosus	2	0	0	2	0
Helodium blandowii	2	0	0	2	0
Kurzia pauciflora	0	2	0	0	0
Lophozia wenzelii	0	1	0	0	0
Meesia longiseta	2	0	0	2?	0
Meesia triquetra	2	0	0	2	0
Meesia uliginosa	1	0	0	1	0
Mylia anomala	0	2	0	0	0
Odontoschisma sphagni	0	2	0	0	0
Pallavicinia lyellii	1	0	0	0	1
Paludella squarrosa	2	0	0	2	0
Palustriella commutata	1	0	1	0	0
Palustriella decipiens	1	0	1	1	0
Philonotis calcarea	1	0	1	0	0
Philonotis fontana	1	0	1	1	0
Plagiomnium ellipticum	1	0	0	1	0
Polytrichum commune	1	1	0	0	1
Polytrichum strictum	1	1	0	1	1
Pseudocampylium radicale	1	0	0	1	1
Rhizomnium pseudopunctatum	2	0	0	1	0
Riccardia chamedryfolia	1	0	0	1	1
Riccardia incurvata	1	0	1	1	0
Riccardia multifida	1	0	0	1	1
Sarmentypnum exannulatum	2	0	0	1	1
Sarmentypnum sarmentosum	2	0	0	1	1
Scapania irrigua	1	0	0	1	1
Scapania paludicola	1	1	0	0	1
Scapania paludosa	1	1	0	0	1
Scorpidium revolvens agg.	2	0	1	1	0
> *Scorpidium cossonii*	2	0	1	1	0
> *Scorpidium revolvens*	2	0	0	2	0
Scorpidium scorpioides	2	0	0	2	0
Schljakovia kunzeana	0	1	0	0	0
Sphagnum affine	1	0	0	0	1
Sphagnum auriculatum agg.	1	0	0	1	1
> *Sphagnum auriculatum*	1	0	0	0	1
> *Sphagnum inundatum*	1	0	0	1	1
Sphagnum austinii	0	2?	0	0	0
Sphagnum balticum	0	2	0	0	0

Taxon	Main mire habitat types		Habitat types of fens		
	fens	bogs	calcareous	rich	poor
Sphagnum capillifolium	1	1	0	0	1
Sphagnum compactum	0	1	0	0	0
Sphagnum contortum	2	0	0	2	0
Sphagnum cuspidatum	0	2	0	0	0
Sphagnum fimbriatum	1	0	0	1	1
Sphagnum fuscum	0	2	0	0	0
Sphagnum lindbergii	0	2	0	0	0
Sphagnum magellanicum agg.	1	1	0	0	1
> *Sphagnum divinum*	1	1	0	0	1
> *Sphagnum medium*	0	2	0	0	0
Sphagnum majus	0	2	0	0	0
Sphagnum molle	1?	0	0	0	1?
Sphagnum obtusum	2	0	0	1	1
Sphagnum palustre agg.	1	0	0	1	1
> *Sphagnum centrale*	1	0	0	0	1
> *Sphagnum palustre*	1	0	0	1	1
Sphagnum papillosum	1	1	0	0	1
Sphagnum platyphyllum	2	0	0	1	1
Sphagnum recurvum agg.	1	1	0	1	1
> *Sphagnum angustifolium*	1	1	0	1	1
> *Sphagnum fallax*	1	1	0	0	1
> *Sphagnum flexuosum*	2	0	0	1	1
Sphagnum riparium	1	0	0	0	1
Sphagnum rubellum	0	2	0	0	0
Sphagnum russowii	1	1	0	0	1
Sphagnum subnitens	2	0	0	1	1
Sphagnum subsecundum	2	0	0	1	1
Sphagnum tenellum	0	2	0	0	0
Sphagnum teres	2	0	0	1	1
Sphagnum warnstorfii	2	0	0	2	0
Splachnum ampullaceum	1	1	0	0	1
Splachnum sphaericum	1	1	0	0	1
Straminergon stramineum	1	1	0	1	1
Tomentypnum nitens	2	0	1	1	0
Warnstorfia fluitans	0	1	0	0	0
Warnstorfia pseudostraminea	1	0	0	0	1
Macrofungi:					
Agrocybe elatella	2	0	0	1	1
Armillaria ectypa	2	0	0	2	0
Arrhenia gerardiana agg.	1	1	0	0	1
> *Arrhenia bigelowii*	1	1	0	0	1
> *Arrhenia gerardiana*	1	1	0	0	1
Arrhenia lobata	2	0	1	1	0
Arrhenia telmatiaea	1	1	0	0	1
Arrhenia turficola	2	0	0	1?	1
Ascocoryne turficola	1	1	0	0	1
Bovista paludosa	2	0	1	1	0
Clavaria sphagnicola	1	1	0	0	1
Cortinarius chrysolitus	1	0	0	0	1
Cortinarius davemallochii	0	1	0	0	0
Entoloma cuspidiferum	1	0	0	0	1
Entoloma elodes	1	1	0	0	1
Entoloma mougeotii	1	0	1	1	0

Taxon	Main mire habitat types		Habitat types of fens		
	fens	bogs	calcareous	rich	poor
Entoloma sphagnorum	1	0	0	1	1
Galerina hybrida	1	1	0	0	1
Galerina mairei	1	1	0	0	1
Galerina norvegica	1	1	0	0	1
Galerina paludosa	1	1	0	0	1
Galerina sphagnicola	0	2	0	0	0
Galerina sphagnorum	1	1	0	0	1
Geoglossum uliginosum	1	0	0	1	1
Gymnopilus fulgens	1	1	0	0	1
Hemileucoglossum pusillum	2	0	1	1	0
Hohenbuehelia longipes	2	0	0	2	0
Hygroaster borealis	0	2	0	0	0
Hygrocybe coccineocrenata	2	0	0	1	1
Hygrocybe conicopalustris	2	0	0	1	1
Hypholoma elongatum	1	1	0	0	1
Hypholoma udum	1	1	0	0	1
Lycoperdon caudatum	1	0	1	1	0
Monilinia baccarum	1	1	0	0	1
Monilinia megalospora	0	1	0	0	0
Monilinia oxycocci	1	1	0	0	1
Monilinia urnula	1	1	0	0	1
Mycena megaspora	1	1	0	0	1
Myriosclerotinia caricis-ampullaceae	2	0	0	0	2
Myriosclerotinia dennisii	1	1	0	0	1
Panaeolus reticulatus	2	0	1	1	0
Phaeogalera stagnina	1	1	0	0	1
Phaeonematoloma myosotis	1	1	0	0	1
Pholiota henningsii	2	0	0	1	1
Psilocybe fuscofulva	1	1	0	0	1
Ramariopsis subarctica	0	2	0	0	0
Simocybe laevigata	1	0	0	1	0
Sphagnurus paluster	1	1	0	0	1
Suillus flavidus	1	1	0	0	1
Trichoglossum hirsutum	2	0	0	1	1

Mapping the distribution of mire specialists and loss of their habitats

Data on the occurrence of vascular plants were obtained from the Pladias database (Wild et al. 2019, Chytrý et al. 2021; accessed 3 March 2025, Supplementary Table S1). Data on bryophyte distribution were sourced from the NDOP database (Species occurrence database of the Nature Conservation Agency of the Czech Republic; accessed 12 January 2025, Supplementary Table S2), supplemented with a comprehensive bryology survey of the Krkonoše National Park (Čejková et al. 2023; the data were uploaded to the NDOP database in June 2026) and literature data (Supplementary Data S2). Data on macrofungi distribution were compiled from Fungaria (BRNU, BRNM, CB, HR, PRM; abbreviations follow Index Herbariorum, https://sweetgum.nybg.org/science/ih) and from the NDOP database (Supplementary Table S2), supplemented by unpublished records of the authors of this study and collaborators (see Acknowledgements).

Mapping the numbers of specialists and habitats based on indicator organisms (i.e. strict specialists in our case) may be sensitive to biases in databases and therefore requires careful data control and filtering (compare Chapman 2005). Major sources of bias include inconsistent taxonomy (Jansen & Dengler 2010), identification mistakes, imprecise or false localizations (Rocchini et al. 2011) and considering intentionally introduced or cultivated populations of some taxa as natural occurrences. The reliability of many database records has been validated by taxonomic experts for the previous studies, mostly regarding the Pladias database (e.g. Kaplan et al. 2015, 2026). Based on an extensive revision of remaining cases, we excluded uncertain or inaccurate records based on our expert knowledge, considering also the historical land use cover (Skokanová et al. 2012, Sychrová et al. 2024) and literature evidence for the non-native occurrences (Jehlík et al. 2012, Kaplan et al. 2022, 2023). For details on data control and filtering, see Supplementary Data S3. Records of specialist occurrences used in this study were collected over approximately the last 120 years, with the majority of records dating to the last 60–70 years (compare Wild et al. 2019). Distribution patterns of specialists and reconstructed distribution of habitats thus reflect a time window spanning from the early period of floristic research to the present.

We used two templates for mapping of total numbers of habitat specialists: (i) standard CEBA (Central European Basic Area) grid template for flora mapping (Ehrendorfer & Hamann 1965) with quadrants divided into four subunits (a, b, c, d) with size of 5 longitudinal × 3 latitudinal minutes (corresponding approximately to 5.5 × 5.9 km; see also Kaplan et al. 2015), and (ii) a finer grid created by further subdividing each subunit into four equal parts, further referred to as "detailed maps". For preparation of the former, a larger number of floristic records was used, including those with less accurate spatial localization. For preparation of detailed maps, specific attention was paid to the exclusion of records with inaccurate location, which is particularly relevant for historical records (for details see Supplementary Data S3). Uncertain cases of specialists and non-specialists with regional affinity to mire habitats were not considered. We mapped separately the numbers of strict specialists and strict plus partial specialists for fens, calcareous fens, rich fens and bogs. For poor fens, which lack strict specialists of vascular plants and bryophytes, only partial specialists were mapped.

Based on maps showing distribution of strict specialists, we finally reconstructed the former distribution of their habitats (fens, calcareous fens, rich fens, and bogs). A habitat was considered once present in a grid if at least one strict specialist had been recorded. The records of different dates indicate the former, but not necessarily the current, occurrence of a mire habitat in a given grid. This reconstruction is based on the premise that mires hosting highly specialized biota (i.e. strict specialists) do not currently initiate in the Czech Republic. As mire development is associated with persistently high water levels and oligotrophic conditions that maintain accumulation of organic matter (peat) and the formation of habitats for specialist species (Joosten et al. 2017), we assume that such conditions rarely arise in the contemporary central-European landscape, which is increasingly affected by eutrophication and drought (Chytrý et al. 2019). Exceptions may include wet nutrient-poor sand pits or quarries after the cessation of extraction. However, such habitats are colonized by specialists mainly if there is a source site nearby, because mire specialists, particularly vascular plants, are often dispersal-limited (Mälson et al. 2008, Horsák et al. 2012).

The reconstructed occurrences of habitats were then compared with the current habitat presence according to the national habitat mapping (Härtel et al. 2009). We used the Habitat Mapping Layer of the Czech Republic (Nature Conservation Agency of the Czech Republic; available at: https://portal.nature.cz/biotopy; accessed 5 March 2026). A habitat within a quadrant was considered present if any mapped polygon overlapped its borders. For a habitat mosaic, we included only those polygons in which a target mire habitat accounted for ≥50% of the area, in order to reduce bias caused by regional differences in mapping criteria and praxis (Divíšek et al. 2014). For comparisons, rich fens were associated with R2.2 habitat (Acidic moss rich fens, see Table 1), while calcareous fens with R2.1 and R1.1 habitats (Calcareous fens and Meadow springs with tufa formation), both corresponding to the vegetation of calcareous fens (the *Caricion davallianae* alliance, see Chytrý et al. 2010). The subordinate units of both fens and bogs used in the system of national habitat mapping were pooled, respectively. Poor fens were not analysed separately due to lack of strict specialists.

Results

List of vascular plant, bryophyte and macrofungi specialists

Altogether 274 taxa (124 vascular plants, 100 bryophytes and 50 macrofungi) were identified as strict or partial specialists either for fens (minerotrophic mires) or bogs (ombrotrophic mires) in the Czech Republic (Table 3, Supplementary Table S3). Of the taxa identified as strict specialists for one of these two main types of mires, 83 display affinity to fens (e.g. *Eriophorum gracile*, *Meesia triquetra*, *Hygrocybe coccineocrenata*) and 26 occur exclusively in bogs (e.g. *Betula nana*, *Sphagnum fuscum*, *Hygroaster borealis*). Whereas vascular plants predominate among the strict specialists for fens (43 taxa), vascular plants and bryophytes occur in approximately equal numbers among the bog strict specialists (10 and 13 taxa, respectively). Of the other considered taxa, 95 were identified as partial specialists only for fens (e.g. *Carex nigra*, *Sphagnum inundatum*, *Entoloma mougeotii*), 13 only for bogs (e.g. *Rhododendron tomentosum*, *Sphagnum compactum*), and 55 for both fens and bogs (e.g. *Carex limosa*, *Sphagnum fallax*, *Galerina hybrida*). A further 19 taxa were assessed as uncertain cases of strict or partial specialists for fens or bogs due to ambiguous habitat associations within the Czech Republic. This group comprises mostly species that are extinct or currently missing (e.g. *Narthecium ossifragum*, *Sphagnum molle*), or those whose historical occurrence has been questioned for different reasons (e.g. *Saxifraga hirculus*, *Spiranthes aestivalis*). Taxa having an affinity to fens or bogs only in some regions of the Czech Republic are listed in Supplementary Table S3.

Within individual types of fens, calcareous fens are characterized by 15 strict specialists with predominance of vascular plants (e.g. *Carex lepidocarpa*, *Schoenus ferrugineus*). The group of strict specialists of rich fens contains 16 species, including all taxonomic groups, but with the highest representation of bryophytes (e.g. *Paludella squarrosa*, *Pseudocalliergon trifarium*, *Sphagnum contortum*). In contrast the group of poor fen strict specialists lacks vascular plants and bryophytes. Altogether 121 taxa were identified as partial specialists for more than one type of fens. Only a small proportion of species were assessed as partial specialists across all three types of fens (e.g. *Eriophorum* *angustifolium*, *Menyanthes trifoliata*). A total of 40 taxa were identified as partial specialists for both calcareous and rich fens (e.g. *Eriophorum latifolium*, *Tomentypnum nitens*, *Bovista paludosa*), and 68 taxa for both rich and poor fens (e.g. *Carex echinata*, *Sphagnum flexuosum*, *Pholiota henningsii*). Species recognized as partial specialists for poor fens frequently also belong to partial specialists for bogs (e.g. *Sphagnum divinum*, *Arrhenia gerardiana*).

Ecological optima of vascular plants specialists along environmental gradients

Ellenberg-type indicator values for moisture, light and nutrients plotted in scatter diagrams (Fig. 1) reveal that strict specialists for fens share similar ecological demands, associated with wet, oligotrophic and predominantly full-light conditions. Ecological optima of partial specialists for fens are more variable with some taxa shifted towards less moistened soils or to moderately nutrient-rich sites. In analogy to strict specialists for fens, strict specialists for bogs are also associated with wet oligotrophic and full-light conditions. Partial specialists for bogs share the same ecological demands, only some of them are semi-shade plants.

Distribution patterns

Records of both strict plus partial specialists for fens come from almost the entire territory of the Czech Republic (Fig. 2). Their reported occurrences are concentrated mainly in highland and mountain areas (the Bohemian-Moravian Highlands, Beskydy Mts, Jeseníky Mts, Krkonoše Mts, Krušné hory Mts, Slavkovský les Mts, Šumava Mts), the Třeboňská pánev Basin and the Doksy region (for definitions and further information on topographic and phytogeographical features of the Czech Republic, see Kaplan 2012, and Chytrý et al. 2017). The distribution patterns of both types of specialists appear similar, although data on the occurrence of strict specialists (Fig. 3) are largely absent from some lowland or middle altitude areas, such as south-western Moravia (phytogeographical district of Znojemsko-Brněnská pahorkatina), foothills of the Krušné hory Mts or some parts of western, north-western and central Bohemia (e.g. Bohemian Karst, southern part of the České Středohoří Mts, Mostecká pánev Basin, the area between the Slavkovský les Mts and the city of Plzeň). Analogous distributional patterns were found for strict plus partial specialists for calcareous fens and rich fens and for partial specialists for poor fens. Strict specialists for calcareous fens were largely concentrated in the Labe river basin and the White Carpathian Mts, while strict specialists for rich fens in the Bohemian-Moravian Highlands, Třeboňská pánev Basin and Jeseníky Mts. Apart from these regions, strict specialists for calcareous and rich fens were also frequently recorded in the Doksy region and Šumava Mts and their foothills. Quadrants harbouring strict specialists for bogs are mostly situated in mountains (Jeseníky Mts, Krkonoše Mts, Krušné hory Mts, Šumava Mts) and Třeboňská pánev Basin. Rarer occurrences are found in the Beskydy Mts, Bohemian-Moravian Highlands, Brdy Mts, Slavkovský les Mts and surroundings, and the Doksy region. Isolated occurrences of strict specialists for bogs are located, for example, in the Orlické hory Mts and their foothills and in central Moravia (Oderské vrchy Hills).

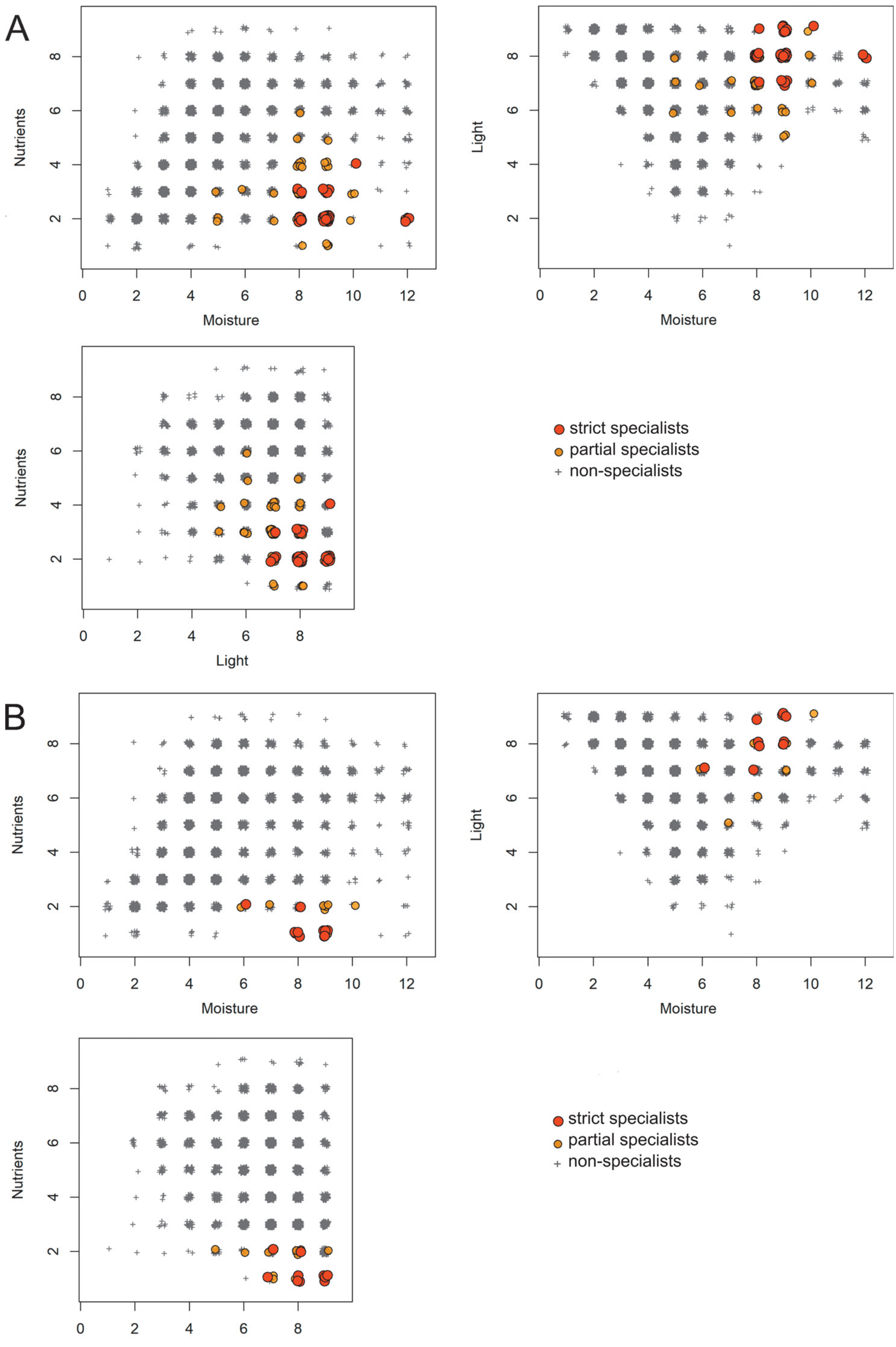


Fig. 1. Pairwise scatter diagram of distribution of fens (A) and bog (B) specialists of vascular plants along main environmental gradients expressed by Ellenberg-type indicator values for the Czech flora.

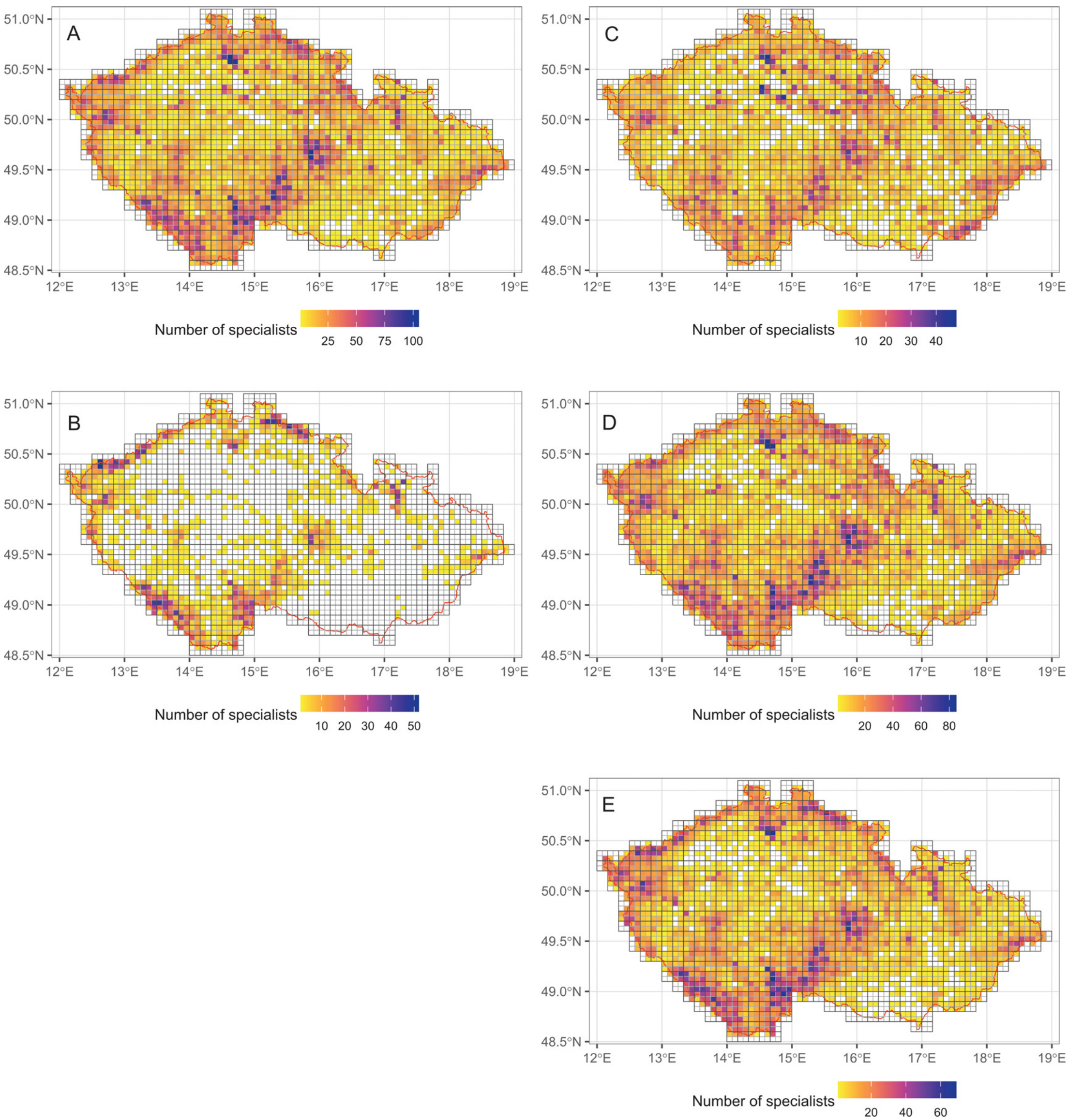


Fig. 2. Spatial distribution of the total number of strict plus partial specialists per grid cell for major mire types, i.e. fens (A) and bogs (B), and for different types of fens, i.e. calcareous fens (C), rich fens (D) and poor fens (E), in the Czech Republic. The presence of a specialist indicates that the taxon has historically been recorded within a given grid cell. Thus, the total number also includes specialists that are no longer present in a grid cell.

Maps, comparing the mire habitat distribution reconstructed from strict specialist occurrences with the current distribution according to the national habitat mapping, showed an overall decline in fens (Fig. 4; Supplementary Table S4). The most pronounced decline concerns areas in lowlands and hilly landscapes (e.g. western and north-

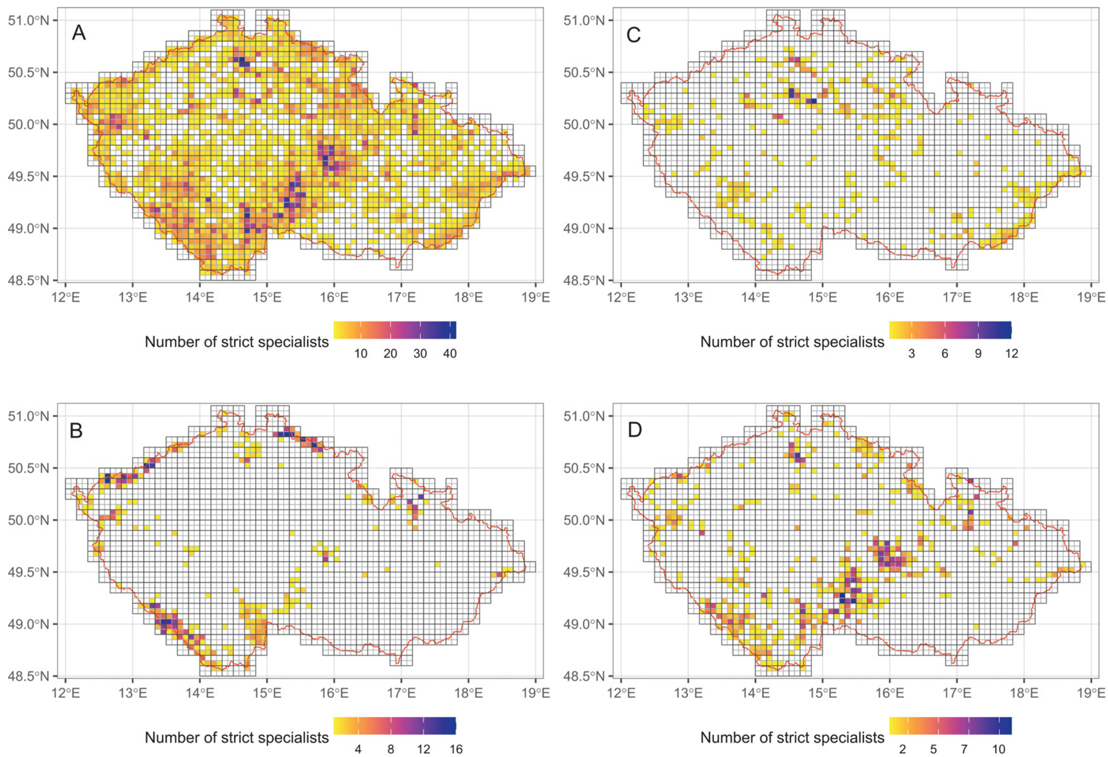
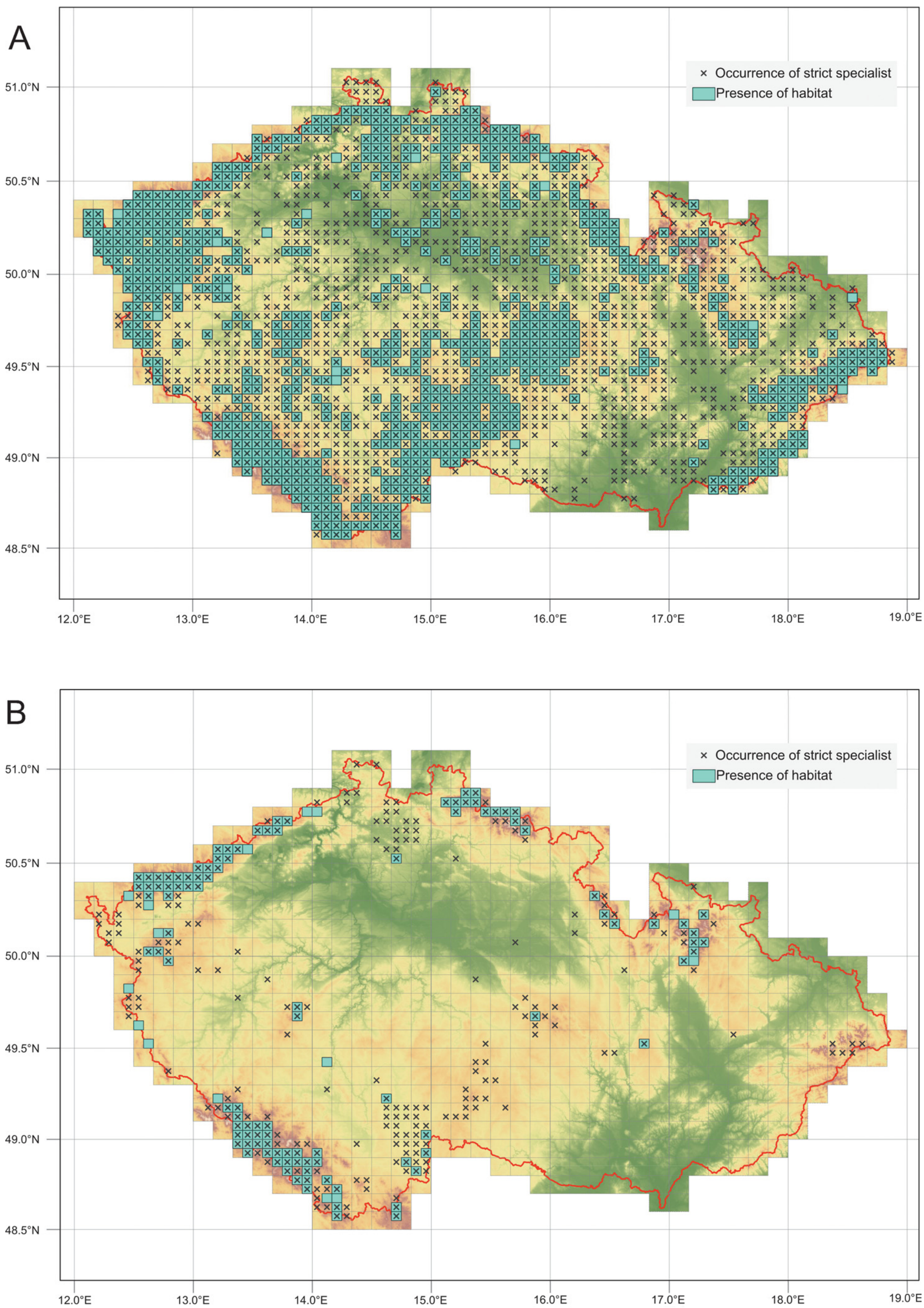
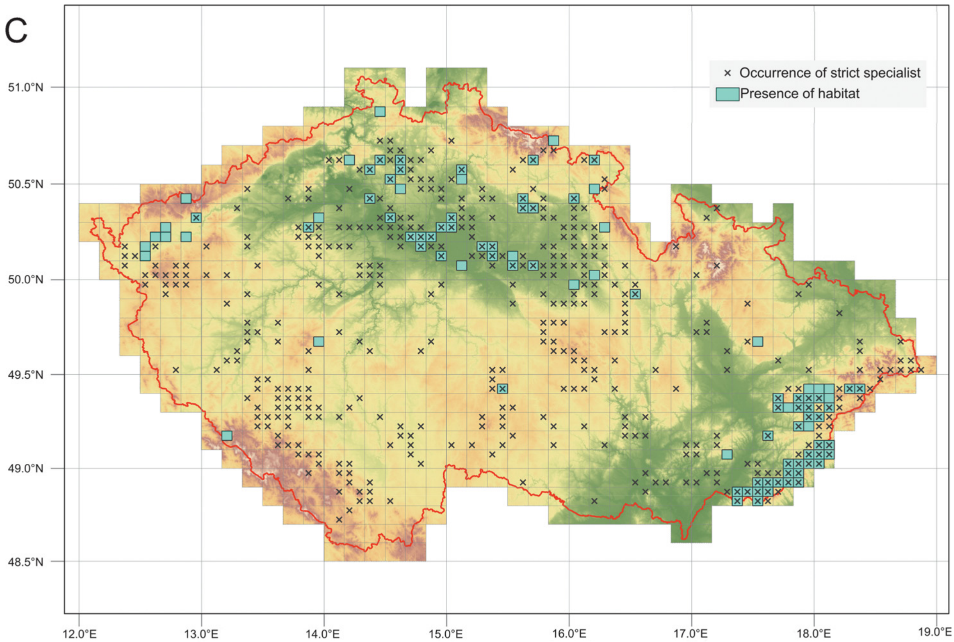


Fig. 3. Spatial distribution of the total number of strict specialists per grid cell for major mire types, i.e. fens (A) and bogs (B), and for different types of fens, i.e. calcareous fens (C) and rich fens (D), in the Czech Republic. Poor fens are not visualized, due to the lack of strict specialists for this habitat. The presence of a specialist indicates that the taxon has historically been recorded within a given grid cell. Thus, the total number also includes specialists that are no longer present in a grid cell.

ern Moravia, central and eastern Bohemia). The comparison further revealed a distinct loss of calcareous fens throughout the Czech Republic, with the exception of the White Carpathian Mts, and their pronounced decline in the Labe River Basin and surrounding areas of Bohemian lowlands. At the quadrant level, the reconstructed and current distributions of rich fens were relatively similar (Supplementary Table S4). Decline of bogs was most apparent in the Beskydy Mts, Bohemian-Moravian Highlands, Třeboňská pánev Basin and some parts of western Bohemia (e.g. Český les Mts, Slavkovský les Mts) and northern Bohemia (the area between the Doksy region and Lužické hory Mts). Detailed maps using a finer grid (Supplementary Data S4) show an identical trend, but further emphasize the decline of rich fens and bogs in some areas (the Bohemian-Moravian Highlands, Třeboňská pánev Basin).


A
Occurrence of strict specialist
Presence of habitat
51.0°N
50.5°N
50.0°N
49.5°N
49.0°N
48.5°N
12.0°E
13.0°E
14.0°E
15.0°E
16.0°E
17.0°E
18.0°E
19.0°E
B
Occurrence of strict specialist
Presence of habitat
51.0°N
50.5°N
50.0°N
49.5°N
49.0°N
48.5°N
12.0°E
13.0°E
14.0°E
15.0°E
16.0°E
17.0°E
18.0°E
19.0°E



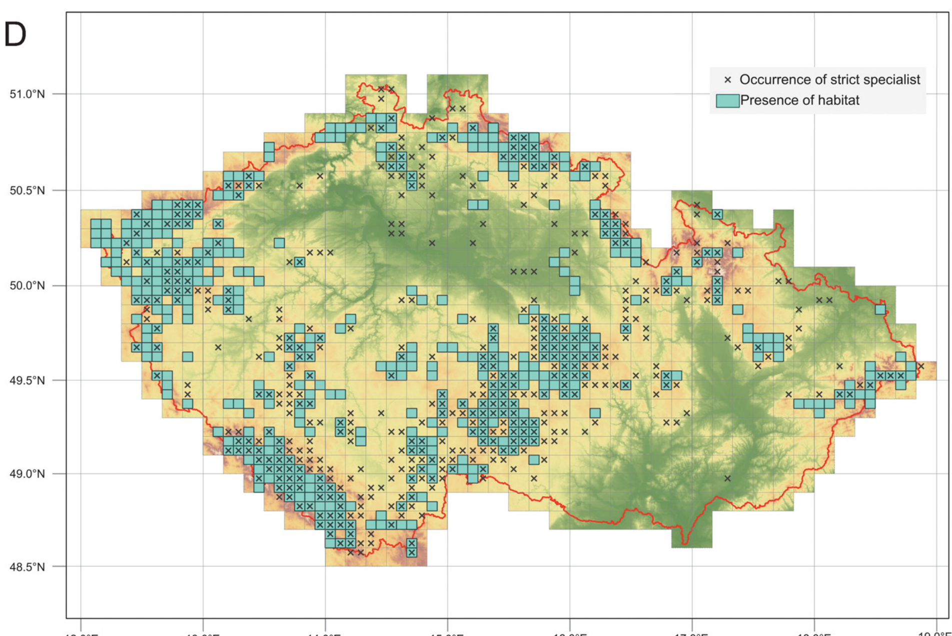


Fig. 4. Current and reconstructed distribution of major mire types, i.e. fens (A) and bogs (B), and different types of fens, i.e. calcareous fens (C) and rich fens (D), in the Czech Republic. Crosses refer to reported occurrences of a strict specialist for a habitat in a quadrant (i.e. reconstructed occurrence of a habitat), bordered blue-green coloured quadrants are those with current presence of a habitat according to national habitat mapping. Poor fens are not visualized, due to the lack of strict specialists for this habitat.

Discussion

Use of an expert-based approach to establish a specialist list

By analogy to scaling or categorizing ecological indicator values (e.g. Ellenberg et al. 1991, Hill et al. 2007) or some plant traits (Klotz et al. 2002, Chytrý et al. 2021), and to preparation of the lists of expansive species (Axmanová et al. 2024) or habitat specialists (Heinken et al. 2022, Dítě et al. 2023), our list was compiled based on expert assessment. Although inherently reliant on arbitrary decisions in ambiguous cases, this approach incorporates comprehensive empirical knowledge on habitat and vegetation preferences of plant and macrofungi taxa. This judgement surpasses the utility of numerical approaches. A subjectivity-based bias may be reduced by integrating the independent experience of many field botanists and mycologists from different regions, habitat contexts and taxonomic expertise, as in our study. In contrast, numerical approaches rely exclusively on limited spot data, such as vegetation plots from databases, often placed preferentially, and on algorithms, such as fidelity calculation (Chytrý et al. 2002), largely disregarding other site characteristics. The utility of vegetation database data is also reduced by the lack of records of rare taxa (e.g. *Dactylorhiza bohemica*, *Drepanocladus lycopodioides*, *Eriophorum gracile*, *Rhynchospora fusca*, *Sagina nodosa*) or inconsistently identified taxa (e.g. *Vaccinium microcarpum*). Moreover, nor are numerical approaches entirely unsupervised and depend on a set of arbitrary decisions, such as definition of a habitat by species composition of vegetation plots, setting the inclusion rules with respect to habitat deterioration, or setting the threshold values for delimiting the specialists. For macrofungi, database data that would allow for numerical delimitation of specialists are missing completely. The numerical approach was nevertheless partially considered even during the preparation of our list, as the candidate list of specialists was also assembled using lists of diagnostic species identified based on fidelity.

Categories and classification

Any list of habitat specialists is inherently dependent on a study scale (Devictor et al. 2010). Continental-scale lists may miss some excellent indicators acting at finer spatial scales. Our list of specialists includes for example the rare glacial-relict moss *Helodium blandowii* which is narrowly associated with fens in the Czech Republic (Štechová et al. 2010, Bradáčová 2011), while it frequently occurs in wet forests and shrublands in northern Europe (Trass et al. 1999, Hedenäs et al. 2014). Therefore, it is not included in the European list of diagnostic taxa for the *Scheuchzerio palustris-Caricetea nigrae* class (compare Mucina et al. 2016). Similar cases are *Calamagrostis varia* and *Sedum villosum,* which, at the European scale, show an optimum in the habitats which are rare in the Czech Republic (moist carbonate rocks and disturbed oceanic springs, respectively).

We also included some taxa with nearly equal distribution in both calcareous springs and fens (the *Palustriella* species) or in both poor fens and bogs (*Vaccinium oxycoccos, Sphagnum angustifolium*) into the list of specialists. These species were not included as diagnostic of the *Scheuchzerio palustris-Caricetea nigrae* class in the list of Mucina et al. (2016) probably because of their assignment to diagnostic taxa of other classes (*Montio-Cardaminetea*, *Oxycocco-Sphagnetea*).

On the other hand, some taxa from continental-scale lists regionally do not prefer mires, because the mire habitat in which they show an optimum is absent for edaphic reasons. When compared to the list of Mucina et al. (2016), our list misses *Carex vaginata*, which occurs in the Czech Republic predominantly in spring ecotones and alpine grasslands, *Carex bigelowii* subsp. *dacica* and *Phleum alpinum* growing predominantly in alpine grasslands, *Allium schoenoprasum* occurring predominantly in springs, *Succisa pratensis* frequently occupying moist and wet grasslands on mineral soils, or *Eleocharis mamillata* preferring mineral-soil reeds (Slavík et al. 2004, Štěpánková 2010, 2024).

The indication potential of a taxon may change also when switching from the scale of the entire Czech Republic to a smaller regional scale. The way to cope with this scale dependency is assembling the modified regional list for a target study area. It therefore means that regional or case researchers may not entirely follow the presented list for the Czech Republic as it is, but may adjust it for a specific region. For these reasons, we adopted the category "Non-specialists with a regional affinity" (0 reg.; Supplementary Table S3), referring to the taxa which have an affinity to some types of mire habitats in some specific regions. For example, *Allium carinatum*, *Phyteuma orbiculare* or *Thalictrum simplex* may be excellent indicators of calcareous fen occurrence in Bohemian lowlands (Sádlo 2000), while they occur exclusively in semi-dry or mineral-soil moist grasslands in the White Carpathian Mts.

Besides taxa with affinity to a habitat (i.e. strict and partial specialists in our case), similarly focused studies sometimes also distinguish taxa that only tolerate environmental conditions of a particular habitat (considered non-specialists in this study). For example, Dítě et al. (2023) list vascular plants not confined to saline habitats but able to tolerate halophytic conditions. In the case of mires, such a group would include meadow species, species spanning from submontane and montane *Nardus* grasslands, or species of marshes and other wetlands. However, mires in the Czech Republic have been generally influenced by shifts in hydrology, an increase in available macronutrients, and abandonment (Navrátilová et al. 2017, Chytrý et al. 2020). Consequently, it is difficult to disentangle which non-specialists may occur even in pristine mires due to the mass effect (Shmida & Wilson 1985, Hettenbergerová & Hájek 2011) and their tolerance to extreme environmental conditions and which enter mire habitats as a result of ongoing, albeit sometimes negligible, site deterioration.

Despite the long tradition of taxonomic and ecological research on vascular plants and bryophytes, new mire taxa are still being discovered in the Czech Republic (*Dactylorhiza maculata* subsp. *averyanovii*; Taraška et al. 2023), or new to science. Recent studies continue to reveal that within a single taxon (most commonly at the species level) multiple distinct genetic entities can be recognized. These entities are subsequently treated as separate species or, where clear morphological diagnostic characters are lacking, as cryptic species. In many cases, they also differ in their ecological requirements and habitat affinity (Hassel et al. 2018, Hedenäs 2020, Majeský et al. 2022, Mikulášková et al. 2024). Thus, the presented list of specialists will be inevitably subjected to future updates with respect to research progress. This holds especially for macrofungi as a still less known group in terms of both taxonomy and habitat affinities (Hofmeister & Hošek 2016).

Present and former distribution of specialists and their habitats

Distribution of strict specialists largely corresponds to regions with suitable environmental conditions for their habitats (compare Chytrý 2011), which is in line with expectations. For example, strict specialists for calcareous fens were mapped in regions with calcium-rich geological substrates, strict specialists for bogs occurred mostly in mountain ranges, where ratio of evapotranspiration to precipitation supports bog development (O'Neill 2000). While strict specialists are associated with one habitat, partial specialists may, however, occur with equal frequency in several mire habitats or even in other habitat types. Therefore, occurrences of partial specialists cannot be automatically interpreted as the presence of a single habitat and maps showing numbers of strict plus partial specialists need to be interpreted with caution. A mapping artefact arises, for example, in the case of the White Carpathian Mts, where partial specialists for poor fens such as *Carex echinata*, *C. nigra* and *Eriophorum angustifolium* are mapped, although the calcareous aquifers do not support the occurrence of poor fens at all.

Strict specialists were used for a more targeted reconstruction of individual habitats. Such reconstruction yielded many historical occurrences of a habitat, not documented by the recent habitat mapping. This pattern is largely associated with the decline of mire habitats, which is most pronounced in calcareous fens. This finding is not surprising, as it corroborates the well known fact that mires in the territory of the Czech Republic have been systematically drained and converted to agricultural or forestry land for more than 150 years (Dohnal et al. 1965, Joosten et al. 2017, Navrátilová et al. 2019). In some regions, these landscape modifications were documented at the level of individual valuable localities (e.g. Klečka 1930, Růžička 1987, Taraška et al. 2021). Moreover, we may assume that many mires disappeared without being recognized (Štechová et al. 2014), and that some localities of strict specialists vanished before these taxa could be documented there. The reconstructed distribution of mire habitats may therefore be underestimated, but less severely than if vegetation data are used. Importantly, the former habitat occurrences reconstructed in our study are typically based on a combination of several strict specialists. For instance, vanished calcareous fens in southern Bohemia were reconstructed based on the occurrences of species such as *Blysmus compressus*, *Carex hostiana*, *Eleocharis quinqueflora*, or *Tofieldia calyculata* (compare Kaplan et al. 2015), which are currently extinct in the region or persist only at a few remnant sites (Lepší et al. 2013). Since quantification of the decline in a habitat's area is one of the criteria used for classifying habitats into IUCN Red List categories (Keith et al. 2013), we assume that the reconstruction presented above may provide a complementary perspective to the evaluation of habitat loss, as conducted by Chytrý et al. (2019).

The seemingly limited decline of rich fens, which are otherwise one of the most vanishing habitats in the Czech Republic (Hájek et al. 2015, Navrátilová et al. 2017, 2022, Chytrý et al. 2019), must likewise be interpreted with caution. It is important to emphasize that the map compares reconstructed and current occurrence of rich fens at the resolution of quadrants of 5.5 × 5.9 km. The present-day occurrence of the habitat, often confined to a single isolated locality, may represent only a minor remnant of the former spatial extent within a given quadrant. In this regard, the detailed maps (with quadrants of one-quarter size; Supplementary Data S4) provide a more informative picture of habitat loss. Moreover, some current presences of rich fens according to the national habitat mapping might be based on occurrences of young fen grasslands of the *Caricetum nigrae* association, that often lack species considered strict specialist in our list (compare Rybníček et al. 1984, Chytrý 2011), while ancient rich fens harbouring strict specialists are no longer present in particular quadrants at all. This is also the probable reason why strict specialists for rich fens have not been recorded in several quadrants with the presence of this habitat according to national habitat mapping.

In some cases, the absence of recent documentation of a habitat within a quadrant, despite its reconstruction here, does not necessarily imply its disappearance. Mires may exhibit fine-scale heterogeneity (Šoltés & Školek 2010, Vicherová et al. 2017), with patches of one mire habitat embedded within a matrix of another mire habitat. Such small-scale occurrences are frequently not captured by habitat mapping conducted at the landscape scale. For example, bogs may occur in the form of smaller hummocks, or initial stages of bog development (the *Eriophoro vaginati-Sphagnetum recurvi* association) within poor fen complexes or as open patches within waterlogged spruce forests. These types of bogs were documented, for instance, in the Beskydy Mts (Duda 1950, Hájek & Malina 1998), the Oderské vrchy Hills (Hradílek & Blahut 2013), or in Třeboňská pánev Basin (Březina et al. 1963).

Other applications

It is important to emphasize that strict specialists are sensitive organisms and site degradation inevitably leads to their decline and finally to extinction (e.g. Rybníček 1974, Bergamini et al. 2009, Hájek et al. 2015, Pollo et al. 2026). At present, the threat to mires and their biota in central Europe continues to increase in connection with rising macronutrient inputs (atmospheric deposition and runoff from surrounding arable land) and declining water table (increase of evapotranspiration, changes in the total amount and seasonal distribution of precipitation; Chytrý et al. 2019). For these reasons, mire specialists should continue to be regarded as highly endangered and in need of conservation attention in the national classification system in forthcoming Red List assessments, as in the previous edition (Grulich 2017). Across all considered taxonomic groups, a high degree of endangerment affects the vast majority of strict specialists for fens and bogs as well as species specialized to mires as a whole occurring both in fens and bogs (e.g. *Carex limosa*, *Drosera rotundifolia*, *Rhynchospora alba*).

In the fields of restoration ecology and bioindication, occurrences of strict specialists may be used for identification of vanished mires. Although the disappearance of mires leads to the loss of specialists, as outlined earlier, recent re-surveys of mire vegetation (Koch & Jurasinski 2015, Hájek et al. 2020) indicate that an increase in non-specialists as a result of mire deterioration can happen relatively quickly, whereas the overall diversity of mire species at a site responds more slowly. Specialists thus may persist at a site for several years after the degradation of their suitable habitat, although the population is then usually affected by the extinction debt (Kuussaari et al. 2009), often consisting of a few remaining individuals or being sterile. The presence of strict specialists even in depauperate vegetation thus indicates a subrecent occurrence of a mire habitat and, consequently, a site potentially suitable for restoration intervention.

Recent studies distinguishing between generalist (matrix-derived) and specialist species (e.g. Pérez-Haase & Ninot 2017, Horsáková et al. 2018, Navrátilová et al. 2022) did not scale specialists according to their exclusivity or facultativeness. The proposed system of strict and partial specialists is more flexible in terms of applications. While strict specialists alone appeared more useful for reconstructing past habitats, their combination with partial specialists may strengthen indications of key environmental factors for mires, such as high moisture and low availability of macronutrients. These groups may also be weighted differently if strict specialists are supposed to bring a more relevant signal in bioindication or biogeography analyses.

Supplementary materials

Data S1. Literature sources used for compilation of the list of mire specialist taxa.
Data S2. Literature excerpted for occurrence records not stored in the NDOP database.
Data S3. Potential sources of bias in floristic data and the countermeasures for their minimization.
Data S4. Detailed maps comparing current and reconstructed distribution of mire habitats.
Table S1. Occurrence records from the Pladias database used for preparation of maps.
Table S2. Occurrence records from the NDOP database used for preparation of maps.
Table S3. Full list of specialists of mire habitats in the Czech Republic, including non-specialists with a regional affinity.
Table S4. Numbers of grid cells with current and reconstructed habitat occurrences.

Supplementary materials are available at https://www.preslia.cz

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Seznam rašeliništních specialistů v České republice (cévnaté rostliny, mechorosty, makromycety)

Druhy lze klasifikovat jako specializované nebo nespecializované pro určitý typ biotopu v závislosti na jejich ekologickém optimu. Specialisté vykazují významnou ochranářskou, funkční i indikační hodnotu a specificky reagují na fragmentaci krajiny a degradaci prostředí. Tyto vlastnosti jsou důležité zejména u vysoce zranitelných biotopů, k jakým patří i rašeliniště. V této studii jsme sestavili seznam specialistů cévnatých rostlin, mechorostů a hub tvořících makroskopicky viditelné plodnice (makromycet) vázaných na slatiniště (minerotrofní rašeliniště) nebo vrchoviště (ombrotrofní rašeliniště) v České republice. U specialistů slatinišť byla dále hodnocena vazba na jednotlivé typy slatinišť (vápnitá slatiniště, slatiniště s kalcitolerantními rašeliníky, chudá slatiniště). Taxony byly rozděleny do dvou hlavních kategorií podle míry jejich specializace: striktní (obligátní) a částeční (fakultativní) specialisté. Celkem 124 taxonů cévnatých rostlin, 100 mechorostů a 50 makromycetů bylo klasifikováno jako striktní nebo částeční specialisté slatinišť nebo vrchovišť. Z tohoto počtu představuje 83 taxonů striktní specialisty slatinišť a 26 taxonů striktní specialisty vrchovišť. Na základě údajů o výskytu striktních specialistů získaných z nálezových databází a dalších datových zdrojů jsme rekonstruovali dřívější rozšíření rašeliništních biotopů v kvadrátech síťového mapování flóry. Porovnání rekonstruovaného a současného rozšíření těchto biotopů ukázalo jejich celkový výrazný úbytek. Významná ochranářská pozornost by měla být nadále věnována naprosté většině striktních specialistů slatinišť i vrchovišť, ale i vybraným částečným specialistům.

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