

Halophytic flora and vegetation in southern Moravia and northern Lower Austria: past and present

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We dedicate this article to the memory of Vít Grulich (1956–2022), a botanist extraordinaire

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Abstract: Halophytic habitats are distinctive components of the landscape in southern Moravia, Czech Republic, and the Pulkau valley in northern Lower Austria. We provide a historical overview of their flora and vegetation since the early 19th century and describe the current state assessed in the field at all remaining sites in 2020. We summarized the historical and current distribution of 17 species with the strongest affinity for saline habitats in the study area: *Bupleurum tenuissimum*, *Cirsium brachycephalum*, *Crypsis aculeata*, *C. schoenoides*, *Galatella cana*, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Samolus valerandi*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum*, *Triglochin maritima* and *Tripolium pannonicum*. Of these, *Galatella cana*, *Salicornia perennans*, *Suaeda prostrata* and *Triglochin maritima* are regionally extinct. We also characterized the bryoflora typical of saline habitats. We classified historical and newly recorded relevés and identified 14 halophytic associations belonging to the alliances *Chenopodion rubri*, *Melilotodentati-Bolboschoenion maritimi*, *Cypero-Spergularion salinae*, *Salicornion prostratae*, *Puccinellion limosae*, *Juncion gerardii* and *Festucion pseudovinae*. The vegetation of the alliance *Salicornion prostratae* had disappeared in the study area by the 1970s. The alliance *Festucion pseudovinae*, with the association *Centaureo pannonicae-Festucetum pseudovinae*, was recognized as a new vegetation type for the Czech Republic. Using soil pH and electrical conductivity measurements, we evaluated the relationships of individual species and vegetation types to soil salinity. This synthetic study shows that the once well-developed halophytic flora and vegetation in the study area steadily declined from the early 19th century to the 1980s, initially mainly due to drainage and after the mid-20th century due to the combination of drainage and cessation of grazing. The introduction of conservation management in the 1990s and ecological restoration contributed to stabilizing plant diversity at the last saline sites. The future of halophytic flora and vegetation depends on the continuation of conservation management.

Keywords: Czech Republic, flora, habitat, halophyte, history, inland saltmarsh, Lower Austria, Moravia, nature conservation, saline, vegetation

Introduction

Inland halophytic flora and vegetation find their optimum mainly in arid and summer-warm areas such as southern Ukraine, southern Russia, Middle and Central Asia and the Middle East (Walter 1974, Eliáš et al. 2020). In such areas, salt steppes and salt meadows are considered intrazonal vegetation within the steppe zone (Mucina et al. 2016). Halophytes are favoured there by high soil salinity caused by intense evaporation, which promotes the upward migration of salts to the upper soil horizons. The high salinity is detrimental to many plant species and favours a small number of adapted species, which are considered obligate halophytes. Macroclimate is a strong driver of the broad-scale distribution of halophytes even in central Europe, where they occur in the dry lowlands. While the saline habitats and specialized halophytes are widespread and common in the central parts of the Great Hungarian Plain (Molnár et al. 2008), they become rarer in the precipitation-richer areas in the foothills of the Carpathians and the Alps (Vicherek 1973). In such marginal areas, including southern Moravia and Lower Austria, other salinity sources are important besides evaporation in dry macroclimate, especially springs in mineral-rich Tertiary deposits. These halophytic habitats also depend on regular disturbance, especially traditional livestock and poultry grazing on villages' common land. Due to their recent decline, they are listed in the European Habitats Directive 92/43/EHS, and most of their remaining sites are protected.

The halophytic flora and vegetation in southern Moravia are confined to the lowlands, including the wider environs of the lower stretches of the Dyje and Svratka rivers, extending slightly into Lower Austria along the Pulkau stream. Their distribution is naturally bounded by colline landscapes of the Bohemian Massif in the west and north-west, the Weinviertler Upland in the south and the Western Carpathian foothills in the east. The halophytic habitats in this area share some common features in vegetation physiognomy and species composition that differ from those of halophytic habitats in eastern Austria, southern Slovakia and Hungary. Consequently, southern Moravia with the adjacent Pulkau valley in Lower Austria can be considered a biogeographically distinct region of halophytic flora and vegetation.

The unique flora of saline habitats has attracted botanists since the beginnings of floristic research in central Europe. The first literature records of halophytic species in the study area date back to the 1820s and mostly refer to the now-vanished natural saline lakes of Kobylí and Čejč (Hochstetter 1825). In the 19th century, some saline habitats were drained, which triggered a discussion among botanists about the decline of halophytic flora (Krzisch 1859, Bubela 1882, Spitzner 1894). In the 19th century, numerous halophytic species were reported in regional floras from different parts of southern Moravia (Rohrer & Mayer 1835, Makowsky 1863, Oborny 1879, 1886, Formánek 1887, 1892) and Lower Austria (Neilreich 1859, Beck 1890–1893, Halácsy 1896). The first comprehensive botanical study of saline habitats in southern Moravia (Laus 1907) contained descriptions of the flora and plant communities at the most important sites. Šmarda (1953) described the state of southern Moravian halophytic flora and vegetation in the mid-20th century, and Vicherek (1962, 1973) described halophytic plant communities based on systematic vegetation sampling in the early 1960s.

Halophytic flora and vegetation declined dramatically in the 1960s and 1970s. Vicherek (1962, 1973) was the last to document with relevés the still well-developed

halophytic plant communities at most southern Moravian sites. The decline of halophytic species after 1950 was mainly related to the cessation of the traditional grazing management in the village's common pastures (Hutweiden), which led to vegetation succession, and exacerbated by interventions into the natural water regime. Although most botanists were aware of this process, the policy-driven intensive agriculture of the 1950s to 1980s did not provide any opportunity to practice management that would conserve the last remnants of halophytic habitats. The succulent halophytes *Salicornia perennans* and *Suaeda prostrata* went extinct in southern Moravia and Lower Austria in the 1970s and 1980s. The quality of halophytic habitats was very bad at that time and continued to decline, as described in the last systematic survey of the southern Moravian halophytic flora by Grulich (1987).

After the political changes of 1989, the Nature Conservation Agency of the Czech Republic launched funding programmes in 1993 to support and manage nationally valuable natural sites. After 2004, these programmes were continued with the EU support. Management by grazing and mowing was introduced at the remaining saline sites (e.g. Dedek 2016). These measures have halted the decline in populations of several endangered halophytic species; however, they have been limited to small protected areas. The general lack of grazing in today's landscape and increasing drought events do not allow for the restoration of halophytic habitats at most of their original sites.

In Austria, land use also changed during the 20th century, although less drastically than in the former Czechoslovakia (Devátý et al. 2019). Currently, the protection of sites with halophytic vegetation in Lower Austria is mainly ensured by designation as Natura 2000 sites. However, the management plans for these areas are not legally binding (Geitzenauer et al. 2016).

This article aims to give a comprehensive overview of the past and present state of halophytic flora and vegetation in southern Moravia and the nearby Pulkau valley in northern Lower Austria. Our main objectives are (i) to describe the main sites of halophytic flora and vegetation, (ii) to review the past and present distribution of plant species with the greatest affinity for saline habitats and (iii) to provide a classification of halophytic communities based on historical and current data. We also describe the bryoflora of saline habitats and evaluate the relationship between individual species and vegetation types and soil salinity.

Methods

Study sites

The study area (Fig. 1) is in southern Moravia (south-eastern Czech Republic) and the Pulkau valley in the adjacent northern part of Lower Austria (north-eastern Austria). Its western part is located in the Western Carpathian foredeep (Dyjsko-svratecký úval), while the eastern part lies in the Lower Morava Valley (Dolnomoravský úval), which is part of the Vienna Basin, and in the Trkmanka stream valley in the hilly landscape of the flysch Carpathians. The halophytic habitats are found in depressions filled with Neogene and Quaternary sediments (Demek & Mackovčín 2006). The last marine regression took place there in the Miocene, leaving saline sediments. Mineral springs rich in sodium, magnesium and sulphates occur in some of these depressions. The mean annual temperature is

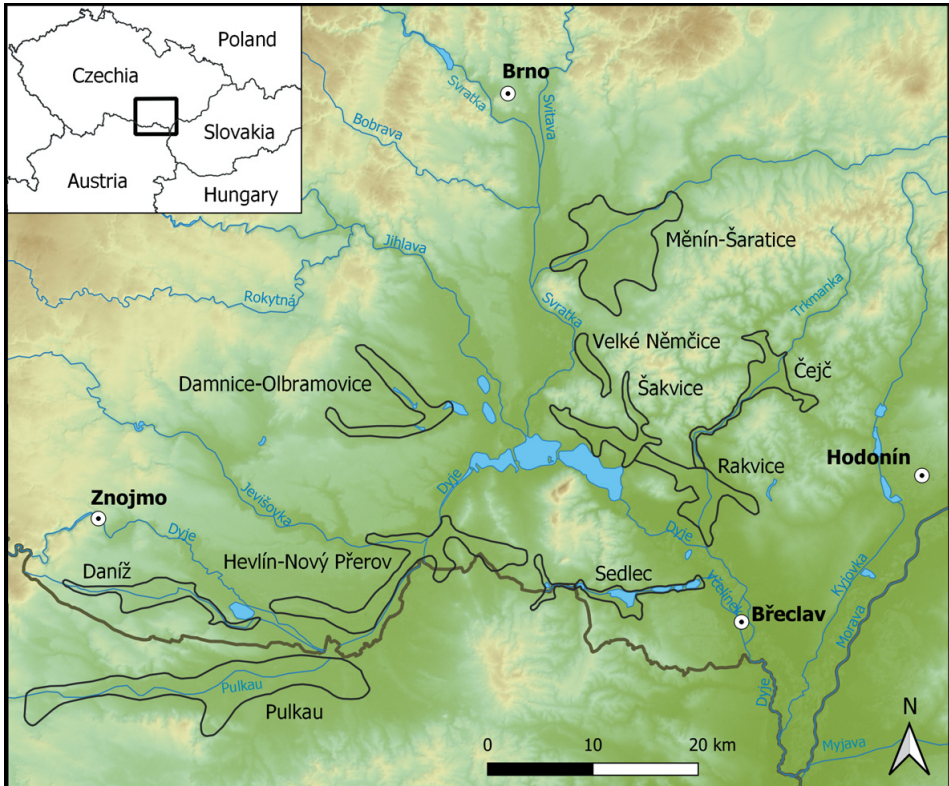


Fig. 1. Halophytic districts in southern Moravia and northern Lower Austria.

9–10 °C, and the annual precipitation total is 450–550 mm (Tolasz et al. 2007). Precipitation peaks in summer, but long droughts can occur in late spring or summer in some years.

Systematic descriptions of the state of halophytic flora and vegetation in southern Moravia in their time were provided by Laus (1907), Šmarda (1953) and Grulich (1987). Many publications dealt with the flora of individual sites or localities of selected halophytes. In 1959–1965, Vicherek (1962, 1964, 1973) carried out systematic vegetation survey and recorded relevés at most sites where halophytic vegetation was still preserved.

We use the regional division of saline sites into districts proposed by Grulich (1987) (Fig. 1; Supplementary Data S1). Each of these districts is a group of nearby sites with extant or vanished halophytic flora and vegetation located in the same basin or drained by the same stream. Grulich (1987) defined eight districts named after the nearby village(s) and, in one case, after a stream (Daníž). He only dealt with halophytes in southern Moravia; therefore, we added the Pulkau district in a nearby area in Lower Austria. We also added another district in Moravia (Damnice-Olbramovice district), which Grulich (1987) did not recognise because of the small number of halophyte records available to him. However, we found another previously neglected source of halophyte records (Oborny 1912) that supported the delimitation of this new district. In addition, we re-assigned the halophyte

occurrences west, south-west and south of the town of Mikulov from the Hevlín-Nový Přerov district to the Sedlec district, as this area is drained by the Včelínek stream, which flows through the Sedlec district.

We reviewed botanical literature from Hochstetter (1825), the first scientific report on Moravian flora, to the present, plant records in the Pladias database, which contains data from botanical literature, herbarium specimens and unpublished observations from the Czech Republic (Wild et al. 2019, Chytrý et al. 2021), the herbarium database JACQ (jacq.org) and relevés (vegetation-plot records) in the Czech National Phytosociological Database (Chytrý & Rafajová 2003). Using these data, we prepared descriptions of the historical status of halophytic flora and vegetation in individual districts and at the most important sites within these districts, especially where halophytic flora and vegetation have survived to the present day.

In many cases, the geographic location of some former halophytic sites was uncertain. To determine such locations, we compared the information from herbarium labels and literature with the maps of the 2nd and 3rd Military Survey of the Habsburg Monarchy, different versions of which are now digitized and publicly available (Anonymous 2001–2017, 2021a, b, Timár et al. 2011). The original topographic sections (scale 1:25,000) of the 3rd Military Survey were particularly useful as they contain information on land use, distinguishing between arable land, meadows and common pastures. To interpret the geographic location of the relevés recorded by J. Vicherek 1959–1965, which contained short and sometimes unclear location information, we used the orthophoto maps based on aerial photographs from the 1950s available on the INSPIRE geoportal (Anonymous 2021b).

We visited all sites with preserved halophytic vegetation on 9–13 August 2020, described their current state, recorded vascular plant species with particular attention to halophytes and subhalophytes, and sampled relevés of halophytic vegetation. We supplemented this primary dataset with records from occasional visits to some sites in summer 2021.

Flora

We reviewed the historical and current distribution of 16 halophytes considered by Grulich (1987) as species with the strongest affinity for the saline habitats in the study area (sometimes referred to as “obligate halophytes”), i.e., *Bupleurum tenuissimum*, *Cirsium brachycephalum*, *Crypsis aculeata*, *C. schoenoides*, *Galatella cana*, *Glaux maritima*, *Plantago maritima* subsp. *ciliata*, *Salicornia perennans*, *Samolus valerandi*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum*, *Triglochin maritima* and *Tripolium pannonicum* subsp. *pannonicum*. We added *Juncus gerardii*, which was omitted by Grulich (1987) due to numerous identification errors in herbaria and literature. We refer to these 17 species as halophytes. There are also other species associated with saline habitats in Moravia, but they also occur on non-saline soil; we refer to them as subhalophytes.

Of the 17 halophytes selected for our study, recently published distribution maps and lists of reviewed records were prepared within the Pladias project for *Crypsis aculeata* and *C. schoenoides* (both Danihelka & Kaplan in Kaplan et al. 2020), *Plantago maritima* (Danihelka & Kaplan in Kaplan et al. 2018), *Salicornia perennans* (Danihelka & Kaplan

in Kaplan et al. 2017), *Spergularia marina* and *S. media* (both Kúr & Ducháček in Kaplan et al. 2016), *Suaeda prostrata* (Daníhelka & Kaplan in Kaplan et al. 2017) and *Tripolium pannonicum* (Daníhelka in Kaplan et al. 2017). A list of verified records and a map for *Cirsium brachycephalum* and *Triglochin maritima* were prepared in collaboration with P. Bureš, those for *Scorzonera parviflora* with V. Grulich and those for *Taraxacum bessarabicum* with J. Štěpánek and J. Zámečník. For the remaining five species, we revised and recorded the specimens available in the herbaria BRNM, BRNU, GM, HR, MMI, MZ, OL, OLM, OP, PR, PRC, VYM and ZMT (acronyms follow Thiers 2021). We found some additional records in these herbaria of the species already covered by the Pladias project. To improve spatial and temporal coverage, we extracted additional records from the literature. For most species, we used numerous literature and unpublished field records available in the Pladias database (www.pladias.cz). However, for *J. gerardii* and, to a large extent, for *T. bessarabicum*, we mainly relied on the records documented by herbarium specimens. The records of halophytes from the Pulkau district were mainly taken from the literature and databases, especially from the JACQ database (www.jacq.org).

The herbarium specimens were revised, their labels photographed and stored in a database together with the records extracted from the literature. They were georeferenced using digital maps from the portal Mapy.cz and various historical maps mentioned above. We then imported them into the Pladias database using its consistency-checking procedures (Wild et al. 2019). The records were further managed in the Pladias database. In several cases, we used information from the literature for herbarium specimens and information from herbarium labels for records extracted from the literature to make a record more precise in terms of time and location. For example, it is known from various sources that Ch. F. Hochsteter lived in Brno in 1817–1824 and that the Měnin Fishpond (Mönitzer See) was drained in 1822. Therefore, his undated specimens can be dated to 1817–1824 and those collected on the shores of Měnin Fishpond to 1817–1821. Similarly, we assigned all records from the 1950s onwards of *Salicornia perennans* and *Suaeda prostrata* from the vicinity of the village of Terežín in the Čejč district to the Zápověď site, as at that time, it was demonstrably the only site in the area where these two succulent halophytes still occurred.

In total, we compiled ~3433 records of halophytes from the nine southern Moravian districts (all stored in the Pladias database) and ~136 records from the Pulkau district in Lower Austria (Supplementary material Data S2). Of the 3433 records, ~1946 records were already available in the Pladias database. We added ~1487 records, of which ~1321 were supported by herbarium specimens. We collected most of the relevant plant records, both from herbarium collections and the literature, that have accumulated since the beginning of botanical research in the area in the early 19th century. Only for the Pulkau district, some herbarium records may be lacking, but it is still the most representative dataset on halophyte flora in the area. The recently added specimens from local collections (e.g. VYM and ZMT) contributed only a few unique records. Based on this experience, we believe that the spatial and temporal pattern of halophyte distribution described here will not change significantly, even if more herbarium specimens and literature records are found in the future.

For all the species and districts, we created graphs showing records of all the 17 halophyte species within each district on the timeline.

The taxonomy and names of vascular plants follow Kaplan et al. (2019) or, for those not occurring in the Czech Republic, Fischer et al. (2008). The Red List categories given in the Species chapter follow the latest Red Lists for the Czech Republic (Grulich 2017) and Austria (Niklfeld 1999).

In addition to vascular plants, we examined the bryoflora of saline habitats. We reviewed the literature from the 20th century and the current literature on the distribution of bryophytes in southern Moravia. Taxonomic concepts and nomenclature follow Kučera et al. (2012).

Vegetation

We extracted all relevés from southern Moravia from the Czech National Phytosociological Database (CNPd; Chytrý & Rafajová 2003) that contained at least one of the above 17 halophytes or subhalophytes *Lotus tenuis* or *Trifolium fragiferum*, and added all the other relevés from publications in which at least one relevé contained at least one of the 17 selected species. We then searched in unpublished sources not digitized in the CNPD for other relevés of halophytic vegetation and added them to this dataset. These newly added relevés came mainly from the unpublished manuscripts of J. Vicherek from the early 1960s and from unpublished reports of protected area surveys conducted in the last two decades.

During our visit at individual sites on 9–13 August 2020, we sampled at least one relevé in a relatively homogeneous area of each visually distinguishable type of halophytic vegetation. All the relevés had a standard size of 10 m². Most of them were squares of 3.16 × 3.16 m, but if there was no homogeneous vegetation in a square area, we used a rectangular plot of 10 m². We measured the geographic coordinates of all four corners of each plot using a GPS (Topcon HiPer SR with Getac PS336 Data Collector) with a positioning accuracy of ~5 cm. In each relevé, we recorded all species of vascular plants and bryophytes and estimated their cover using the nine-grade Braun-Blanquet scale (Westhoff & van der Maarel 1978). In total, we sampled 67 relevés. This dataset is available in the Zenodo repository (Danihelka et al. 2021).

For vegetation classification, we used a selection of relevés from the CNPD, added the relevés newly digitized from the literature, and the new relevés sampled in the field. This dataset contained 729 relevés. All the newly digitized and newly sampled relevés were deposited in the CNPD. We corrected errors in species identifications that we had discovered based on our field experience and examination of herbarium specimens. We also replaced broad species concepts used in the older literature with currently established concepts of narrower taxa that occur at saline sites. For example, records of *Carex vulpina* and *Festuca valesiaca* at saline sites were changed to *C. otrubae* and *F. pulchra*, respectively. Groups of closely related species often misidentified by botanists were combined into aggregates. For example, because the herbarium collections showed a high proportion of *Juncus compressus* specimens from saline sites to be misidentified as *J. gerardii*, we had to combine these two species into the *J. compressus* agg.

We classified this relevé dataset using the expert system CzechVeg-ESy, developed for the national vegetation classification of the Czech Republic (Chytrý 2007, 2011). We replaced the original definitions of marsh associations, as available in version 1-2020-01-12 of the expert system (Chytrý et al. 2020), with the definitions developed by Landucci

et al. (2020). The classification was performed using the Juice 7.1 program (Tichý 2002). We carefully reviewed the classification of each relevé by the expert system and investigated why some relevés were misclassified, not classified at all, or assigned to more than one association. Based on this experience, we improved the expert system by refining the logical definitions of associations of specialized halophytic vegetation. For some refined definitions, we used new features implemented in the expert system language for vegetation classification (ESy) described by Tichý et al. (2019). This refinement increased the number of correctly classified relevés.

It was not our aim to define new associations that are not recognized in Vegetation of the Czech Republic (Šumberová 2007a, b, Šumberová et al. 2007, 2011). However, we noticed that our data from 2020 and some newly obtained datasets contain several relevés corresponding to the association *Centaureo pannonicae-Festucetum pseudovinae*, described from Slovakia and not recognized in the national vegetation classification of the Czech Republic (Šumberová et al. 2007). Therefore, we added this association to the expert system.

Most halophytic associations are species-poor vegetation types defined by the dominance of a single highly specialized species. However, this is not the case for the halophytic grasslands of the class *Festuco-Puccinellietea*. To test whether the associations of this class defined by the expert system reflect real patterns of species composition, we compared the expert-system-based classification of this class with an unsupervised divisive classification (Twinspan; Hill 1979). We applied Twinspan to the relevés assigned by the expert system to any association of the class *Festuco-Puccinellietea*. We used the R package Twinspan (Oksanen 2019) with pseudospecies cut levels corresponding to 0, 2, 5, 10 and 20% cover. To avoid classification bias due to a disproportionate number of similar relevés from some sites, we performed a stratified resampling of the dataset. We took only two randomly selected relevés from each group of relevés assigned to the same association and sampled by the same researcher at the same site and in the same year. This stratification reduced the number of *Festuco-Puccinellietea* relevés from 293 to 166. These relevés were classified by Twinspan. Because Twinspan tends to divide groups into subgroups of similar size, vegetation types represented by a few relevés may not be recognized at higher division levels. Therefore, we interpreted groups at different hierarchical levels and accepted those that were most similar to the accepted associations or corresponded to ecologically defined subgroups within the associations. We then compared the associations defined by the expert system with a set of accepted Twinspan groups using alluvial diagrams created with the R library ggaluvial v. 0.12.3 (Brunson 2020).

From the classified dataset of 729 relevés, we selected 426 relevés assigned by the expert system to the associations of specialized halophytic vegetation. We considered the associations that were either defined by a dominance of one halophytic species or contained multiple halophytic species. We applied the same stratified resampling as described above, resulting in 246 relevés. We used this resampled dataset to create a synoptic table and calculate the diagnostic, constant and dominant species of each association.

All the halophytic associations of the classes *Bidentetea*, *Phragmito-Magno-Caricetea*, *Crypsietea aculeatae* and *Thero-Salicornietea strictae* were defined through the dominance of a single halophytic species. Consequently, their classification was straightforward within the concept of dominance-based associations and did not require further testing. However, the classification of halophytic grasslands of the class *Festuco-Puccinellietea* was based mainly on the combination of the occurrence of sociological

species groups. Therefore, we tested whether this classification reflects the patterns of variation in total species composition using two methods. First, we calculated the Twinspan classification of the stratified subset of 166 relevés assigned to the associations of the *Festuco-Puccinellietea* class and compared the Twinspan clusters with these associations. Second, we prepared a DCA ordination (Hill & Gauch 1980, calculated using the `vegan` v. 2.5-7 library in R; Oksanen et al. 2020) of the same relevés and plotted the association assignment of each relevé by the expert system onto the ordination diagram.

Diagnostic species were defined based on the frequency of their presence/absence within and outside the groups of relevés belonging to different associations. To be considered diagnostic, a species had to meet four conditions simultaneously: (i) to have a value of the phi coefficient of association with the group of relevés greater than 0.25, (ii) to have a probability of observed occurrence concentration within that group based on Fisher's exact test of less than 0.05, (iii) to have the greatest frequency in the relevés of the focal association with a constancy ratio greater than 0.25, and (iv) to have more than one occurrence in the dataset. The phi coefficient was calculated for the virtually equalized sizes of relevé groups according to Tichý & Chytrý (2006). The constancy ratio is defined as the ratio between the percentage species frequency within the focal group in which frequency is highest and the next highest frequency in any other group (Dengler 2003). If a species had a phi coefficient greater than 0.50, it was considered highly diagnostic.

Constant species were defined as those occurring in more than 40% of the relevés assigned to the focal association. Species occurring in more than 80% of the relevés were considered highly constant.

Dominant species were defined as those occurring in more than 20% of relevés with a cover greater than 25% or a lower cover that is greatest in the relevé. If they fulfilled these conditions in more than 50% of the relevés, they were considered highly dominant.

Relationships to salinity

We collected soil samples from a depth of 2–10 cm in 3–4 places within each relevé sampled in August 2020. We mixed these samples for each relevé and measured the pH and electrical conductivity of the mixed sample in a suspension with distilled water (soil:water ratio ~ 2:5) using the Hach HQ40D multimeter (Hach, Loveland, CO, US). To evaluate the relationships between individual plant species and salinity, we related the presence/absence data of all species to measured soil pH and conductivity using a generalized linear model with binomial distribution and logit link function. We used the `glm()` function from the R-core package `stats` (R Core Team 2020). We used McFadden's pseudo- R^2 (McFadden 1974) to quantify the proportion of variation explained by the model. For species with significant ($p < 0.05$) or marginally significant ($p < 0.1$) models, we drew the plots of species occurrence probability using the packages `ggplot2` (Wickham 2016), `ggtext` (Wilke 2020), `gtools` (Warnes et al. 2020) and `gridExtra` (Auguie 2017).

Sites

Měnin-Šaratice district

This district lies between the villages of Blučina, Otmarov, Sokolnice, Šaratice, Otnice, Těšany and Moutnice in a large and shallow depression of the Litava, Dunávka and Říčka streams (Grulich 1987). This is the northernmost part of southern Moravia where halophytes occurred naturally. It includes the area of the former large Měnin Fishpond (Mönitzer Teich) with some smaller fishponds and mineral water springs between the villages of Nesvačilka (Neudorf) and Šaratice (Scharatitz).

The former Měnin Fishpond was between the villages of Měnin, Blučina and Moutnice. Although mostly referred to as a lake in the literature, it was an artificial pond created in 1492 (Hurt 1960). Soils on its shores were rich in salt, especially calcium and magnesium sulphate (Laus 1907). The fishpond was drained in 1822 and converted mainly into arable land (Hurt 1960). The nearby smaller fishponds were also drained during the 19th century, and most of the natural springs were adjusted for collecting water using a system of tubes and wells during the 20th century (Laus 1907, Grulich 1987).

In the past, this district harboured all the 17 halophytes except *Samolus valerandi* and *Triglochin maritima*. The past occurrence of *Glaux maritima* is uncertain: the single non-dated herbarium specimen allegedly collected near Měnin may be mislabelled.

The only records of the halophytic flora at the Měnin Fishpond before its drainage are from Hochstetter (1825). He explored the area likely between 1817–1821 because his 1825 article indicates he was unaware of the fishpond drainage. He observed vegetation with *Cirsium brachycephalum* (*Cnicus polyanthemus*), *Crypsis aculeata*, *Plantago maritima*, *Salicornia perennans*, *Scorzonera parviflora* and *Suaeda prostrata* on the fishpond shores. He also collected *Galatella cana* in a nearby grove and *Taraxacum bessarabicum* (*Leontodon lividus*) in an adjacent wet meadow. He further collected *Bupleurum tenuissimum*, *Scorzonera parviflora*, *Spergularia media* (misidentified as *S. salina*) and *Tripolium pannonicum*, but these records were published only later by Rohrer & Mayer (1835).

Makowsky (1856) found *Crypsis aculeata* and *C. schoenoides* in saline habitats near the villages of Měnin, Moutnice and Otmarov and confirmed the occurrence of *Salicornia perennans*, *Suaeda prostrata* and *Tripolium pannonicum*. He returned to the area several times and collected most of the halophytes once recorded by Hochstetter. However, the occurrences of *Cirsium brachycephalum* and *Galatella cana* have not been confirmed since Hochstetter's times (for the latter, see Danihelka 2008). *Scorzonera parviflora* was last recorded in 1900. The halophytic sites near Otmarov were repeatedly visited by Brno botanists from the late 1860s because of their easy accessibility via railway, and numerous herbarium specimens have been preserved. However, already Laus (1907: 14), who visited the area in 1894, reported that the area had been cultivated, and the occurrences of halophytes reduced to a few spots, mainly ditches and road verges in villages' common pastures. He considered the surroundings of Vladimirov farmstead near Otmarov, where he collected *Crypsis aculeata*, as the best-preserved halophytic site. Halophytic flora gradually disappeared near Otmarov, although some halophytes, e.g. *Bupleurum tenuissimum* and *Plantago maritima*, survived there until the 1930s.

Krist (1935) referred to the site near the village of Šaratice as almost destroyed, harbouring only *Plantago maritima* and *Tripolium pannonicum*. Šmarda (1953) described, partly based on information from the algologist J. Bílý Jr., remnants of halophytic

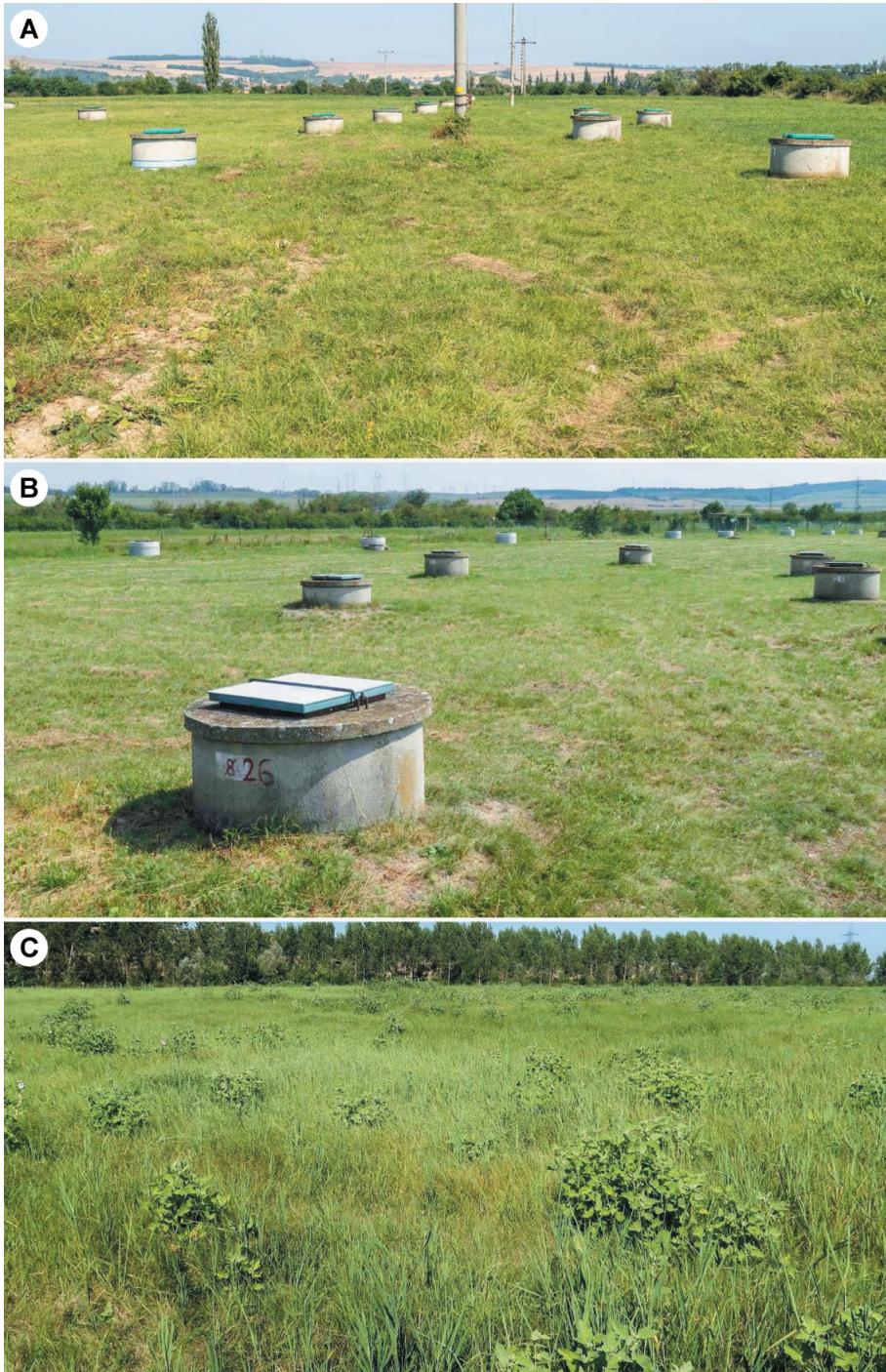


Fig. 2. Halophytic localities in the Měnin-Šaratice district: (A) Kalužiny 2020, (B) Zřídla u Nesvačilk 2020, (C) Císařská obora 2020. Photo credits: K. Chytrý (A), M. Chytrý (B), E. Šmerdová (C).

vegetation at several sites within the district but reported few halophytic species. Fragments of halophytic vegetation were still preserved along the Dunávka stream west of Sokolnice between the railway and the road. In 1950, J. Šmarda recorded there *Bupleurum tenuissimum*, *Juncus gerardii*, *Plantago maritima* and *Spergularia media*. *Salicornia perennans*, collected there in 1912, and *Suaeda prostrata*, found in 1912 and 1922, were no longer present. The last specimens of *Salicornia perennans* were collected by S. Staněk and J. Suza around mineral springs near the villages of Nesvačilka and Šaratice in the early 1920s, and the last specimen of *Suaeda prostrata* was collected by J. Šourek near Nesvačilka in 1946.

Vicherek (1973) was still able to record relevés of halophytic vegetation in a shallow depression between Moutnice and Nesvačilka, probably near the springs of the Nesvačilka stream. Between 1962 and 1964, he found there *Crypsis aculeata*, *C. schoenoides*, *Spergularia marina*, *S. media*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. This site may be identical with the place recorded on herbarium labels as Luža, where E. Vitek collected *Crypsis aculeata*, *Salicornia perennans* and *Suaeda prostrata* in 1912. These last spots were destroyed by drainage probably in the 1960s. In 1982, only *Plantago maritima* was known to survive in the district, occurring at two sites. However, targeted searches after 2000 also yielded a few records of *Bupleurum tenuissimum* and *Spergularia marina*. Nowadays, strongly impoverished fragments of halophytic vegetation remain mainly at the three small sites described below.

Kalužiny (Fig. 2A). – This site is located ~1.75 km S of the village of Šaratice. In old herbarium labels, it is referred to as “Šaratica”, “prameny Šaratice”, “prameny hořké vody” or “gradovna”. Currently, it is covered mainly with meadows dominated by *Bromus erectus* in drier places and meadows with *Festuca arundinacea*, *Inula britannica* and *Serratula tinctoria* in wetter places. A meadow with *Medicago sativa* and *Festuca pratensis* was sown along the eastern edge of the site. These meadows are regularly mown, and the wet places are disturbed by heavy machinery. Only a few small wet depressions still contain halophytes and subhalophytes, such as *Plantago maritima* and *Lotus maritimus*. The site is protected as a natural water source.

Zřídla u Nesvačilký (Fig. 2B). – The Natura 2000 site Zřídla u Nesvačilký, also protected as a natural water source, consists of two non-contiguous sites. The larger one, in old herbarium labels usually referred to as “Wolfovy studánky” or “prameny Šternovky”, is located ~2 km NE of the village of Nesvačilka. Currently, there are some wet places between the wells in a fenced area. In 2006, a few individuals of *Lactuca saligna* were recorded there by J. Podhorný and J. Komárek (Grulich in Hadinec & Lustyk 2007). In 2020, we observed *Plantago maritima* in one place outside the fenced area as the last species of the 17 halophytes studied here. There were patches of *Festuca pulchra* grassland (association *Centaureo pannonicae-Festucetum pseudovinae*). However, the dominant vegetation type in this area is dry to mesic non-halophytic grassland. The smaller site is located ~2 km NE of Nesvačilka. It is covered by a grassland composed of generalist species with no halophytes. Both sites are regularly cut and mulched. Although the most appropriate management for halophytes is grazing with soil surface disturbances, it would be at odds with using the site for collecting mineral water (Pekárová 2015).

Císařská obora (Fig. 2C). – The Císařská obora (Emperor’s Game Preserve) site is located ~5 km S of the village of Měnin, south of the former Měnin Fishpond. It is a part of the Natura 2000 site Rumunská bažantnice. Not much is known about its past. According to the 2nd Military Survey maps (in Moravia dating to 1836–1840), the site was covered mainly by meadows. The 3rd Military Survey maps (1876–1878) showed it covered by a forest (Galdhof-Wald), with a small patch of arable land in the middle. The aerial photographs from the 1950s are difficult to interpret, but the area was mainly covered by meadows and (possibly) clearings. Currently, the site is located inside a fenced game preserve. There are ditches and small fishponds with islands created in the late 1990s (Juřica et al. 2015). *Phragmites australis* stands occur on fishpond shores and stands of *Bolboschoenus maritimus*, *B. planiculmis*, *Carex distans* and *C. otrubae* near ditches. Islands are covered by unmown ruderal grasslands dominated by *Calamagrostis epigejos* and *Agrostis gigantea* with tall herbs *Althaea officinalis*, *Cirsium canum* and *Dipsacus fullonum*. Other grasslands in the area are mown. Subhalophytes such as *Centaureium pulchellum*, *Lotus maritimus*, *L. tenuis*, *Melilotus dentatus* and *Teucrium scordium* are scattered in the area, but we found none of the 17 halophytes studied here.

Velké Němčice district

This district lies in a shallow depression along the Starovický stream between the villages of Velké Němčice (Gross Niemtschitz), Uherčice (Auerschitz) and Starovice (Steurowitz). In the north, it borders the Měnin-Šaratice district.

In the past, this district supported all the 17 halophytes except *Cirsium brachycephalum*, *Galatella cana*, *Samolus valerandi* and *Triglochin maritima*. The past occurrence of *Glaux maritima* is uncertain: there are two records from relevés recorded by J. Vicherek (Vicherek 1962), but no herbarium specimen has been found. There are also historical records of *Triglochin maritima* (e.g. Vicherek 1962), but we consider them erroneous because the only herbarium specimen reported for this district (cf. Bureš 2010) corresponds to *T. palustris*.

The occurrences of halophytes in this district were discovered by botanists as late as 1921. Fietz et al. (1923) described patches of halophytic vegetation developed around a small fishpond (Hofteich) at the southern edge of Velké Němčice, now filled with earth and built up. At this site, they recorded *Bupleurum tenuissimum*, *Crypsis schoenoides*, *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina* and *Tripolium pannonicum*. They found the best-developed patches of halophytic vegetation ~1.3 km SSE of the town. This “Niemtschitzer Salzsteppe” (later referred to as Plácky or Brodač) was a small remnant of the former extensive saline meadows and pastures in the shallow valleys of the Starovický and Křepický streams. It had an approximately triangular shape (like the current Plácky Nature Monument) and an estimated area of 5 ha. Fietz et al. (1923) described various vegetation types, including patches dominated by annual species of *Atriplex*, *Juncus gerardii*, *Tripolium pannonicum* and *Festuca* (probably *F. pulchra*) and patches co-dominated by *Salicornia perennans* and *Suaeda prostrata*. In addition, they noted the occurrence of *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina* and *S. media*. Some halophytes, including *Salicornia perennans* and *Suaeda prostrata*, were also abundant on a dirt road close to the site. Non-succulent halophytes occurred in

a broader area because Fietz et al. (1923) reported patches of halophytic vegetation also east of the road Velké Němčice–Hustopeče.

The Plácky site was frequently visited by botanists in the 1920s and 1930s, as documented by numerous herbarium specimens. *Bupleurum tenuissimum*, *Crypsis aculeata*, *C. schoenoides*, *Salicornia perennans*, *Scorzonera parviflora*, *Spergularia marina*, *Suaeda prostrata* and *Tripolium pannonicum* were collected at the Plácky site in large quantities for the exsiccate series Herbarium florae Reipublicae bohemicae slovenicae and distributed worldwide. However, Krist (1935) reported that the halophytic site near Velké Němčice had been “reduced”, and the surrounding wetlands drained by deep ditches. Consequently, the site remained dry throughout the year.

From the 1940s onwards, the Plácky site was repeatedly surveyed by V. Vlach, whose unpublished records were summarized by Husák & Jatiová (1984). In 1942, Vlach recorded *Crypsis aculeata*, *Juncus gerardii*, *Salicornia perennans*, *Spergularia media*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. According to his records, local conditions for halophytic flora, grazed by livestock, were optimal until 1945. In that year, a weir on the Svratka river was removed, and the drought of 1947 caused a significant decline in groundwater level. Consequently, halophytes started to decline, and ruderal species increased. In 1950, Vlach failed to confirm the occurrence of *Crypsis aculeata* and *Taraxacum bessarabicum*, while *Salicornia perennans* was only represented by a few individuals. Jan Šmarda studied this site in 1950, recording *Bupleurum tenuissimum*, *Plantago maritima*, *Salicornia perennans*, *Suaeda prostrata* and *Taraxacum bessarabicum* (Šmarda 1953). He considered Plácky as one of the most valuable halophytic sites in Moravia and recommended its strict protection. Although the site was put under conservation in 1950, the decline of halophytic vegetation continued. Between 1958 and 1965, the area south of Velké Němčice was drained by subsurface pipe drainage, and a system of drainage ditches was established around the perimeter of the Plácky site a few years later. Still, J. Vicherek was able to record relevés of vegetation dominated by *Salicornia perennans* and *Suaeda prostrata* between 1959 and 1965 (Vicherek 1973). This was the last record of the former, while for *Suaeda prostrata*, there is a herbarium specimen collected by F. Weber allegedly in 1973. In the mid-1970s, only *Plantago maritima*, *Spergularia media*, *Scorzonera parviflora* and *Tripolium pannonicum* were observed at the site (Husák & Jatiová 1984). A visit to the site in 2001 by J. Danihelka yielded no records of halophytes. Conservation management was restored in 2005 when regular mowing was introduced. Since 2017, the site has been grazed by horses (M. Hájek, pers. comm.). The current halophytic flora of Plácky is extremely impoverished. J. Danihelka & K. Fajmon collected *Spergularia marina* next to the southwestern edge of the reserve in 2007, and P. Novák observed a small population of *Bupleurum tenuissimum* and probably also *Juncus gerardii* in 2012. In addition, *Chenopodium chenopodioides* was repeatedly recorded in the southern part of the reserve. Currently, there are no well-developed halophytic plant communities there (Fig. 3A). Some parts of the reserve, especially its north-western corner, are dry and covered by subruderal grasslands dominated by *Carex praecox*, *Festuca rupicola* and *Poa angustifolia*. Wet depressions are overgrown by *Carex riparia*.



Fig. 3. Halophytic localities in the Velké Němčice, Šakvice and Rakvice districts (A) Pláčky 2020, (B) Štinkovka 2021, (C) Trkmanec-Rybníčky 2020. Photo credits: K. Chytrý (A), M. Chytrý (B), E. Šmerdová (C).

Starovický Fishpond, the second major halophytic site of the Velké Němčice district, was located at the northern edge of the village of Starovice northeast of Hustopeče. The 3rd Military Survey maps (1876–1878) show two small fishponds near the northern edge of the village, surrounded by a common pasture. Aerial photographs from the 1950s show a similar pattern, with a football playground replacing pasture at the south-eastern corner of the area. The halophytes occurred around the fishponds and possibly also in a pasture land strip along the Starovický stream up to 1 km towards the north-west. Probably in the late 1960s or during the 1970s, the southern part of the halophytic site was built up, and its northern part was destroyed by enlarging the fishpond towards the village. The western half of the former site (west of the Starovický stream) is now completely drained and partly used as a tennis playground, while most of the remaining area is covered by ruderal grassland (in places with *Carex otrubae*). The fishpond littoral is largely overgrown by *Phragmites australis*.

The occurrences of halophytes near Starovice were discovered by botanists in the early 1920s. At this site or nearby, they collected *Bupleurum tenuissimum*, *Crypsis schoenoides*, *Juncus gerardii*, *Plantago maritima*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. The first description of the Starovice site was published by Šmarda (1953), who in 1951 recorded *Bupleurum tenuissimum*, *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum* and *Tripolium pannonicum*.

Vicherek (1962, 1973), who studied the Starovice site in 1959–1965, confirmed the occurrence of *Bupleurum tenuissimum*, *Glaux maritima*, *Plantago maritima*, *Salicornia perennans*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. He was still able to record vegetation dominated by both succulent halophytes. However, the halophytic habitats were destroyed soon after his survey. The last herbarium specimen of *Suaeda prostrata* is from 1968. Still, a few halophytes survived until the 1970s: *Tripolium pannonicum* was last collected in 1977 and *Plantago maritima* in 1980.

In 1961, F. Kühn studied weed flora of patches with saline soils on arable land in the surroundings of Velké Němčice (Kühn 1963). He found *Spergularia marina* at about ten sites, at some of them accompanied by *Crypsis schoenoides* (in Table 1 of his article reported as *Heleochloa alopecuroides+schoenoides*). Of the formerly rich halophytic flora in the Velké Němčice district, only *Bupleurum tenuissimum*, *Spergularia marina* and probably also *Juncus gerardii* have survived until recently, all in tiny populations.

Some subhalophytes still occur in the floodplain of the Starovický stream ~1 km N to 1.5 km NNW of Starovice. Shallow pools were created there in 2013–2015 as a part of a restoration project. In 2021, the edges of the *Phragmites australis* stands fringing the pools contained several subhalophytes such as *Bolboschoenus maritimus*, *B. planiculmis*, *Carex otrubae*, *C. secalina*, *Centaurium pulchellum*, *Lotus tenuis*, *Melilotus dentatus*, *Puccinellia distans* and *Trifolium fragiferum* (Chytrý & Danihelka 2021). However, the site is relatively dry and unmown, which does not provide good conditions for halophytes. None of the 17 halophytes studied in this article was found there.

Šakvice district

This district encompasses the shallow depressions of the Popický and Štinkovka streams between the village of Pouzdřany (Pausram) in the west, the town of Hustopeče (Auspitz) in the north and the village of Starovičky (Klein-Steurowitz) in the east. Some halophytes also occurred in narrow stream valleys north of Popice (Poppitz) and Hustopeče.

The flora of the district included *Bupleurum tenuissimum*, *Crypsis aculeata*, *C. schoenoides*, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Samolus valerandi*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum*, *Triglochin maritima* and *Tripolium pannonicum*. It is likely that *Cirsium brachycephalum* also occurred in this district, but no herbarium specimen has been found.

The most valuable and well-known halophytic site was around the Šakvice railway station (formerly called Hustopeče station, Bahnhof Auspitz or Nordbahn-Station Auspitz). It was discovered in the 1860s by J. Wessely, then a parish priest in Hustopeče. Because of its location on the railway from Vienna to Brno (opened in 1839), botanists frequently visited this site, and its flora was documented by numerous herbarium specimens. All the species listed in the previous paragraph except *Cirsium brachycephalum* occurred there. *Triglochin maritima* was discovered there as a new species of the Moravian flora in 1900. There is also a herbarium specimen of *Samolus valerandi* allegedly collected from this site, but it may be a labelling mistake.

Laus (1907) was the first to describe the halophytic flora around the Šakvice railway station in detail. At that time, halophytes occurred on both sides of the railway, but the best-developed halophytic vegetation was found in the place where the local railway to Hustopeče branched off. In this narrow triangle, Laus observed stands dominated by *Salicornia perennans* and probably also by *Suaeda prostrata*.

Laus (1907) already reported that one part of the saline habitats was destroyed in 1894 when the local railway to Hustopeče was built. Another part disappeared when the second railway track and a flyover were built in the early 1920s (Krist 1935). *Triglochin maritima* was last collected in 1923. As reported by J. Bílý (sec. Šmarda 1953), it once occurred in a small saline meadow north-west of the station. The last specimen of *Suaeda prostrata* was collected in 1927 and that of *Salicornia perennans* in 1931. Krist (1935) recorded *Plantago maritima* and *Tripolium pannonicum* but no other halophytes. Šmarda (1953) only found *Juncus gerardii* (last collected in 1952) and *Plantago maritima*, and concluded that the once-famous halophytic site near the Šakvice station “belongs to the past age”. Indeed, these were the last records of halophytes from this site.

Another halophytic site occurred ~1.8 km W of the village of Starovičky on both banks of the Štinkovka stream. The 2nd Military Survey maps (1836–1840) show there meadows on the bottom of a drained fishpond (still referred to as a fishpond: Un. Steurowitzer Teich). Halophytes occurred in these wet saline meadows and along the Starovičský stream roughly up to the village centre (Šmarda 1953), where *Glaux maritima* was recorded in 1952. The flora of this site was rich in halophytes, including *Bupleurum tenuissimum*, *Crypsis schoenoides*, *Glaux maritima*, *Plantago maritima*, *Samolus valerandi*, *Scorzonera parviflora*, *Spergularia marina*, *S. media* and *Tripolium pannonicum*. Šmarda explored the site in 1952 and found *Plantago maritima*, *Scorzonera parviflora*, *Taraxacum bessarabicum* and *Tripolium pannonicum* (Šmarda 1953). Also in

1952, V. Skřivánek (sec. Šmarda 1953) found *Scorzonera parviflora* and *Taraxacum bessarabicum* somewhere between this site and the village. Jiří Vicherek still sampled saline grasslands of the association *Scorzonero parviflorae-Juncetum gerardii* with *Plantago maritima*, *Scorzonera parviflora* and *Tripolium pannonicum* in 1962 or 1963 (Vicherek 1973). *Plantago maritima* and *Tripolium pannonicum* were last collected in 1971, while *Juncus gerardii* was still recorded there in 2021 (Chytrý & Danihelka 2021).

A targeted search in summer 2021 along the Štinkovka stream between the south-eastern edge of Hustopeče and a dam of the Lower Nové Mlýny reservoir resulted in the discovery of halophytic habitats on a temporarily abandoned wet arable land and ex-arable land converted to semi-natural areas as a part of restoration projects (Chytrý & Danihelka 2021). The richest halophytic and subhalophytic flora, including whole halophytic plant communities, was found along the Štinkovka between Šakvice and Starovičky. Of the halophytes, *Crypsis schoenoides*, *Juncus gerardii*, *Samolus valerandi* and *Spergularia marina* were recorded, each species at two sites.

In the past, some halophytes also occurred further upstream along the Štinkovka at the north-western outskirts of Hustopeče. The site was referred to as an ice-skating rink (Eislaufplatz) and later a swimming school (Schwimmschule) on herbarium labels. *Samolus valerandi* was collected there repeatedly from 1897 and last observed in 1954 or 1955 (J. Tománek sec. Sedláček & Dvořák 1983). It co-occurred with *Plantago maritima*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. Šmarda (1953) considered the site destroyed. Today, there is an open-air swimming pool and a swimming hall. In 2018, *S. valerandi* was found (together with a few subhalophytes) on the drained bottom of the Přední Fishpond ~2 km north of its former site in Hustopeče (Ambrozek & Melichar in Lustyk & Doležal 2019).

Further well-developed patches of halophytic vegetation once existed in a shallow depression of the Popický stream near the road ~1.5 km SE of the village of Popice. The 3rd Military Survey map (1876–1878) shows strips of grasslands along the Popický stream and its left-hand tributary. This site most likely hosted *Suaeda prostrata*, collected there or nearby in 1894–1913, as well as *Crypsis aculeata*, *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina* and *Tripolium pannonicum*. The record of *Cirsium brachycephalum* (Šmarda 1953) may also refer to this site. The last record of *Tripolium pannonicum* dates back to 1930. In 1984, V. Grulich and R. Řepka collected *Plantago maritima* and *Spergularia marina* between this site and the railway. However, the site was destroyed in the same year by reclamation (Grulich 1987).

The occurrences of halophytes along the Popický stream above the north-western edge of Popice were discovered probably by Šmarda (1953), who recorded only *Juncus gerardii*. Local vegetation was described by Vicherek (1962). His relevés include *Cirsium brachycephalum*, *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. These saline habitats were probably destroyed in the 1960s, as suggested by the absence of newer records of halophytes. In addition, Šmarda (1953) found *Juncus gerardii*, *Plantago maritima*, *Spergularia marina* and *Tripolium pannonicum* in grazed places along the stream in the village and on the local playground.

Halophytic vegetation also occurred further westwards between the villages of Popice and Pouzdřany, probably ~1.5 km WNW of Popice, but the exact location is unknown. Laus (1907) recorded there *Bupleurum tenuissimum*, *Plantago maritima*, *Spergularia*

marina, *S. media*, *Suaeda prostrata* and *Tripolium pannonicum*. Šmarda (1953) observed *Plantago maritima*, *Spergularia marina* and *Tripolium pannonicum* somewhere in that area in 1952. Single records of halophytes also exist from other places in the district, e.g. from the eastern shores of the former Šakvický Fishpond south-east of the village of Šakvice, now flooded by the Lower Nové Mlýny reservoir.

The first halophyte species to disappear from the Šakvice district was *Triglochin maritima* in the 1920s, while both succulent halophytes vanished in the late 1920s or early 1930s. *Plantago maritima* was last observed in the district in the mid-1980s. Nowadays, *Crypsis schoenoides*, *Juncus gerardii*, *Samolus valerandi* and *Spergularia marina* occur in the district, except for *J. gerardii* in large populations.

Restored halophytic sites along the Štinkovka stream near Šakvice (Fig. 3B). – Since 2017, the village of Šakvice has implemented a series of ecological restoration projects aimed at converting the wet arable land along the Štinkovka stream into areas with semi-natural vegetation. They created a pond and several shallow pools, planted forests, sowed grasslands and left some areas on the former arable land without management. After rains, some places in these areas are shallowly flooded. In summer 2021, several halophytic species and plant communities were found in these areas (Chytrý & Danihelka 2021). One site occurs on the right bank of the Štinkovka between the road Šakvice–Starovičky and the railway Brno–Břeclav ~2.2–2.8 km ESE of Šakvice. There were large populations of *Crypsis schoenoides* and *Samolus valerandi* in the stands of *Bolboschoenus maritimus* and *B. planiculmis* (association *Tripleurospermo inodori-Bolboschoenetum planiculmis*). Several species of subhalophytes also occurred in the stands of *Carex secalina* (*Agrostio stoloniferae-Juncetum ranarii*) and ephemeral wetlands on wet ex-arable land (*Veronico anagalloidis-Lythretum hyssopifoliae*). Another site, restored in 2018, occurred near a new fishpond on both sides of Štinkovka 1.5–1.9 km E of Šakvice. Also here, abandoned wet arable land was overgrown by *Bolboschoenus planiculmis* stands containing large populations of *Crypsis schoenoides*, *Samolus valerandi* and *Spergularia marina*. In places, there were patches with salt efflorescences on the soil surface and species-poor vegetation with *Crypsis schoenoides*, corresponding to the association *Heleochloëtum schoenoidis*. The deposit of the substrate removed from the pond and pools were covered by extensive stands of *Carex secalina* (*Agrostio stoloniferae-Juncetum ranarii*) and in trampled places by open grasslands dominated by *Puccinellia distans* and *Spergularia marina* (association *Puccinellietum limosae*). Narrow reed stands dominated by *Schoenoplectus tabernaemontani* developed along the banks of the new fishpond. Large populations of *Samolus valerandi* and *Spergularia marina* were also found in wet maize fields on the right bank of the Štinkovka adjacent to the north-eastern edge of this restored site.

Rakvice district

The Rakvice district lies in a shallow depression along the lower Trkmanka stream and its left-hand tributary Bílovický stream between the southern edge of the town of Velké Pavlovice, the village of Velké Bílovice, the town of Podivín (Kostel) and the village of Rakvice (Rakwitz). Towards the north-west, halophytes occurred along the railway as far as the Zaječí (Saitz) station. The latter site, drained by Zaječí stream (a left-hand tributary

of the Štinkovka stream), might be considered as a part of the Šakvice district. However, we prefer to follow the district delimitations proposed by Grulich (1987). In the north, this district borders the Čejč district. In the south-west, it reaches the Dyje floodplain, but it is impossible to draw a sharp border. While succulent halophytes never occurred within reach of floods, *Bupleurum tenuissimum*, *Crypsis schoenoides* and *Cirsium brachycephalum* were repeatedly recorded on pasture land inundated during extreme floods or even within floodplains.

The earliest known herbarium specimen of a halophyte from southern Moravia was collected in this district by H. Schott, most likely between 1786 and 1792. The specimen of *Plantago maritima* labelled “auf der Huthweide bey Kostel” is now preserved in the herbarium of the Hungarian Natural History Museum in Budapest (BP; Sutorý 1995). However, this record remained unknown to Moravian botanists for the next two centuries.

The halophytic flora of the Rakvice district was rich in species and included all the 17 halophytes except for *Galatella cana* and *Triglochin maritima*. Both succulent halophytes only occurred near the Zaječí railway station. There are numerous herbarium specimens of *Salicornia perennans* from the site near the Rakvice railway station but only one, possibly mislabelled, specimen of *Suaeda prostrata*.

The first halophytic site discovered in this district was near the Zaječí railway station. Alexander Makowsky collected *Crypsis aculeata* there in 1874 and *Bupleurum tenuissimum* and *Salicornia perennans* in 1879. Laus (1907) reported halophytes to occur mainly in the ditches along the southern side of the railway and on arable land south-west of the railway station. However, he noted that they were strongly declining due to reclamation. *Suaeda prostrata* was last collected there in 1921, and *Salicornia perennans* (by Laus already considered disappeared) in 1924. Other halophytes vanished from this site roughly at the same time, except for *Tripolium pannonicum*, which was last collected in 1952. Šmarda (1953) observed only *Bolboschoenus maritimus* agg. and *Lotus maritimus* at this site.

Species-rich halophytic sites, discovered as late as 1907 by H. Laus, were around the village of Rakvice (Laus 1909). North of the railway station, he observed *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans* and *Scorzonera parviflora*. South of the railway next to the station, *Crypsis aculeata*, *C. schoenoides* and *Spergularia media* occurred in a marshland grazed by geese. In 1909, he also collected *Taraxacum bessarabicum*, while *Samolus valerandi* was found there in 1926. Halophytes also occurred along the southern and south-eastern edge of the village. A small fishpond was indicated on the 3rd Military Survey map (1876–1878) at the southern edge of the village. Then it was probably surrounded by halophytic vegetation, but now it is filled with earth and built up. South and south-east of the village, the map showed large tracts of common pastures and reed beds. As documented by numerous herbarium specimens of halophytes, these pastures and wetlands were at least partly saline. They extended further east of the village towards the Trkmanka stream and the town of Podivín. Some halophytes, e.g. *Crypsis schoenoides* and *Spergularia marina*, may have occurred further in the south-east, near Podivín, but locality information on herbarium labels is vague.

Šmarda (1953) confirmed the occurrence of halophytes at both sites near Rakvice. In 1950, he found *Crypsis schoenoides*, *Glaux maritima*, *Juncus gerardii*, *Spergularia marina* and *Tripolium pannonicum* in saline marshlands south-east of the village. Two

years later, he recorded *Cirsium brachycephalum* in railway ditches next to the station, along with *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora* and *Tripolium pannonicum*. In 1959–1964, the halophytic vegetation around Rakvice was documented by Vicherek (1962, 1973), who recorded numerous relevés containing most of the halophytes that occurred at both major sites.

However, both halophytic sites near Rakvice were destroyed. *Salicornia perennans* was last collected near the railway station in 1932 and vanished probably in the 1930s. *Suaeda prostrata* was allegedly collected there in 1925 by F. Weber; however, this may be a mislabelled specimen, and the species may have never occurred at that site. The halophytic habitats south and south-east of the village were destroyed probably in the 1960s. In contrast, halophytes in the ditches next to the railway station survived longer: *Scorzonera parviflora* and *Tripolium pannonicum* were last observed in 1981 (Grulich 1987).

The large saline marshlands northeast of Rakvice and south of the Trkmanský dvůr settlement (below referred to as Trkmanec-Rybníčky and Trkmanské louky) were discovered by S. Staněk and J. Bílý Jr. in 1922, when they collected *Cirsium brachycephalum* and *Tripolium pannonicum* there. However, this site was almost disregarded by Šmarda (1953), who cited a few records of subhalophytes provided by F. Kühn. In 1962 or 1963, J. Vicherek sampled there a relevé of a saline marshland with *Bolboschoenus maritimus* agg., *Cirsium brachycephalum*, *Juncus gerardii* and *Scorzonera parviflora* (Vicherek 1973), providing the only record of the latter species from this site. *Samolus valerandi* was discovered there only in 1982, and it has been observed repeatedly since then.

The last major halophytic site in the Rakvice district existed around the Fabián Fishpond at the northern edge of the town of Velké Bílovice. It was discovered in 1921 by J. Podpěra, who collected *Bupleurum tenuissimum*, *Glaux maritima* and *Spergularia media* on the shores of this small fishpond. During the following decades, *Crypsis aculeata*, *C. schoenoides*, *Plantago maritima*, *Spergularia marina* and *Tripolium pannonicum* were repeatedly collected at this site. Šmarda visited the site in 1951 and recorded *Crypsis aculeata*, *Glaux maritima*, *Spergularia marina* and *Tripolium pannonicum*, and probably also *Juncus gerardii* (Šmarda 1953). Halophytic vegetation was still present there in the early 1960s (Vicherek 1962). Last halophytes, namely *Crypsis aculeata* and *Spergularia marina*, were collected in 1971 and 1978, respectively. The fishpond was filled with earth probably at the turn of the 1970s, and currently, the area is used as a playground with no remnants of halophytic vegetation.

The current halophytic flora of the Rakvice district is enormously impoverished. Both succulent halophytes disappeared already in the 1920s. *Crypsis aculeata* and *Glaux maritima* were last collected in 1964, and *Bupleurum tenuissimum* in 1969. *Plantago maritima*, *Scorzonera parviflora* and *Tripolium pannonicum* vanished during the early 1990s. Only *Cirsium brachycephalum*, *Crypsis schoenoides*, *Juncus gerardii*, *Samolus valerandi* and *Spergularia marina* still survive. *Spergularia media*, nowadays also present in the district, was collected only twice in 1909 and 1918, and then again in 2008 and 2014 along the motorway. However, the recent occurrences may not be derived from the autochthonous populations.

Trkmanec-Rybníčky and Trkmanské louky. – This site is located ~2 km E to NE of the Rakvice village. The 2nd Military Survey map (1836–1840) shows a fishpond (Rakwitzer

Teich) occupying a large part of this area, and the 3rd Military Survey map (1876–1878) shows the fishpond to be drained and converted to meadows and probably reed beds. The latter map also indicates small areas of meadows and common pastures between the southern corner of this area and the railway. In the 1970s, when the motorway Praha–Bratislava was built, the road Velké Pavlovice–Podivín, originally following the right bank of the already channelized Trkmanka stream, was abandoned. The stream channel was relocated to the east, and the motorway separated the area into the larger northern and the smaller southern part. The northern part has been protected since 2008 as the Trkmanec-Rybníčky Nature Monument, while the southern part has been proposed but not yet designated as the Trkmanské louky Nature Monument. Both sites are protected as Natura 2000 sites.

The Trkmanec-Rybníčky Nature Monument (Fig. 3C) lies in a triangle between the road Velké Pavlovice–Velké Bílovice, the Trkmanka stream and its tributary Bílovický stream. In the 1980s and early 1990s, this area was arable land drained by a channel, from which water was pumped into the Trkmanka stream. The operation of this drainage system ceased and the arable fields were gradually abandoned between 1996 and 2006. Waterlogging of a large part of the area resulted in the succession of *Phragmites australis* stands. In 2006–2008, the area was restored, the reed stands were reduced and shallow pools were dug, in which *Crypsis schoenoides* and other halophytes appeared. At present, Trkmanec-Rybníčky comprises areas with different water regimes. The northern part encompasses halophytic pastures currently managed by horse grazing and mowing. In wetter parts, these pastures contain halophytes such as *Samolus valerandi*. The pastures occur in a mosaic with halophytic marshes with *Bolboschoenus planiculmis*, *Schoenoplectus tabernaemontani* (associations *Astero pannonici-Bolboschoenetum compacti* and *Schoenoplectetum tabernaemontani*) and other types of wetland vegetation (e.g. *Bidentifondosae-Atriplicetum prostratae*). The central and southern parts of the site are dominated by marshes, and there are also a few ponds, in which stands of *Heleochoëtum schoenoidis* were sampled in 2011 and 2015 by P. Lustyk and P. Dřevojan (Dřevojan et al. 2017).

The Trkmanské louky site (Fig. 4A) is currently managed mainly as arable land. The proposed Nature Monument aims to protect the critically endangered *Cirsium brachycephalum*, which grows in fragmentary stands of the association *Agrostio stoloniferae-Juncetum ranarii*. Besides crop cultures, *Phragmitetum communis* is the most widespread vegetation, accompanied by scrub patches with *Cornus sanguinea* and *Calamagrostis epigejos* indicating ongoing succession. Subhalophytes such as *Melilotus dentatus* and *Centaurium pulchellum* can be found rarely at the edges of these extensive stands. In more disturbed and wet places on arable land where crops grow weakly, saline vegetation develops with dominant *Bolboschoenus planiculmis*, accompanied by *Cirsium brachycephalum* (*Tripleurospermo inodori-Bolboschoenetum planiculmis*).

Čejč district

This district included halophytic sites in the valley of the Trkmanka stream and its tributaries around the former salt lakes of Čejč (Čejčské jezero, Tscheitscher See) and Kobylí (Kobylské jezero, Kobylér See), and a small lake or a fishpond (Smradák, Smradaker Teich) between the villages of Terezín (Theresiendorf) and Čejč (Tscheitsch). Towards

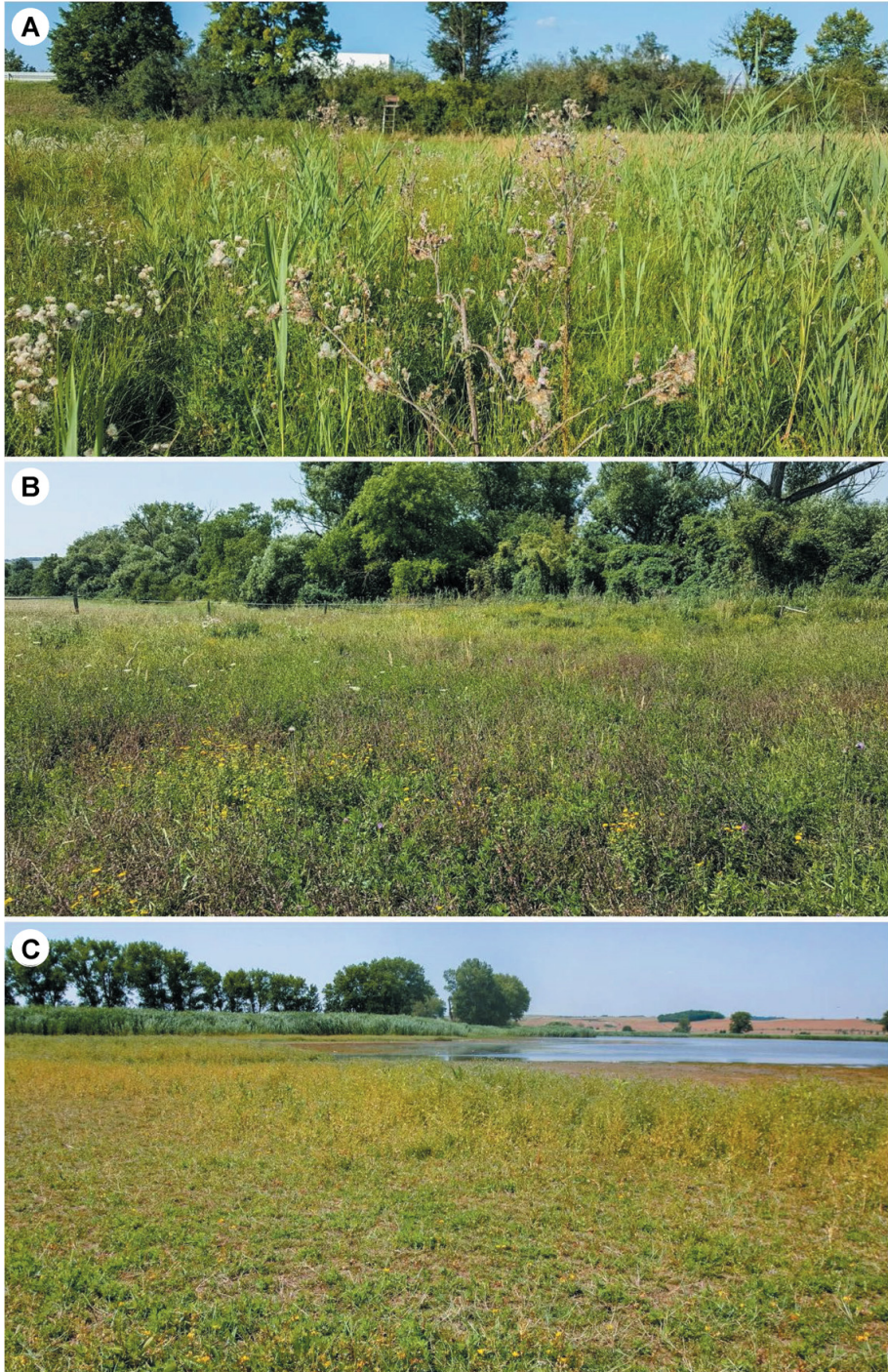


Fig. 4. Halophytic localities in the Rakvice, Čejč and Sedlec districts: (A) Trkmanské louky 2020, (B) Zápověď 2020, (C) Drained bottom of the Nesyt Fishpond in its southern bay 2020. Photo credits: F. Kratoš (A, B), M. Chytrý (C).

the north, saline habitats occurred in the valley of the Kašnice stream as far as the former railway station Klobouky u Brna at the eastern edge of the town and along the Spálený stream as far as the former Kumstát (or Kunštát) mill north of the village of Krumvíř. Towards the south, the occurrences of some halophytes once continued along the Trkmanka roughly to the southern edge of Velké Pavlovice, i.e. to the arbitrary border with the Rakvice district.

The halophytic flora of the Čejč district was rich in species and included all the 17 halophytes except for *Galatella cana* and *Triglochin maritima*. The occurrence of *Cirsium brachycephalum* is uncertain because there is only a single record from a relevé (Vicherek 1962).

The salt lake surrounded by saline marshes, fen meadows and steppe slopes harbouring rare species attracted numerous botanists who praised the local flora in superlatives. For instance, Hochstetter (1825) described it as a place where the Moravian flora “no doubt develops its rarest products”. Wiesner (1854) referred to the vicinity of Čejč as “Flora’s treasury in Moravia”, while Bubela (1882) described it as “Eldorado of Moravian botanists”.

Čejč Lake was situated ~0.9 km SSE of the village of Čejč. The earliest description of the lake is found in a book about the healing waters of the Margraviate of Moravia (Jordán z Klauzburku 1580: 284–293). The author described the lake's water as awfully bitter, comparing its taste to *Centaurium*, *Gentiana*, *Artemisia absinthium* and the galls of some animals. He also noticed that no fish could live in the lake, and its water was toxic to livestock from elsewhere but not to animals from local farms. He further reported that in summer, the water level was low, and the shores were white [from salt efflorescences]. Much to botanists’ regret, Čejč Lake was drained in 1858 (Krzisch 1859).

Kobylí Lake occupied a shallow depression of the Trkmanka stream between the villages of Kobylí, Brumovice and Terezín. It was ~5 km long and in its north-eastern part up to 1.5 km wide. Its water was less saline than that of Čejč Lake (Vlach 1952). It was reportedly drained as soon as 1834 or 1835 (Spitzner 1894, Vlach 1952), but its northern part is shown on the 2nd Military Survey map (1836–1840) as still filled with water.

The small lake or a fishpond between the villages of Terezín and Čejč, referred to as Smraďák (Smradaker Teich) or Rybníček, was located ~0.5 km S of the village of Terezín (Theresiendorf). It was drained at the same time as Čejč Lake. The bottoms of all three lakes are now used mainly as arable land. While the shapes of the former Čejč and Kobylí Lakes may be still traced on current topographic maps, and both place names are still in use, the former area of the small Smraďák Fishpond has been dissected into three parts by the local railway Zaječří–Hodonín (opened in 1897) and its branch to Klobouky u Brna.

This district was first floristically explored independently by Ch. F. Hochstetter and A. Carl, then a county physician in the town of Uherské Hradiště. In 1821, A. Carl collected *Scorzonera parviflora* and *Tripolium pannonicum* near Čejč Lake. Next year, he found *Plantago maritima* near the villages of Vrbice and Čejč. The first published floristic records from this district are those from Hochstetter (1825). He reported that the low shores of Kobylí Lake were richly covered with the succulent halophytes *Salicornia perennans* and *Suaeda prostrata* (*Chenopodium maritimum*) as well as *Chenopodium chenopodioides* (*C. serotinum*) and *Lepidium coronopus*. At Čejč Lake, he found *Carex distans* and *Scorzonera parviflora*. Wilhelm Tkany and Friedrich Kolenati, reporting on their excursion to the Čejč surroundings with J. Bayer in 1851 (Kolenati 1852), listed

Glaux maritima, *Salicornia perennans* and *Scorzonera parviflora* among the species found. Bayer (Anonymous 1853), in addition, observed *Bupleurum tenuissimum*, *Crypsis aculeata*, *Plantago maritima*, *Spergularia marina*, *Suaeda prostrata* (*Schoberia maritima*) and *Tripolium pannonicum* near Čejč Lake. However, already Krzisch (1859), who found only a few hardly surviving halophytes in the surroundings of Čejč Lake, regretted the lake's drainage and envisaged the decline of halophytes.

The drainage of both lakes and the Smraďák Fishpond did not cause immediate destruction of all halophytic habitats or local extinction of halophytes. For instance, Steiger (1880) noted *Plantago maritima* in meadows near Brumovice, probably near the fishpond at the eastern edge of the village. Bohuňovský (1880) confirmed the occurrence of *Salicornia perennans* in a pasture near Terezín and discovered *Samolus valerandi* at the site referred to as Na Rybníčku, which corresponds to the remnants of the drained Smraďák Fishpond. This site was explored by Bubela (1882), who confirmed the occurrence of *Samolus valerandi* and recorded *Crypsis aculeata*, *C. schoenoides*, *Salicornia perennans*, *Suaeda prostrata* and *Tripolium pannonicum* in the saline reed bed and on dry mud, while *Bupleurum tenuissimum*, *Plantago maritima*, *Spergularia marina*, *S. media* and *Taraxacum bessarabicum* occurred in the adjacent meadow. In the late 1890s, the site was disturbed during the construction of the railway Zaječív–Hodonín, but halophytes continued to occur there. The succulent halophytes were last collected at this site in the mid-1940s, and the habitats must also have been destroyed in the 1940s because Šmarda (1953) did not mention this site at all.

Botanists continued visiting this district, repeatedly confirming the presence of halophytes at various sites. For instance, Formánek (1884) recorded *Scorzonera parviflora* and *Tripolium pannonicum* near Terezín, and (probably during a second trip) *Bupleurum tenuissimum*, *Crypsis aculeata* (near the sulphur water spring Heliga), *C. schoenoides*, *Glaux maritima*, *Plantago maritima*, *Spergularia marina* and *Suaeda prostrata* near Čejč. According to Spitzner (1894), who explored the area in 1887, the western shores of the former Kobylí Lake (east of the village of Brumovice) hosted *Salicornia perennans*, *Suaeda prostrata* and *Tripolium pannonicum*. *Glaux maritima* occurred alongside the stream that once connected Čejč and Kobylí Lakes, i.e. somewhere near the site Na Rybníčku, while *Samolus valerandi* was found in cattle tracks on the bottom of the former Čejč Lake. *Spergularia marina* grew on the bottom of the former Kobylí Lake, and *Crypsis aculeata* and *C. schoenoides* in ditches probably south-west of the village. *Samolus valerandi* was abundant on cattle paths in the former Čejč Lake (Spitzner 1894). Heinrich Laus visited the district in 1906 and observed only *Spergularia marina* and *Tripolium pannonicum* in the area of the former Čejč Lake (Laus 1907). He did not find anything of the former halophytic flora between Terezín and Kobylí but still observed a few sites with halophytes in the district, such as near the Rovinský dvůr (Rovinka) farm south of Krumvíř.

Some well-preserved remnants of the halophytic vegetation survived for a long time at the north-eastern edge of the former Kobylí Lake. Between 1927 and 1929, the surroundings of Terezín were thoroughly explored by Gilli (1930). He paid particular attention to the patches of halophytic vegetation between the railway and the road to Krumvíř ~1.3 km NNW(–N) of the village, i.e. to the site now referred to as Zápověď. He described the place as a marshland with a reed stand in the middle. *Tripolium pannonicum* was found in large quantities at the edge of the reed stand, *Glaux maritima*, *Juncus gerardii*, *Plantago*

maritima, *Scorzonera parviflora* and *Spergularia media* occurred in the surroundings, and *Salicornia perennans* was present at one spot with salt efflorescences. The Zápověď site, on the 3rd Military Survey maps (1876–1878) indicated as a common pasture, was frequented by botanists from the 1930s onwards, as documented by numerous herbarium specimens. This site was spared from draining due to its location in a narrow strip of land between the road and railway. It was managed as a nature reserve by a non-governmental nature conservation society from 1944 and designated as a State Nature Reserve in 1952 (Vlach 1952, Smejkalová 1990). In 1949, the site was explored by Šmarda (1953) and roughly at the same time also by Vlach (1952). The latter author described the site in detail and noted several vegetation types, including stands with both succulent halophytes. He recorded *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. Šmarda (1953) found the same species as Vlach and, in addition, collected *Bupleurum tenuissimum*. Jiří Vicherek studied halophytic vegetation in the Čejč district in 1959–1964. In the relevés from the Zápověď site, he recorded *Bupleurum tenuissimum*, *Crypsis aculeata*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Scorzonera parviflora*, *Spergularia media*, *Suaeda prostrata*, *Taraxacum bessarabicum* and *Tripolium pannonicum* (Vicherek 1962, 1973). However, his record of *Suaeda prostrata* in two relevés from 1959–1961 is the last record of this species from the site. *Salicornia perennans* was last collected in 1967. Other halophytes disappeared in Zápověď by the early 1970s, primarily due to the drainage of the surrounding land (Grulich 1987).

Gilli (1930), apart from describing the Zápověď site in detail, reported the occurrence of halophytes elsewhere in the northern part of the district. He found *Bupleurum tenuissimum*, *Plantago maritima* and *Tripolium pannonicum* in the meadows between the road and the Trkmanka stream north of Zápověď towards Krumvíř. *Plantago maritima* dominated vegetation in some places, and *Spergularia media* occurred on arable land. He further recorded *Spergularia media* around a small fishpond in the southern part of Krumvíř, and *Plantago maritima*, *Scorzonera parviflora* and *Tripolium pannonicum* in the meadows along the Spálený stream between the village and the Kumstát mill. In contrast, he did not confirm the occurrence of *Scorzonera parviflora* near the railway station Klobouky u Brna, where it was once found by Steiger (1880). In the early 1950s, Marvanová & Marvan (1959) found *Spergularia marina* along the Spálený stream south of Krumvíř, *Samolus valerandi* together with *Juncus gerardii* in a drained fishpond south-west of the Rovinský dvůr farmstead and *Plantago maritima* at two sites near Čejč and on a path to the *Samolus* site south of Krumvíř. Vicherek (1962, 1973) recorded relevés of saline marshlands with *Juncus gerardii*, *Plantago maritima*, *Samolus valerandi*, *Taraxacum bessarabicum* and *Tripolium pannonicum* along the Trkmanka stream north of the Zápověď site towards Krumvíř, which is the area once explored by Gilli (1930) and Marvanová & Marvan (1959). He also sampled saline marshlands with *Juncus gerardii* and *Scorzonera parviflora* near the Trkmanka stream between the villages of Terezín and Brumovice. These were probably the last remaining sites with halophytic vegetation suitable for vegetation sampling in the Čejč district.

As mentioned above, occurrences of some halophytes continued along the Trkmanka stream as far as the southern edge of the town of Velké Pavlovice. There were several records of *Glaux maritima* between 1857 and 1949 from saline grasslands next to the

village of Bořetice, probably somewhere close to its northern edge. *Glaux maritima* also used to occur at the northern edge of Velké Pavlovice along the Trkmanka stream and east of the railway station at its southern periphery; the last observation from the latter site dates back to 1952 (Z. Hrabal sec. Šmarda 1953). *Juncus gerardii* was collected somewhere near the town in 1931.

In the mid-1980s, no occurrences of halophytes in the Čejč district were known apart from a single record of *Spergularia marina* from 1983 at the northern edge of Terezín (Grulich 1987). In the late 1980s, the protection of the degraded Zápověď site was recommended for abolition, which happened probably in the early 1990s (Buček & Smejkalová 1987; but see Smejkalová 1990). However, in 2003, the Zápověď site was restored by bulldozing shallow pools of different depths at the formerly saline sites. Halophytic vegetation quickly developed around them (Slavík in Hadinec & Lustyk 2009). Beside these shallow pools, a fishpond was built in 2005, but it is deep and therefore unsuitable for halophytic vegetation. The upper soil layer of the shallow pools was removed in the 2010s to support the halophytes dependent on early successional stages (P. Slavík, pers. comm.). *Spergularia media* emerged there in 2005, *Glaux maritima* in 2007, *Crypsis aculeata* in 2008 and *Spergularia marina* in 2015, all probably from the soil seed bank. The site currently hosts halophytes and subhalophytes such as *Bolboschoenus maritimus*, *Carex secalina*, *Glaux maritima* and *Spergularia media* (Fig. 4B). Grasslands around the pools are regularly mown. In drier parts, there are saline grasslands of *Loto tenuis-Potentilletum anserinae*, while the places flooded for a longer time but drying out in summer are occupied by a *Puccinellietum limosae* grassland with *Puccinellia distans* and *Spergularia media*. Reed stands of *Phragmites australis* dominate deeper parts of the pools usually flooded throughout the year. Stands of *Bolboschoenus maritimus* and *B. planiculmis* (*Astero pannonicus-Bolboschoenetum compacti*) occur at the edges of these reed beds and in other flooded places.

Apart from the new occurrences of halophytes at Zápověď, *Samolus valerandi* was found in 2017 in a wet meadow in the Trkmanka valley ~2.5 km south-east of the village of Krumvíř, i.e. near the sites where it was once recorded by Marvanová & Marvan (1959) and Vicherek (1962).

Sedlec district

The Sedlec district lies in the shallow valley of the Včelínek (Niklasgraben) stream roughly between the towns of Mikulov (Nikolsburg) and Lednice (Eisgrub). In the west, it also includes a small area adjacent to the western edge of Mikulov drained by a nameless left-hand tributary of the Včelínek and a small area in Lower Austria drained by the Niklasgraben stream, which is the uppermost reach of the Včelínek. The soil salinity in the district is caused by sulphates (mainly magnesium sulphate) from Tertiary deposits, but in the village of Sedlec (Voitelsbrunn, Selce), it was formerly strengthened by a mineral spring. In the 15th century, several fishponds were built on the Včelínek stream between Mikulov and Lednice, just on the historical border between Moravia and Lower Austria. They included the Porzteich Fishpond (now partly preserved as Nový Fishpond) west of Sedlec and a series of four fishponds east of Sedlec, namely Nesyt (Nimmersatteich or Steindammteich), Hlohovecký (Bischofwarter Teich), Prostřední (Mitterteich) and Mlýnský (Mühlteich). The Czech name Nesyt and its German equivalent

Nimmersatteich mean Sateless pond, which refers to water shortage in this dry and warm area.

The halophytic flora of the Sedlec district used to be rich in species and included all the 17 halophytes considered here except *Cirsium brachycephalum*, *Galatella cana* and *Triglochin maritima*. The presence of *Glaux maritima* is doubtful. However, the district was poorly accessible from both Brno and Vienna due to its peripheral location. Therefore, it was rarely visited by botanists, and the occurrence of halophytes was reported relatively late. The earliest record of a halophyte from the district is that of *Tripolium pannonicum* in the Flora of Lower Austria (Neilreich 1859), but the origin of this record is unknown. *Plantago maritima*, *Scorzonera parviflora*, *Spergularia media* (*Lepigonium marginatum*) and *Tripolium pannonicum* were collected by F. R. Müncke, who served as a pharmacist in the Prussian army and explored the site during the Prussian military campaign against Austria in 1866 (Müncke 1868). His records are labelled Valtice (Feldsberg) and probably refer to the occurrences of halophytes at the south-eastern edge of the Nesyt Fishpond. Formánek (1887, 1892) reported *Spergularia marina*, *Taraxacum bes-sarabicum* and *Glaux maritima* from Sedlec. However, the occurrence of *G. maritima* has never been documented by a herbarium specimen, and the records in the relevés from the 1960s are most likely mistakes. The occurrences of the succulent halophytes, *Salicornia perennans* and *Suaeda prostrata*, were discovered in 1914 by F. Zimmermann (Wildt 1915, Zimmermann 1916). In 1922, J. Bílý Jr. found *Samolus valerandi* on the Nesyt shores near the Sedlec railway station. At that time, well-developed halophytic vegetation was found along both banks of the Včelínek stream near the western shore of Nesyt, an area marked as a common pasture on the 3rd Military Survey maps.

Since the 1920s, the sites around the Nesyt Fishpond have been repeatedly visited by Moravian botanists. Anton Fröhlich, a secondary school teacher in Mikulov, reported *Bupleurum tenuissimum* in 1933 and made numerous observations about local halophytic flora and vegetation (Fröhlich 1935, 1940, 1943). Zapletálek (1933, 1939) provided a description of the flora and vegetation in the surroundings of the Nesyt Fishpond. His description of vegetation developed on the drained Nesyt bottom, summarized in an unpublished thesis, was partly reproduced by Šmarda (1953). Jan Šmarda visited the site in 1950 and confirmed the occurrence of *Bupleurum tenuissimum*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Scorzonera parviflora*, *Spergularia marina*, *S. media* and *Suaeda prostrata* near the Sedlec railway station (Šmarda 1953). At that time, a concentric zonation of halophytic vegetation was still preserved, with the stands of *Puccinellia distans* and *Salicornia perennans* in the lowest part in the middle of the site. Fröhlich summarized his observations in a brief report (Fröhlich & Švestka 1956) accompanied by a distribution map of selected species around the western half of the Nesyt Fishpond. Many of the records were indicated as old; however, this map shows that some halophytes, including *Suaeda prostrata*, once occurred quite far in the south-west, south of the railway. The aerial photographs from the 1950s show a sizable treeless area on both sides of the Včelínek stream between the western tip of the Nesyt Fishpond and the village of Sedlec. The area was crossed by walking paths and contained trampled patches with sparse vegetation. It was probably still used as a common pasture and provided suitable conditions for halophytic vegetation.

In the early 1960s, the vegetation on the western shores of the Nesyt Fishpond was explored by Vicherek (1962, 1973). His relevés are not dated, but he collected herbarium

specimens at this site in 1960–1962. He still recorded stands with *Salicornia perennans* and *Suaeda prostrata*, patches with annual grasses *Crypsis aculeata* and *C. schoenoides*, and saline marshlands with *Scorzonera parviflora*. Most of these relevés were probably sampled in the current nature reserve and on the drained Nesyt bottom. However, he also recorded stands with *Crypsis aculeata* at the northern margin of the fishpond and saline grassland with *Plantago maritima*, *Puccinellia distans*, *Spergularia media*, *Taraxacum bessarabicum* and *Tripolium pannonicum* at the southern and south-eastern shores. This suggests that the halophytic vegetation was still well preserved and relatively widespread at that time.

Since the 1960s, the occurrences of halophytes were gradually restricted to the area of the current Slanisko u Nesytu National Nature Reserve. This reserve was officially established in 1961, but there was some kind of protection earlier, probably from 1953 (Grulich 1987), as Fröhlich & Švestka (1956) refer to the site as a halophytic reserve. The common pasture between the Včelínek stream and the southern edge of the village of Sedlec was later converted into a football playground. The frequent mowing and trampling by football players turned out to support halophytes. *Spergularia marina* and *Taraxacum bessarabicum* survived on the playground until 1999; however, we found none of them at this site in 2020. During the 1960s, grazing at the Slanisko u Nesytu site gradually ceased, perhaps partly due to its legal protection. No goose grazing was observed there in the 1970s (V. Grulich, pers. comm.). Consequently, the habitat quality deteriorated, and both succulent halophytes, *Salicornia perennans* and *Suaeda prostrata*, went locally, hence also nationally, extinct there in 1976 and 1986, respectively (Grulich 1987).

In the past, halophytes also occurred scattered elsewhere around the Nesyt Fishpond. For instance, *Scorzonera parviflora* was collected in the southern bay of the Nesyt Fishpond in 1930 by J. Zapletálek. Fröhlich & Švestka (1956) reported *Crypsis aculeata* and *C. schoenoides* from that place. Vicherek (1973) recorded a relevé with *Juncus gerardii*, *Orchis palustris* and *Tripolium pannonicum*, probably in the same place, in the early 1960s. Small patches of halophytic vegetation with *Bupleurum tenuissimum*, *Plantago maritima*, *Spergularia marina* and some subhalophytes once existed along a walking path on the southern shores of the Výtopa Fishpond (adjacent to the south-eastern corner of Nesyt) and in a shallow depression next to the north-eastern corner of Výtopa (Danihelka & Hanušová 1995). Both sites were indicated as common pastures on the 3rd Military Survey maps. The early records of halophytes by Müncke (1868) may also refer to this part of the district. To our knowledge, *Bupleurum tenuissimum* was last seen there in 2004, while *Plantago maritima* and *Juncus gerardii* were still present in 2020 and 2021.

Further eastwards, some halophytes, namely *Crypsis schoenoides*, *Samolus valerandi* and *Tripolium pannonicum*, were scattered on the shores and drained bottoms in the Lednice Fishpond system. *Crypsis schoenoides* was collected on the drained bottom of the Hlohovecký Fishpond in 2021. The easternmost halophytic site in this district was at the western edge of the Dyje floodplain below the dam of the Mlýnský Fishpond (Mühlteich) south-east of Lednice. In the early 1960s, Vicherek (1973) recorded there a relevé of a saline marshland with *Juncus gerardii*, *Plantago maritima* and *Tripolium pannonicum*. One herbarium specimen of *Juncus gerardii* from 1960 and a few specimens of *Taraxacum bessarabicum* from the 1920s–1960s were probably collected at the same site. However, no halophytes have been found in this part of the district since the 1960s.

Although concentrated to the western shore of the Nesyt Fishpond, some halophytes also occurred along the Včelínek stream westwards as far as south and west of Mikulov. There was a herbarium specimen from the mid-19th century and a literature record from 1949 (J. Bílý sec. Šmarda 1953) of *Plantago maritima* from that area. *Scorzonera parviflora* once occurred near the Tiergartenhof north-west of the village of Kleinschweinbarth in Lower Austria (S. Domas sec. Makowsky 1863). Also, the herbarium records of *Crypsis schoenoides* from the Seeäcker saline meadows along the border between Moravia and Lower Austria may be attributed to the Sedlec district. In 2007, a large population of *Samolus valerandi* developed temporarily in a saline marshland with *Bolboschoenus planiculmis* in a shallow wet depression on arable land ~1.6 km W of Mikulov, north of the railway to Znojmo (Paukertová & Sedláček in Hadinec & Lustyk 2007: 326). Several subhalophytes (e.g. *Centaurium pulchellum*, *Lythrum hyssopifolia* and *Schoenoplectus tabernaemontani*) were also found there.

Currently, the Sedlec district has the best-preserved halophytic flora of all the ten districts considered in this study. Although both succulent halophytes have disappeared, *Bupleurum tenuissimum*, *Crypsis aculeata*, *C. schoenoides*, *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina*, *S. media* and *Tripolium pannonicum* still occur at the Slanisko u Nesytu site. Moreover, *Crypsis schoenoides* and *Samolus valerandi* have been repeatedly recorded on the drained bottoms of the Nesyt and Hlohovecký fishponds. A few individuals of *Crypsis aculeata* and *Tripolium pannonicum* were observed in 2020 on the drained bottom of the Nesyt Fishpond in its southern bay (Fig. 4C). In addition, *Juncus gerardii* and *Plantago maritima* have survived at another site south of the small Výtopa Fishpond.

Slanisko u Nesytu (Fig. 5A). – The Slanisko u Nesytu National Nature Reserve, the most species-rich halophytic site in the study area, is located ~0.4 km S of the village of Sedlec along the western margin of the Nesyt Fishpond. The reserve is divided into the western and eastern parts by a shallow ditch. Most of its area is currently covered by subhalophytic grasslands. The occurrences of halophytes are confined mainly to shallow depressions in both parts of the reserve, being slightly more common in the eastern part. Until the 1990s, targeted conservation management was limited. In the mid-1970s, shallow ditches were dug in the western part of the reserve to create a habitat for annual halophytes (Grulich 1987). The ditches had a positive effect for some years until they were overgrown by *Agrostis stolonifera*. In 1986, a square-shaped pit was dug in the eastern part of the reserve to re-establish *Salicornia perennans* (Grulich 1987, in litt. 2021). This attempt failed, and the pit was ultimately overgrown by *Phragmites australis* (Danihelka 2005). In 1991, topsoil was removed in a strip about 100 m long and 3 m wide in the western part of the reserve (Danihelka & Hanušová 1995). This shallow ditch now harbours small populations of *Crypsis aculeata* and *C. schoenoides*, particularly in rainy years (Dřevojan et al. 2017), and sometimes also several individuals of *Samolus valerandi* (population derived from seeds collected from the bottom of Nesyt) and *Scorzonera parviflora*. Regular mowing was re-established in 1993, and sheep grazing was introduced in 2000. The intensity and spatial extent of these management measures have increased since then. Nowadays, the halophytic vegetation is grazed by horses, which seems to be a particularly suitable management practice for saline habitats (Kmet et al. 2018). The best developed halophytic community (association *Puccinellietum*

limosae) with *Bupleurum tenuissimum*, *Plantago maritima*, *Taraxacum bessarabicum* and *Tripolium pannonicum* is preserved in the eastern part of the reserve. Slightly wet to mesic parts of the site are covered by the grasslands of *Loto tenuis-Potentilletum anserinae* and drier parts with *Festuca pulchra* by *Centaureo pannonicae-Festucetum pseudovinae*. Wet halophytic grasslands of *Scorzonero parviflorae-Juncetum gerardii*, once common at the site, were developed in the 1990s in a ditch created for conservation purposes in the western part (Hanušová 1995) and last recorded there by J. Danihelka in 2004.

Slanisko v trojúhelníku. – This recently discovered small halophytic site is located ~1.6 km W of the town of Mikulov in a shallow wet depression on arable land north of the railway Mikulov–Znojmo. In 2006, a part of the depression was filled with earth. In 2007, a population of *Samolus valerandi*, counting several thousands of individuals, was discovered there (Paukertová & Sedláček in Hadinec & Lustyk 2007: 326). Later, a part of the earth was removed to support the occurrence of halophytes. In 2020, the site was relatively dry, covered with a mosaic of bare soil and annual ruderal vegetation. Small plants of *S. valerandi* occurred in large numbers in pits dug in the previous year as a part of conservation management. However, the prospects of this site are uncertain because it is located in the route of a planned motorway.

Slanisko u Výtopy. – Small remnants of halophytic vegetation are preserved along the walking path south of the Výtopa Fishpond ~1.9 km N of the Valtice railway station. A small population of *Plantago maritima*, counting about 100 individuals, occurs in the *Centaureo pannonicae-Festucetum pseudovinae* grassland dominated by *Festuca pulchra*. *Juncus gerardii* occurs on wet arable land next to the south-eastern bay of the fishpond.

Damnice-Olbramovice district

The Damnice-Olbramovice district includes the former halophytic sites in a shallow valley of the Miroslavka stream between the Miroslavský Fishpond south-west of the village of Suchohrdly u Miroslavi in the west and the village of Vlasatice in the east, as well as a shallow valley of the Olbramovický stream between the village of Olbramovice in the north-west and Vlasatice in the south-east. This district is proposed here in addition to the eight districts recognized in the Moravian part of the study area by Grulich (1987).

The flora of the Damnice-Olbramovice district has always been poor in halophytes for its peripheral location and likely a low degree of soil salinity. As botanists rarely visited the district, some halophyte occurrences may have vanished without being recorded. Of the 17 halophytes, the district used to harbour *Glaux maritima*, *Plantago maritima*, *Spergularia marina*, *Tripolium pannonicum*, and probably also *Juncus gerardii* (Šmarda 1953).

The first botanist to discover halophytes in this district was H. Zimmermann. In 1883, he collected *Plantago maritima* in a meadow north-west of the village of Damnice (Damitz) and noted *Spergularia marina* and *Tripolium pannonicum* as co-occurring species on the herbarium label of this *Plantago* specimen (see also Oborny 1886). Andreas Ripper explored the area a few years later and recorded *Glaux maritima* in the villages of Damnice, Jiřice u Miroslavi (Iritz) and Troskotovice (Treßkowitz; Oborny 1912). He also confirmed the occurrence of *Plantago maritima* at the site discovered earlier by Zimmermann

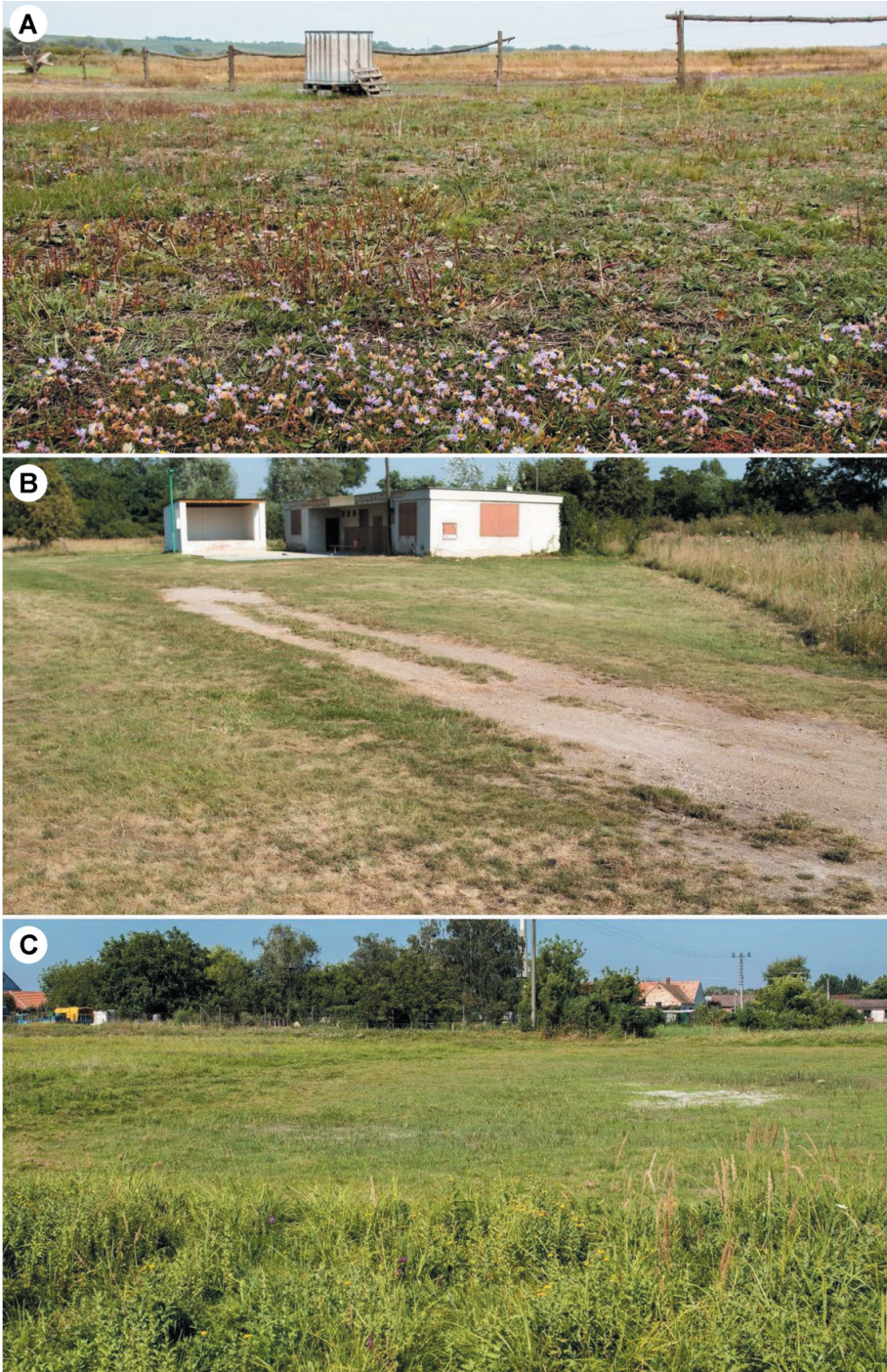


Fig. 5. Halophytic localities in the Sedlec and Hevlín-Nový Přerov districts: (A) Slanisko u Nesytu 2016, (B) Dobré Pole 2020, (C) Novosedly 2020. Photo credits: M. Chytrý (A), K. Chytrý (B, C).

(“between Damnice and the Miroslav railway station”) and added another record near Troskotovice. The halophytic site north-west of Damnice survived at least until 1952 when J. Šmarda and M. Součková collected *Plantago maritima* and *Tripolium pannonicum* and observed *Juncus gerardii* there. They also found some subhalophytes in a wet meadow upstream below the Suchohrdelský Fishpond (Šmarda 1953).

The occurrences of halophytes along the Olbramovický stream were discovered even later. Johann Hruby collected *Plantago maritima* at the margin of the village of Malé Želovice (Klein-Seelowitz, currently part of Olbramovice) in 1927. In 1948, J. Horňanský Sen. collected this species near the road between Olbramovice and Branišovice, i.e. roughly in the same place. In 1951, F. Kühn added a record of *Tripolium pannonicum* from a ditch north-east of Branišovice (Šmarda 1953). *Spergularia marina* was collected near Branišovice by J. Vicherek in 1962 and for the second time by L. Bravencová in 2007, which is the latest record of any halophyte from our list in this district. To our knowledge, no halophytic vegetation has been preserved in the district.

Hevlín-Nový Přerov district

The Hevlín-Nový Přerov district includes halophytic sites adjacent to the left side of the Dyje river floodplain between the villages of Dyjákovice (Tajax), Hevlín (Höflein), Hrabětice (Grafendorf) and Jevišovka (Fröllersdorf, Frélichov), halophytic sites adjacent to the right side of the Dyje floodplain between Nový Přerov (Neu-Prerau) and Novosedly (Neusiedl, Nové Sídlo), as well as those in a shallow basin drained by the Mikulovka/Polní stream east of the town of Mikulov (Nikolsburg). Most sites were in southern Moravia, but a few halophytes also occurred in the adjacent part of Lower Austria east of the settlement of Alt-Prerau. Grulich (1987) also included in this district the area with halophytes west of the town of Mikulov, but we consider it part of the Sedlec district because it is drained by the Včelínek stream.

The halophytic flora of the Hevlín-Nový Přerov district was originally rich in species and included all the 17 halophytes except *Galatella cana* and *Triglochin maritima*. The first records of halophytes from this area date back to the early 1840s. Siegfried Reissek (Reisseck 1841) found *Salicornia perennans*, *Spergularia marina* and *Suaeda prostrata* on the way from the town of Drnholec (Dürnholz) to the village of Dobré Pole (Guttenfeld), probably somewhere near Novosedly. However, the exact location of the site is unknown as the description in the original source does not match the locations of halophytic sites as currently known.

The halophytic site in Nový Přerov was discovered by A. Oborny in 1883. He collected there *Bupleurum tenuissimum*, *Crypsis aculeata*, *C. schoenoides*, *Salicornia perennans*, *Samolus valerandi*, *Spergularia media*, *Suaeda prostrata* and *Taraxacum bessarabicum*. Schierl (1896) reported the occurrence of *Glaux maritima*. All these records refer to the surroundings of a small fishpond in the northern part of the village and saline meadows between the northern part of the village and the railway from Novosedly to the town of Laa an der Thaya in Lower Austria, abandoned in the 1920s.

In 1920 the site was explored by H. Iltis, a secondary school teacher in Brno. He collected most of the species found there once by A. Oborny, including both succulent halophytes and, in addition, *Glaux maritima*. In 1922, J. Bílý Jr. and S. Staněk collected *Bupleurum tenuissimum*, *Plantago maritima*, *Salicornia perennans*, *Scorzonera parviflora*,

Spergularia media and *Suaeda prostrata* in saline meadows between Nový Přerov and Jevišovka. It is unclear whether these finds are from the same site as those collected by A. Oborny and H. Iltis, as the site is referred to as “beyond the railway”, i.e. possibly between the abandoned railway and the Dyje floodplain.

For the subsequent decades, the Nový Přerov halophytic site was almost neglected. Šmarda (1953) did not visit it. Jiří Vicherek studied its vegetation probably in 1962. His relevés (Vicherek 1973) contained *Bupleurum tenuissimum*, *Crypsis aculeata*, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Spergularia marina*, *S. media*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. In 1980–1984, V. Grulich collected there herbarium specimens of *Bupleurum tenuissimum*, *Juncus gerardii*, *Plantago maritima*, *Spergularia marina*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. At that time, the halophytes were confined to the bottom and shores of a small fishpond at the village's northern edge. Vicherek returned to the site in 1994 and collected *Bupleurum tenuissimum* and *Plantago maritima*. The last record of *Tripolium pannonicum* dates back to 1992. The fragments of saline habitats south-west of the fishpond were destroyed by afforestation in 1998. However, a small population of *Plantago maritima* still survives in trampled places ~250 m NNE of the church.

The occurrences of halophytes in Novosedly or nearby, possibly observed already by S. Reissek, were rediscovered in 1883 by A. Ripper, a theology student, and A. Oborny, who found *Crypsis aculeata* and *C. schoenoides* somewhere between Jevišovka and Novosedly (Oborny 1883). In 1884, H. Zimmermann collected *Crypsis aculeata* in the village or nearby. Probably at the same time, A. Ripper (sec. Oborny 1912) recorded *Glaux maritima* directly in the village (“auf Dorfanger”). Šuk (1956) described the halophytic vegetation in the surroundings of Novosedly as nearly destroyed by intensive grazing. He listed only a few subhalophytes. Jiří Vicherek studied the vegetation of this site probably in 1962. His relevés contained *Bupleurum tenuissimum*, *Crypsis aculeata*, *Juncus gerardii*, *Plantago maritima*, *Spergularia marina*, *S. media*, *Taraxacum bessarabicum* and *Tripolium pannonicum* (Vicherek 1973). Vít Grulich visited the site in 1982 and 1983 and collected *Crypsis aculeata*, *C. schoenoides*, *Juncus gerardii*, *Spergularia marina*, *S. media* and *Taraxacum bessarabicum*. He considered the site relatively well preserved (Grulich 1987). Since the 1980s, the site has been repeatedly visited by botanists. In 1993, a nature reserve was established there to protect the remaining occurrences of halophytes. However, most of them disappeared due to the lack of management, and *Crypsis schoenoides* is the only halophyte still found there, though irregularly.

There were other halophytic sites near Novosedly in the past. For instance, H. Zimmermann collected *Salicornia perennans* and *Crypsis schoenoides* near Jevišovka in 1884. This site may have been located either in a common pasture ~1.5 km W of the village or, less likely, on the right bank of the Dyje river towards Nový Přerov. Roughly at the same time, A. Ripper found *Bupleurum tenuissimum* and *Tripolium pannonicum* in common pastures between Jevišovka and the town of Hrušovany nad Jevišovkou (Grußbach), possibly in the same place where H. Zimmermann found *Crypsis* and *Salicornia*, and *Glaux maritima* even further towards the east near Hrušovany nad Jevišovkou. A record of *Plantago maritima* and *Tripolium pannonicum* from 1949 (or already from the 1920s?) in a common pasture near Jevišovka (J. Bílý sec. Šmarda 1953) may also refer to this site. However, all these occurrences were destroyed a long time ago.

The halophytic site at the village of Dobré Pole was also discovered by A. Ripper, who recorded abundant populations of *Glaux maritima* and *Bupleurum tenuissimum*; he also found the former species near the village of Březí (Brattlesbrunn). In 1934, O. Thenius and F. Teuber, hobby botanists from Brno, collected *Glaux maritima*, *Spergularia marina* and *S. media* near a small fishpond in Dobré Pole, which is the halophytic site preserved until now. Anton Fröhlich collected *Glaux maritima* in Dobré Pole repeatedly between 1924 and 1954, *Tripolium pannonicum* in 1941 and a non-dated specimen of *Spergularia marina*. All of these 20th-century herbarium records certainly originated from the area of the current nature reserve at the southern edge of the village. Šmarda (1953) did not visit this site. He only reported the occurrence of *Glaux maritima* (“in large quantities”) based on the information from J. Bílý Jr. The undocumented record of *Cirsium brachycephalum*, reportedly based on the information provided to him by F. Švestka, is likely erroneous. Vratislav Šuk, in the early 1950s working as a pharmacist in Mikulov, listed *Glaux maritima*, *Plantago maritima*, *Spergularia media*, *Taraxacum bessarabicum* and *Tripolium pannonicum* from the Dobré Pole site (Šuk 1956). Jiří Vicherek recorded no relevés at this site (see Vicherek 1973). Vít Grulich visited the site repeatedly during the 1980s and documented the occurrence of *Glaux maritima*, *Plantago maritima*, *Spergularia marina*, *S. media*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. He considered the site relatively well preserved (Grulich 1987) and recommended it for conservation. In the early 1990s, *Bupleurum tenuissimum* was rediscovered at the Dobré Pole site after more than a century; the latest record of this species is from 2008.

The occurrences of halophytes in the western part of the district were also discovered by A. Ripper. Probably in 1884, he found *Bupleurum tenuissimum* and *Tripolium pannonicum* near Hevlín and *B. tenuissimum* near the Travní dvůr (Trabinghof) farmstead west of Hrabětice. The site north of Hevlín was rediscovered half a century later by Tomaschek (1933). In a saline meadow located ~1.1 km NNE of the village (currently, there is a brick factory), Tomaschek confirmed the presence of *Tripolium pannonicum* and added *Plantago maritima* and *Taraxacum bessarabicum* as new records. In addition, he found *Plantago maritima* south-west of Travní Dvůr and discovered the westernmost halophytic site of this district ~1 km NW of Dyjákovice. At the latter site, described as a small saline meadow with ditches, he found *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina*, *S. media* and *Tripolium pannonicum*, accompanied by numerous subhalophytes. Though no exact information is available, all these occurrences must have vanished probably a long time ago. The only surviving halophyte in this part of the district is *Spergularia marina*, collected near Hevlín between 1992 and 2012 (Němec et al. 2014). The find of *Cirsium brachycephalum* in an abandoned loam pit ~1.2 km ENE of Hevlín (Dřevojan 2017; still present there in 2020) is the only reliable record of this species from the Hevlín-Nový Přerov district.

The current halophytic flora in this district is enormously impoverished. The two succulent halophytes, *Salicornia perennans* and *Suaeda prostrata*, were last collected in 1922. *Samolus valerandi* was last collected even a year earlier. *Scorzonera parviflora* was last seen in the early 1930s. *Crypsis aculeata* was last seen at the Novosedly site in 1994. *Glaux maritima*, *Plantago maritima*, *Spergularia marina*, *S. media*, *Taraxacum bessarabicum* and *Tripolium pannonicum* still survive in this district, but their occurrences have mostly been reduced to a single site.

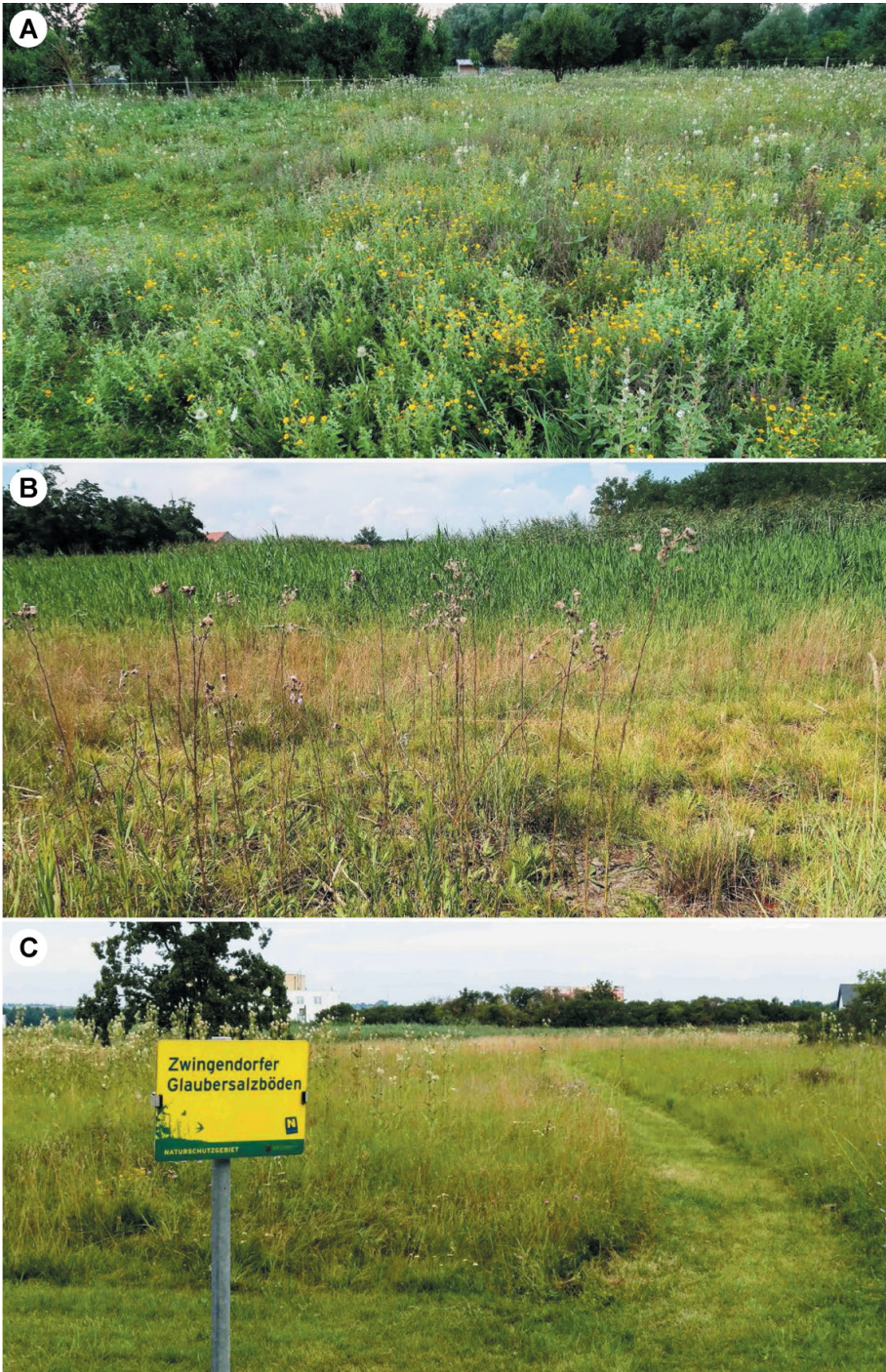


Fig. 6. Halophytic localities in the Hevlín-Nový Přerov and Pulkau districts: (A) Nový Přerov 2020, (B) Hevlín 2020, (C) Hintausacker 2020. Photo credits: E. Šmerdová (A, B), M. Chytrý (C).

Nový Přerov (Fig. 6A). – A remnant patch of halophytic and subhalophytic habitats is located at the north-eastern edge of the village of Nový Přerov ~250 m NNE of the church. Nowadays, *Plantago maritima* occurs there as the only halophyte. In 2020, the area was grazed with a mixed herd of sheep, goats and one horse and covered by a subhalophytic pasture with *Achillea collina*, *Althaea officinalis*, *Dipsacus laciniatus*, *Inula britannica*, *Lotus tenuis*, *Pulicaria dysenterica* and *Senecio erraticus*. Subhalophytic trampled grasslands with *Lotus maritimus*, *L. tenuis*, *Pulicaria dysenterica* and *Trifolium fragiferum* (*Loto tenuis-Potentilletum anserinae*) also occur in the village along pedestrian paths.

Dobré Pole (Fig. 5B). – The Dobré Pole saline site is located at the southern edge of the village of Dobré Pole. A part of the area has been used as a football playground for decades. In the 1980s, a pond at the saline site was deepened to collect waste and sewage water from the village (Lysák 2016a). This intervention disrupted the water regime and, together with some other measures, caused desalination of its soils. Since the disruption of the water regime, the saline site has been drying out, and the herb layer cover is increasing (Lysák 2016a). After a wastewater treatment plant was constructed in the village, the pond sediment was removed and nowadays, it is only used for collecting the wastewater. The football playground and its surroundings (~4 ha in total) were designated as the Slanisko Dobré Pole Nature Reserve in 1993. Trampling on the playground and in the surroundings supports some competitively weak halophytes and subhalophytes. The playground is covered mainly by the *Loto tenuis-Potentilletum anserinae* association, and the heavily trampled spots, partly on the access road, are covered by the *Centaureo pannonicae-Festucetum pseudovinae* and in places also by *Puccinellietum limosae* grasslands. *Glaux maritima* is restricted to a depression north of the fishpond. The area between the pond and the core of the saline site is covered by a subhalophytic tall-forb community of *Althaea officinalis*, *Dipsacus laciniatus* and *Pulicaria dysenterica*. This community also occurs in several slightly wet spots in the broader surroundings of the saline site. Currently, the site is regularly mown. In addition, the areas outside the playground are grazed as part of conservation management.

Novosedly (Fig. 5C). – This saline site is located at the north-eastern edge of Novosedly. Its area was used by local people for hay making and poultry grazing. However, it was gradually abandoned and changed into an illegal dumping place for waste and building rubble. In the late 1980s, some digging and earth moving disrupted the water regime, which may have caused desalination and supported the spread of *Phragmites australis* (V. Grulich, in litt. 2021). Although the site was put under conservation in 1993 (Slanisko Novosedly Nature Reserve), most of the remaining halophytes disappeared in the subsequent years due to the lack of management and succession of *Phragmites australis* and other competitive grasses. In 2008, P. Šmarda recorded only subhalophytes *Carex distans*, *Chenopodium chenopodioides*, *Melilotus dentatus*, *Pulicaria dysenterica*, *Schoenoplectus tabernaemontani* and *Trifolium fragiferum* (Šmarda 2008), but none of the 17 halophytes analyzed in the current study. Still, *Taraxacum bessarabicum* was collected there a year later. In 2011, dense reed stands were removed together with the topsoil, waste and building rubble. Since then, the site has been regularly grazed for conservation purposes (Lysák 2016b), which resulted in the re-appearance of *Crypsis schoenoides*. In 2020, the

area was covered mainly by subhalophytic grassland of the *Loto tenuis-Potentilletum anserinae* association dominated by *Agrostis stolonifera*, *Carex otrubae*, *Deschampsia cespitosa*, *Festuca pratensis* agg. and *Potentilla anserina*, with the occurrence of *Carex distans*, *Lotus maritimus*, *L. tenuis*, *Melilotus dentatus*, *Pulicaria dysenterica* and *Trifolium fragiferum*. An artificial depression was created in the central part of the site to support halophytes. In favourable years, its bottom is inhabited by *Atriplex prostrata*, *Carex secalina*, *Chenopodium chenopodioides* and *Crypsis schoenoides* (Lysák 2016b). The peripheral parts of the reserve are covered by semi-dry grasslands with *Achillea collina*, *Agrimonia eupatoria*, *Brachypodium pinnatum*, *Centaurea jacea*, *Festuca rubra*, *F. rupicola*, *Origanum vulgare* and *Petrorhagia prolifera*.

Hevlín (Fig. 6B). – This site, an abandoned and flooded sand or loam pit ~1.2 km ENE of Hevlín, is indicated as such already on the 3rd Military Survey map (1876–1878). No detailed information about its flora had been available until recently. In 2014, reed beds were partly removed from its northern and southern parts. In 2016, P. Dřevojan found there a population of *Cirsium brachycephalum* (Dřevojan 2017). Although this species has never been reported from this area, it may have been present there for a long time. Conservation management was introduced in 2020, aimed at reducing reed stands at the *C. brachycephalum* sites.

Daníž district

The Daníž district includes the halophytic sites once found along the Daníž stream south-east of Znojmo (Znaim) between the town of Šatov (Schattau) in the west and the village of Jaroslavice (Joslowitz) in the east, as well as along the Vrbovecký stream, a tributary of Daníž. Although *Plantago maritima* was found at the northern edge of the district near the village of Vrbovec (Urbau) as early as 1871 (Oborny 1872), the halophyte-rich sites along the Daníž had remained unknown. They were discovered in the late 1920s or early 1930s by O. Tomaschek, a primary school teacher in Jaroslavice. His report (Tomaschek 1933) comprehensively summarized the distribution of halophytes in the Znojmo administrative district, representing the westernmost occurrence of halophytes in Moravia. He provided detailed descriptions of the four most valuable halophytic sites near the villages of Jaroslavice, Strachotice (Rausenbruck), Dyjákovičky (Klein-Tajax) and Šatov. However, halophytes were more widespread within the district (for instance, he recorded *Plantago maritima* at 14 additional sites). František Švestka collected *Glaux maritima* in Šatov in 1946 and near the village of Chvalovice in 1947. However, no other information is available about the halophytic flora and vegetation at these sites. Of the 17 halophytes dealt with in this study, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina*, *Taraxacum bessarabicum*, and *Triglochin maritima* used to occur in the Daníž district.

The largest halophytic grassland once existed ~3 km WSW to 2 km WNW of Jaroslavice, in a valley of a right-side tributary of the Daníž stream, lined by steep hill-sides in the south-east. Tomaschek (1933) recorded there *Glaux maritima*, *Plantago maritima*, *Scorzonera parviflora*, *Taraxacum bessarabicum* and *Triglochin maritima*, as well as numerous subhalophytes. In addition, *Juncus gerardii* was collected there in 1947. The occurrences of all the species found by Tomaschek (1933) were allegedly

confirmed by Švestka (1947a); however, his brief report published in a natural history journal for teachers may have been entirely based on the records published by Tomaschek (1933).

The next halophytic site upstream along the Daníž was located south-west of Strachotice (Rausenbruck) near the road to the hamlet of Hnízdo (Gnast). *Glaux maritima*, *Scorzonera parviflora* and *Plantago maritima*, accompanied by some subhalophytes, occurred in this saline grassland surrounded by arable fields (Tomaschek 1933).

The third halophytic site was located near a brick factory south of the village of Dyjákovičky. Tomaschek (1933) observed *Plantago maritima* and *Taraxacum bessarabicum* there, the latter in large numbers, and five subhalophytes. Halophytic vegetation also occurred in grazed places in the village. In 1963 or 1964, J. Vicherek recorded there five relevés containing *Glaux maritima*, *Spergularia marina* and *Taraxacum bessarabicum* (Vicherek 1973).

The westernmost halophytic site, located between the villages of Šatov and Hnanice (Gnadlersdorf), hosted fewer halophytes than the previous sites, and the only halophyte, noted by Tomaschek (1933) and Švestka (1947b), was *Glaux maritima*, accompanied by some subhalophytes.

The halophytic vegetation in the Daníž district disappeared probably during the 1950s and 1960s. In the early 1960s, Vicherek found halophytic vegetation worth sampling only in the village of Dyjákovičky (Vicherek 1973). Grulich (1987) reported that all the halophytes that formerly occurred in the Daníž district had vanished. However, at least *Juncus gerardii* still survives at a handful of sites, as documented by the records from the eastern edge of the village of Šatov (2012), the southern edge of the village of Vrbovec (2011) and the former halophytic site south-west of Strachotice (2011; Němec et al. 2014).

Pulkau district

This district lies in the shallow valley of the Pulkau stream in northern Lower Austria. It is a long and narrow area between the village of Zellerndorf (south of the town of Retz) and the town of Laa an der Thaya, as well as in the shallow depression of the Entersgraben stream between Laa an der Thaya and the town of Staats. The best-developed halophytic vegetation occurred in the past between the town of Seefeld-Kadolz and the village of Wulzeshofen, particularly around the village of Zwingendorf.

The 3rd Military Survey maps from the early 1870s show numerous large tracts of meadows and common pastures along the Pulkau stream and its tributaries. Some of these meadows and especially common pastures, particularly in the eastern part of the district, were likely saline and hosted halophytic species, including both succulent halophytes. However, the stream channelization to prevent floods started already in the 1830s (Kalbrunner 1855). Since the 1930s, large areas have been drained. The groundwater level dropped by 0.5 m or more, and large tracts of meadows and pastures were converted to arable fields (Oberleitner et al. 2006). Consequently, many saline habitats and occurrences of halophytes were probably destroyed before being described by botanists. In addition, the occurrences of halophytes in the Pulkau valley have always been considered less attractive and less visited by Austrian botanists than those around Lake Neusiedl. Therefore, they received less attention, and the available information is scarce.

The flora of the Pulkau district used to be rich in halophytes. It included *Bupleurum tenuissimum*, *Crypsis aculeata*, *C. schoenoides*, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Samolus valerandi*, *Scorzonera parviflora*, *Taraxacum bessarabicum*, *Spergularia marina*, *S. media* and *Suaeda prostrata*. It has always been the only area in Austria with the occurrence of *Glaux maritima*.

Based on the opinion of Neilreich (1859), the earliest record of a halophyte species in the Pulkau district may be found in Schultes (1814), who reported the occurrence of *Salicornia perennans* (*S. herbacea*) near the town of Ernstbrunn. Although Ernstbrunn is located ~20 km S of the Pulkau valley, this is a reasonable interpretation of Schultes' record. Dolliner (1842) found *Glaux maritima* in wet places around the village of Staatz. The occurrences of most halophytes in the district were discovered by H. Kalbrunner, a pharmacist and the mayor of the town of Langenlois (Kalbrunner 1855). In the village of Mailberg, he observed *Glaux maritima*, covering the shores of the Schlossteich Fishpond, and near the village, he also found *Scorzonera parviflora* and *Spergularia marina*. *Glaux maritima* was also very common along the Pulkau between the town of Seefeld-Kadolz and the village of Wulzeshofen. Kalbrunner further found *Plantago maritima* around the village of Zwingendorf, and *Suaeda prostrata* (*Schoberia maritima*) around the village of Hadres. Based on information from A. Unger, Neilreich (1859) added the records of *Crypsis aculeata* from the area between Staatz and Laa an der Thaya and the surroundings of Zwingendorf. Based on a record by M. Matz, he reported *Salicornia perennans* to occur between the villages of Platt and Watzelsdorf south of the town of Retz and between the village of Haugsdorf and Laa an der Thaya, in places very abundant. He added the records of *Suaeda prostrata* from near Seefeld, Zwingendorf and Laa an der Thaya, a record of *Spergularia marina* near Zwingendorf, and records of *S. media* along the Pulkau stream from Mailberg as far as Laa an der Thaya. According to the same source, *Plantago maritima* occurred all over the district.

The eastern part of the Pulkau district became easily accessible by train from Vienna in 1870 when a new railway line Vienna–Brno was put in operation. In July 1871, the halophytic flora between Laa an der Thaya and Seefeld was explored by August L. Reuss, his brother and their friends (Reuss 1873). They observed halophytes in ditches and field margins along the road from Laa an der Thaya to Wulzeshofen. Further westwards, between Wulzeshofen and Zwingendorf, they reported large tracts of infertile ground, in many places with a thick layer of salt efflorescences. Halophytes were becoming less frequent towards Seefeld. They collected *Cirsium brachycephalum* in road ditches and in a reed bed north of the road Laa an der Thaya–Wulzeshofen, *Crypsis schoenoides* and *Juncus gerardii* between Wulzeshofen and Zwingendorf, *Salicornia perennans* in ditches between Hanfthal and Wulzeshofen, *Samolus valerandi* in a ditch, *Scorzonera parviflora* and *Tripolium pannonicum* in a dried-out wetland between Wulzeshofen and Zwingendorf, and *Spergularia marina* and *S. media* between Laa an der Thaya and Wulzeshofen. *Spergularia media* occurred as far as Zwingendorf. *Plantago maritima* was common, while *Glaux maritima* occurred in large quantities in the villages and along road ditches from Wulzeshofen as far as Zwingendorf and beyond. Reuss (1873) concluded that there was no other area in Lower Austria with such well-developed halophytic flora.

For the next 100 years, a small number of plant records are available from the Pulkau district. In the late 1870s or early 1880s, *Scorzonera parviflora* was recorded near Laa an der Thaya by H. Braun, and near Kadolz by A. Oborny (Halácsy & Braun 1882).

Roughly at the same time, K. Rechinger collected *Glaux maritima* in Zwingendorf for the exsiccate series Flora exsiccata austro-hungarica. In 1897, J. Haring collected *Tripolium pannonicum* in a meadow near the Zellerndorf railway station, roughly in the same place where M. Matz recorded *Salicornia perennans* in the 1850s. Probably in 1904, A. Teyber found *Bupleurum tenuissimum* in Zwingendorf, which was the first record of this species in the district. In 1953, H. Melzer recorded *Glaux maritima*, *Salicornia perennans*, *Scorzonera parviflora*, *Suaeda prostrata* and *Tripolium pannonicum* on the bottom of a former fishpond, probably at the Hintausacker site near Zwingendorf, and also found *Cirsium brachycephalum* somewhere nearby (Melzer 1955). In 1960, he collected *Salicornia perennans* and *Suaeda prostrata* at the site known as Saliterweide (also Saliterwiese or Saliterheide) ~2.4 km ESE of Zwingendorf.

The Hintausacker site at the NW edge of Zwingendorf was still used as a goose pasture in the 1970s. However, the number of grazing animals dropped, and some parts of the site were used as a waste place. Waste was repeatedly removed from the area. In 1979, the Hintausacker site was purchased by the Land Niederösterreich and, together with Saliterweide, included in the newly designated Zwingendorfer Glaubersalzböden Nature Reserve (Naturschutzgebiet). In the mid-1990s, the site was cleaned from waste again, bulldozed, and some earth was removed. Reed stands were reduced by repeated mowing, and some spontaneously established trees and shrubs were cut. In contrast, Saliterweide was left almost unmanaged, except for some interventions into the water regime, such as removing subsurface drainage pipes and enlarging the pond (Holzer et al. 2002).

From the mid-1920s to the 1970s, halophytic flora in the area was documented by Jurasky (1980). At the Hintausacker site, he recorded *Glaux maritima*, *Plantago maritima*, *Salicornia perennans*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. A wet depression ~1 km E of Zwingendorf, north of the road to Wulzeshofen, probably a former ice pond, harboured both the succulent halophytes and *Scorzonera parviflora*, *Spergularia media* and *Tripolium pannonicum*. This habitat was later destroyed by filling with earth (Oberleitner et al. 2006). In contrast, at the Saliterweide site, Jurasky only found *Plantago maritima*, but he reported the occurrence of salt efflorescences at the margins of adjacent arable fields. Hütterer & Albert (1993) sampled *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Spergularia media*, *Taraxacum bessarabicum* and *Tripolium pannonicum* for an ecophysiological study at the Hintausacker site in 1989. They also sketched a vegetation map of the site, which roughly corresponds to the situation as observed in 2020. A shallow pond in the north-eastern corner of the site was surrounded by *Phragmites australis* stands except for the southern side, which was probably disturbed by horses, poultry or people and fringed by the *Astero pannonici-Bolboschoenetum compacti* vegetation. The next vegetation zone in slightly drier places was *Loto tenuis-Potentilletum anserinae* with *Melilotus dentatus* and *Tripolium pannonicum* and trampled (perhaps also grazed) *Potentilla anserina* grassland, in places with *Glaux maritima* and *Inula britannica*.

Holzer et al. (2002) recorded *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Spergularia media* and *Tripolium pannonicum* at the Hintausacker site in 2001. They reported a mosaic of various vegetation types, including shallow ponds either with *Bolboschoenus* marshes or completely occupied with *Phragmites* reed beds, open stands with *Glaux maritima*, wet to intermittently wet saline meadows, monodominant stands of

Calamagrostis epigejos and a young self-established stand of *Fraxinus excelsior* and *Acer negundo*. Some halophytes were also present on an abandoned arable field south-west of the reserve. *Cirsium brachycephalum*, *Juncus gerardii*, *Plantago maritima* and *Tripolium pannonicum* still occurred at Saliterweide. Holzer et al. (2002) discovered an additional halophytic site between the farmstead Alicenhof and the western edge of Zwingendorf, including a large reed bed with *Phragmites australis* and a saline meadow. Of the halophytes, *Glaux maritima*, *Plantago maritima* and *Tripolium pannonicum* were present at this site. In summer 2021, we found none of these species there.

The current halophytic flora of the Pulkau district is strongly impoverished and includes *Cirsium brachycephalum* (last record from 2016), *Glaux maritima*, *Plantago maritima*, *Scorzonera parviflora*, *Spergularia marina*, *S. media* and *Tripolium pannonicum*. Locally disappeared halophytes include *Crypsis aculeata* and *C. schoenoides* (last recorded in the late 19th century), *Salicornia perennans* and *Suaeda prostrata* (persisting until the late 1970s or early 1980s), *Taraxacum bessarabicum* (last observed about ten years later) and *Samolus valerandi* (last record in 1988). All the remaining occurrences of halophytes in the Pulkau district are confined to both Zwingendorf sites, especially Hintausacker. However, subhalophytes still occur at other sites in the Pulkau district. In July 2021, we observed *Bolboschoenus maritimus*, *Centaurium pulchellum*, *Lotus tenuis* and *Melilotus dentatus* in wet places on arable land 1.5 km E of Obritz, *Bolboschoenus maritimus*, *Carex otrubae*, *Lotus tenuis*, *Melilotus dentatus*, *Puccinellia distans*, *Rumex stenophyllus* and *Trifolium fragiferum* in the sports grounds and around ponds at the southern edge of Seefeld-Kadolz, and *Achillea asplenifolia*, *Bolboschoenus maritimus*, *Carex distans*, *C. otrubae*, *Lotus maritimus*, *L. tenuis*, *Melilotus dentatus* and *Rumex stenophyllus* in reed beds and meadows between the western edge of Zwingendorf and the Alicenhof farmstead.

Hintausacker (Fig. 6C). – This last well-preserved site of halophytic vegetation in the Pulkau district is located at the north-western edge of the village of Zwingendorf north to north-east of the church. It is one of the two parts of the protected area Zwingendorfer Glaubersalzböden with an area of 5.38 ha. Nowadays, it is the only Austrian locality of *Glaux maritima*. The southern part of the site is covered by a mesic meadow dominated by *Festuca arundinacea* and *Arrhenatherum elatius*. The most widespread halophytic vegetation at this site corresponds to the association *Loto tenuis-Potentilletum anserinae*. The meadows and subhalophytic grasslands are left unmown or mown in longer than annual intervals, which allows tall grasses and herbs to dominate and suppress competitively weak halophytes. Most halophytes and subhalophytes, including *Carex distans*, *C. secalina*, *Centaurium pulchellum*, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Puccinellia distans*, *Scorzonera parviflora*, *Spergularia media* and *Tripolium pannonicum* occur in the *Puccinellietum limosae* vegetation in shallow depressions with relatively sparse vegetation, including the places where topsoil was removed. At wetter places, there are also patches of saline marshes with *Bolboschoenus maritimus* (*Astero pannonici-Bolboschoenetum compacti*). Two shallow ponds in the northern part of the site are surrounded by stands of *Phragmites australis*, *Bolboschoenus maritimus* agg. and *Carex riparia*.

Saliterweide. – This abandoned pasture is located between arable fields ~2.4 km ESE of the church in Zwingendorf, south of the road to Wulzeshofen. It is the second of the two

parts of the protected area Zwingendorfer Glaubersalzböden with an area of 10.33 ha. The largest part of the site is covered with an unmanaged grassland with *Agrostis gigantea*, *A. stolonifera*, *Dactylis glomerata*, *Elytrigia repens*, *Festuca rupicola* and *Poa angustifolia*, here and there with individuals of *Plantago maritima*. Trampled places and grassy roads are dominated by *Festuca pulchra* with abundant *Plantago maritima* (association *Centaureo pannonicae-Festucetum pseudovinae*). Stands of *Phragmites australis* and rich populations of *Bolboschoenus maritimus*, *Lotus tenuis* and *Plantago maritima* occur around a small pond in the south-western part of the site. *Cirsium brachycephalum* is reported from this site, but we did not find it in July 2021.

Other occurrences of halophytes

Some occurrences of halophytes were also recorded at a few sites outside the above-described districts. *Plantago maritima*, *Taraxacum bessarabicum*, *Tripolium pannonicum*, and probably also *Juncus gerardii* were recorded in a shallow depression of the Jevišovka stream near or in the village of Stošíkovice na Louce north-east of the town of Znojmo in the early 1950s (Šmarda 1953). *Juncus gerardii* and *Tripolium pannonicum* once occurred around a fishpond at the south-eastern edge of the village of Hodonice east of Znojmo (Šmarda 1953). In the 1880s, *Taraxacum bessarabicum* and *Tripolium pannonicum* were found on common pastures somewhere between the towns of Břeclav and Lanžhot and the village of Moravská Nová Ves (A. Ripper in Oborny 1912). The exact location of this site is unknown. While *J. gerardii* may be still present at the Hodonice site (last collected in 2013), all the remaining occurrences likely disappeared a long time ago.

Species

Here we review the historical and current distribution and ecology of 17 halophytes that are (or were) significantly related to saline habitats in Moravia. Their Red List classification in the Czech Republic and Austria is given in brackets after the species names, following Grulich (2017) and Niklfeld (1999), respectively: RE – regionally extinct; CR – critically endangered, EN – endangered; VU – vulnerable.

The presence of these species in the halophytic districts of southern Moravia and the Pulkau valley since the 1820s is summarized in Figs. 7 and 8. Individual occurrence records mentioned in the text and shown in these figures are summarized in Supplementary Data S2. Although we prepared the occurrence dataset with extraordinary care, it is most likely not free of mistakes. Labelling mistakes in herbaria are probably more frequent in halophytes than in other vascular plants. As halophytes have never been widespread, they were often collected for exchange or used as a present to other botanists. The new owners sometimes replaced the original locality information with new labels, which may contain imprecise information. Also, specimens collected during excursions may have been labelled without knowledge of local topography and reliable maps. There are also errors in the collection date. In addition, some botanists collecting in large quantities and selling their specimens to museums, e.g. F. Weber, may have deliberately misdated specimens to reduce the number of duplicates. For these reasons, if a single record or specimen of a species exists from a particular site, the occurrence of this species should be considered uncertain. The same holds for temporal outliers.

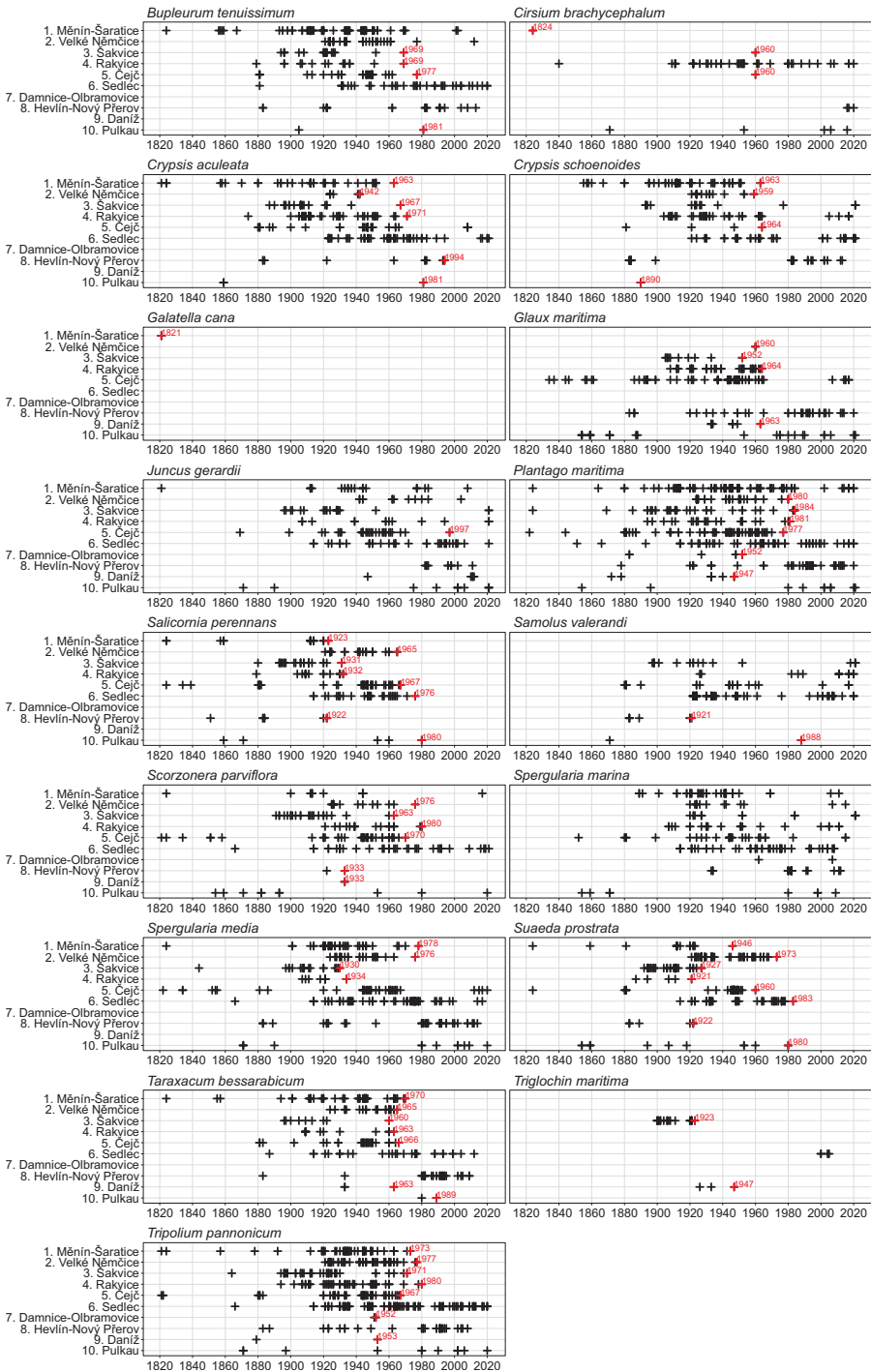


Fig. 7. Recorded occurrences of 17 halophytic species in individual halophytic districts. Red crosses with a date indicate the last record for locally extirpated species, defined as those not recorded in the district after 2000. Many records are not shown because they are not dated. This applies particularly to herbarium specimens from the 19th century.

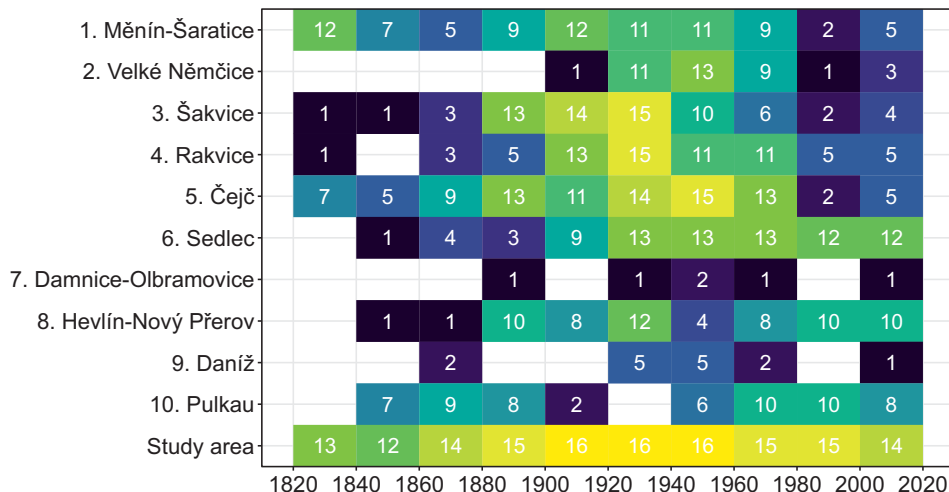


Fig. 8. Number of species of the 17 halophytes dealt in this study recorded per two-decade periods in individual halophytic districts of southern Moravia and northern Lower Austria and across all the districts (Study area). This Figure summarizes the records for individual species shown in Fig. 7. The period 2001–2020 also includes several records from the year 2021.

Bupleurum tenuissimum (Red Lists: CZ: CR; AT: EN)

Bupleurum tenuissimum is an annual herb occurring in the western Mediterranean, in the Atlantic parts of Europe from Spain to Denmark, including Great Britain, the western Baltic area, central Germany and the Pannonian region, with scattered occurrences towards the east reaching as far as southern Ukraine (Meusel et al. 1978).

This species is a competitively weak halophyte usually growing in open, often disturbed vegetation. In the study area, it was recorded in nearly all the types of saline grasslands of the class *Festuco-Puccinellietea*.

Bupleurum tenuissimum was present in all the halophytic districts except Damnice-Olbramovice and Daníž. The last records in the Rakvice and Šakvice districts date back to 1951 and 1953, respectively. In the Čejč district, it was last collected in 1977. In the Pulkau district, it was discovered near the village of Zwingendorf in 1904 by A. Teyber (Anonymous 1905) and re-recorded roughly at the same site in 1981. Currently, the largest population of this species, comprising thousands of individuals, occurs at the Slanisko u Nesytu site in the Sedlec district. There are also recent records from the Měnin-Šaratice, Velké Němčice and Hevlín-Nový Přerov districts, in each of them from a single site, but the populations are small. Due to its inconspicuous appearance, this plant can be easily overlooked in the field, and the size of its populations fluctuates depending on the weather of a particular year. Therefore, it may have survived unnoticed at some additional sites.

Apart from the occurrences in the halophytic districts, *Bupleurum tenuissimum* was once found near the village of Komárov at the southern periphery of the city of Brno (A. Makowsky sec. Oborny 1886) and at two sites near the village of Popovice east of the town of Uherské Hradiště (Staněk 1926). However, both occurrences have not been confirmed since then.

Cirsium brachycephalum (Red Lists: CZ: CR, AT: EN; EU Habitats Directive 92/43/EEC)

Cirsium brachycephalum is a biennial to short-lived monocarpic species, seldom reproducing vegetatively (Prokešová 2013). It is endemic to the Carpathian Basin, having most localities in Hungary and southern Slovakia and the westernmost distribution limit in southern Moravia and Lower Austria (Meusel & Jäger 1992).

Cirsium brachycephalum is a competitively weak and moisture-demanding species. It prefers heavy, saline soils that are at least occasionally flooded. It is usually considered a halophyte (Grulich 1987), although its affinity for saline habitats is not as strong as generally believed (Zlinská 2004, Prokešová 2013). It also grows in subhalophytic marshes and meadows, margins of reed beds, wet fallows, wetlands on arable land and at other occasionally disturbed sites (Bureš 2004). In the study area, it was recorded mainly in saline marshes of the alliance *Meliloto dentati-Bolboschoenion maritimi* and saline grasslands of the association *Agrostio stoloniferae-Juncetum ranarii*.

Unlike most other halophytes, *Cirsium brachycephalum* has always been rare in the study area. It was first collected on the shores of the Měnin Fishpond between 1817 and 1821 (Hochstetter 1825, see also Danihelka in Hadinec & Lustyk 2007). Reisseck (1841) reported this species to occur somewhere north-east of the town of Lednice. Albin Wildt found it near the village of Rakvice in 1909 and 1911. Currently, *C. brachycephalum* occurs in a few places north-east of this village at the Trkmanec-Rybníčky and Trkmanské louky sites. In the past, the species was also recorded in the ditches along the railway south-east and north-west of Rakvice and in the Dyje floodplain south of the village (herbarium specimens and records from 1950–1969). There is also a herbarium specimen allegedly collected near the village of Terezín (F. Weber 1930 PR) and a record from a relevé sampled north of Terezín in 1958–1961 (Vicherek 1962), both in the Čejč district. In addition, *C. brachycephalum* was recorded in a saline marsh north-west of the village of Popice in the Šakvice district in 1958–1961 (Vicherek 1962). A single record from the village of Dobré Pole (F. Švestka sec. Šmarda 1953) in the Hevlín-Nový Přerov district is probably erroneous. The recent find of *C. brachycephalum* near the village of Hevlín (Dřevojan 2017) is the first reliable record of this species in that district. Currently, it is the only site of this species in the Czech Republic besides the sites near Rakvice. This site is close to the occurrences in the Pulkau district in Lower Austria. In this district, the species was reported from the village of Unternalb south of the town of Retz (Adler et al. 1996) and the area between the village of Zwingendorf and the town of Laa an der Thaya. A small population of *C. brachycephalum* was observed in 2016 at the Saliterweide site near Zwingendorf (N. Sauberer sec. Dřevojan 2017), being the last population of this species in northern Lower Austria. However, we did not find this species at Saliterweide in July 2021.

In addition to the occurrences described above, *Cirsium brachycephalum* was collected in a fen meadow at the edge of the Morava river floodplain south of the village of Moravský Písek in 1946. This is the only record from that site, and the occurrence probably vanished soon after being discovered.

Crypsis aculeata (Red Lists: CZ: CR; AT: VU)

Crypsis aculeata is an annual grass distributed in the submeridional and meridional zones in Europe, Asia and northern Africa. It also occurs in some areas of the temperate zone with continental climates. Its occurrences in Lower Austria, southern Moravia and south-

ern Slovakia are located at the northern limit of its range (Conert 1998, Danihelka & Kaplan in Kaplan et al. 2020).

Typical habitats of this halophyte in Moravia are periodically flooded places, such as temporary pools on pastures and arable land, shores and bottoms of drained fishponds with saline water, and margins of saline reed beds. *Crypsis aculeata* is a dominant species of the association *Crypsietum aculeatae*. It occurs on heavy soils rich in nitrogen and soluble sulphates and chlorides.

Crypsis aculeata was once present in all the districts but Damnice-Olbramovice and Daníč. However, it started to decline with the drainage of saline lakes and fishponds in the 19th century. Its decline accelerated in the early 20th century with the drainage of saline pastures followed by their conversion to arable land. Its occurrence at the Plácky site, the only one in the Velké Němčice district, was last documented in 1942. The occurrence near the village of Moutnice in the Měnin-Šaratice district (Vicherek 1973) vanished probably soon after 1963. The last herbarium record from the Šakvice district dates back to 1967. In the Rakvice district, *C. aculeata* was last collected in 1971 at the saline site surrounding the former Fabián Fishpond, now filled with earth, in the town of Velké Bílovice. In the Čejč district, it was recorded frequently until 1966, e.g. at the Zápověď site near the village of Terezín, but was not found for the next few decades. In 2008, it was rediscovered at Zápověď in a shallow pool dug in 2003 as a part of an ecological restoration project (Hadinec & Lustyk 2009). The last record of this species at the Novosedly site in the Hevlín-Nový Přerov district dates back to 1994 (J. Vicherek sec. Hanušová 1995). Only one small population, once established from seeds collected from another site at the Nesyt Fishpond (Danihelka & Hanušová 1995), still survives at the Slanisko u Nesytu site near the village of Sedlec. In addition, a few plants were seen on the drained bottom near the southern bay of the Nesyt Fishpond in 2020. For the Pulkau district, only two 19th-century records and one record from 1981 exist for *C. aculeata*.

Crypsis schoenoides (Red Lists: CZ: CR; AT: CR)

Crypsis schoenoides is an annual grass with a similar life history and distribution as *C. aculeata*. It occurs in the submeridional and meridional zones and the continental part of the temperate zone in Europe, western and Central Asia, Siberia, northern and subtropical Africa and Madagascar. The northern range limit of this species is in south-eastern Austria, southern Moravia and southern Slovakia (Conert 1998, Danihelka & Kaplan in Kaplan et al. 2020).

Crypsis schoenoides grows at periodically flooded sites such as shores and bottoms of regularly drained fishponds and oxbows and temporary pools in saline grasslands and arable fields. It is a dominant species of the association *Heleochloëtum schoenoidis*. It grows on heavy soils rich in nitrogen, phosphorus, sulphates and chlorides. However, its affinity for saline habitats is weaker than in *C. aculeata* (Šumberová 2007a).

Crypsis schoenoides was once present in all the districts but Damnice-Olbramovice and Daníč. It declined similarly and for the same reasons as *C. aculeata* but slower because of its weaker affinity for saline habitats. The last herbarium specimen in the Velké Němčice district was collected in 1959, probably at the Plácky site. The last records from the Měnin-Šaratice and Čejč districts date back to the 1960s. Only two 19th-century records of *C. schoenoides* exist for the Pulkau district (Beck 1890–1893). After

2000, *C. schoenoides* was observed in saline habitats in four districts: In the Šakvice district, where the last records were from 1977, two populations of this species were found in summer 2021 on abandoned wet arable land along the Štinkovka stream between the villages of Šakvice and Starovičky (Chytrý & Danihelka 2021). In the Rakvice district, it still occurs at the Trkmanec-Rybníčky site. In the Hevlín-Nový Přerov district, it was found at the Slanisko Novosedly site, and in the Sedlec district, it still occurs at the Slanisko u Nesytu site and on the drained bottom of the Nesyt Fishpond, locally in large quantities (Dřevojan et al. 2017).

In addition to the occurrences at sites described above, *Crypsis schoenoides* was repeatedly recorded in 1994–2012 on gravel bars and in an oxbow of the Dyje river south-west of the town of Lanžhot.

Galatella cana (Red Lists: CZ: RE; AT: EN)

Galatella cana is a perennial clonal herb endemic to the western and southern margin of the Pannonian Lowland. It was recorded in southern Moravia, eastern Austria, Hungary, northern Serbia and south-western Romania (Wagenitz 1979, Grulich & Feráková 1999).

Galatella cana was found only once on the territory of the current Czech Republic between 1817 and 1821 by Ch. F. Hochstetter, somewhere near the eastern shores of the former Měnin Fishpond in the Měnin-Šaratice district (Hochstetter 1825). Hochstetter described its habitat as follows: “In einem kleinen Gehölze seitwärts vom See steht eine neue Pflanze für Deutschlands Flora, nämlich *Aster canus* W. et K., ebendasselbst *Senecio tenuifolius* [i.e. *S. erucifolius*]...!”. This corresponds to the circumstances known from the closest sites of this species near the village of Baumgarten an der March in Lower Austria and at the Šúr site near Bratislava in south-western Slovakia (Grulich & Feráková 1999). For a long time, no herbarium specimen of this species from the Měnin site had been known (Grulich 1987), and its former occurrence in Moravia was sometimes questioned. However, a specimen collected by Hochstetter near Měnin was found in the herbarium of the University of Vienna in 2007 (Danihelka 2008). Other specimens from the same site were later discovered in the State Museum of Natural History Stuttgart (Danihelka 2009) and recently in the Silesian Museum in Opava, the latter with a transcribed label. No records of *G. cana* exist from the Pulkau district.

Glaux maritima (Red Lists: CZ: CR; AT: CR)

Glaux maritima is a low-growing perennial herb with a circumpolar distribution. It occurs mainly along the coasts of western and northern Europe, eastern Asia, and western and eastern North America, as well as in inland saline habitats in areas with arid climates in eastern Europe, Siberia and North America. It also occurs scattered in saline habitats across central and western Europe (Meusel et al. 1978).

In the study area, *Glaux maritima* prefers wet saline sites, in the past grazed mainly by geese and ducks, often in villages along ditches and streams and around fishponds (Grulich 1987). It occurs in halophytic grasslands of the associations *Puccinellietum limosae*, *Scorzonero parviflorae-Juncetum gerardii* and *Loto tenuis-Potentilletum anserinae*.

Glaux maritima used to occur in most Moravian districts of halophytic flora. However, some of the records are uncertain. Only one herbarium specimen is known from the

Měnin-Šaratice district, allegedly collected near the village of Měnin in the late 19th century; however, it could be a labelling mistake. Only three records exist from the Velké Němčice district, all from relevés recorded by Vicherek (1962, 1973) at the southern edge of the village of Velké Němčice and near the village of Starovice probably in 1960 and 1965. In the Šakvice district, *G. maritima* occurred near the Šakvice railway station and in the village of Starovičky; at the latter site, it was last collected in 1952. From the Rakvice district, *G. maritima* disappeared during the 1960s. The species was also abundant in the Čejč district, but some occurrences disappeared already in the 19th century after the lakes of Kobylí and Čejč were drained. At the Zápověď site near the village of Terezín, *G. maritima* used to be collected frequently until 1965; thereafter, it disappeared but was found again in 2007 after shallow pools were created in the former nature reserve. The species was also present in at least three villages of the Damnice-Olbramovice district; however, these occurrences, recorded most likely in the 1880s (A. Ripper sec. Oborny 1912), disappeared probably in the early 20th century. *Glaux maritima* still survives at the Dobré Pole site in the Hevlín-Nový Přerov district. In the Daníž district, it was recorded in four villages, with the last record in the village of Dyjákovičky dating back to 1962 or 1963 (Vicherek 1973). It was once widespread in the Pulkau district; a large population still survives at the Hintausacker site near Zwingendorf. There are also three undocumented records from the Sedlec district, but we consider them erroneous. The earliest one (Formánek 1887) is probably based on a misidentification. One of the records in two different relevés by Vicherek (1962) is a misprint, and the other one may be a location mistake.

In addition to the occurrences described above, there is an undocumented record of *Glaux maritima* from the Hrubá louka site north of the town of Hodonín (J. Bílý sec. Šmarda 1953) and an unclear record from the surroundings of Retz (Janchen 1977).

Juncus gerardii (Red Lists: CZ: CR; AT: VU)

Juncus gerardii is a perennial graminoid distributed along the coasts of Europe and the eastern coasts of North America, as well as at inland saline sites of Europe, western temperate Asia, Siberia and North America (Hultén & Fries 1986).

The species occurs in wet saline meadows and marshes, at mineral springs and rarely in wetlands on arable land. It is also found on non-saline but mineral-rich clayey soil. In southern Moravia, it frequently occurs in most types of saline vegetation, often dominating or co-dominating the saline grasslands of the *Juncion gerardii* alliance.

Juncus gerardii is very similar to the frequently co-occurring *J. compressus*, and both species have often been misidentified. For instance, there are ~100 *Juncus* specimens originally identified as *J. gerardii* from the Czech Republic at BRNU, of which ~50 were reidentified as *J. compressus* in our revision. Consequently, records of *J. gerardii* not documented by a herbarium specimen, especially records from relevés, are unreliable. For this reason, we accept only a few records of this species that are not supported by a herbarium specimen, thus certainly underestimating the species' frequency. In vegetation analyses, we merged *J. compressus* and *J. gerardii* into the *J. compressus* agg.

Among the 17 halophytes dealt with in this study, *Juncus gerardii* is the most widespread species, both in southern Moravia and Lower Austria. It has several isolated occurrences outside the ranges of other halophytes. Also, it is usually the last surviving

halophyte at former halophytic sites. Based on the inspected herbarium specimens and field experience, we assume that in the past, it was present in all the districts, though there is no herbarium specimen from the Damnice-Olbramovice district. There are also recent records from all the other districts, most of them supported by herbarium specimens collected after 1990.

Plantago maritima (Red Lists: CZ: CR; AT: VU)

Plantago maritima is a perennial clonal herb with a cosmopolitan but fragmented distribution. In Europe, it occurs mainly along its western Atlantic and northern coasts, in the mountains of its southern part and inland saline habitats in the areas with continental climates (Meusel et al. 1978). Three to six subspecies are recognised in Europe (Chater & Cartier 1976, Marhold 2011). Plants occurring in the steppe zone of Eurasia are traditionally separated as *P. maritima* subsp. *ciliata* (Chrtek 2000), which is the taxon found in the study area.

Plantago maritima naturally occurs in grasslands on alkaline to neutral, heavy soils. In the study area, it occurs in most types of halophytic vegetation, ranging from salt marshes of the *Meliloto dentati-Bolboschoenion maritimi* alliance through annual saline vegetation of the alliances *Cypero-Spergularion salinae* and *Thero-Salicornion* to the saline grasslands of the alliances *Puccinellion limosae*, *Juncion gerardii* and *Festucion pseudovinae*. It is most frequent in the association *Centaureo pannonicae-Festucetum pseudovinae*.

Plantago maritima once occurred in all the districts of halophytic flora in the study area. However, the last record from the Daníč district dates back to 1947 and that from the Damnice-Olbramovice district to 1952. In the late 1970s and during the 1980s, its populations disappeared from the Velké Němčice, Šakvice, Rakvice and Čejč districts. The species still occurs in the Měnin-Šaratice, Sedlec, Hevlín-Nový Přerov and Pulkau districts, usually at one or two sites in each district. However, most populations consist of a small number of individuals. The largest population survives at the Slanisko u Nesytu site.

In the study area, *Plantago maritima* occurred far beyond the ranges of other halophytes except for *Juncus gerardii*, usually on heavy, saline to slightly saline or mineral-rich soils. In the west, its range extended to the village of Podmolí west of the town of Znojmo, in the north to the city of Brno, and in the east the towns of Kyjov and Hodonín. However, none of the populations at the limits of its historical range has survived until now. In addition, this species was recorded at two isolated sites in the Bílé Karpaty Mts; the occurrence in an abandoned loam pit west of the town of Uherský Brod may still exist. Recently, *P. maritima* is spreading along the roads where salt is used for winter de-icing (Danihelka & Kaplan in Kaplan et al. 2018). However, no such records are available from the study area.

Salicornia perennans (Red Lists: CZ: RE; AT: VU)

The taxonomy of the genus *Salicornia* is still insufficiently resolved (Kadereit et al. 2007). The populations once found in southern Moravia and Lower Austria are now assigned to *S. perennans* (syn. *S. prostrata*), but records under the name *S. herbacea* in earlier literature also refer to this species. It is an annual diploid succulent herb occurring at inland saline sites from the Carpathian Basin in the west to the Aral Sea in the east (Kadereit et al. 2007). The southern Moravian sites were at the north-western limit of its range (Danihelka & Kaplan in Kaplan et al. 2017).

The southern Moravian stands of *Salicornia perennans* were confined to the parts of saline sites with strongly saline soils that were flooded in the spring but usually turned very dry in the mid-summer. The dominance of this species defined the association *Salicornietum prostratae*, but it also co-occurred in stands dominated by the other annual succulent halophyte species, *Suaeda prostrata*.

Salicornia perennans was once present in all the districts but Daníč. It was likely abundant in pastures on the flat shores of the former Měnin Fishpond and Kobylí and Čejč lakes (Hochstetter 1825, Krzisch 1859). Some populations survived at other sites, but their decline accelerated in the early 20th century. After World War II, *S. perennans* was only observed in four districts: two of the occurrences (both in nature reserves) vanished during the 1960s because of the drainage of the surrounding agricultural land. At the Slanisko u Nesytu site in the Sedlec district, this species survived for another decade, but the population size gradually diminished during the early 1970s (Grulich 1987). The likely causes of population decline include abandonment (especially cessation of poultry grazing), changes in water regime and desalination. In 1976, when the fate of the last surviving *Salicornia* population became clear, the remaining five dwarfish specimens were collected and later deposited at the BRNU herbarium. The last records from two sites near the village of Zwingendorf in the Pulkau district date back to the early 1970s or 1980s (Jurasky 1980).

In 1986, an unsuccessful attempt was made by P. Tomšovic from the Institute of Botany in Průhonice to re-introduce *Salicornia perennans* at the Slanisko u Nesytu site. The seeds were collected at Lake Neusiedl. However, the seeds sown at the site did not germinate, while young plants grown in a greenhouse and transplanted to the site failed to fructify (Grulich 1987, in litt. 2021, Danihelka 2005).

Samolus valerandi (Red Lists: CZ: CR; AT: EN)

Samolus valerandi is an annual halophyte distributed mainly in the Mediterranean, western Europe, along the Baltic coast and in the steppe zone of western Asia, towards the east reaching Pakistan and north-western India. It is also found in southern Africa. Its distribution in central Europe is fragmented, confined to saline marshes (Meusel et al. 1978). The populations of the New World are now separated at the species level as *S. parviflorus* (Choleva 2009).

In the study area, *Samolus valerandi* is found in saline marshes of the alliance *Melilotodentati-Bolboschoenion maritimi* and wet saline grasslands of the alliance *Juncion gerardii*, in ditches, on the bottoms of drained fishponds and in temporary pools on arable land. It never reaches high cover.

Although being native to the study area, *Samolus valerandi* was first collected as late as 1871 near the village of Zwingendorf in the Pulkau district (Reuss 1873) and 1880 between the villages of Terezín and Čejč in the Čejč district (Bohuňovský 1880). It has been recorded in the Šakvice, Rakvice, Čejč, Sedlec, Hevlín-Nový Přerov and Pulkau districts. In the Hevlín-Nový Přerov district, *S. valerandi* was last collected in 1921. In the Čejč district, it was last collected in 1962 and, after more than 50 years, again in 2017 in a wet saline meadow north of the village of Terezín. In the Šakvice district, it once occurred at the northern edge of the town of Hustopeče, with the last record dating back to 1955. In 2017, a small population was discovered on the drained bottom of the Přední

Fishpond ~1.5 km N of the former site. In 2021, large populations were discovered on abandoned wet arable land along the Štinkovka stream between the villages of Šakvice and Starovičky. There are numerous recent records from the Rakvice and Sedlec districts. In the Rakvice district, an abundant population of *S. valerandi* was recently found mainly at the Trkmanec-Rybníčky site. In the Sedlec district, this species has been repeatedly observed since the 2000s, mainly on the drained bottom of the Nesyt Fishpond and once also on the drained bottom of the Hlohovecký Fishpond. A new occurrence was discovered in 2007 in a wet part of an arable field ~1.6 km W of the town of Mikulov. In the Pulkau district, *S. valerandi* was only found in the surroundings of the village of Zwingendorf in 1871 and for the second time in 1988.

In addition to the occurrences associated with halophytic sites, *Samolus valerandi* was recorded in a fen meadow in the Dyje floodplain west of the village of Brod nad Dyjí in 1922 and a reed bed west of the village of Pavlov in 2002.

Scorzonera parviflora (Red Lists: CZ: CR; AT: EN)

Scorzonera parviflora is a perennial herb with a large continuous distribution range in the steppe zone in south-eastern European Russia, Kazakhstan, adjacent parts of western Siberia and Kyrgyzstan. It also occurs in Transcaucasia, central Anatolia, the Carpathian Basin, central Germany and southern France, with scattered occurrences mainly in southern Ukraine, Romania and northern Bohemia (Meusel & Jäger 1992).

In the study area, *Scorzonera parviflora* was recorded mainly in periodically wet saline meadows of the association *Scorzonera parviflorae-Juncetum gerardii* on heavy, clayey soils. However, it also occurs in saline marshes and other types of halophytic vegetation.

The species was once present in all the districts except Damnice-Olbramovice. In the Měnin-Šaratice district, it occurred near the village of Měnin (last collected in 1900) and in saline meadows at mineral springs south of the village of Šaratice, where it was last seen in 1944 and then again in 2017. In the Velké Němčice district, this species was repeatedly collected at the Plácky site, with the last record from 1975 or 1976 (Husák & Játiová 1984). There is also one record from the southern edge of the village of Velké Němčice approximately from 1963 (Vicherek 1973) and another one from the village of Starovice from 1950 (Šmarda 1953), but at least the latter is uncertain. In the Šakvice district, the *S. parviflora* population near the railway station was destroyed in the early 1920s. However, another population survived at the saline site west of the village of Starovičky until about 1963 (Vicherek 1973). In the Čejč district, this species was particularly abundant, but the last record from the Terezín site dates back to 1970. In the Rakvice district, *S. parviflora* once occurred at several sites; the population in wet railway ditches next to the Rakvice railway station survived until the early 1980s (Grulich 1987). The species was once abundant on the western shores of the Nesyt Fishpond, but it also occurred along its southern shores and in the railway ditches west of the village of Sedlec (Fröhlich 1940). One of the two last extant populations of *S. parviflora* in the study area occurs at the Slanisko u Nesytu site. Its size fluctuates depending on moisture, declining in dry years. Only small numbers of individuals were observed during the 2010s. However, numerous plants were observed in 2021, supported by a humid spring of that year. The species was also recorded north of the village of Kleinschweinbarth in Lower Austria (*S. Domas* sec. Makowsky 1863). In the Hevlín-Nový Přerov district,

S. parviflora was collected near the village of Nový Přerov in 1922, and there has been no other reliable record since then. In the Daníč district, it was found by Tomaschek (1933) at three sites, but these populations were probably destroyed in the 1950s. In the Pulkau district, *S. parviflora* once occurred at several sites between the villages of Großkadolz and Mailberg and the town of Laa an der Thaya (Halácsy 1896); however, it has only survived until the present at the Zwingendorf site.

There are old literature records of *Scorzonera parviflora* from the southern margin of the city of Brno (Oborny 1886) and the surroundings of the town of Rajhrad (F. Mitrowsky sec. Oborny 1886), both relatively close to the occurrences in the Měnin-Šaratice district. The undocumented records from the surroundings of the towns of Uherské Hradiště (L. Schlögl sec. Oborny 1886) and Hodonín (C. Theimer sec. Oborny 1886) are almost certainly erroneous as no suitable sites have ever existed in those areas.

Spergularia marina (Red Lists: CZ: CR; AT: CR)

Spergularia marina is an annual or short-lived perennial prostrate to ascending herb. It has a nearly cosmopolitan distribution, but it is unclear which parts of its distribution range are primary and where it has been introduced. In the Old World, it occurs mainly along the European and Mediterranean coasts and in inland saline habitats of the Carpathian Basin, steppe zone of eastern Europe, western Siberia and Central Asia (Meusel et al. 1965, Kúr & Ducháček in Kaplan et al. 2016).

This competitively weak species grows in sparse vegetation, in which it can be locally one of the most abundant species. In the study area, it has been most often recorded on wet shores and drained bottoms of ponds, especially in annual vegetation of the associations *Chenopodietum rubri*, *Crypsietum aculeatae*, *Heleochoëtum schoenoidis* and *Spergulario marginatae-Suaedetum prostratae*. It also occurs in halophytic grasslands and on wet arable land but seems to avoid saline marshes.

Spergularia marina was once present in all the districts, though there is no herbarium specimen known to us from the Daníč district. Records after the year 2000 are available from all the districts except Daníč. In the Šakvice district, the last herbarium specimen was collected in 1984, and only in 2021, large stands of this species were found at restored sites and abandoned wet arable land east of the village of Šakvice. This demonstrates that *S. marina* can survive in wet saline places on arable land unnoticed for decades.

While declining in its original habitats, *Spergularia marina* is now spreading along roads salted for winter de-icing and in cities (Kúr & Ducháček in Kaplan et al. 2016).

Spergularia media (Red Lists: CZ: CR; AT: VU)

Spergularia media is a prostrate to ascending perennial herb. It is native to coastal areas and inland saline sites in Europe, northern Africa, Kazakhstan and northern Iran (Meusel et al. 1965, Kúr & Ducháček in Kaplan et al. 2016).

Spergularia media has similar habitat requirements as *S. marina* but is less frequent on exposed wet bottoms and more frequent on spring-wet and summer-dry soils with high salt concentration, especially in the *Puccinellietum limosae* grasslands. In the past, it was constantly present in the stands of succulent halophytes (alliance *Thero-Salicornion*). It also occurs in the stands of annual halophytic grasses (alliance *Cypero-Spergularion salinae*). Unlike *S. marina*, it is less tolerant to mechanical disturbances and is mainly found in natural habitats.

Spergularia media was once present in all the districts but Damnice-Olbramovice. There is only one literature record (not supported by a herbarium specimen) from the Daníž district, namely from the saline site north-west of the village of Dyjákovice (Tomaschek 1933). *Spergularia media* declined together with other halophytes, mainly due to drainage. It first disappeared from the Šakvice district, where it was last collected in 1929. The last herbarium specimen from the Velké Němčice district is from 1963, when it was collected at the Starovice site. In the Měnin-Šaratice district, the species was last collected in 1978 at the Zřídla u Nesvačilky site. In the Čejč district, *S. media* was repeatedly collected from the 1820s until 1967, when it was last found at the Zápověď site. It was rediscovered there in 2005 after the creation of shallow pools. In the remaining districts, this species still survives at one or a few sites.

Recently, *Spergularia media* has also been recorded along roads treated by de-icing salt. However, the number of such records is much smaller than for *S. marina* (Kúr & Ducháček in Kaplan et al. 2016).

Suaeda prostrata (Red Lists: CZ: RE; AT: EN)

Suaeda prostrata is a prostrate to ascending annual succulent herb. It is a member of the taxonomically difficult *S. maritima* aggregate, which in Europe comprises four species (Uotila 2011). *Suaeda prostrata* is a continental species distributed from the Carpathian Basin to south-western Siberia (Freitag et al. 1996, Freitag & Lomonosova 2006). It reaches the north-western limit of its range in southern Moravia, where it is the only species of *Suaeda*. The records of *S. maritima* and *S. pannonica* in earlier sources from the study area also belong to this species (Daníhelka & Kaplan in Kaplan et al. 2017).

The stands dominated by *Suaeda prostrata* (association *Spergulario marginatae-Suaedetum prostratae*) developed on strongly saline soils that were at least shortly flooded in the spring but dried out in summer. This species was more tolerant to the high content of nitrogen than *Salicornia perennans* (Šumberová 2007b).

Like *Salicornia perennans*, *Suaeda prostrata* was once present in all the districts but Damnice-Olbramovice and Daníž. Both species usually co-occurred and also declined simultaneously. The occurrences in the Šakvice, Rakvice and Nový Přerov districts vanished already in the 1920s. After World War II, *Suaeda prostrata* was only observed in five districts: the occurrence in the Měnin-Šaratice district vanished probably in the 1940s, the last remaining population in the Čejč district at the Zápověď site disappeared in the late 1960s, and two populations in the Velké Němčice district vanished in the late 1960s or early 1970s. The population decline at the Slanisko u Nesytu site in the Sedlec district started around the year 1980 (Grulich 1987). In the Pulkau district, *S. prostrata* was last recorded in the late 1970s at two sites (Jurasky 1980), namely Hintausacker next to the village of Zwingendorf and in a shallow wet depression ~1 km E of the village, now filled with earth.

Taraxacum bessarabicum (Red Lists: CZ: CR; AT: EN)

Taraxacum bessarabicum is a small perennial herb. It is one of the few easily identifiable *Taraxacum* species, a member of the *Taraxacum* sect. *Piesis*, which comprises late-flowering (summer to autumn), sexually reproducing halophytic species. It has an extensive distribution range from western Europe to Central Asia. Unlike apomictic species,

T. bessarabicum is morphologically variable but this variation exhibits no spatial pattern across its geographic range (Meusel & Jäger 1992, Kirschner et al. 1994, 2011).

Taraxacum bessarabicum is confined to nutrient-rich saline soils (Kirschner et al. 1994, Dudáš et al. 2016). In the study area, it was recorded most frequently in the association *Puccinellietum limosae* but also occurred in other types of halophytic grasslands and annual halophytic vegetation.

In the past, *Taraxacum bessarabicum* occurred in all the halophytic districts of the study area. However, there is only one record from the Damnice-Olbramovice district, by A. Ripper from the village of Troskotovice, which may be dated to the 1880s (Oborny 1912). In the Šakvice district, this species was last collected in 1922. There are only two records of *T. bessarabicum* from the Daníž district undocumented by herbarium specimens, near the villages of Dyjákovičky and Slup (Tomaschek 1933); these occurrences probably disappeared soon after World War II. The last populations in the Velké Němčice, Čejč and Rakvice districts disappeared probably in the 1960s. The last herbarium specimen collected in the Měnin-Šaratice district near the village of Otmarov dates back to 1970; this species disappeared from this district in the early 1970s. In the Pulkau district, *T. bessarabicum* was last observed in 1989 at the Hintausacker site near the village of Zwingendorf. Recent records have only been known from the Hevlín-Nový Přerov and Sedlec districts. In the former, this species still may survive at the Novosedly and Dobré Pole sites, whereas a small population at the Nový Přerov site vanished in the 1990s. The occurrences in the Sedlec district, once surrounding the whole Nesyt Fishpond, have been reduced to the Slanisko u Nesytu site, while the occurrence in slightly saline meadows south-east of the town of Lednice was documented by herbarium specimens in 1921–1962.

In addition to the occurrences described above, there is a herbarium specimen of *Taraxacum bessarabicum* collected in 1860 by A. Makowsky in Královo Pole, now a part of the city of Brno; however, this record is dubious as it is not listed in his flora of the Brno county published three years later (Makowsky 1863). Based on the record by A. Ripper (sec. Oborny 1912) from the 1880s, this species also occurred in slightly saline pastures between the town of Břeclav and the village of Tvrdonice.

Triglochin maritima (Red Lists: CZ: RE; AT: VU)

Triglochin maritima is a perennial herb with a wide distribution range in Europe, Asia and the Americas. In Europe, it is most common in the western and northern European coastal areas and on the Baltic coast. It is also scattered along the Mediterranean coast. Further, it occurs around the Black Sea and in the Pontic and Pannonian regions (Hultén & Fries 1986).

Triglochin maritima was one of the rarest halophytes in the study area. It naturally occurred only in two districts. In 1900 it was discovered near the Šakvice railway station. However, this occurrence was destroyed in the early 1920s when the second track was built (cf. Krist 1935). Another population existed in the Daníž district in a saline meadow west of the village of Jaroslavice. It was first observed there in 1926 by Tomaschek (1933) and for the last time collected by F. Šmarda in 1947. The species was considered extinct until 2000 when two individuals were found in a shallow ditch at the Slanisko u Nesytu site in the Sedlec district (Danihelka & Šmarda 2001). The last plant was observed at that site in 2005. The species was likely planted there.

In addition to the occurrences at the sites with halophytic vegetation, *Triglochin maritima* was collected in 1947–1949 east of the village of Ratíškovice between the towns of Bzenec and Hodonín. However, this occurrence probably disappeared shortly after being discovered. Although Bureš (2010) accepted some additional undocumented records from southern Moravia, we consider them erroneous because of numerous identification mistakes we have seen in herbaria. The specimen cited therein from the Starovice site (J. Dvořák 1959 OP) is *T. palustris*.

Tripolium pannonicum (Red Lists: CZ: CR; AT: VU)

Tripolium pannonicum is a short-lived perennial or annual herb. It has a discontinuous distribution range from the British Isles through the temperate zone in eastern Europe, southern Siberia and Central Asia to China and Japan. This species is very variable, and its populations distributed along the European coast are sometimes separated as *T. pannonicum* subsp. *tripolium*. The inland populations, assigned to the type subspecies, are scattered from north-eastern Spain over central Germany, the Carpathian Basin, south-eastern and eastern Europe to the temperate zone of Asia (Meusel & Jäger 1992).

Tripolium pannonicum grows on heavy clayey or loamy saline soils well supplied with nutrients. Being a weak competitor, it requires disturbance by grazing cattle or poultry (Danihelka in Kaplan et al. 2017). In southern Moravia and the Pulkau valley, it occurs or previously occurred in most types of halophytic vegetation, being most frequent in the halophytic grasslands of the associations *Puccinellietum limosae* and *Scorzonero parviflorae-Juncetum gerardii* and the stands of succulent halophytes of the alliance *Thero-Salicornion*.

Tripolium pannonicum was once present in all the districts. During the 1950s, it disappeared from the Šakvice, Damnice-Olbramovice and Daníž districts. From each of the latter two districts, only one herbarium specimen and one field record exist. In the Měnín-Šaratice district, *T. pannonicum* survived until the early 1970s near the village of Otnice, while the last record from the frequently visited Zřídla u Nesvačilký site dates back to the early 1960s (Vicherek 1973). In the Velké Němčice district, *T. pannonicum* was last collected in 1973 at the Starovice site. In the Čejč district, this species survived until the late 1960s at the Zápověď site, while in the Rakvice district, it was last collected in 1980 in the railway ditches near the Rakvice railway station. At present, *T. pannonicum* occurs in a large population at the Slanisko u Nesytu site in the Sedlec district. A few plants were also found on the drained bottom near the southern bay of the Nesyt Fishpond in 2018 and 2020. Populations found at the Dobré Pole site in the Hevlín-Nový Přerov district and at the Hintausacker site near Zwingendorf in the Pulkau district are smaller.

In addition to the occurrences described above, *Tripolium pannonicum* was observed in slightly saline pastures between the town of Břeclav and the village of Tvrdonice. This record (A. Ripper sec. Oborny 1912) dates back to the 1880s.

Bryophytes

Most records of bryophytes from saline sites were provided by J. Podpěra in the series Results of the bryological research in Moravia (Podpěra 1906, 1913, 1923). He described, as new to science, *Chrysohypnum helodes* var. *salinum* (current name *Campyliadelphus elodes*) from the saline habitats along the railway near the Šakvice station

(Podpěra 1906) and recorded it repeatedly there (Podpěra 1913, 1923). This taxon was also found by Fietz et al. (1923) at the Plácky site near Velké Němčice. However, according to Bradáčová et al. (2015), populations of *Campyliadelphus elodes* do not differ between saline and non-saline habitats. Furthermore, these authors found a mixture of *C. elodes* and the halophytic bryophyte *Conardia compacta* in Podpěra's syntype stored in the herbarium PR. In 1912, J. Podpěra discovered *Hennediella heimii*, a moss species characteristic of saline habitats, near the railway between the village of Rakvice and the town of Podivín (Podpěra 1912, 1913). In the 1990s, it was considered as critically endangered (Váňa 1995) and afterwards as missing (Kučera & Váňa 2005) until it was rediscovered in 2017 at the Slanisko u Nesytu site near Sedlec (Kučera et al. 2017). Along with *H. heimii*, Kučera et al. (2017) found other endangered or critically endangered halophytic bryophytes at this site, namely *Conardia compacta*, *Didymodon tophaceus* subsp. *sicculus* and *Pterygoneurum* cf. *kozlovii*.

The specialized halophytic mosses co-occur at halophytic sites with species characterized by broad distribution and broad ecological niches. At the sites with *Hennediella heimii*, Podpěra (1912) also recorded *Trichostomum crispulum*. Other non-specialist species, such as *Leptodictyum riparium*, *Physcomitrium pyriforme*, *Pterygoneurum subsessile*, *P. ovatum*, *Tortula protobryoides* and *T. truncata* were observed at saline sites by Šmarda (1953). Bryological surveys of the Slanisko u Nesytu site in 2004 (Kubešová & Novotný 2004) and 2017 (Kučera et al. 2017) yielded ~30 species, including *Amblystegium serpens*, *Barbula unguiculata*, *Brachythecium rutabulum*, *Drepanocladus aduncus*, *Homalothecium lutescens*, *Hygroamblystegium humile*, *Leptodictyum riparium*, *Physcomitrium pyriforme*, *Syntrichia papillosa* and *Tortula acaulon*.

In August 2020, we collected bryophytes in relevés at the sites with preserved halophytic vegetation in southern Moravia and the Pulkau district. Among altogether 86 bryophyte specimens collected, we identified 29 terricolous species. However, none of them was a specialist of saline habitats. The most frequent species were *Brachythecium rutabulum*, *Drepanocladus aduncus*, *Homalothecium lutescens*, *Hygroamblystegium humile*, *Leptodictyum riparium*, *Oxyrrhynchium hians* and various *Bryum* species, e.g. *B. caespiticium*. All the identified bryophytes are classified as least concern in the Czech Republic except for *Drepanocladus polygamus*, which is considered vulnerable (Kučera et al. 2012). Although this species regularly occurs in some saline habitat types, these habitats are endangered in general, and individual populations are small. A complete list of bryophytes may be extracted from the table of our relevés (Danihelka et al. 2021).

Vegetation

Vegetation classification: overall patterns

The modified expert system CzechVeg-ESy classified the dataset of 729 relevés to the associations. Of these, 426 relevés were classified to 14 associations dominated by halophytes or defined through their occurrence (hereafter called “halophytic associations”; Supplementary Data S3). Other relevés were classified to non-halophytic associations, remained unclassified or were transitional (i.e. classified to more than one association).

A comparison of the *Festuco-Puccinellietea* associations classified by the expert system with Twinspan classification is shown in an alluvial diagram (Fig. 9). Some sister clusters in the Twinspan dendrogram were merged to match the classification by the

expert system as much as possible. Still, the match of both classifications was not perfect. The associations TCA01 *Puccinellietum limosae* and *Centaureo pannonicae-Festucetum pseudovinae* were almost entirely contained within one Twinspan cluster each. However, each of these two clusters also contained a significant proportion of the relevés of another association. The associations of the alliance *Juncion gerardii* corresponded to 2–4 clusters each.

In the DCA ordination, the first axis corresponded to soil moisture increasing from left to right (Fig. 10). The second axis corresponded to increasing salinity and the proportion of halophytes from the bottom to the top. The *Puccinellietum limosae* (TCA01) and *Centaureo pannonicae-Festucetum pseudovinae* (TCC01) relevés were located mainly at the edges of the triangular cloud of points in the ordination diagram, which corresponded to the classification of these two associations to separate alliances. However, the three associations of the *Juncion gerardii* were overlapping, with *Loto tenuis-Potentilletum anserinae* (TCB02) encompassing the largest variation in species composition, spanning from the mesophytic types on the bottom left to the wet types from drained fishpond bottoms on the right.

These two comparisons indicate a mismatch between the traditional classification of the *Juncion gerardii* to the associations (here formalized in the expert system) and the pattern of total species composition (here represented by the Twinspan classification and DCA ordination). While the traditional classification defines associations based on the occurrence of a few halophytes that reflect specific habitat conditions within the complexes of halophytic vegetation, the variation in total species composition reflects mainly the gradients of moisture availability and salinity, i.e. the factors that indicate the decrease in the habitat quality over the past decades.

Vegetation types

The 14 associations dominated or defined through the occurrence of halophytes were classified according to the national vegetation classification system of the Czech Republic (Chytrý 2007, 2011) as follows:

- MB *Bidentetea* Tüxen et al. ex von Rochow 1951
 - MBB *Chenopodion rubri* (Tüxen 1960) Hilbig et Jage 1972
 - MBB01 *Chenopodietum rubri* Tímár 1950
 - MBB02 *Bidentii frondosae-Atriplicetum prostratae* Poli et J. Tüxen 1960
corr. Gutermann et Mucina 1993
 - MBB04 *Chenopodio chenopodioidis-Atriplicetum prostratae* Slavnič 1948
corr. Gutermann et Mucina in Mucina et al. 1993
- MC *Phragmito-Magno-Caricetea* Klika in Klika et Novák 1941
 - MCB *Meliloto dentati-Bolboschoenion maritimi* Hroudová et al. 2009
 - MCB01 *Astero pannonici-Bolboschoenetum compacti* Hejný et Vicherek
ex Ofaheřová et Valachovič in Valachovič 2001
 - MCB02 *Schoenoplectetum tabernaemontani* De Soó 1947
- TA *Crypsietea aculeatae* Vicherek 1973
 - TAA *Cypero-Spergularion salinae* Slavnič 1948
 - TAA01 *Crypsietum aculeatae* Wenzl 1934

- TAA02 *Heleochloëtum schoenoidis* Topa 1939
- TB *Thero-Salicornietea strictae* Tüxen in Tüxen et Oberdorfer 1958
- TBA *Salicornion prostratae* Géhu 1992
- TBA01 *Salicornietum strictae* Soó 1964
- TBA02 *Spergulario marinae-Suadetum prostratae* Vicherek in Moravec et al. 1995
- TC *Festuco-Puccinellietea* Soó ex Vicherek 1974
- TCA *Puccinellion limosae* Soó 1933
- TCA01 *Puccinellietum limosae* Soó 1933
- TCB *Juncion gerardii* Wendelberger 1943
- TCB01 *Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943
- TCB02 *Loto tenuis-Potentilletum anserinae* Vicherek 1973
- TCB03 *Agrostio stoloniferae-Juncetum ranarii* Vicherek 1962
- TCC *Festucion pseudovinae* Soó 1933
- TCC01 *Centaureo pannonicae-Festucetum pseudovinae* Klika et Vlach 1937

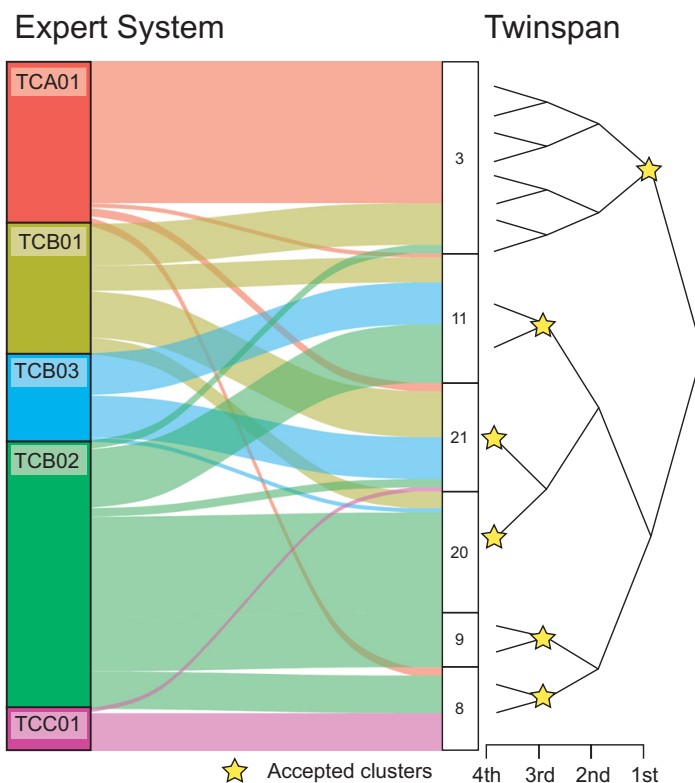


Fig. 9. A comparison of the associations of the *Festuco-Puccinellietea* class classified by the expert system with clusters based on the Twinspan classification. TCA01 = *Puccinellietum limosae*, TCB01 = *Scorzonero parviflorae-Juncetum gerardii*, TCB02 = *Loto tenuis-Potentilletum anserinae*, TCB03 = *Agrostio stoloniferae-Juncetum ranarii*, TCC01 = *Centaureo pannonicae-Festucetum pseudovinae*.

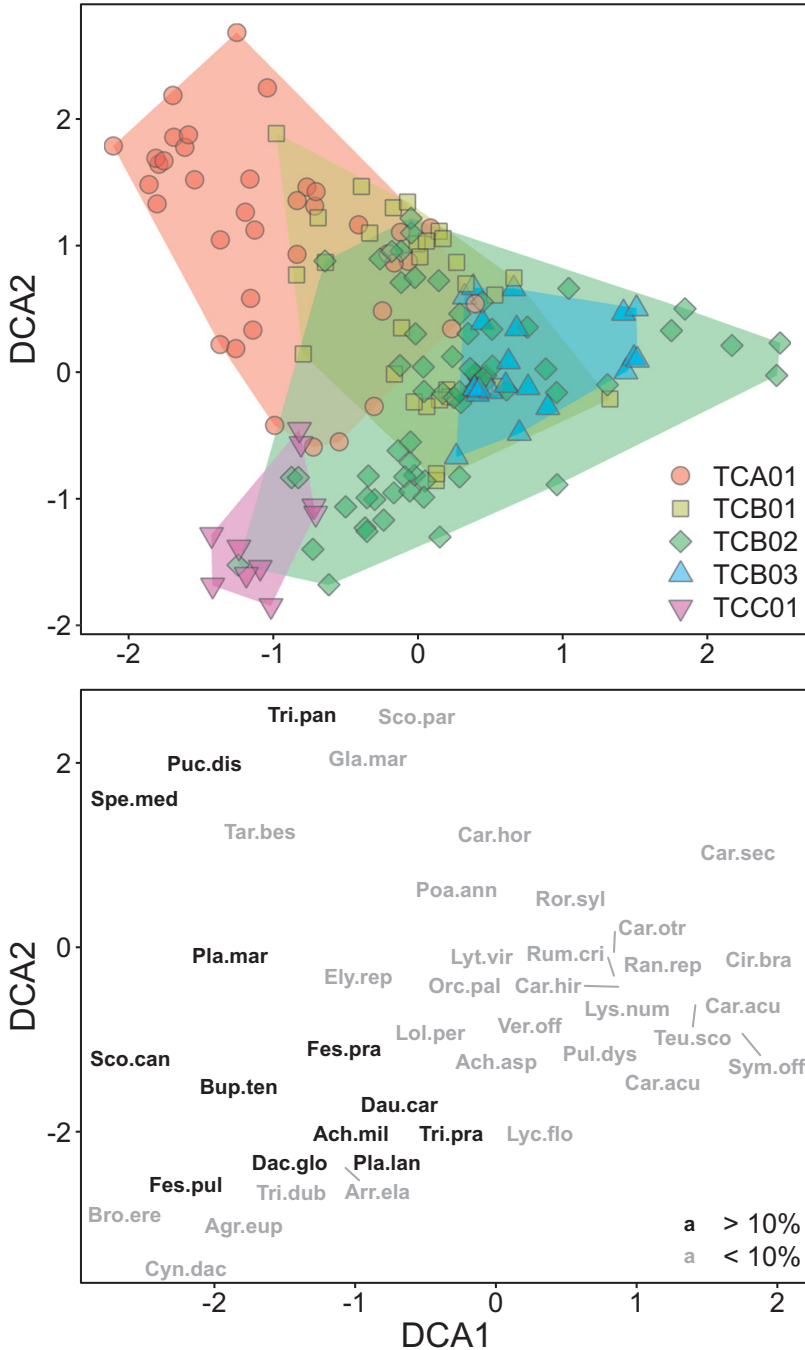


Fig. 10. Ordination (detrended correspondence analysis, DCA) of the relevés assigned to the *Festuco-Puccinellietea* associations by the expert system. Different colours and symbols indicate the associations (see Fig. 9 for the code legend). The lower plot shows only diagnostic species of the associations (see Table 1): black and grey letters indicate species with a fit to the first two axes higher and lower than 10%, respectively.

Table 1. Synoptic table of 14 halophytic associations based on the relevés classified by the expert system. The numbers are the percentage occurrence frequencies (constancies). In the associations defined by the dominance of a single species, the dominant species are indicated by dark shading. Light shading indicates diagnostic species of individual associations sorted by decreasing values of the phi coefficient of association. Frequencies of bryophytes were calculated only from our relevés sampled in 2020. Therefore, the associations not sampled in that year do not contain any bryophyte records. A full version of this table is available as Supplementary Table S1.

Association number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of relevés	10	5	1	17	13	9	10	9	6	38	29	62	28	10
Number of relevés with bryophytes	.	1	.	7	7	.	19	4	5
Diagnostic species														
1 – MBB01 <i>Chenopodietum rubri</i>														
<i>Chenopodium glaucum</i>	100	.	.	6	.	22	40	.	17	11	.	2	11	.
<i>Gnaphalium uliginosum</i>	30	4	2	.	.
2 – MBB02 <i>Bidenti-Atriplicetum prostratae</i>														
<i>Atriplex prostrata</i> subsp. <i>latifolia</i>	10	100	100	53	.	33	80	11	17	45	25	13	21	10
3 – MBB04 <i>Chenopodio chenopodioidis-Atriplicetum prostratae</i>														
<i>Chenopodium chenopodioides</i>	.	.	100	.	.	.	30
4 – MCB01 <i>Astero pannonic-Bolboschoenetum compacti</i>														
<i>Bolboschoenus maritimus</i> agg.	10	60	100	100	92	11	70	.	.	13	32	18	68	.
<i>Mentha aquatica</i>	.	.	.	24	3	4	.
5 – MCB02 <i>Schoenoplectetum tabernaemontani</i>														
<i>Schoenoplectus tabernaemontani</i>	10	.	.	47	100	.	10	.	.	.	7	5	14	.
<i>Persicaria amphibia</i>	.	.	.	18	69	.	10	3	.	.
<i>Eleocharis palustris</i> agg.	.	.	.	6	77	29	2	14	.
<i>Hippuris vulgaris</i>	31
<i>Equisetum fluviatile</i>	23
<i>Carex disticha</i>	15
<i>Lythrum salicaria</i>	.	.	.	24	38	.	10	.	.	3	4	8	14	.
6 – TAA01 <i>Crypsietum aculeatae</i>														
<i>Crypsis aculeata</i>	40	.	.	6	.	100	20	.	.	3	4	.	.	.
7 – TAA02 <i>Heleochloetum schoenoidis</i>														
<i>Crypsis schoenoides</i>	33	100	.	.	5	4	3	.	.
<i>Chenopodium album</i> agg.	.	20	40	3	.	.
<i>Solanum tuberosum</i>	20
<i>Matricaria chamomilla</i>	20	.	.	3
<i>Chenopodium rubrum</i>	20	.	.	3	.	3	.	.
<i>Anagallis arvensis</i>	10	20	3	.	.
8 – TBA01 <i>Salicornietum prostratae</i>														
<i>Salicornia perennans</i>	11	.	100	67	5
9 – TBA02 <i>Spergulario marginatae-Suaedetum prostratae</i>														
<i>Suaeda prostrata</i>	33	100	8
10 – TCA01 <i>Puccinellietum limosae</i>														
<i>Taraxacum bessarabicum</i>	10	11	17	58	11	13	.	10
<i>Glaux maritima</i>	21	4	10	.	.
11 – TCB01 <i>Scorzonero parviflorae-Juncetum gerardii</i>														
<i>Scorzonera parviflora</i>	23	.	.	33	.	5	68	3	.	10
<i>Orchis palustris</i>	15	25	.	.	.
<i>Carex acuta</i>	11	2	.	.

Association number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Achillea asplenifolia</i>	3	21	6	4	.
<i>Teucrium scordium</i>	.	.	.	6	14	5	.	.
<i>Lychnis flos-cuculi</i>	7	.	.	.
12 – TCB02 <i>Loto tenuis</i>-<i>Potentilletum anserinae</i>														
<i>Poa annua</i>	3	11	19	.	.
<i>Cerastium holosteoides</i>	5	.	19	4	10
<i>Verbena officinalis</i>	8	.	.
<i>Pulicaria dysenterica</i>	10	.	.	8	14	24	7	.
<i>Arenaria serpyllifolia</i>	3	.	10	.	.
13 – TCB03 <i>Agrostio stoloniferae</i>-<i>Juncetum ranarii</i>														
<i>Carex otrubae</i>	10	20	.	18	46	32	24	89	20
<i>Ranunculus repens</i>	.	.	.	12	31	3	32	39	68	.
<i>Carex hirta</i>	18	16	36	.
<i>Cirsium brachycephalum</i>	.	.	.	12	15	11	.	36	.
<i>Rumex crispus</i>	.	.	.	24	15	.	10	.	.	.	11	24	50	10
<i>Carex secalina</i>	.	20	.	12	5	.	2	32	.
<i>Lythrum virgatum</i>	3	7	.	18	.
<i>Rorippa sylvestris</i>	7	13	21	.
<i>Carex hordeistichos</i>	17	.	4	.	25	10
<i>Symphytum officinale</i> agg.	.	.	.	6	3	14	.
<i>Lysimachia nummularia</i>	2	11	.
14 – TCC01 <i>Centaureo pannonicae</i>-<i>Festucetum pseudovinae</i>														
<i>Festuca pulchra</i>	11	.	5	.	100
<i>Achillea millefolium</i> agg.	.	.	.	6	11	4	34	14	90
<i>Cynodon dactylon</i>	30
<i>Scorzonera cana</i>	11	4	.	.	40
<i>Plantago lanceolata</i>	7	26	4	50
<i>Daucus carota</i>	.	20	16	4	23	.	60
<i>Dactylis glomerata</i>	18	4	40
<i>Centaurea jacea</i>	10	8	29	24	4	60
<i>Bupleurum tenuissimum</i>	11	7	6	.	40
<i>Plantago maritima</i>	.	.	.	6	38	.	10	44	33	47	29	11	.	90
<i>Arrhenatherum elatius</i>	6	4	30
<i>Bromus erectus</i>	20
<i>Agrimonia eupatoria</i>	2	.	20
<i>Festuca pratensis</i> agg.	24	36	34	25	60
<i>Trifolium dubium</i>	7	2	4	20
<i>Trifolium pratense</i>	14	13	11	30
Species diagnostic for more than one association														
<i>Elymus repens</i>	10	80	.	29	8	11	10	11	.	24	25	31	36	80
<i>Tripolium pannonicum</i>	.	40	.	24	15	33	20	100	50	84	46	10	25	10
<i>Spergularia media</i>	.	.	.	6	.	22	30	89	83	71	4	.	.	10
<i>Puccinellia distans</i>	20	.	.	24	.	22	40	89	100	87	32	16	36	.
<i>Lolium perenne</i>	11	11	39	.	40
<i>Poa pratensis</i> agg.	11	7	37	7	50
Other species with > 5% frequency across the whole table														
<i>Lotus tenuis</i>	10	20	100	29	8	.	20	11	.	68	96	100	68	90
<i>Juncus compressus</i> agg.	10	60	.	53	77	.	30	56	50	47	100	45	79	40
<i>Agrostis stolonifera</i> agg.	10	40	.	65	77	33	30	.	.	39	79	56	96	30
<i>Potentilla anserina</i>	20	20	.	59	46	.	20	.	.	47	93	68	82	10
<i>Trifolium fragiferum</i>	16	50	69	64	40

Association number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Phragmites australis</i>	10	20	.	59	54	11	50	.	.	34	61	24	39	20
<i>Melilotus dentatus</i>	.	20	100	29	8	.	10	.	.	29	46	47	61	30
<i>Odonites vernus</i> subsp. <i>serotinus</i>	.	.	.	6	21	36	58	39	40
<i>Taraxacum</i> sect. <i>Taraxacum</i>	10	.	.	13	32	50	57	40
<i>Plantago uliginosa</i>	10	20	.	24	15	.	50	.	.	3	36	32	64	.
<i>Inula britannica</i>	10	20	.	29	15	.	20	.	.	18	25	35	25	30
<i>Carex distans</i>	.	.	.	6	8	43	29	36	50
<i>Polygonum aviculare</i> agg.	.	20	.	18	.	22	40	.	.	32	7	26	14	.
<i>Senecio erraticus</i>	.	.	.	12	.	.	10	.	.	13	32	27	25	30
<i>Spergularia marina</i>	70	20	.	.	.	56	40	11	67	13	7	13	4	.
<i>Mentha pulegium</i>	43	24	36	.
<i>Centaureum pulchellum</i>	40	.	.	18	11	14	21	32	10
<i>Potentilla reptans</i>	8	3	32	29	21	10
<i>Tripleurospermum inodorum</i>	.	40	100	29	23	.	30	.	.	6	18	21	8	.
<i>Cirsium canum</i>	10	.	.	12	3	25	21	25	.
<i>Lotus maritimus</i>	11	29	13	21	30
<i>Plantago major</i>	10	40	100	18	5	7	23	14	.
<i>Medicago lupulina</i>	.	.	100	3	.	32	4	40
<i>Juncus bufonius</i> agg.	60	.	100	6	.	.	10	.	.	3	.	11	36	.
<i>Scorzoneroides autumnalis</i>	3	11	26	18	10
<i>Poa trivialis</i>	38	21	11	29	.
<i>Cirsium arvense</i>	.	.	100	6	8	.	20	.	.	8	4	10	25	20
<i>Pulicaria vulgaris</i>	3	18	23	11	.
<i>Pastinaca sativa</i>	.	20	5	4	23	7	10
<i>Bidens tripartitus</i>	20	.	.	6	11	21	.	.
<i>Trifolium hybridum</i>	.	.	100	12	14	8	21	.
<i>Rumex maritimus</i>	10	.	100	6	.	.	20	.	.	.	7	16	4	.
<i>Sonchus arvensis</i>	.	20	.	6	.	.	20	.	.	11	4	8	11	.
<i>Trifolium repens</i>	3	7	19	.	20
<i>Potentilla supina</i>	.	.	100	12	.	.	50	.	.	.	4	6	7	.
<i>Calamagrostis epigejos</i>	3	.	13	18	.
<i>Sonchus asper</i>	.	.	.	12	.	.	10	.	.	5	18	2	14	.
<i>Echinochloa crus-galli</i>	.	20	100	6	.	.	50	.	.	.	4	6	4	.
<i>Athaea officinalis</i>	10	.	.	6	.	11	.	.	.	3	11	10	4	.

Bryophytes: diagnostic species**4 – MCB01 *Astero pannonicum-Bolboschoenetum compacti***

<i>Physcomitrium pyriforme</i>	–	.	–	29	–	–	–	–	–	.	–	.	.	.
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14 – TCC01 *Centaureo pannonicae-Festucetum pseudovinae*

<i>Brachythecium albicans</i>	–	.	–	.	–	–	–	–	–	.	–	.	.	40
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Bryophytes: other species with > 5% frequency across the whole table

<i>Drepanocladus aduncus</i>	–	.	–	14	–	–	–	–	–	14	–	11	.	40
<i>Drepanocladus polygamus</i>	–	.	–	14	–	–	–	–	–	.	–	21	.	20
<i>Brachythecium rutabulum</i>	–	.	–	.	–	–	–	–	–	.	–	21	25	.
<i>Hygroamblystegium humile</i>	–	.	–	.	–	–	–	–	–	14	–	11	.	20
<i>Bryum caespiticium</i>	–	.	–	14	–	–	–	–	–	.	–	5	25	.
<i>Leptodictyum riparium</i>	–	.	–	.	–	–	–	–	–	.	–	16	.	.
<i>Brachythecium salebrosum</i>	–	.	–	.	–	–	–	–	–	.	–	5	25	20

A synoptic table summarizing the species composition of these 14 halophytic associations was prepared based on the stratified subset of relevés assigned to these associations by the expert system (Table 1). The time axes showing the occurrence of each association and the total number of associations in halophytic districts of the study area are shown in Figs. 11 and 12. We provide the descriptions of individual associations in the following text. The highly diagnostic, highly constant or highly dominant species (see Methods) are shown in bold.

MBB01 *Chenopodietum rubri* (Fig. 13A)

Diagnostic species: ***Chenopodium glaucum***, *Gnaphalium uliginosum*, *Juncus bufonius* agg., *Spergularia marina*

Constant species: ***Chenopodium glaucum***, *Juncus bufonius* agg., *Spergularia marina*

Dominant species: ***Chenopodium glaucum***

The species-poor annual vegetation dominated by *Chenopodium glaucum* was described by Vicherek (1973) from several halophytic sites in southern Moravia. It occurred on fishpond shores or in shallow depressions in the complexes of saline grasslands. The soils were bare, strongly saline and nutrient-rich, wet in spring but drying out in summer. Vicherek (1973) classified this vegetation to the subassociation *Crypsietum aculeatae chenopodietosum glauci*, despite the rare occurrence of *Crypsis aculeata* in these stands. He considered this vegetation transitional between the association *Crypsietum aculeatae* and ephemeral wetland vegetation of the class *Isoëto-Nano-Juncetea*. Following the concept accepted in the Vegetation of the Czech Republic (Šumberová & Lososová 2011), this vegetation belongs to the association *Chenopodietum rubri*, which comprises stands of both *Chenopodium glaucum* and *C. rubrum*, occurring in both saline and non-saline, mainly anthropogenic habitats. Vicherek (1973) documented this vegetation by relevés sampled in the early 1960s in the Velké Němčice, Rakvice, Sedlec and Hevlín-Nový Přerov districts. There are no newer records from the study area except for a relevé dominated by *Chenopodium glaucum* recorded during the Natura 2000 mapping in 2001 on a bottom of an artificial pool in the Císařská obora site in the Měnin-Šaratice district. However, this relevé is much richer in species than the relevés recorded by Vicherek (1973). Although this vegetation seems to be absent from halophytic sites in the study area today, it can temporarily develop on exposed bottoms of fishponds (e.g. Nesyt) and pools.

MBB02 *Bidentifrondosae-Atriplicetum prostratae* (Fig. 13B)

Diagnostic species: *Atriplex prostrata* subsp. *latifolia*, *Atriplex sagittata*, *Elymus repens*, *Euphorbia platyphyllos*
Constant species: ***Atriplex prostrata* subsp. *latifolia***, *Bolboschoenus maritimus* agg., *Elymus repens*, *Juncus compressus* agg.

Dominant species: ***Atriplex prostrata* subsp. *latifolia***, *Bolboschoenus maritimus* agg., *Juncus compressus* agg., *Phragmites australis*, *Spergularia marina*, *Tripolium pannonicum*

This species-poor community is dominated by *Atriplex prostrata* subsp. *latifolia*, a therophyte with an affinity for saline soils, though often occurring also in non-saline anthropogenic habitats. It develops in places with the fluctuating water level, especially at the bottoms of summer-drained fishponds and pools. The decay of phytoplankton and aquatic macrophytes increases nutrient availability, which supports the high productivity of this vegetation and the occurrence of some species of marshes (e.g. *Bolboschoenus*

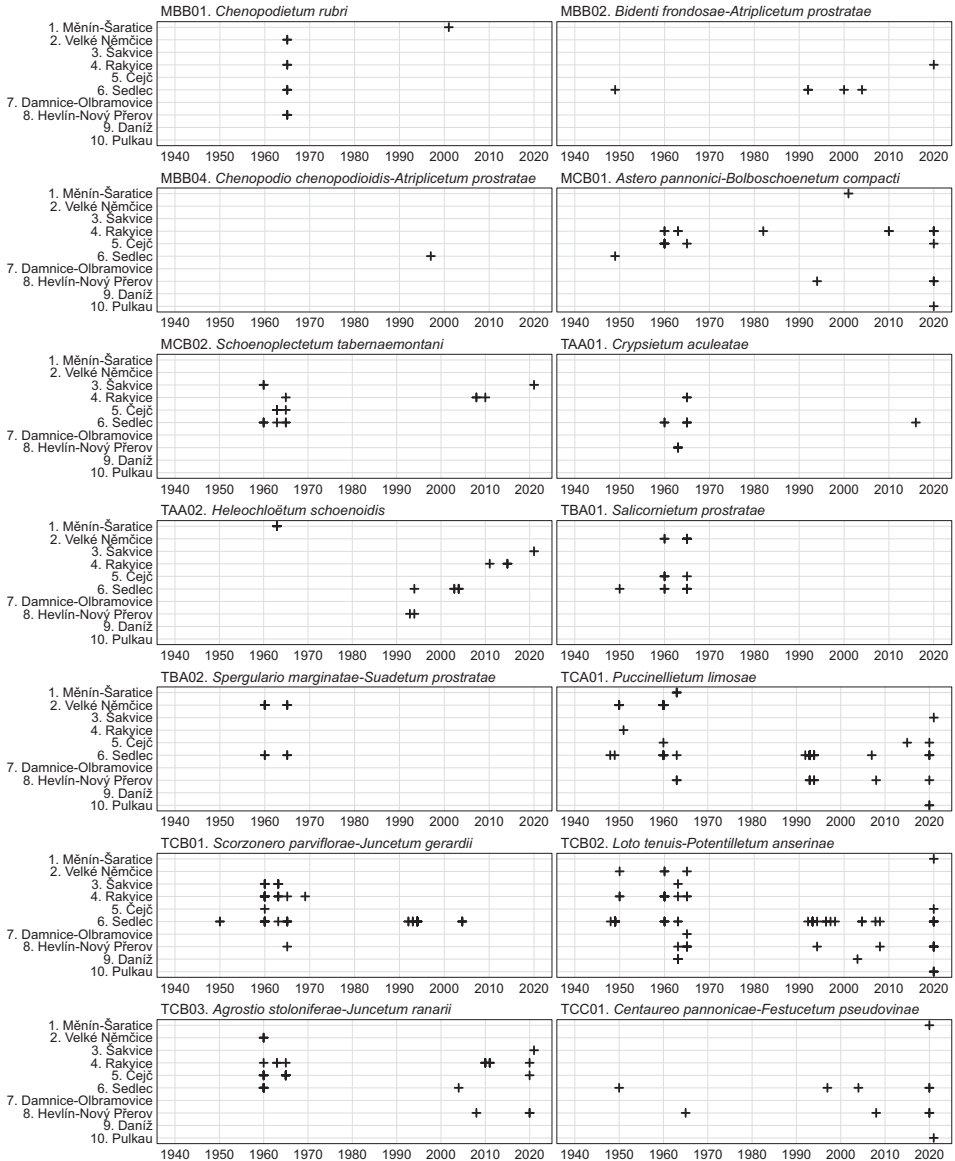


Fig. 11. Records of halophytic associations in individual halophytic districts of southern Moravia and northern Lower Austria. Each cross indicates a relevé classified to the association by the expert system. The gap between 1965 and 1990 is due to the absence of research.

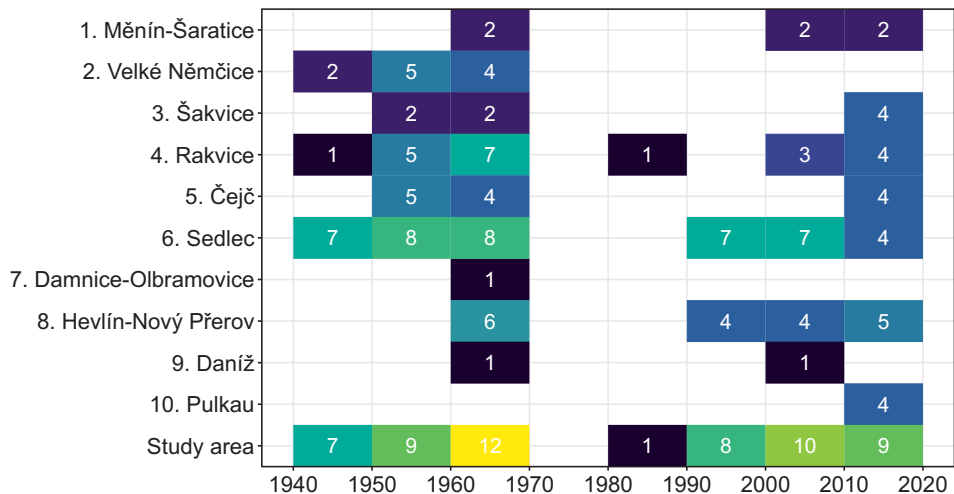


Fig. 12. Numbers of halophytic associations recorded per two-decade periods in individual halophytic districts of southern Moravia and northern Lower Austria and across all the districts (Study area). This figure summarizes the records for individual associations shown in Fig. 14. The gap in the 1970s and 1980s indicated the absence of research between 1965 and 1990. The period 2001–2020 also includes records from the Šakvice and Pulkau districts from 2021.

maritimus agg. and *Phragmites australis*) and ruderal species (e.g. *Atriplex sagittata* and *Elymus repens*). There are also competitively weak halophytes typical of the early successional stages, especially *Spergularia marina*. Different authors repeatedly sampled this vegetation on the shores or exposed bottom of the Nesyt Fishpond in the Sedlec district. In 2020, we also recorded it at the Trkmanec-Rybníčky site in the Rakvice district.

MBB04 *Chenopodio chenopodioidis*-*Atriplicetum prostratae* (Fig. 13C)

This association comprises natural vegetation of saline, periodically flooded soils dominated or co-dominated by the halophyte *Chenopodium chenopodioides*, accompanied by different species of ephemeral wetlands and some halophytes. The soils are rich in nitrogen and show various degrees of salinity (Šumberová & Lososová 2011). In the modified expert system, we re-defined this association through dominance or co-dominance of *Chenopodium chenopodioides* to make it consistent with the definitions of other associations. The modified definition is more restrictive than the definition in the Vegetation of the Czech Republic (Šumberová & Lososová 2011), which required >5% cover but not the dominance of this species. As a result, only one relevé recorded by K. Šumberová on the bottom of Hlohovecký Fishpond in the Sedlec district in 1997 was classified to this association. Nevertheless, *Chenopodium chenopodioides* is repeatedly found on bare wet soil at other halophytic sites of southern Moravia. Vegetation with significant participation of this species was documented by relevés, for example, at Zápověď site in the Čejč district (by K. Šumberová in 2007) and the Trkmanec-Rybníčky site in the Rakvice district (here partly in the annual vegetation of the association *Heleochoëtum schoenoidis*, by P. Lustyk in 2000 and 2011, and P. Dřevojan in 2015). However, the species has also been

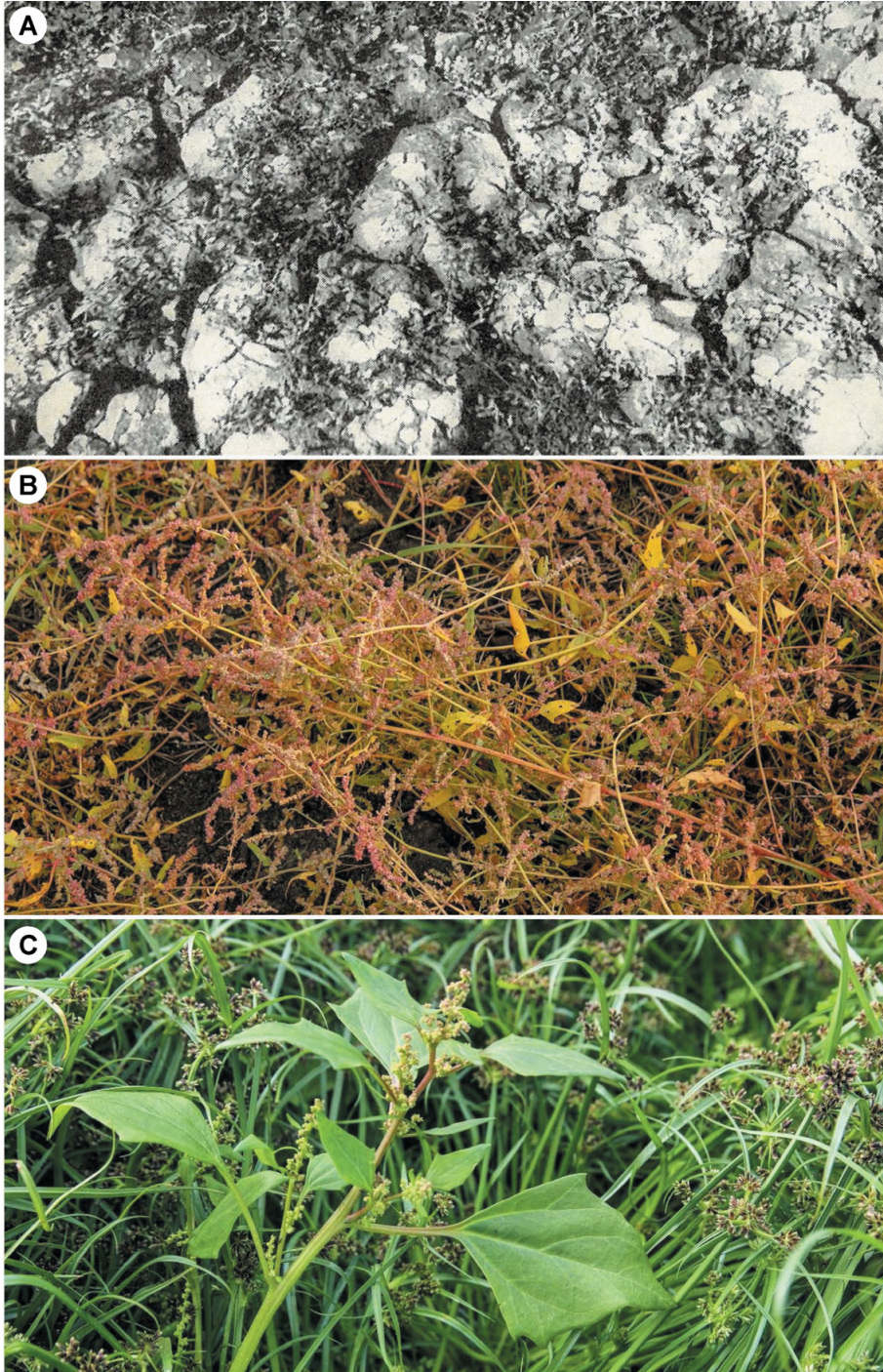


Fig. 13. Associations of halophytic vegetation in southern Moravia and northern Lower Austria: (A) MBB01 *Chenopodietum rubri*, Sedlec, early 1960s; (B) MBB02 *Bidenti-Atriplicetum prostratae*, Slanisko u Nesytu 2016; (C) MBB04 Fragmentary stand of *Chenopodio chenopodioidis-Atriplicetum prostratae*, Zápověď 2020. Photo credits: J. Vicherek (A), M. Chytrý (B), K. Chytrý (C).

repeatedly recorded at various southern Moravian sites that lack well-developed halophytic vegetation, especially in fishponds and other wet habitats (Dřevojan & Šumberová in Kaplan et al. 2018). Therefore, vegetation corresponding to this association may also be found at other sites not reported here.

MCB01 *Astero pannonici-Bolboschoenetum compacti* (Fig. 14A)

Diagnostic species: *Bolboschoenus maritimus* agg., *Lycopus europaeus*, *Mentha aquatica*, *Schoenoplectus tabernaemontani*; *Physoctenium pyriforme*

Constant species: *Agrostis stolonifera* agg., *Atriplex prostrata* subsp. *latifolia*, ***Bolboschoenus maritimus* agg.**, *Juncus compressus* agg., *Phragmites australis*, *Potentilla anserina*, *Schoenoplectus tabernaemontani*

Dominant species: ***Bolboschoenus maritimus* agg.**

This relatively species-poor halophytic marsh vegetation occurs in the littoral zones of water bodies, near mineral springs and in wet depressions in the complexes of halophytic vegetation (Hroudová et al. 2009). The dominant species are *Bolboschoenus maritimus* and *B. planiculmis*, which can occur either separately or in mixed stands. These species are accompanied by other halophytes, including *Juncus gerardii*, *Lotus tenuis*, *Melilotus dentatus*, *Puccinellia distans* and *Tripolium pannonicum*. This association is one of the most common types of (sub)halophytic vegetation in the study area, repeatedly documented by relevés from several halophytic districts (e.g. by Vicherek 1973 under the name *Bolboschoenetum maritimi continentale*). We also recorded relevés belonging to this association in four districts in 2020. Similar stands develop on temporarily flooded arable land. They are usually dominated by *Bolboschoenus planiculmis*, contain some arable weed species, and are classified as the association *Tripleurospermo inodori-Bolboschoenetum planiculmis* Hroudová et al. 2009. Halophytes can also occur in this association, as documented from wet arable land near Šakvice by Chytrý & Danihelka (2021).

MCB02 *Schoenoplectetum tabernaemontani* (Fig. 14B)

Diagnostic species: *Bolboschoenus maritimus* agg., *Carex disticha*, *Carex riparia*, ***Eleocharis palustris* agg.**, *Equisetum fluviatile*, ***Hippuris vulgaris***, *Lythrum salicaria*, ***Pericaria amphibia***, *Poa trivialis*, ***Schoenoplectus tabernaemontani***

Constant species: *Agrostis stolonifera* agg., ***Bolboschoenus maritimus* agg.**, *Carex otrubae*, *Eleocharis palustris* agg., *Juncus compressus* agg., *Pericaria amphibia*, *Phragmites australis*, *Potentilla anserina*, ***Schoenoplectus tabernaemontani***

Dominant species: ***Schoenoplectus tabernaemontani***

This vegetation develops on saline or calcium-rich clayey soils at periodically waterlogged sites with changing dry and wet periods (Vicherek 1962, Šumberová et al. 2011). The dominant species *Schoenoplectus tabernaemontani* forms dense stands, which may contain ruderal, subhalophytic and halophytic species such as *Carex otrubae*, *Juncus gerardii*, *Plantago maritima* and *Potentilla anserina*. Vicherek (1973) documented *Schoenoplectetum tabernaemontani* near the villages of Popice (Šakvice district), Kobylí (Čejč district), Lednice and at the Nesyt Fishpond (both Sedlec district). In 2020, we observed (but not sampled) this vegetation at the Trkmanec-Rybníčky site (Rakvice district), Nesyt Fishpond and Novosedly site (Hevlín-Nový Přerov district). It also occurs at the shore of a new fishpond at restored sites near Šakvice (Šakvice district; Chytrý & Danihelka 2021).

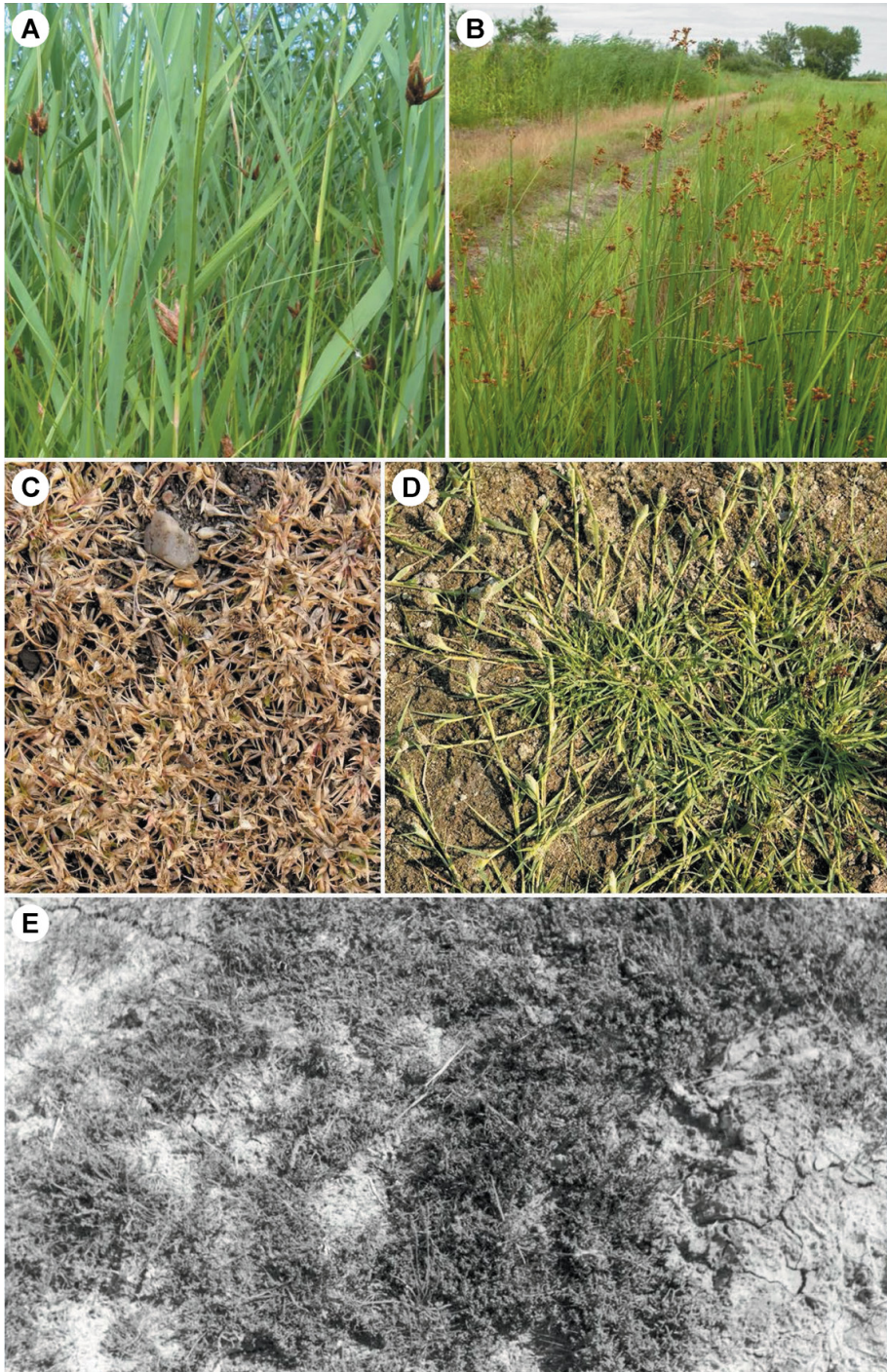


Fig. 14. Associations of halophytic vegetation in southern Moravia and northern Lower Austria: (A) MCB01 *Astero pannonici-Bolboschoenetum compacti*, Zápověď 2020; (B) MCB02 *Schoenoplectetum tabernaemontani*, Rakvice 2020; (C) TAA01 *Crypsietum aculeatae*, Slanisko u Nesytu 2016; (D) TAA02 *Heleocholetum schoenoidis*, eastern shore of the Nesyt Fishpond 2020; (E) TBA01 *Salicornietum prostratae*, Terežín 1961. Photo credits: M. Chytrý (A, C), K. Šumberová (B), K. Chytrý (D), J. Vicherek (E).

TAA01 *Crypsietum aculeatae* (Fig. 14C)

Diagnostic species: *Crypsis aculeata*

Constant species: *Crypsis aculeata*, *Spergularia marina*

Dominant species: *Crypsis aculeata*, *Spergularia media*

This species-poor vegetation is characterized by a high cover or dominance of *Crypsis aculeata*, often accompanied by *Spergularia marina* or *S. media*. It occurs on exposed fishpond shores and in periodically inundated depressions that dry out in summer. The extent of individual stands rarely exceeds 1 m². In the study area, *Crypsietum aculeatae* was only recorded near Rakvice, at the Nesyt Fishpond (Sedlec district) and near Novosedly (Hevlín-Nový Přerov district; Vicherek 1973). The populations were reduced dramatically in the 1990s (Danihelka & Hanušová 1995), and later on, this association was considered to have disappeared from the Czech Republic (Šumberová 2007a). In 2008, a population of *C. aculeata* was found on the wet bottom of a pool dug at the Zápověď site in the Čejč district as a part of an ecological restoration project (Hadinec & Lustyk 2009). However, it was not documented by a relevé. In 2016, this vegetation developed near the western shore of the Nesyt Fishpond. However, the population of *C. aculeata* has rapidly declined at this site since then, and we found only one individual in 2020. This fluctuation in population size is natural, and the association can re-appear in the future once bare wet soil is exposed.

TAA02 *Heleochloëtum schoenoidis* (Fig. 14D)

Diagnostic species: *Anagallis arvensis*, *Chenopodium album* agg., *Chenopodium rubrum*, *Crypsis schoenoides*, *Echinochloa crus-galli*, *Matricaria chamomilla*, *Potentilla supina*, *Solanum tuberosum*

Constant species: *Atriplex prostrata* subsp. *latifolia*, *Bolboschoenus maritimus* agg., *Crypsis schoenoides*, *Echinochloa crus-galli*, *Phragmites australis*, *Plantago uliginosa*, *Potentilla supina*

Dominant species: *Crypsis schoenoides*, *Spergularia marina*

These low-growing, open annual grasslands are dominated by *Crypsis schoenoides*. Other species, usually occurring in low abundances, include halophytes such as *Spergularia marina*, species of drained fishpond bottoms such as *Chenopodium rubrum* and *Potentilla supina*, and ruderal plants such as *Echinochloa crus-galli* or *Chenopodium album*. The association occurs on bottoms of drained fishponds or pools and in seasonally wet depressions, sometimes on arable land. The soils are wet in spring but dry out in summer when cracks appear on the surface (Šumberová 2007a). *Crypsis schoenoides* survives in a seed bank and can appear on the bare ground after several years since the last occurrence. Although Vicherek (1973) recorded this vegetation only at one site near the village of Moutnice, it used to be probably more common in the study area, as inferred from floristic records of *C. schoenoides*. In 1993–1994, this vegetation was documented by relevés at the Nesyt Fishpond (Sedlec district) and near the village of Novosedly (Hevlín-Nový Přerov district; Danihelka & Hanušová 1995). In 2004, M. Chytrý and J. Danihelka sampled large stands of *Heleochloëtum schoenoidis* near the Výtopa Fishpond close to the eastern shore of the Nesyt Fishpond. At this site, it occurred in a spring-flooded field depression in which mud removed from the Nesyt bottom was deposited. This observation indicates that the species can survive long periods in a seed bank on pond bottoms. The association was also observed at the Trkmanec-Rybníčky site near Rakvice and documented by relevés in 2011 by P. Lustyk and in 2015 by P. Dřevojan

(Lustyk in Hadinec & Lustyk 2013, Dřevojan et al. 2017). We observed this vegetation on the exposed bottom of the eastern shore of the Nesyt Fishpond in 2020. We also sampled this association on abandoned wet arable land along the Štinkovka stream east of Šakvice in 2021 (Chytrý & Danihelka 2021), which is the first record of its occurrence in the Šakvice district. It is likely that in the future, *Heleochoëtum schoenoidis* will also reappear at other sites by regeneration of the dominant species from the seed bank following mud dredging and depositing or the emergence of wet bare soil.

TBA01 *Salicornietum strictae* (Fig. 14E)

Diagnostic species: *Puccinellia distans*, *Salicornia perennans*, *Spergularia media*, *Tripolium pannonicum*
 Constant species: *Juncus compressus* agg., *Plantago maritima*, *Puccinellia distans*, *Salicornia perennans*,
Spergularia media, *Tripolium pannonicum*
 Dominant species: *Salicornia perennans*

This species-poor vegetation once occurred in highly saline and moist spots dominated by *Salicornia perennans*, an annual succulent plant forming sparse and low-growing stands. In places, this species was accompanied by other halophytes such as *Plantago maritima*, *Puccinellia distans*, *Spergularia media*, *Suaeda prostrata* and *Tripolium pannonicum*. *Salicornietum strictae* used to occur in depressions at halophytic sites, where salt precipitated on the soil surface and, at the same time, the surface was relatively wet (Vicherek 1973). This vegetation also occurred on dirt roads crossing the complexes of halophytic vegetation, where it was supported by disturbance. For example, V. Grulich (pers. comm.) observed it in the tracks of horse-drawn carriages still in the early 1970s. In the 19th century, this vegetation may have been common along the shores of the former Měnin Fishpond and salt lakes in the Čejč district. Vicherek (1973) documented *Salicornietum strictae* by relevés from the early 1960s recorded at the Plácky site (Velké Němčice district), Zápověď site (Čejč district) and the Nesyt Fishpond (Sedlec district). However, the populations of the dominant species declined rapidly during the 1960s and entirely disappeared in the 1970s. This process was related to the cessation of the traditional management of saline vegetation such as goose and livestock grazing and soil desalination.

TBA02 *Spergulario marinae-Suaedetum prostratae* (Fig. 15A)

Diagnostic species: *Puccinellia distans*, *Salicornia perennans*, *Spergularia marina*, *Spergularia media*,
Suaeda prostrata
 Constant species: *Juncus compressus* agg., *Puccinellia distans*, *Salicornia perennans*, *Spergularia marina*,
Spergularia media, *Suaeda prostrata*, *Tripolium pannonicum*
 Dominant species: *Suaeda prostrata*

This association included open, species-poor stands dominated by *Suaeda prostrata*. Other species, occurring in low abundances, included *Juncus gerardii*, *Puccinellia distans*, *Salicornia perennans*, *Spergularia marina*, *S. media* and *Tripolium pannonicum*. The community used to occur in similar habitats as the previous association: shallow depressions with an extremely high concentration of salt and nitrates in the soil, often on livestock and poultry pastures (Vicherek 1973). This vegetation may have been once common on the shores of the former Měnin Fishpond, Kobyly Lake and Čejč Lake. In the early 1960s, relevés of this association were recorded by Vicherek (1962, 1973) at the

Plácky site and near the village of Starovice (both in the Velké Nēmčice district) and at the Nesyt Fishpond near Sedlec. These occurrences vanished in the 1970s and 1980s when *Suaeda prostrata* went extinct in the Czech Republic.

TCA01 *Puccinellietum limosae* (Fig. 15B)

Diagnostic species: *Glaux maritima*, *Puccinellia distans*, *Spergularia media*, *Taraxacum bessarabicum*, *Tripolium pannonicum*

Constant species: *Atriplex prostrata* subsp. *latifolia*, *Juncus compressus* agg., *Lotus tenuis*, *Plantago maritima*, *Potentilla anserina*, ***Puccinellia distans***, *Spergularia media*, *Taraxacum bessarabicum*, ***Tripolium pannonicum***

Dominant species: ***Puccinellia distans***

This short open grassland is characterized by the occurrence, and in places also high cover, of *Puccinellia distans*. This species can be accompanied by *Glaux maritima*, *Plantago maritima*, *Spergularia media*, *Taraxacum bessarabicum* and *Tripolium pannonicum*. The community further contains species otherwise typical of subhalophytic meadows such as *Lotus tenuis* and *Potentilla anserina*. *Puccinellietum limosae* develops in places that are wet in spring but dry out during summer. Most species of this community tolerate trampling, hence the community also develops on footpaths. *Puccinellietum limosae* was once common at most halophytic sites in southern Moravia (Vicherek 1962, 1973) but declined in the 1960s. However, as it is less dependent on the water regime, its decline was less pronounced than the decline of some other associations. During our survey in 2020, we documented this association by relevés in the Čejč, Sedlec, Hevlín-Nový Přerov and Pulkau districts. In 2021, we also sampled it near Štinkovka stream in the Šakvice district (Chytrý & Danihelka 2021).

TCB01 *Scorzonero parviflorae*-*Juncetum gerardii* (Fig. 15C)

Diagnostic species: *Achillea asplenifolia*, *Carex acuta*, *Carex distans*, *Juncus compressus* agg., *Lotus tenuis*, *Lychnis flos-cuculi*, *Mentha pulegium*, *Orchis palustris*, *Potentilla anserina*, *Potentilla reptans*, ***Scorzonera parviflora***, *Teucrium scordium*

Constant species: *Agrostis stolonifera* agg., *Carex distans*, ***Juncus compressus* agg.**, *Lotus tenuis*, *Melilotus dentatus*, *Mentha pulegium*, *Phragmites australis*, ***Potentilla anserina***, *Scorzonera parviflora*, *Trifolium fragiferum*, *Tripolium pannonicum*

Dominant species: *Carex distans*, *Juncus compressus* agg., *Scorzonera parviflora*

This association of wet saline grasslands occurs in shallow depressions at halophytic sites. It is physiognomically similar to wet meadows. The stands are usually dominated by graminoids, in particular, *Juncus gerardii*, *J. compressus* or *Carex distans*. Graminoids are accompanied by various halophytic dicot herbs, most notably *Scorzonera parviflora* and *Tripolium pannonicum*, which can both attain a high cover. In the early 1960s, this vegetation occurred at most of the southern Moravian halophytic sites (Vicherek 1962, 1973). However, with further draining and desalination, it gradually changed to the subhalophytic grasslands with fewer specialist species (*Loto tenuis*-*Potentilletum anserinae*) or non-halophytic grasslands. Later on, this vegetation was documented by relevés only from the Slanisko u Nesytu site in the early 1990s (Hanušová 1995) and in 2004 (by J. Danihelka). During our vegetation survey in 2020, we did not record any relevé corresponding to this association.

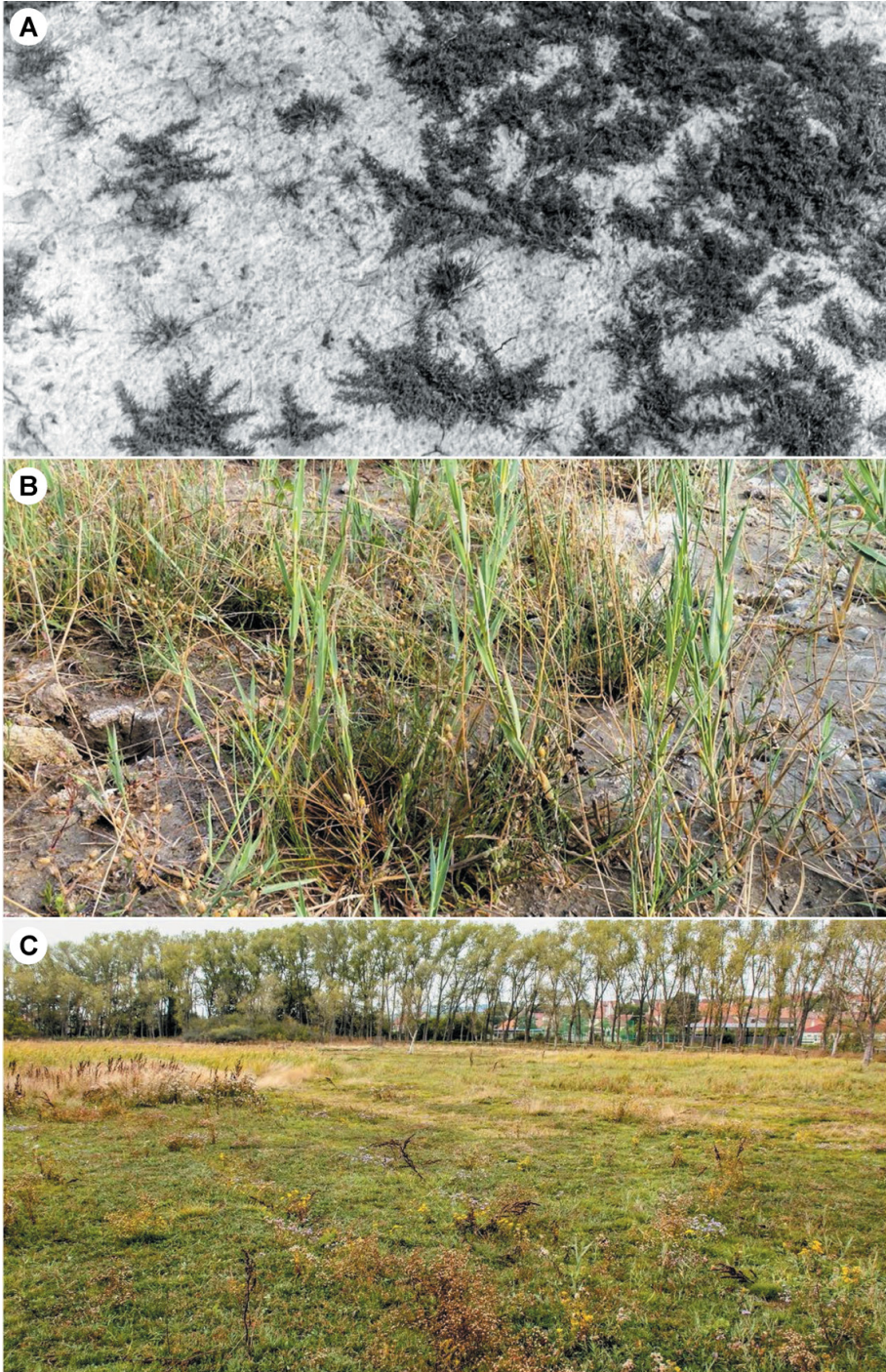


Fig. 15. Associations of halophytic vegetation in southern Moravia and northern Lower Austria: (A) TBA02 *Spergulario marginatae-Suaedetum prostratae*, Starovice 1962; (B) TCA01 *Puccinellietum limosae*, Zápověď 2020; (C) TCB01 *Scorzonero parviflorae-Juncetum gerardii*, Slanisko u Nesytu 2016. Photo credits: J. Vicherek (A), M. Chytrý (B, C).

TCB02 *Loto tenuis*-*Potentilletum anserinae* (Fig. 16A)

Diagnostic species: *Arenaria serpyllifolia*, *Cerastium holosteoides*, *Lolium perenne*, *Lotus tenuis*, *Odontites vernus* subsp. *serotinus*, *Poa annua*, *Poa pratensis* agg., *Pulicaria dysenterica*, *Pulicaria vulgaris*, *Scorzoneroides autumnalis*, *Taraxacum* sect. *Taraxacum*, *Trifolium fragiferum*, *Verbena officinalis*

Constant species: *Agrostis stolonifera* agg., *Juncus compressus* agg., ***Lotus tenuis***, *Melilotus dentatus*, *Odontites vernus* subsp. *serotinus*, *Potentilla anserina*, *Taraxacum* sect. *Taraxacum*, *Trifolium fragiferum*

Dominant species: *Potentilla anserina*

This association is currently the most common type of saline grassland in the study area. It consists mainly of the graminoids *Agrostis stolonifera*, *Juncus compressus* and *J. gerardii*, and subhalophytic herbs *Lotus tenuis*, *Melilotus dentatus*, *Potentilla anserina*, *Pulicaria dysenterica* and *Trifolium fragiferum*. Besides halophytes and subhalophytes, various species of mesophilous grasslands, wet soils and ruderal sites are also present, including *Cerastium holosteoides*, *Lolium perenne*, *Poa annua*, *P. pratensis* agg. and *Taraxacum* sect. *Taraxacum*. Two subtypes of this association can be distinguished, mesic and wet. The mesic subtype, characterized by species of mesic meadows and ruderal vegetation, occurs in trampled areas such as village lawns, paths and extensively managed football playgrounds. In the past, this subtype was typical of pastures around villages, and also today, it occurs in places where grazing was reintroduced for conservation purposes. The wet subtype, characterized by *Melilotus dentatus* and annual species of ephemeral wetlands, occurs in wet depressions in the complexes of halophytic vegetation and on exposed fishpond shores and bottoms. This association represents a transition between halophytic and non-halophytic vegetation. It was probably always common at most halophytic sites in the study area. As the only type of halophytic grasslands, it also occurred outside the natural complexes of halophytic vegetation, e.g. within some villages. Following the decrease in groundwater level and subsequent soil desalination, various types of halophytic vegetation lost the most specialized species of saline habitats, resulting in a change to the grasslands with subhalophytic species of the association *Loto tenuis*-*Potentilletum anserinae*.

TCB03 *Agrostio stoloniferae*-*Juncetum ranarii* (Fig. 16B)

Diagnostic species: *Agrostis stolonifera* agg., *Calamagrostis epigejos*, *Carex hirta*, *Carex hordeistichos*, ***Carex otrubae***, *Carex secalina*, *Cirsium brachycephalum*, *Lysimachia nummularia*, *Lythrum virgatum*, *Mentha pulegium*, *Plantago uliginosa*, *Potentilla anserina*, *Ranunculus repens*, *Rorippa sylvestris*, *Rumex crispus*, *Symphytum officinale* agg., *Taraxacum* sect. *Taraxacum*, *Trifolium fragiferum*

Constant species: ***Agrostis stolonifera* agg.**, *Bolboschoenus maritimus* agg., ***Carex otrubae***, *Juncus compressus* agg., *Lotus tenuis*, *Melilotus dentatus*, *Plantago uliginosa*, ***Potentilla anserina***, *Ranunculus repens*, *Rumex crispus*, *Taraxacum* sect. *Taraxacum*, *Trifolium fragiferum*

Dominant species: *Agrostis stolonifera* agg., *Carex otrubae*

This type of halophytic grassland is typical of the sites with the repeatedly disturbed soil surface. It is dominated by graminoids such as *Agrostis stolonifera*, *Carex hordeistichos*, *C. otrubae* and *C. secalina*. Ruderal species such as *Calamagrostis epigejos*, *Carex hirta*, *Ranunculus repens*, *Rumex crispus* and *Taraxacum* sect. *Taraxacum* are also common. The rare halophyte *Cirsium brachycephalum* also occurs or once occurred in this vegetation at some sites. Vicherek (1973) divided this vegetation into three associations based on the prominence of different sedge species, *Agrostio-Caricetum distantis* Soó 1939, *Agrostio-Caricetum secalinae* Vicherek 1973 and *Meliloto-Caricetum otrubae* Vicherek

1973. However, the differences in species composition and ecology of these associations are small, with various transitions; therefore, Šumberová et al. (2007) merged them into a single association, and our results support this broader concept. Vicherek (1962, 1973) recorded this association from the Velké Němčice, Šakvice, Rakvice, Čejč and Sedlec districts. In the latter district, at Slanisko u Nesytu site, relevés were made by J. Danihelka in 2004. In our vegetation survey in 2020, we recorded this vegetation at the Trkmanské louky site (Rakvice district), Zápověď site (Čejč district) and near the village of Hevlín (Hevlín-Nový Přerov district). In 2021, we also recorded it along the Štinkovka stream near Šakvice (Šakvice district).

TCC01 *Centaureo pannonicarum-Festucetum pseudovinae* (Fig. 16C)

Diagnostic species: *Achillea millefolium* agg., *Agrimonia eupatoria*, *Arrhenatherum elatius*, *Bromus erectus*, *Bupleurum tenuissimum*, *Carex distans*, *Centaurea jacea*, *Cynodon dactylon*, *Dactylis glomerata*, *Daucus carota*, *Elymus repens*, *Festuca pratensis* agg., *Festuca pulchra*, *Lolium perenne*, *Plantago lanceolata*, *Plantago maritima*, *Poa pratensis* agg., *Scorzonera cana*, *Trifolium dubium*, *Trifolium pratense*; *Brachythecium albicans*

Constant species: *Achillea millefolium* agg., *Carex distans*, *Centaurea jacea*, *Daucus carota*, *Elymus repens*, *Festuca pratensis* agg., *Festuca pulchra*, *Lotus tenuis*, *Plantago lanceolata*, *Plantago maritima*, *Poa pratensis* agg.

Dominant species: *Festuca pulchra*

This association comprises grasslands dominated by salt-tolerant narrow-leaved tussock-forming grass *Festuca pulchra*, which forms dense stands. Subhalophytic and halophytic species such as *Bupleurum tenuissimum*, *Lotus tenuis* and *Plantago maritima* frequently occur in this vegetation. The stands are often adjacent to non-halophytic mesic grasslands and contain their typical species, e.g. *Achillea millefolium* agg. (usually *A. collina*), *Arrhenatherum elatius*, *Centaurea jacea*, *Dactylis glomerata*, *Festuca arundinacea*, *F. pratensis*, *Plantago lanceolata* and *Poa pratensis* agg. This association occurs at the margins of saline sites where the soil is not inundated, being mesic in spring and dry in summer. Most stands are trampled, such as at the edges of dirt roads and in pastures. This association, first described from south-eastern Slovakia (Klika & Vlach 1937), was not included in the national vegetation classification of the Czech Republic (Šumberová et al. 2007) because of the lack of relevés at that time. Still, Vicherek (1973) published one relevé from the Nový Přerov site, which he classified to the association *Achilleo-Festucetum pseudovinae* Soó (1933) 1947, although all the other relevés of this association in his study were from southern Slovakia. A relevé corresponding to this vegetation was recorded already by Šmarda (1953) at the Nesyt Fishpond (with the dominant species misidentified as *Festuca valesiaca*), and other such relevés were recorded by J. Danihelka in 2004 at the same site, and by P. Šmarda in 2008 at the Dobré Pole site. In 2020, we sampled this vegetation at the Zřídla u Nesvačilký site (Měnin-Šaratice district), near both western and eastern edge of the Nesyt Fishpond (Sedlec district) and at Dobré Pole site (Hevlín-Nový Přerov district), and observed it at the Plácky site (Velké Němčice district). In 2021, we also observed it at the Saliterweide site near Zwingendorf (Pulkau district). The higher number of relevés from recent years can be due to avoidance of this vegetation type by earlier researchers, who may have considered it degraded vegetation transitional to other vegetation types. An alternative explanation would be the relatively recent spread of this vegetation, which developed on solonchak soils after the drop of the

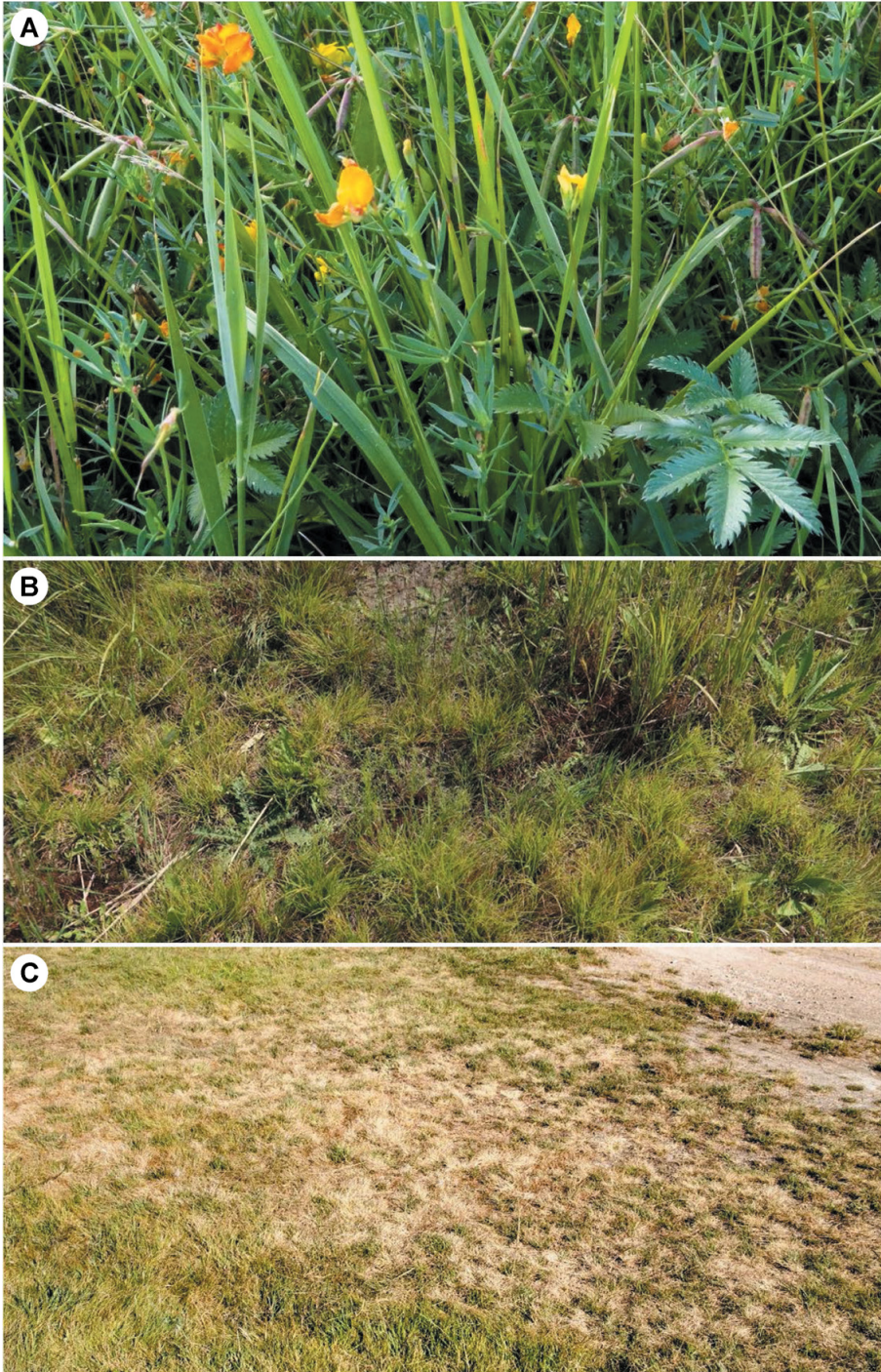


Fig. 16. Associations of halophytic vegetation in southern Moravia and northern Lower Austria: (A) TCB02 *Loto tenuis*-*Potentilletum anserinae*, Zápověď 2020; (B) TCB03 *Agrostio stoloniferae*-*Juncetum ranarii*, Hevlín 2020; (C) TCC01 *Centaureo pannonicae*-*Festucetum pseudovinae*, Dobré Pole 2020. Photo credits: M. Chytrý (A), E. Šmerdová (B), K. Chytrý (C).

water table. This association may represent a degradation phase of the former saline grasslands of the alliances *Puccinellion limosae* or *Juncion gerardii*.

The association *Centaureo pannonicae-Festucetum pseudovinae* belongs to the alliance *Festucion pseudovinae* Soó 1933. This alliance, which comprises dry grasslands of the salt steppe, is distributed mainly in Hungary and southern Slovakia but is also found at Lake Neusiedl in Austria, in Vojvodina and the Pannonian part of Romania (Eliáš et al. 2013, Dítě et al. 2014). Vicherek (1973) reported *Festucion pseudovinae* for the Czech Republic based on the above-mentioned single relevé from Nový Přerov. However, this alliance was not accepted in the subsequent overviews of Czech vegetation (Vicherek & Řehořek in Moravec et al. 1995, Šumberová et al. 2007) due to the lack of other records. Here we add this alliance to the vegetation classification system of the Czech Republic. During our fieldwork in 2020 and 2021, we sampled this vegetation in three halophytic districts and observed it in the other two. Compared to the other halophytic associations, it is characterized by low conductivity and significantly lower pH, indicating possible recent degradation of the former solonchak soils.

Non-halophytic vegetation types in the complexes of halophytic vegetation

Besides the above-mentioned associations dominated or characterized by the occurrence of halophytes, complexes of halophytic vegetation in the study area also include some associations defined by non-halophytes but containing some halophytes as a minor component of their species composition. The most common of such associations are *Phragmitetum australis* Savič 1926 and *Caricetum distichae* Nowiński 1927.

Phragmitetum australis includes species-poor stands dominated by *Phragmites australis*. Its halophytic subtype often contains *Bolboschoenus maritimus*, *Juncus compressus*, *J. gerardii* and *Potentilla anserina*. Some more specialized or rare halophytes such as *Cirsium brachycephalum*, *Samolus valerandi*, *Scorzonera parviflora* and *Tripolium pannonicum* can also occur in this vegetation.

Caricetum distichae is dominated by *Carex disticha*, which forms dense and extensive stands through its clonal growth. Other moisture-demanding species such as *Carex otrubae* and *Iris pseudacorus* frequently occur in this vegetation. At the halophytic sites, *Caricetum distichae* can be enriched by halophytes such as *Juncus gerardii*, *Plantago maritima*, *Scorzonera parviflora* and *Tripolium pannonicum*. Vicherek (1962) described such vegetation as the subassociation *Caricetum distichae juncetosum gerardii* Vicherek 1962.

Further vegetation types found in the complexes of halophytic vegetation and containing some halophytic species include annual wetland vegetation of drained fishpond bottoms and temporary pools on arable land. This vegetation appears in irregular intervals, depending on the water level fluctuations, particularly on the fishponds Nesyt, Výtopa and Hlohovecký in the Sedlec district. The associations found there include *Cyperetum micheliani* Horvatić 1931 (alliance *Eleocharition ovatae*), *Veronico anagalloidis-Lythretum hyssopifoliae* Wagner ex Holzner 1973 (*Verbenion supinae*) and *Rumici maritimi-Ranunculetum scelerati* Oberdorfer 1957 (*Bidention tripartitae*).

There are also weed and ruderal plant communities, especially where halophytic sites border on arable land or where saline soil was ploughed. These include especially the associations *Setario pumilae-Echinochloetum cruris-galli* Felföldy 1942 corr. Mucina in

Mucina et al. 1993 (alliance *Spergulo arvensis-Erodion cicutariae*) and *Convolvulo arvensis-Elytrigietum repentis* Felföldy 1943 (*Convolvulo arvensis-Elytrigion repentis*), which were particularly common at the Trkmanské louky and Trkmanec-Rybníčky sites during our survey in 2020, but also occurred at other halophytic sites. If wet arable land is abandoned, it can be quickly (within 1–2 years) overgrown by *Bolboschoenus planiculmis* stands with weed species. These stands belong to the association *Tripleurospermo inodori-Bolboschoenetum planiculmis* Hroudová et al. 2009 (*Eleocharito palustris-Sagittarion sagittifoliae*). They often contain various subhalophytes and, in some places, also more demanding halophytes. For example, *Crypsis schoenoides*, *Samolus valerandi* and *Spergularia marina* occurred in the stands of this association on abandoned wet arable land along the Štinkovka stream in the Šakvice district in 2021 (Chytrý & Danihelka 2021).

Relationships to salinity

The pH of soil sampled in the relevés of halophytic vegetation in 2020 ranged from 6.8 to 8.5 (mean 7.8) and conductivity ranged from 238 to 5010 (mean 1633) $\mu\text{S}/\text{cm}$.

The generalized linear models identified 39 species with significant ($P < 0.05$) or marginally significant ($P < 0.1$) relationship to pH or conductivity (Table 2 and graphs in Supplementary Fig. S1). Contrary to the generally accepted view, *Festuca pulchra* and *Plantago maritima* tended to be significantly more frequent on soils with lower pH and lower conductivity. In contrast, *Agrostis stolonifera* and *Phragmites australis*, species with a broad ecological range, tended to be more common on high-pH, saline soils. It is important to interpret these results strictly within the context of the halophytic dataset. Both *Agrostis* and *Phragmites* are species occurring across a broad range of pH and salinity, including non-saline habitats. At the halophytic sites, they occur in wetter places, which are also more saline. Therefore, their correlation with saline, high-pH soils in the current dataset is likely mediated through an indirect effect of moisture.

A comparison of vegetation types in terms of pH and conductivity of their soils was possible for five associations with at least three soil samples (Fig. 17). *Loto tenuis-Potentilletum anserinae* (TCB02) and *Centaureo pannonicae-Festucetum pseudovinae* (TCC01) had the lowest mean for both the variables, which corresponds to their status of “degraded” halophytic vegetation occurring on desalinated soils or transitional vegetation to other grassland types in the marginal zones of halophytic vegetation complexes. However, the only significant difference was for pH between *Centaureo-Festucetum* and the other associations.

Table 2. Results of the generalized linear models linking species occurrence to soil pH and conductivity. Species occurring more frequently on higher-pH vs lower-pH soils are called basiphilous vs neutrophilous, respectively. Species occurring more frequently on soils with higher vs lower electric conductivity are called halophytes vs glycophytes, respectively. Only species with significant ($P < 0.05$) and, in brackets, marginally significant ($P < 0.1$) models are shown.

Species	pH	Soil conductivity
<i>Achillea collina</i>	neutrophilous	glycophyte
<i>Agrimonia eupatoria</i>	(neutrophilous)	-
<i>Agrostis stolonifera</i>	(basiphilous)	halophyte
<i>Arenaria serpyllifolia</i>	-	glycophyte
<i>Bolboschoenus maritimus</i>	basiphilous	-
<i>Bolboschoenus planiculmis</i>	-	(halophyte)
<i>Bromus erectus</i>	neutrophilous	-
<i>Carduus acanthoides</i>	neutrophilous	-
<i>Carex secalina</i>	basiphilous	(halophyte)
<i>Centaurea jacea</i>	neutrophilous	(glycophyte)
<i>Cerastium holosteoides</i>	-	glycophyte
<i>Cirsium brachycephalum</i>	basiphilous	-
<i>Cirsium canum</i>	neutrophilous	-
<i>Conyza canadensis</i>	-	glycophyte
<i>Dactylis glomerata</i>	(neutrophilous)	glycophyte
<i>Daucus carota</i>	neutrophilous	-
<i>Dispacus fullonum</i>	neutrophilous	-
<i>Elymus repens</i>	neutrophilous	-
<i>Festuca pratensis</i>	neutrophilous	-
<i>Festuca pulchra</i>	neutrophilous	(glycophyte)
<i>Glaux maritima</i>	(basiphilous)	halophyte
<i>Inula britannica</i>	(neutrophilous)	-
<i>Juncus compressus</i> agg.	basiphilous	halophyte
<i>Linaria vulgaris</i>	neutrophilous	-
<i>Lolium perenne</i>	-	(glycophyte)
<i>Medicago lupulina</i>	-	glycophyte
<i>Myosotis arvensis</i>	neutrophilous	-
<i>Phragmites australis</i>	basiphilous	halophyte
<i>Plantago lanceolata</i>	(neutrophilous)	glycophyte
<i>Plantago maritima</i>	-	glycophyte
<i>Plantago uliginosa</i>	-	(halophyte)
<i>Poa angustifolia</i>	(neutrophilous)	glycophyte
<i>Potentilla reptans</i>	(neutrophilous)	-
<i>Puccinellia distans</i>	basiphilous	halophyte
<i>Serratula tinctoria</i>	neutrophilous	-
<i>Sonchus arvensis</i>	(basiphilous)	-
<i>Trifolium pratense</i>	(neutrophilous)	-
<i>Trifolium repens</i>	neutrophilous	(glycophyte)

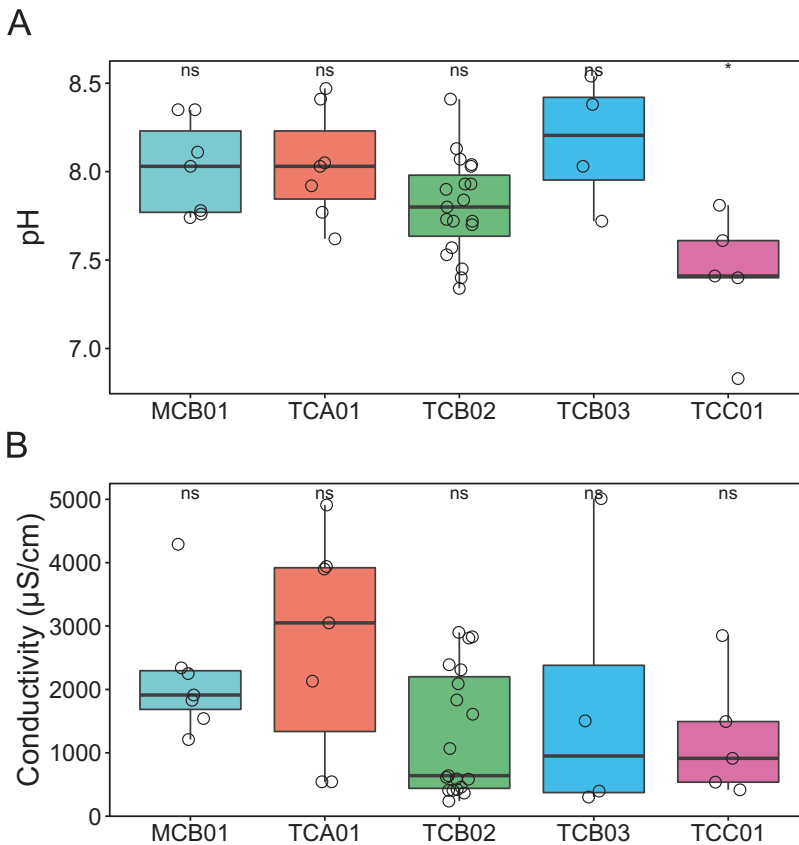


Fig. 17. A comparison of soil pH and conductivity among halophytic associations with at least three soil measurements. Data are based on soil samples from the relevés we recorded in 2020. Non-significant differences are indicated by “ns”; a significant difference at $P < 0.05$ is indicated by an asterisk. See the syntaxonomic synopsis for the association codes.

Discussion

Broader biogeographic context

The study area of southern Moravia and the nearby Pulkau valley in northern Lower Austria is located on the north-western edge of the Carpathian (= Pannonian) Basin, the largest inland area of well-developed halophytic flora and vegetation in Europe west of the steppe zone (Wendelberger 1950, Molnár & Borhidi 2003, Eliáš et al. 2013). The similarities and differences between the halophytic flora of the Carpathian Basin and the inland halophytic flora of Bohemia, Germany, Poland, eastern Romania, the steppe zone of Eastern Europe and Central Asia, as well as the halophytic flora of the European coasts have been discussed, for example, by Wendelberger (1950) and Vicherek (1973).

In the north-west of the Carpathian Basin, halophytic vegetation is best developed around Lake Neusiedl (e.g. Wendelberger 1950, Vicherek 1973, Eliáš et al. 2013, 2020). This area comprises various saline habitats with different water regimes and degrees of salinity

including salt pans (Boros et al. 2013). The extent of saline habitats there is large, which makes local extinctions less likely and colonizations easier than in the more peripheral parts of the Carpathian Basin with small patches of halophytic habitats, such as in southern Moravia. Consequently, the halophytic flora at Lake Neusiedl includes some species that have never been recorded in the study area, e.g. the Pontic-Pannonian *Suaeda pannonica* (Freitag et al. 1996), *Puccinellia limosa* and the Pannonian endemic *P. peisonis* (Fischer et al. 2008). In contrast, *Glaux maritima*, which occurs in southern Moravia and the Pulkau valley, is not found in the other parts of the Carpathian Basin today.

Traditionally, the halophytic flora and vegetation of southern Moravia and the Pulkau valley have been compared with the halophytic flora and vegetation of south-western and southern Slovakia, which lies on the northern edge of the Carpathian Basin (Krist 1940, Vicherek 1973). In general, both areas have similar flora and vegetation, but there are some notable differences. For example, the two succulent halophytes *Salicornia perennans* and *Suaeda prostrata* have never been found in southern Slovakia; consequently, the vegetation of the alliance *Thero-Salicornion* has never occurred there either. *Crypsis aculeata* and *Glaux maritima* have always been very rare there; *G. maritima* disappeared already in the 19th century. In contrast, several species typical of salt steppes of the alliances *Festucion pseudovinae* and *Puccinellion limosae* occurring in southern Slovakia have never occurred in the study area. Such species include *Artemisia santonicum*, *Camphorosma annua*, *Carex divisa*, *Hordeum geniculatum*, *Lepidium cartilagineum*, *Limonium gmelinii*, *Pholiurus pannonicus* and *Plantago tenuiflora*. This can be explained by different ecological conditions, especially by the prevalence of solonetz, a drier, three-horizon type of saline soils at the Slovak halophytic sites. Such soils favour the development of salt steppes, which are widespread in Hungary (Molnár et al. 2008), and also occur in southern Slovakia, where they are represented by several associations (Vicherek 1973, Dítě et al. 2014). In southern Moravia and the Pulkau valley, salt steppe is only represented by two associations, *Puccinellietum limosae* and *Centaureo pannonicae-Festucetum pseudovinae*, the latter reported here as a new association for this area. Higher precipitation and lower summer temperatures in this area do not support the formation of solonetz. The local halophytic flora and vegetation occur on solonchak, a wetter, two-horizon type of saline soil that often develops near mineral-water springs (Vicherek 1973). The prevalence of different salts (mainly sulphates in the study area vs sodium carbonate in southern Slovakia and on the Hungarian Plain; Vicherek 1973, Boros et al. 2013) may also contribute to regional differences in halophytic flora. In addition, differences in land use and stochastic processes, such as local extinction events, may have had an influence. In contrast to the extensive plains of Hungary, Vojvodina, north-western Romania, southern Slovakia and Burgenland, the study area is much smaller, and the distribution of saline habitats is restricted to small halophytic districts in lowland areas surrounded by hilly landscapes. Small populations of halophytes in restricted areas may be at greater risk of extinction.

The halophytic flora and vegetation of the study area also show some similarities with those occurring in isolated inland halophytic areas in more north-western and northern parts of central Europe, namely north-western Bohemia (Toman 1976, 1988, Šumberová et al. 2007), Saxony-Anhalt and Thuringia in central Germany (Altehege & Rossmann 1939, Schubert 2001, Piernik 2012, Dítě et al. 2022) and the Kujawy region in Poland (Wilkoń-Michalska 1963, Piernik 2012). The Bohemian sites have always had a limited

number of halophytic species, probably due to their isolated location and a small area of saline habitats. Several continental halophytes occurring in southern Moravia (e.g. *Cirsium brachycephalum*, *Crypsis aculeata*, *C. schoenoides*, *Salicornia perennans*, *Suaeda prostrata* and *Tripolium pannonicum*) have never been found there (Kaplan et al. 2019). Accordingly, halophytic vegetation is poorly developed in Bohemia and only represented by the alliances *Chenopodion rubri*, *Meliloto dentati-Bolboschoenion maritimi* and *Juncion gerardii* (Šumberová et al. 2007). In contrast, German and Polish inland saline habitats are richer in specialist species, including the succulent halophytes *Salicornia europaea* and *Suaeda maritima*. Traditionally, halophytic vegetation in these inland areas has been classified in the coastal saltmarsh alliances described from the North Sea or the Baltic Sea (Schubert 2001, Matuszkiewicz 2007). However, Dítě et al. (2022) compared the species composition of German and Polish inland halophytic grasslands with corresponding plant communities on the Baltic coast and in the Carpathian Basin. They found these grasslands to be more similar to inland Pannonian than to coastal halophytic vegetation. Consequently, they proposed reclassifying the German and Polish inland halophytic grasslands to the continental inland alliances *Puccinellion limosae* and *Juncion gerardii*.

Saline habitats: partly natural, partly man-made

The halophytic flora and vegetation in southern Moravia and northern Lower Austria are restricted to small areas, mostly shallow depressions with clayey subsoil over Tertiary deposits rich in magnesium and sodium sulphates. In the dry and summer-warm climate in this area, the salt was pushed up in the soil and locally formed efflorescences on the surface. Unique conditions occurred in the salt pan of the former Čejč Lake, which had no outlet (Jordán z Klauzburku 1580: 284–293). In places, the salt content in the soil was increased by water from mineral springs, such as near the villages of Šaratice, Nesvačilka, Čejč and Sedlec. At least in some places, soil salinity was high enough to allow the occurrence of the *Salicornion prostratae* vegetation with low-competitive succulent halophytes *Salicornia perennans* and *Suaeda prostrata*. For millennia, halophytes were supported by livestock grazing (Vicherek 1973, Eliáš et al. 2020), which protected the competitively weak but stress-tolerant halophytes from competing non-halophytes on moderately saline soils. Since the Middle Ages, new saline habitats had probably developed around newly created fishponds (Hurt 1960). These fishponds were surrounded by pastures and meadows, which were wet in the spring but dried out in the summer. Many fishponds were later drained, but some halophytes survived in grasslands developed on their drained bottoms.

Additional habitats were created when the Vienna–Brno railway was built in the late 1830s. Halophytes readily colonized the ditches along the railway near the villages of Rakvice and Šakvice. Halophytes also occurred directly in settlements. The common land in the villages was freely accessible for grazing livestock, domestic pigs and poultry. There was hardly any paving, and each village had at least one small pond with unpaved shallow banks used for horse bathing and domestic geese and ducks. Such sites were suitable for halophytes. Records from the 19th and early 20th century show that *Glaux maritima* occurred in many villages in the Damnice-Olbramovice, Hevlín-Nový Přerov, Daníž and Pulkau districts (e.g. Reuss 1873, Oborny 1912). In halophytic districts, *Glaux*

maritima, *Plantago maritima* and *Spergularia media* occurred almost continuously (e.g. Kalbrunner 1855, Fietz et al. 1923, Gilli 1930). Overall, historical records prove that humans have long promoted the spread of halophytic flora and vegetation in the study area.

Not only man-made but also destroyed by man

Halophytic habitats, confined to small areas with a specific combination of topography, soil properties, moisture, climate and management, were fragile and vulnerable to disruptions, especially changes in the water regime. Such interventions began in the early 19th century when sugar beet was introduced as a new crop (Tomšovic 1990) to replace cane sugar, which became unavailable due to the naval blockade of the European continent during the Napoleonic wars. Sugar beet is salt-tolerant, and its cultivation on drained, albeit somewhat saline, arable land was much more profitable than grazing or haymaking on saline grassland. For this reason, the Měnin Fishpond, Kobylí Lake and Čejč Lake were drained and converted to arable land between 1822 and 1855 (Krzisch 1859, Spitzner 1894, Hurt 1960).

In some areas, draining of agricultural land was made possible only by river channelization. For instance, the lower section of the Pulkau stream and the Dyje river section between its confluence with the Pulkau and the village of Nový Přerov were channelized already in 1832 (Kalbrunner 1855). The Dyje section between the villages of Nový Přerov and Mušov was channelized in 1888–1902 (Fiala & Štěpánek 1992). In the Pulkau district, the once channelized bed of the Pulkau was further deepened downstream the village of Hadres in 1958, and the channelization continued further upstream to the village of Zellerndorf (Lindermayer 2008). These measures caused a drop in the groundwater level in the floodplain, which enabled large-scale drainage and subsequent conversion into arable land of wet habitats adjacent to the stream corridor. The large-scale draining of agricultural land started in the late 1950s, and 105,000 ha of land were drained in the former South Moravian region by 1973 (Března et al. 1974).

Already the 19th-century botanists saw the drainage as a cause of the decline of halophytes (e.g. Krzisch 1859). Still, these interventions were not fatal in the short term because small patches of halophytic habitats remained preserved at less affected sites. For instance, in the Čejč district, even the succulent halophytes survived at the Zápověď and Na Rybníčku sites for more than a century after the drainage of both saline lakes. However, the halophytic habitats were continuously reduced in size and fragmented, and the population size of individual halophytes shrank. The decline of well-known halophytic sites in southern Moravia was briefly discussed by Krist (1935). He also underlined the drop in groundwater level, caused by drainage, as the main threat to halophytes, pointing to the drainage of the Plácky site near Velké Němčice. As reported by Husák & Jatiová (1984), the surroundings of the Plácky site, put under conservation in 1950, was repeatedly drained in 1958–1965 and again in 1970. In 1968–1972, drainage ditches were dug out around the whole nature reserve, and the groundwater level dropped to depths of 120–150 cm. Consequently, most halophytes disappeared by the mid-1970s.

Another factor that strongly accelerated the decline of halophytes was the land-use change. Grazing livestock and poultry were almost ubiquitous in and around villages until the 1950s. Common pastureland (Hutweide) indicated in the 3rd Military Survey

maps, usually in wet parts of the landscape, often corresponds with the localities of halophytes reported in the literature and on herbarium labels. Grazing animals transported diaspores of halophytes (e.g. *Plantago maritima*) along driveways to new suitable sites and made their occurrence possible on moderately saline soils through disturbances. However, livestock grazing almost disappeared from southern Moravia with the introduction of collective farming during the 1950s. The surroundings of small fishponds and other places in villages and their peripheries continued to be grazed by domestic geese and ducks until the 1960s. However, free-running poultry also gradually disappeared from rural areas. For instance, the Slanisko u Nesytu site was still grazed by a large number of domestic geese in the 1960s, but there was no longer any grazing in the 1970s (Danihelka 2005). Husák & Jatiová (1984) reported that the livestock grazing at the Plácky site ceased in the mid-1960s. In contrast, the Hintausacker site near Zwingendorf in Lower Austria was grazed by geese until the 1980s, and one of the small ponds there was used for horse bathing (Holzer et al. 2002). This spontaneous management was able to keep at least some parts of the site without tall-growing vegetation, i.e. suitable for less competitive halophytes. However, many abandoned halophytic grasslands outside the villages were overgrown by dense stands of *Phragmites australis*.

The changes in land use were paralleled by the changes in rural settlements. The public space in the villages was gradually changed to resemble towns. Along with the elimination of small dumping places and free-roaming domestic animals, roads were paved, streams deepened, straightened, channelized or hidden into subsurface pipes, and small village ponds, initially with flat shores and fluctuating water level, were either filled with earth or changed into water reservoirs with a vertical embankment of stone and concrete. Unpaved public spaces were converted to regularly mown lawns or small city-like parks, often with plantations of ornamental trees and shrubs. As a result, habitats suitable for halophytes completely disappeared from most villages or were reduced to small and isolated patches. Vegetation types with specialized halophytes (e.g. the alliance *Salicornion prostratae* or associations *Puccinellietum limosae*, *Scorzonero parviflorae-Juncetum gerardii* and *Agrostio stoloniferae-Juncetum ranarii*) were converted into species-poor grasslands dominated by generalist grasses such as *Festuca arundinacea* and *Lolium perenne*. In a better case, they were transformed to the *Loto tenuis-Potentilletum anserinae* grasslands containing a few less demanding subhalophytes. In southern Moravia, these changes were almost finished by the late 1970s, while this process was somewhat delayed in Lower Austria. As a result, *Glaux maritima*, once recorded directly in village centres, completely disappeared from these sites during the 1960s. In 1963, this species was recorded from grazed places in the village of Dyjákovičky in the Daníž district, which was the last such record in southern Moravia.

In summary, most of the halophytic habitats in southern Moravia and the Pulkau valley were destroyed by draining and subsequent conversion into arable land. Small patches of halophytic habitats in villages were also destroyed directly through improvements of public spaces. The remaining halophytic habitats at the village peripheries and those outside villages, usually too small for intensive farming, were abandoned and, consequently, disappeared due to a secondary succession of reed stands and woody vegetation.

These patterns and causes of the decline of halophytic flora and vegetation were similar to those observed in the whole Carpathian Basin (e.g. Eliáš et al. 2020), southern Slovakia (Vicherek 1973, Dítě et al. 2014) and elsewhere in eastern Austria (Oberleitner

et al. 2006). However, the timing and relative importance of human interventions and succession after abandonment were site-specific.

From the non-intervention conservation to targeted management and restoration

The fast decline of saline habitats during the 20th century stimulated interest in their conservation and led to designating several sites as protected areas, namely Zápověď u Terezína (designated as a private reserve in 1944, as a Nature Reserve in 1952 and abolished in the early 1990s), Plácky (designated in 1950, now Nature Monument), Slanisko u Nesytu (1961, now National Nature Reserve), Zwingendorfer Glaubersalzböden (1979, Naturschutzgebiet consisting of two parts, Hintausacker and Saliterweide), Slanisko Dobré Pole and Slanisko Novosedly (both 1993, now Nature Reserves) and Trkmanec-Rybníčky (2008, Nature Monument). Other localities without a status of (National) Nature Reserve or (National) Nature Monument were designated as the Sites of Community Importance (SCI) within the Natura 2000 network: Zřídla u Nesvačilký, Rumunská bažantnice (including Císařská obora) and Trkmanské louky. Consequently, the most valuable of the remaining halophytic sites in southern Moravia and the Pulkau valley are currently under protection except for Zápověď, the site with *Cirsium brachycephalum* near Hevlín and the newly discovered halophytic sites along the Štinkovka stream near Šakvice.

Around the mid-20th century, nature conservationists supported non-intervention as the primary conservation approach because disturbances were considered detrimental. For instance, Krist (1935) described the remaining halophytic patches at the Plácky site as “trampled by cattle” and referred to the vegetation as “destroyed”. He considered grazing pressure as one of the causes of halophyte decline, in addition to drainage. Fröhlich & Švestka (1956), describing the Slanisko u Nesytu site near Sedlec, complained about the “spread of weeds” and disturbances of “natural plant communities” caused by grazing and mowing. However, referring to the attempts to convert a part of this site to arable land in 1932, they already recognized the positive effect of disturbances on halophytes: “luckily, former attempts to use saline soils for economic purposes failed [...]. The cultivation of soil supported the occurrence of halophytes, while the crops suffered”.

Until the mid-1970s, there was no conservation management in any of the protected halophytic sites. Only the sites at village peripheries were managed spontaneously by local people who used them for grazing by free-roaming chickens, occasional haymaking (e.g. Dobré Pole), and sometimes waste removal (e.g. Hintausacker near Zwingendorf; Holzer et al. 2002). The Dobré Pole site, for some decades the only site of *Glaux maritima* in southern Moravia, was saved by local footballers, who mowed and trampled the playground and the adjacent area. In contrast, the legally protected Zápověď and Plácky sites, both located far from the nearest villages, were entirely abandoned and lost their halophytic flora and vegetation.

Nature conservation authorities realized the importance of management in halophytic reserves in the 1970s. In 1976, they proposed a project to raise the groundwater level at the Plácky site, but it was not implemented (Husák & Jatiová 1984). At the Slanisko u Nesytu reserve, shallow ditches were dug out in the mid-1970s to create suitable habitats for halophytes (Grulich 1987, in litt. 2021). However, these ditches were left unmanaged and overgrew by perennial grasses, mainly *Agrostis stolonifera* (Danihelka

2005, Čtyroký et al. 2007). Husák & Jatiová (1984) recommended regular disturbances of soil surface at the Plácky site to reduce vegetation cover and create suitable conditions for competitively weak halophytes. These proposals failed partly due to the political and economic situation in Czechoslovakia at that time: nature conservation authorities had limited power and almost no financial resources for conservation management. Even if some money was allocated for conservation purposes, finding a company or a cooperative farm with required machinery and free working capacities was challenging. Nevertheless, the situation of the Hintausacker site in Zwingendorf was similar despite the different political and socioeconomic conditions in Austria. Although the site has been formally protected since 1979, conservation management by bulldozing, scrub removal and mowing started as late as 1995 (Holzer et al. 2002).

The Slanisko u Nesytu site was probably the first halophytic reserve in the study area with regular conservation management. In 1991, a shallow ditch was created in the western part of the reserve, in which halophytic grasslands of *Scorzonero parviflorae-Juncetum gerardii* developed spontaneously (Daníhelka & Hanušová 1995, Hanušová 1995). Since 1993, the reserve has been mown regularly. Grazing was restored in 2000, first with a small flock of sheep and goats and in two-year intervals (Daníhelka 2005, Čtyroký et al. 2007). All these early management measures were limited by the lack of money and logistic difficulties. There were neither small farmers with necessary machinery nor private persons specialized in the management of protected areas. The local cooperative farm was also unable to work in small areas and perform fine-scale conservation management. The traditional shepherding skills were forgotten, and no animals were available. However, funding was slowly increasing, and nature conservation authorities gradually improved their skills and experience in active management.

Regular grazing was established at some sites after 2010. Among livestock, horses proved to be the most effective agents in restoring saline habitats for their high mobility and weight (Kmet et al. 2018). Apart from the plant biomass removal, they disturb the soil surface, and by compressing the soil, they enhance evaporation, hence salt precipitation at the soil surface. The establishment of grazing resulted in pronounced improvement of conditions at some saline sites. Some protected areas are also affected by eutrophication due to their direct contact with surrounding arable fields and, in the absence of management, by expanding competitively strong species, both native such as *Phragmites australis* and alien such as *Solidago gigantea*.

Recent evidence also shows that restoration of saline habitats is possible at some sites where they have disappeared. Two notable examples of successful (yet unintentional) restoration of halophytic vegetation are the Zápověď site near Terezín and saline habitats along the Štinkovka stream near Šakvice. At both sites, no halophytes were recorded for several decades. However, after creating shallow pools and depositing removed earth in the surroundings, several halophytic species appeared spontaneously in large populations, most probably by germinating from the soil seed bank. For example, *Crypsis aculeata*, *Glaux maritima*, *Spergularia marina* and *S. media* appeared at Zápověď after its restoration in 2003 (Slavík in Hadinec & Lustyk 2009) while *Crypsis schoenoides*, *Samolus valerandi* and *Spergularia marina* appeared near Šakvice after wet arable land was transformed into a semi-natural area in 2018 (Chytrý & Daníhelka 2021). Moreover, the whole halophytic plant communities corresponding to well-defined phytosociological associations soon developed at these sites. Similar developments occurred after

the restoration of the Trkmanec-Rybníčky site in 2006-2008. These cases of successful restoration of halophytic habitats and their specialized flora and vegetation are important examples for future restoration projects, demonstrating that partial return of halophytes to the landscape is possible. However, the long-term preservation of halophytic flora and vegetation at restored sites requires continued management, including the removal of reeds and other tall plants through grazing, mowing and periodical disturbance of the soil surface.

Our database of exactly located relevés sampled in 2020 (Danihelka et al. 2021) provides the basis for the future monitoring of vegetation and habitat changes, which can support proper management planning. However, the disrupted water regime at most halophytic sites and their surroundings limits the full recovery of halophytic flora and vegetation. Restoration of the water regime in protected areas is currently the main challenge for in situ conservation of halophytic flora and vegetation and restoration of its habitats.

Halophytes: those lost and those to be saved

Halophytic sites in the study area lost a considerable proportion of their former floristic diversity. The pattern shown in Fig. 8 resulted from two different processes. From the beginning until the 1930s, the graph mainly shows progress in floristic research, whereas in later years, it mainly reflects the destruction of individual sites and species. The recent halophytic flora of the study area is strongly impoverished. *Galatella cana*, *Salicornia perennans*, *Suaeda prostrata* and *Triglochin maritima* went regionally extinct. These losses are hardly replaceable, at least in the short time, as shown by the failed attempt to re-establish the population of *Salicornia perennans* at the Slanisko u Nesytu site in the mid-1980s (V. Grulich, in litt. 2021). At least the two succulent halophytes require a much higher salinity degree than currently encountered in the study area. At present, conservation efforts should thus focus on protecting the remaining 13 halophytes still occurring in the area and their habitats.

Of the remaining species, the least endangered ones are *Juncus gerardii*, *Plantago maritima* and *Spergularia marina*. *Juncus gerardii* can survive even in degraded saline habitats as long as they are humid in the spring. Although it is often neglected and confused with *J. compressus*, it seems to be the most widespread halophyte of the study area. *Plantago maritima* is still present at several sites, and at least the populations at the Slanisko u Nesytu, Dobré Pole, Hintausacker and Saliterweide sites are still large enough not to be in immediate danger of local extinction. Its survival may be explained by its relatively loose relations to salinity: in our dataset, it tends to grow preferably at sites with lower salinity (Table 2). *Spergularia marina* occurs in most halophytic districts, but most of its populations are small. It is more often found on wet arable land next to the halophytic sites than directly within these sites. Conservation management of this species includes continued cultivation of periodically flooded arable land. The species appears there in wet years when the crop fails to develop or when a wet patch is left uncultivated. *Plantago maritima*, *Spergularia marina* and *S. media* have recently spread along roads salted for winter de-icing and in cities (Ducháček & Kúr in Kaplan et al. 2016, Danihelka & Kaplan in Kaplan et al. 2018). However, nothing is known about the genetic relationship between the autochthonous populations from saline habitats and the recently spreading populations.

Glaux maritima and *Tripolium pannonicum* currently occur at three sites. Both of them have two populations that are large enough to escape the immediate risk of extinction. These species readily respond to mowing and grazing applied as a part of conservation management. The current status of *Spergularia media* is similar to the previous two species. *Cirsium brachycephalum* is currently present at two or three sites; the population at the Trkmanec-Rybníčky and Trkmanské louky sites seems to be stabilized and large enough, while the populations at the Hevlín and Saliterweide sites are small and require monitoring and conservation management. We failed to confirm the occurrence at Saliterweide in July 2021. Only two of the populations of *Samolus valerandi* known to us are found in protected areas, both being large enough and monitored by nature conservation authorities. In addition, there are recent records from further five sites, and other occurrences may be discovered in the future on drained fishpond bottoms somewhere else in the area. At the Nesyt Fishpond, *S. valerandi* co-occurs with *Crypsis schoenoides*. The latter species forms locally large stands there on exposed parts of the bottom in dry years and does not seem to be in danger. However, this may change in the future if non-saline water from the Dyje river was pumped into the Lednice Fishpond system, as currently discussed. This happened already in the early 1980s and may have been one of the factors causing the desalination at the Slanisko u Nesytu site (Danihelka & Hanušová 1995).

The populations of four remaining species, *Bupleurum tenuissimum*, *Crypsis aculeata*, *Scorzonera parviflora* and *Taraxacum bessarabicum*, require monitoring and targeted management. Of them, only *Bupleurum tenuissimum* is not in immediate danger because the population at the Slanisko u Nesytu site is rich in individuals and well responding to management. *Taraxacum bessarabicum* may have survived only at two or three sites, in populations counting less than several hundred or several dozen plants. *Crypsis aculeata* and possibly also *Scorzonera parviflora* are on the brink of extinction in the study area. Populations of both species have suffered from a series of dry years since 2015. However, *S. parviflora* profited from the humid spring of 2021, and an abundant population appeared at the Slanisko u Nesytu site. Relatively rich population occurs at the Hintausacker site near Zwingendorf, and two plants were observed at the Kalužiny site in the Měnin-Šaratice district in 2017. *Crypsis aculeata* has survived at one to three sites: it was last recorded at the Zápověď site in 2008, while at the Slanisko u Nesytu site, it is confined to a few square meters in an artificial ditch, and the population size fluctuates from a few to several hundred plants. A few plants were observed on the drained bottom of the Nesyt Fishpond in 2020.

Although the decline of saline vegetation in the last two centuries was caused mainly by human activities, some halophytes were able to take advantage of those changes. During the last decades, some halophytes spread massively along motorways. The critically endangered species *Puccinellia distans* and *Spergularia marina* became common elements of salted roadsides while being at extinction risk in natural habitats. The former species dominated ruderal grasslands along salted roads in the cities already in the late 1970s (Hadač et al. 1983). *Limonium gmelinii*, a species of continental salt steppes, was found as a new non-native species of Moravian flora on a motorway edge near Brno in 2009 (Kocián et al. 2016). Since the roadsides can be a partial substitute for some drier types of natural saline habitats, their colonization by other halophytes is possible.

Despite the spread of some halophytes in anthropogenic habitats, natural and semi-natural occurrences of halophytes and their plant communities are in general decline. In the long term, most halophyte species are at risk of regional extinction due to the extinction debt phenomenon (Figueiredo et al. 2019). The reasons are obvious: many populations are small in numbers, some survive in suboptimal conditions, and there are no suitable habitats to colonize. Therefore, targeted management of the remaining halophytic habitats and restoration at selected sites where they have disappeared seems to be the only way to conserve their populations.

Supplementary materials

Fig. S1. – Results of the generalized linear models (binomial distribution, logit link function) linking the probability of species occurrence to soil pH and conductivity

Table S1. – Full version of the synoptic table (Table 1) of 14 halophytic associations based on the relevés classified by the expert system

Data S1. – Shape files with the delimitation of ten halophytic districts of southern Moravia and northern Lower Austria

Data S2. – Floristic records of the 17 halophytic species analyzed in this study

Data S3. – Metadata on relevés classified by the expert system

Supplementary materials are available at www.preslia.cz

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Halofytní flora a vegetace jižní Moravy a severních Dolních Rakous: minulost a současnost

Slaniska představují významnou součást jihomoravské krajiny v území mezi Znojmem, Brnem a Břeclaví, jakož i v údolí Pulkavy v příhraniční části Dolních Rakous. V této studii shrnujeme historii slanomilné flóry a vegetace tohoto území od počátku 19. století a na základě terénního výzkumu v létě 2020 popisujeme současný stav zbylých halofytních lokalit. Lokality slanisk dělíme do deseti okrsků, a to měnínsko-šaratického, velkoněmčického, šakvického, rakvického, čejčského, sedleckého, damnicko-olbramovického, hevlínsko-novopřerovského, danížského a pulkavského. Nejlépe vyvinutá slaniska se v minulosti nacházela ve velkoněmčickém, šakvickém, rakvickém, čejčském a sedleckém okrsku. V současnosti se nejlépe zachovalé halofytní biotopy nacházejí v sedleckém, hevlínsko-novopřerovském a pulkavském okrsku. Dále jsme zpracovali přehled současného a historického rozšíření 17 druhů, které se ve studovaném území vzhledem k silné vazbě na zasolené půdy považují za halofilní, a to *Bupleurum tenuissimum*, *Cirsium brachycephalum*, *Crypsis aculeata*, *C. schoenoides*, *Galatella cana*, *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Salicornia perennans*, *Samolus valerandi*, *Scorzonera parviflora*, *Spergularia marina*, *S. media*, *Suaeda prostrata*, *Taraxacum bessarabicum*, *Triglochin maritima* a *Tripolium pannonicum*. Z nich *Galatella cana*, *Salicornia perennans*, *Suaeda prostrata* a *Triglochin maritima* už na jižní Moravě i v údolí Pulkavy vyhynuly. Fytoocenologické snímky halofytní vegetace jsme klasifikovali do 14 asociací, které patří do svazů *Chenopodion rubri*, *Meliloto dentati-Bolboschoenion maritimi*, *Cypero-Spergularion salinae*, *Salicornion prostratae*, *Puccinellion limosae*, *Juncion gerardii* a *Festucion pseudovinae*. Na základě půdní reakce a konduktivity změřené z půdních vzorků jsme analyzovali vztah jednotlivých druhů a vegetačních typů k míře zasolení půdy. Naše syntéza ukazuje, že kdysi dobře vyvinutá halofytní flóra a vegetace ve studovaném území trvale ustupovala od počátku 19. století až do 80. let minulého století, zpočátku většinou v důsledku odvodňování a od poloviny 20. století také vlivem ukončení pastvy. Ochranná péče od 90. let zastavila úbytek halofytů na posledních několika lokalitách. Budoucnost halofytních biotopů závisí na dlouhodobé a cílené ochranné péči a ekologické obnově.

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