



A comprehensive study of the sedge species *Carex pseudocyperus* in Slovakia: distribution and syntaxonomy

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Received: 27 May 2025 / Accepted: 11 August 2025 / Published online: 7 October 2025
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Abstract

Carex pseudocyperus is a wetland species listed in the European and IUCN Plant Red Lists. However, its distribution and vegetation affinity are poorly known in Slovakia. We aimed to revise the chorology of this sedge species at a national level using all available herbarium, literature and field records and to provide vegetation synthesis of phytosociological relevés with its occurrence. Most species records occurred in the lowlands of south-western and eastern Slovakia (Pannonian phytogeographical region), whereas they were less common in the northern and mountainous regions. Although several past localities disappeared and many other species populations were reduced, *C. pseudocyperus* was also newly found in natural and anthropogenic habitats. TWINSpan classification divided the dataset of 161 phytosociological relevés into 4 clusters of forest and shrub vegetation and 9 clusters of non-forest vegetation. Forest and shrub vegetation were syntaxonomically identified as follows: (1) alliance *Alnion incanae*, (2) transition between first and third group, (3) alliance *Alnion glutinosae*, and (4) alliance *Salicion cinereae*. The species composition of the non-forest plant communities was much more heterogeneous and interpreted as: (1) alliance *Charion vulgaris*, (2) class *Lemnetea*, (3) alliance *Carici-Rumicion hydrolapathi*, (4) alliance *Eleocharito palustris-Sagittarion sagittifoliae*, (5) alliance *Phragmition communis*, (6) alliances *Magnocaricion elatae* and *Magnocaricion gracilis*, (7) alliance *Bidention tripartitae*, (8) order *Nanocyperetalia* and (9) alliance *Molinion caeruleae*. Vegetation analysis revealed that the species in Slovakia predominantly occupied riparian forest and non-forest marshy vegetation, with sporadic occurrence in other plant communities. It exhibited a particularly high frequency and cover in alder swamp forests (*Alnion glutinosae* alliance) and marshy vegetation of the *Phragmito-Magnocaricetea* class. *Carex pseudocyperus* should be of conservation or at least monitoring concern, as it inhabits different wetland and floodplain ecosystems susceptible to ongoing human pressure and environmental changes.

Keywords Chorology · Cyperaceae · Floodplains · Herbaria · Phytosociology · Wetlands

Introduction

Wetlands are among the most valuable ecosystems in the world (Cui et al. 2020; Keddy 2023). These ecotonal areas between terrestrial and aquatic ecosystems have an exceptionally high level of biodiversity and habitat heterogeneity, offering multiple ecosystem functions and services (Xu et al. 2020; Eric et al. 2022). They significantly contribute to the regional species pool, flood protection, and water storage and filtration (Houlahan et al. 2006; Salimi et al. 2021). Although their conservation should be a primary goal of society, freshwater wetlands are currently considered the most endangered ecosystems worldwide. Wetlands host numerous rare and threatened biological organisms and their communities (Dudgeon and Strayer 2025) but are prone

Dedicated to the memory of Vít Grulich (2 October 1956 – 24 February 2022), an expert on the genus *Carex*, great botanist, colleague and friend who loved nature in Slovakia.

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to human pressure. Their area is constantly shrinking due to pervasive land use modifications, the invasion of non-native species, ongoing climate warming and associated environmental changes (Brinson and Malvárez 2002; Cui et al. 2020). Human-induced threats, such as eutrophication, deforestation and construction (Houlahan et al. 2006; Keddy 2023), modify the water regime, productivity levels and biotic interactions, which lead to habitat fragmentation and degradation (Cui et al. 2020). These processes have important ecological consequences at different levels of the biological hierarchy – from species to ecosystems. Understanding the ecology and distribution patterns and temporal trends in species populations seems crucial for ensuring its adequate conservation and to guide optimal management activities. In Central Europe, several comprehensive studies have focused on the chorology and vegetation patterns of plant species with affinity to wetland and aquatic habitats, such as *Calla palustris* (Dudáš et al. 2021), *Carex secalina* (Lembicz et al. 2009; Eliáš et al. 2012), *Coleanthus subtilis* (Richert et al. 2016), *Ranunculus lingua* (Dudáš et al. 2023) or *Wolffia arrhiza* (Pietryka et al. 2023). However, plenty of other wetland species have not been studied, as complex revision of distribution and vegetation data is time- and personnel-consuming. In-depth research is also lacking in the attractive and easily determined cyperus sedge species – *Carex pseudocyperus* (Fig. 1).

The genus *Carex* is the largest, most widespread, ecologically important, cosmopolitan genera within the *Cyperaceae* family. This genus, common known as sedges, comprises ca 2000 species worldwide (Reznicek 1990; Roalson et al. 2021; Koopman et al. 2025). They occur across a wide range of environments, including dry areas and deserts (Kukkonen 1987; Abudurehman et al. 2016; Grzelak et al. 2019), but many others thrive in marshy, flooded and wet habitats in the temperate and subarctic zones (Leck and Schütz 2005). The subject of our research is the species *Carex pseudocyperus*, which is a perennial sub-cosmopolitan sedge found in North America, Eurasia and north Africa (Meusel et al. 1965). In Europe, it is distributed from southern regions of central Finland, southwards to central Spain, Sicilia and Macedonia. It is only missing in the northernmost and southernmost European regions (Meusel et al. 1965; Chater 1980). This sedge species is widespread among wetland habitats, such as marshes, ditches (Laghi et al. 2015), littoral areas of lakes and fishponds (Laghi et al. 2015; Nikolin et al. 2016), oxbows, ponds, and flooded gravel pits (Dančák and Kocián 2018), with moist to waterlogged sandy soils (Muñoz-Secilla and Sánchez-García 2013). In Slovakia, the species populations are considered stable, but in other countries, *C. pseudocyperus* is included in national (e.g. Czech Republic – Grulich 2012; Grulich and Chobot 2017; Austria – Hohla et al. 2009) or regional Plant Red Lists (e.g. Andalusia – Cabezudo et al. 2005; Kärnten – Kniely et al. 1995).

In the Czech Republic, it is classified as near threatened (NT) and requires attention because there are recent indications of its population decline (Grulich and Chobot 2017). *Carex pseudocyperus* is listed in the category Least Concern (LC) in the European Red List of Vascular Plants (Bilz et al. 2011), which implies monitoring of its populations in the future. This status overlaps with the IUCN Red List at the global level (<https://www.iucnredlist.org>). This species prefers both forest and non-forest wetlands, especially freshwater marshes of the class *Phragmito-Magnocaricetea* and swamp forests of the *Alnetea glutinosae* class (Douda et al. 2016; Landucci et al. 2020). However, no comprehensive vegetation synthesis of plant communities with the occurrence of *C. pseudocyperus* has yet been conducted in Slovakia. Most vegetation records are limited to local phytosociological studies focusing on wetlands and floodplains, which has led to its inclusion in the list of diagnostic species for the classes *Alnetea glutinosae* and *Phragmito-Magnocaricetea*, including their lower syntaxonomical units (Jarolímek and Šibík 2008).

Various sources of chorological data related to the species' occurrence suggest significant discrepancies. The earliest published records originate from Bratislava and Kežmarok as well as from the Danube and Tisa Riverbeds in the mid-nineteenth century, where it formed locally abundant stands (Reuss 1853). This is in contrast to much more recent literature sources, which have not regarded it as a common sedge species but rather a species with mostly fragmented and small populations (e.g. Dostál and Červenka 1992). Details of the spatial dynamics of the species distribution need to be critically revised. This research may offer initial background for assessing its ecological and conservation importance. Specifically, we aimed (1) to provide a comprehensive overview of the distribution of *C. pseudocyperus* in Slovakia based on all available data, including herbarium specimens, literature sources and original field records and (2) to describe the vegetation affinity of this species in Slovakia.

Materials and methods

Data collection

Herbarium, literature and database records (including several private records) as well as our original field observations were assembled to determine the distribution range of *Carex pseudocyperus*. National herbaria and local museum collections were used to examine herbarium specimens from the current territory of Slovakia. Herbarium material of *C. pseudocyperus* was deposited in the Slovak herbaria of BRA, KO, LTM, NI, POP, SAV, SLO, SMBB, SNV and TM. The herbarium collection of the Matej Bel University



Fig. 1 *Carex pseudocyperus* and some of its habitats: a – upper part of the plant (Photo by M. Slezák, Nové Mesto nad Váhom, 2022), b – close-up of the female spikes (Photo by R. Hrivnák, Nolčovo, 2018), c – black alder swamp forests of the *Carici elongatae-Alnetum glutinosae* (Photo by M. Slezák, Nature Reserve Šúr, 2023), d – non-forest habitat of the *Cicuto-Caricetum pseudocyperi* (Photo by R. Hrivnák, Leles, 2019)

in Banská Bystrica is not indexed; thus, we set the abbreviation (MBU) for this purpose. No herbarium specimen of target species or incorrectly determined specimens were found in BBZ, HLO, HUM, MOP, MPS, PMK, VSM, ZAM, ZV, Orava Museum in Oravský Podzámok or Museum of Homeland Studies in Považská Bystrica. The Slovak collections were supplemented by specimens from other relevant Central European herbaria, such as BP, BRNM, BRNU,

nosae (Photo by M. Slezák, Nature Reserve Šúr, 2023), d – non-forest habitat of the *Cicuto-Caricetum pseudocyperi* (Photo by R. Hrivnák, Leles, 2019)

PRC and W, except for WU, where no relevant materials were found. Additionally, some items available on the online JACQ herbarium (<https://www.jacq.org/#database>) were included, namely BRNU (12 items) and W (4 items). Herbarium acronyms followed Thiers (2023), and in the case of small local museum collections, they followed Vozárová and Sutorý (2001). To complete the list of occurrences, the online databases iNaturalist (<https://www.inaturalist.org/>)

home) and GBIF – the Global Biodiversity Information Facility (<https://www.gbif.org>) were used. Distribution and vegetation records were gathered and processed from 2015 to 2025. A distribution map was created with the program Corel Draw using the quadrants of the Central European Flora Mapping System (Niklfeld 1971), with a total of 1577 subgrid cells covering the entire territory of Slovakia (all cells that fully or partially cover the territory of Slovakia were included). We georeferenced distribution records without geographic coordinates based on the description of the locality present either in the labels of herbarium specimens or in the literature. To avoid incorrect identification of the locality, especially the oldest records were confronted with historical maps of Slovakia (<https://www.staremapy.sk>). All localities of *C. pseudocyperus* are presented in Appendix 1 and sorted according to their phytogeographical affiliation (Futák 1984).

Vegetation survey

Vegetation with the presence of *Carex pseudocyperus* was studied using the traditional Zürich–Montpellier approach (Westhoff et al. 1973) with the modified Braun–Blanquet scale (Dengler et al. 2008). The vegetation affinity of *C. pseudocyperus* was analysed based on the 123 phytosociological relevés provided by the Slovak Vegetation Database (GIVD ID EU-SK-001; <https://ibot.sav.sk/cdf>) and completed by 38 unpublished relevés. The final dataset included 161 relevés (91 for non-forest and 70 for forest and shrub vegetation; Appendix 2), stored in the Turboveg database (Hennekens and Schaminée 2001). They were processed in the Juice program (Tichý 2002). Species taxonomy was unified using the concept of broadly defined plant taxa with few aggregate taxa (Appendix 3). Two datasets, i) forest and shrub and ii) non-forest vegetation, were created and separately evaluated. Numerical classification was performed using the TWINSpan algorithm (Hill 1979) with four pseudospecies cut levels (0, 25, 50 and 75%). The diagnostic species of each cluster were determined using frequency and fidelity thresholds (Φ – phi coefficient; Chytrý et al. 2002), which were set as follows: frequency > 20%, phi coefficient ≥ 0.20 and difference in frequency between clusters > 20%. If a particular species was constant (frequency reached > 50%) in two or more clusters, it was not accepted as a diagnostic. Fisher's exact test ($p < 0.05$) was used to eliminate species with a non-significant occurrence in a given cluster (Tichý and Chytrý 2006). The TWINSpan algorithm and diagnostic species approach were accompanied by the dominant species approach, typical for aquatic and marshy vegetation (e.g. Chytrý 2011; Landucci et al. 2020). Manual reassignment of some relevés was performed based on the prevalence of diagnostic species, presence of

dominant species and our expert judgement; less than 10% of non-forest vegetation relevés were moved.

Nomenclature

The nomenclature of the plant species followed Marhold and Hindák (1998), and the names of the syntaxa followed Mucina et al. (2016).

Results

Distribution records of *Carex pseudocyperus* in Slovakia over time

Carex pseudocyperus was recorded at more than 150 locations in Slovakia (excluding unspecified records; Fig. 2), covering 98 subgrid cells (~6% of the total) within the Central European Flora Mapping System. The total number of species records in Slovakia approached 250 when multiple temporal data points were counted for a single locality (Appendix 1). The distribution pattern covered five phytogeographical districts in the *Pannonicum* and 17 phytogeographical districts in the *Carpathicum occidentale* region. Most species records were found in the warm areas of the Záhorská nížina and Východoslovenská nížina lowlands, with the species frequency decreasing towards higher elevations. The elevational maximum of 885 m was recorded on the Muránska planina Mts, in the Mokrý Poľana Nature Reserve, which contrasted with its lowest elevations documented in the Latorica River basin (several locations around 100 m; Appendix 1). All species localities in Slovakia from the period 1853–2025 are reported, but only seven were available before 1900, including three without a more detailed locality description. Between 1900 and 1950, 26 new localities were documented with the species. The number of records continued to grow gradually, with a notable increase during the latter half of the twentieth century. This period yielded an additional 62 new localities, in addition to those documented before 1950. Recent observations (since 2000) included 59 additional findings distributed throughout the country. The oldest record of *C. pseudocyperus* was published by Reuss (1853), who reported its presence in the cities of Bratislava and Kežmarok and along the Danube and Tisa Rivers. The population in the Šúr Nature Reserve (near the village of Svätý Jur, southwestern Slovakia) represents the most consistently recorded locality of *C. pseudocyperus* in the country, with repeated observations from the mid-nineteenth century to the present. This site also yielded the oldest herbarium specimen (Wiesbauer 1865 W) and one of the earliest published records (Kornhuber 1858).

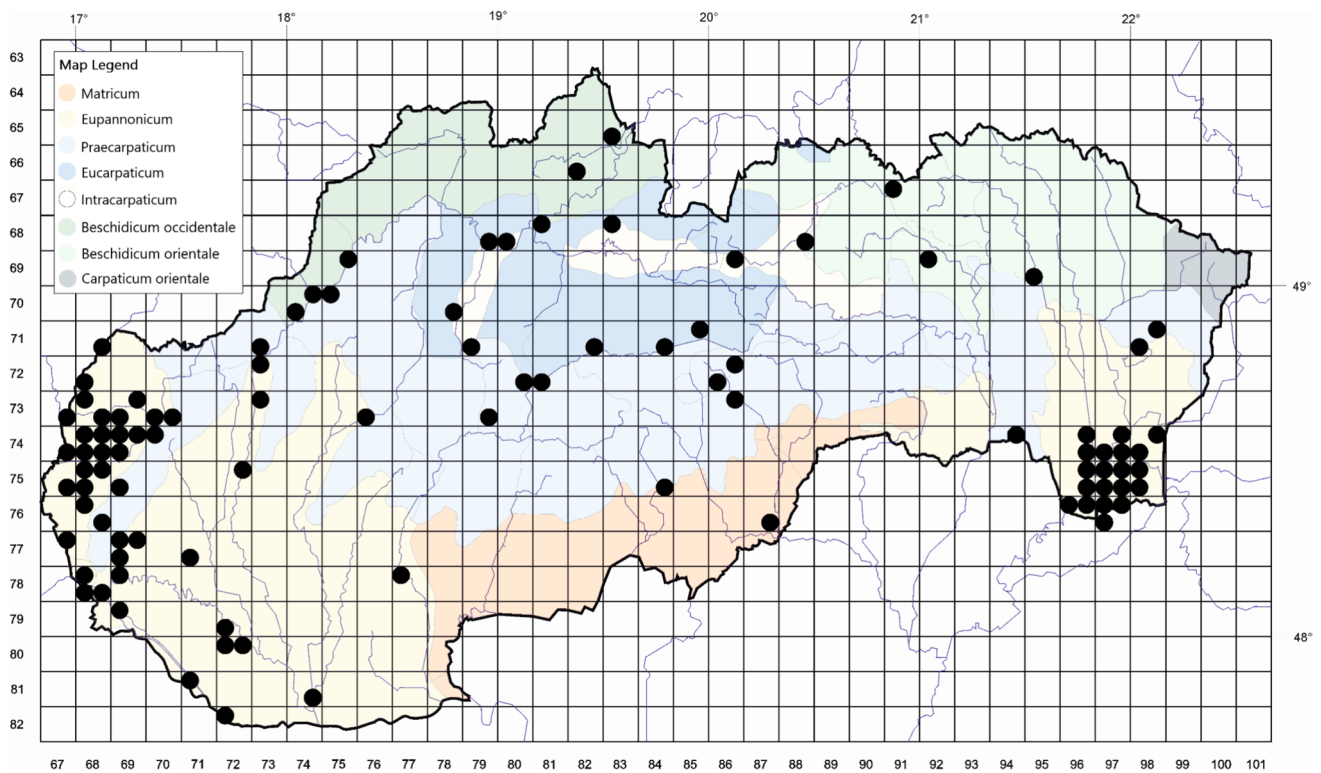


Fig. 2 Distribution of *Carex pseudocyperus* in Slovakia based on the Central European Flora Mapping System. Different colours indicate the phytogeographical division of Slovakia (sensu Futák 1984)

Vegetation affinity

Overall, 409 vascular plant taxa were identified in phytosociological relevés with the occurrence of *Carex pseudocyperus* (350 in forest and shrub vegetation and 203 in non-forest vegetation). After *C. pseudocyperus*, the most common plant species in the whole dataset were *Lycopus europaeus* (occurrence in 73% of the relevés), *Lysimachia vulgaris* (63%), and *Lythrum salicaria* (52%), followed by *Solanum dulcamara* (50%). Only 12 vascular plants had a frequency higher than 50% in forest and shrub vegetation (the first 3 of the most occurring plants were *Lysimachia vulgaris*, *Lycopus europaeus* and *Solanum dulcamara*). Non-forest vegetation seemed to be much more heterogeneous than woodland vegetation, which was also indicated by the fact that only two species (*Lycopus europaeus* and *Lythrum salicaria*) exceeded a frequency of 50% in the dataset.

Four clusters were identified in forest and shrub vegetation by TWINSpan classification (Table 1). The first cluster was represented by vegetation dominated by trees *Alnus incana* and *Picea abies*. The forest understorey of these riparian stands in mountainous areas was composed of hygrophilous and acidophilous plants (e.g. *Chaerophyllum hirsutum*, *Cirsium oleraceum*, *Luzula sylvatica* and *Vaccinium myrtillus*). They were classified in the alliance

Alnion incanae (class *Alno glutinosae-Populetea albae*). The second cluster, which showed a transitional position between alder swamps and lowland riparian alder forests of the alliance *Alnion incanae* (Table 1), were composed of the tree *Alnus glutinosa* and shrub *Salix cinerea*. The most frequent woody species also reached higher cover values in the third and fourth clusters. Hygrophilous graminoid and herb species (e.g. *Glyceria maxima*, *Peucedanum palustre* and *Typha* species) were typical in the understorey for the third and fourth clusters, which completed the list of forest mesophilous plants (e.g. *Brachypodium sylvaticum* and *Mycelis muralis*) in the second cluster. The vegetation of the third and fourth clusters corresponded to alder swamp forests of the alliance *Alnion glutinosae* (class *Alnetea glutinosae*; Fig. 1c) and to willow carrs of the alliance *Salicion cinereae* (class *Franguletea*), respectively.

Nine clusters were distinguished in non-forest vegetation, which was formed by an abundant group of wetland plants (e.g. *Glyceria maxima*, *Lycopus europaeus*, *Lysimachia vulgaris*, *Lythrum salicaria* and *Rumex hydrolapathum*), less frequently by aquatic species (*Lemna minor* and *Stratiotes aloides*) and occasionally by hygrophilous species (e.g. *Agrostis stolonifera* agg. and *Juncus effusus*; Table 2). These stands were syntaxonically interpreted mostly at the level of alliance. The first two clusters were characterised by the

Table 1 Shortened synoptic table of forest and shrub plant communities with *Carex pseudocyperus* with percentage frequency and cover range (in upper index). Diagnostic taxa (see Method chapter) are presented in individual clusters according to decreasing of phi-coefficient; other taxa according to decreasing of frequency in all clusters. Abbreviations: E₀ – moss layer, E₁ – herb layer, E₂ – shrub layer, E₃ – tree layer

Cluster	1	2	3	4
No. of relevés	2	4	40	24
Dominants of tree layer				
<i>Picea abies</i> (E ₃)	100 ^{a-4}	.	.	.
<i>Picea abies</i> (E ₂)	100 ¹⁻³	.	.	.
<i>Picea abies</i> (E ₁)	100 ⁺	.	.	.
<i>Alnus incana</i> (E ₃)	50 ^a	.	.	.
<i>Alnus incana</i> (E ₁)	50 ¹	.	.	.
<i>Alnus glutinosa</i> (E ₃)	50 ^a	100 ⁴⁻⁵	100 ³⁻⁵	.
<i>Alnus glutinosa</i> (E ₂)	.	75 ⁺¹	72 ^{r-a}	17 ^{+a}
<i>Alnus glutinosa</i> (E ₁)	50 ¹	50 ⁺	12 ⁺¹	.
Cluster 1: <i>Alno glutinosae</i>-<i>Populetea albae</i>, <i>Alnion incanae</i>				
<i>Tephrosia crista</i>	100 ^{+a}	.	.	.
<i>Soldanella hungarica</i>	100 ⁺¹	.	.	.
<i>Lonicera nigra</i>	100 ¹⁻³	.	.	.
<i>Vaccinium myrtillus</i>	100 ^a	.	.	.
<i>Equisetum sylvaticum</i>	100 ^{+a}	.	.	.
<i>Cirsium oleraceum</i>	100 ^{1-a}	.	.	.
<i>Chaerophyllum hirsutum</i>	100 ^{1-b}	.	.	.
<i>Luzula sylvatica</i>	100 ^{a-b}	.	.	.
<i>Lonicera nigra</i> (E ₂)	100 ⁺	.	.	.
<i>Lonicera nigra</i> (E ₁)	100 ⁺	.	.	.
<i>Gymnocarpium dryopteris</i>	100 ^{+a}	.	.	.
<i>Pleurozium schreberi</i> (E ₀)	100 ^{+a}	.	.	.
<i>Tetraphis pellucida</i> (E ₀)	100 ⁺	.	.	.
<i>Rhytidadelphus triquetrus</i> (E ₀)	100 ¹	.	.	.
<i>Myosotis palustris</i> agg.	100 ⁺¹	.	5 ⁺¹	.
<i>Valeriana dioica</i> agg.	100 ¹⁻³	.	8 ⁺³	.
<i>Plagiomnium undulatum</i> (E ₀)	100 ^{1-a}	25 ⁺	.	.
<i>Cardamine amara</i>	100 ¹⁻³	25 ¹	.	.
<i>Plagiomnium affine</i> (E ₀)	100 ⁺	25 ⁺	2 ⁺	.
<i>Caltha palustris</i>	100 ³	25 ^b	10 ^{+b}	.
<i>Calliergonella cuspidata</i> (E ₀)	100 ⁺¹	25 ⁺	.	12 ⁺¹
Cluster 2: transitional position between <i>Alnion incanae</i> and <i>Alnion glutinosae</i>				
<i>Rubus hirtus</i> s. lat.	.	75 ⁺	2 ⁺	.
<i>Padus avium</i> (E ₂)	50 ¹	50 ¹	50 ^{r+}	4 ⁺
<i>Padus avium</i> (E ₁)	.	75 ^{+a}	2 ¹	.
<i>Brachypodium sylvaticum</i>	.	75 ^{+a}	5 ¹	.
<i>Carex acutiformis</i>	.	75 ^{+a}	15 ¹⁻⁴	.
<i>Impatiens parviflora</i>	.	50 ⁺¹	.	.
<i>Festuca gigantea</i>	.	50 ⁺	.	.
<i>Plagiomnium</i> sp. (E ₀)	.	50 ⁺¹	2 ¹	.
<i>Mycelis muralis</i>	.	50 ^r	2 ⁺	.
<i>Viburnum opulus</i> (E ₁)	.	50 ⁺	5 ⁺¹	.

Table 1 (continued)

Cluster	1	2	3	4
No. of relevés	2	4	40	24
Cluster 3: <i>Alnetea glutinosae</i>, <i>Alnion glutinosae</i>				
<i>Eupatorium cannabinum</i>	.	.	58 ⁺¹	8 ⁺
<i>Symphytum officinale</i>	.	.	42 ^{r-a}	12 ⁺¹
<i>Poa trivialis</i>	.	.	30 ^{+a}	.
<i>Bidens tripartita</i>	.	.	25 ^{r-1}	.
<i>Peucedanum palustre</i>	.	25 ¹	65 ^{+a}	42 ^{+a}
<i>Carex paniculata</i>	.	.	22 ^{+a}	.
<i>Equisetum fluviatile</i>	.	25 ¹	45 ^{+b}	25 ^{+a}
Dominant of shrub layer				
<i>Salix cinerea</i> (E ₂)	100 ⁺	.	45 ^{r-a}	100 ^{a-5}
<i>Salix cinerea</i> (E ₁)	50 ⁺	.	2 ¹	17 ^{+a}
Cluster 4: <i>Franguletea</i>, <i>Salicion cinereae</i>				
<i>Typha angustifolia</i>	.	.	.	50 ⁺³
<i>Rumex hydrolapathum</i>	.	.	.	46 ⁺¹
<i>Typha latifolia</i>	.	.	2 ⁺	42 ⁺¹
<i>Hygrohypnum</i> sp. (E ₀)	.	.	.	38 ^{+a}
<i>Eurhynchium schleicheri</i> (E ₀)	.	.	.	33 ^{+a}
<i>Glyceria maxima</i>	.	.	30 ^{+b}	58 ^{+a}
<i>Salvinia natans</i>	.	.	.	25 ^{1-a}
<i>Hydrocharis morsus-ranae</i>	.	.	.	25 ¹⁻³
<i>Stratiotes aloides</i>	.	.	.	25 ^{+a}
<i>Phragmites australis</i>	.	.	20 ^{r+}	50 ⁺⁴
Other taxa with occurrence at least 10% of all relevés				
<i>Carex pseudocyperus</i>	100 ^{+a}	100 ⁺¹	100 ^{r-b}	100 ⁺⁴
<i>Lysimachia vulgaris</i>	50 ^a	100 ^{+a}	98 ⁺³	79 ^{r-a}
<i>Lycopus europaeus</i>	.	100 ^{r-1}	98 ^{+a}	83 ⁺³
<i>Solanum dulcamara</i>	50 ^a	50 ^{r-a}	90 ⁺³	79 ⁺³
<i>Thelypteris palustris</i>	.	50 ^{r+}	82 ⁺⁴	67 ¹⁻⁵
<i>Carex elongata</i>	50 ⁺	100 ¹⁻³	88 ⁺⁴	38 ⁺³
<i>Galium palustre</i>	50 ⁺	50 ⁺	82 ^{+a}	46 ^{+a}
<i>Scutellaria galericulata</i>	.	75 ⁺	45 ^{r-a}	67 ^{+a}
<i>Lythrum salicaria</i>	.	25 ⁺	52 ⁺¹	62 ^{+a}
<i>Dryopteris carthusiana</i> agg.	50 ^a	75 ^{1-a}	70 ⁺³	4 ¹
<i>Calamagrostis canescens</i>	50 ⁺	25 ¹	50 ^{r-a}	46 ⁺³
<i>Frangula alnus</i> (E ₂)	50 ^a	50 ³	65 ⁺³	8 ^{+a}
<i>Cicuta virosa</i>	.	.	35 ^{+a}	54 ⁺¹
<i>Urtica dioica</i>	50 ⁺	50 ⁺¹	52 ^{r-3}	8 ⁺¹
<i>Carex elata</i>	.	.	45 ^{+a}	29 ^{+a}
<i>Rubus caesius</i>	50 ⁺	25 ¹	50 ⁺¹	8 ^{a-3}
<i>Stachys palustris</i>	.	.	42 ⁺³	25 ⁺¹
<i>Iris pseudacorus</i>	.	25 ¹	40 ^{+a}	21 ⁺¹
<i>Phellandrium aquaticum</i>	.	.	35 ⁺³	29 ^{+a}
<i>Athyrium filix-femina</i>	100 ^{+a}	100 ^{a-3}	35 ^{+a}	.
<i>Cirsium palustre</i>	.	25 ⁺	42 ^{r-a}	8 ⁺
<i>Carex riparia</i>	.	.	32 ⁺⁵	29 ⁺⁴
<i>Ranunculus repens</i>	100 ^{1-a}	25 ⁺	30 ^{r-a}	12 ⁺¹
<i>Lemna minor</i>	.	.	20 ^{r-3}	29 ⁺³
<i>Lysimachia nummularia</i>	50 ⁺	.	25 ^{+a}	12 ⁺³
<i>Frangula alnus</i> (E ₁)	50 ⁺	75 ⁺	25 ⁺¹	.

Table 1 (continued)

Cluster	1	2	3	4
No. of relevés	2	4	40	24
<i>Epilobium palustre</i>	.	.	25 ⁺	17 ⁺¹
<i>Deschampsia cespitosa</i>	50 ⁺	100 ⁺	20 ⁺¹	.
<i>Bidens cernua</i>	.	.	15 ⁺¹	29 ⁺¹
<i>Carex remota</i>	100 ⁺¹	100 ^{+a}	15 ^{+a}	.
<i>Alisma plantago-aquatica</i>	.	.	22 ^{r-a}	12 ⁺¹
<i>Juncus effusus</i>	.	50 ^{r+}	20 ^{r-a}	4 ⁺
<i>Calystegia sepium</i>	.	.	20 ⁺³	12 ⁺¹
<i>Sium latifolium</i>	.	.	12 ^{r-1}	25 ⁺
<i>Mentha aquatica</i>	.	25 ⁺	18 ⁺¹	8 ⁺
<i>Phalaroides arundinacea</i>	.	20 ^{+a}	18 ^{r-a}	4 ⁺
<i>Carex appropinquata</i>	.	.	20 ^{+a}	8 ⁺¹
<i>Oxalis acetosella</i>	100 ¹	100 ⁺³	8 ⁺	.
<i>Brachythecium rivulare</i> (E ₀)	.	25 ^b	2 ⁺	29 ^{+a}
<i>Dryopteris cristata</i>	.	.	20 ^{+a}	4 ^a
<i>Carex vesicaria</i>	.	.	20 ⁺⁴	4 ⁺
<i>Menyanthes trifoliata</i>	.	.	8 ⁺¹	25 ⁺³
<i>Sparganium erectum</i>	.	.	12 ^{+a}	17 ⁺¹
<i>Persicaria amphibia</i>	.	.	8 ⁺	25 ⁺
<i>Equisetum palustre</i>	50 ⁺	.	15 ⁺¹	43
<i>Cardamine pratensis</i>	50 ⁺	.	8 ⁺	17 ⁺¹
<i>Carex acuta</i>	.	.	8 ⁺¹	21 ^{+a}
<i>Sorbus aucuparia</i> (E ₁)	50 ¹	100 ⁺¹	5 ^{r+}	.
<i>Sorbus aucuparia</i> (E ₂)	50 ⁺	100 ^{r-1}	5 ⁺	.
<i>Betula pubescens</i> (E ₃)	.	.	2 ⁺	.
<i>Betula pubescens</i> (E ₂)	.	.	12 ^{+a}	8 ⁺
<i>Erechtites hieraciifolius</i>	.	.	15 ⁺¹	4 ¹
<i>Myosoton aquaticum</i>	.	.	18 ⁺¹	.

occurrence of aquatic plants with a low frequency and cover of marshy species. Although macroscopic alga *Chara vulgaris* dominated in the first cluster, a set of hydrophytes determined the physiognomy of the second cluster (Table 2). This species composition is typical for the submerged macroalgal stonewort swards of the alliance *Charion vulgaris* (class *Charetea intermediae*; first cluster) and for pleustophytic aquatic vegetation of the *Lemnetea* class (second cluster). The third cluster was mainly composed of *Cicuta virosa*, *Rumex hydrolapathum*, *Thelypteris palustris* and pleustophytic hydrophytes. It represented the vegetation of the non-stabilised organic substrates of the alliance *Carici-Rumicion hydrolapathi* (class *Phragmito-Magnocaricetea*; Fig. 1d). The vegetation of the fourth cluster was relatively rare and contained only four phytosociological relevés (Table 2). These stands were dominated by species of shallow lentic and lotic habitats with fluctuating water, such as *Leersia oryzoides* and *Phellandrium aquaticum*. They were classified into the alliance *Eleocharito palustris-Sagittarion sagittifoliae* (class *Phragmito-Magnocaricetea*). The vegetation of littoral zones and shallow flooded terrain depressions

was primarily created by competitively strong species (*Equisetum fluviatile*, *Glyceria maxima*, *Phragmites australis* and *Typha angustifolia*) or by marshy tall-sedges (*Carex elata*, *C. riparia*, *C. rostrata* and *C. vesicaria*). This floristic spectrum indicates that the fifth cluster grouped reed swamp vegetation of the alliance *Phragmition communis* (class *Phragmito-Magnocaricetea*), while the sixth cluster included sedge-bed marsh vegetation of the alliances *Magnocaricion elatae* and *Magnocaricion gracilis* (*Phragmito-Magnocaricetea*). The last three clusters were poorly documented by phytosociological relevés. Species of the genus *Bidens* (*B. cernua* and *B. tripartita*) found an ecological optimum in the seventh cluster, which corresponded to the summer-annual pioneer vegetation of periodically nutrient-rich riverbanks and drained muddy bottoms of eutrophic waterbodies within the alliance *Bidention tripartitae* (class *Bidentetea*). Species of the exposed bottom, such as *Cyperus fuscus* and *Juncus articulatus*, were rich in cluster eight. These stands of the pioneer ephemeral dwarf-cyperaceous vegetation of periodically freshwater flooded habitats were interpreted as the order *Nanocyperetalia* (class *Isoëto-Nanojuncetea*). The last cluster was differentiated by the graminoids *Molinia caerulea* agg. and *Juncus effusus* (Table 2), representing the vegetation of wet meadows on nutrient-poor soils of the alliance *Molinion caeruleae* (class *Molinio-Arrhenatheretea*).

Although the occurrence of *C. pseudocyperus* was recorded in the vegetation of nine phytosociological classes, the species frequency and cover values revealed its ecological affinity, especially to habitats of the classes *Phragmito-Magnocaricetea* (~ 50% of all relevés), *Alnetea glutinosae* (~ 25%) and *Franguletea* (~ 15%). Overall, this species occurred in the following plant communities: class *Alnetea glutinosae* (alliance *Alnion glutinosae*), class *Alno glutinosae-Populetea albae* (alliance *Alnion incanae*), class *Bidentetea* (alliance *Bidention tripartitae*), class *Charetea intermediae* (alliance *Charion vulgaris*), class *Franguletea* (alliance *Salicion cinereae*), class *Isoëto-Nanojuncetea* (order *Nanocyperetalia*), class *Lemnetea* (including all alliances which belong to the class, *Lemnion minoris*, *Stratotion* and *Utricularion vulgaris*), class *Molinio-Arrhenatheretea* (alliance *Molinion caeruleae*) and class *Phragmito-Magnocaricetea* (alliances *Carici-Rumicion hydrolapathi*, *Eleocharito palustris-Sagittarion sagittifoliae*, *Magnocaricion gracilis*, *Magnocaricion elatae* and *Phragmition communis*).

Discussion

A detailed revision of chorological records based on herbarium specimens, published literature and database sources, combined with robust vegetation and chorological observations, provided novel insights into the current distribution,

Table 2 Shortened synoptic table of non-forest plant communities with *Carex pseudocyperus* with percentage frequency and cover range (in upper index). Diagnostic taxa (see Method chapter) and dominant taxa (with cover medium $\geq 2b$) are presented in individual clusters according to both decreasing of phi-coefficient; other taxa according to decreasing of frequency in all clusters

Cluster	1	2	3	4	5	6	7	8	9
No. of relevés	1	9	16	4	25	27	3	4	2
Cluster 1: <i>Charetea intermediae</i>, <i>Charion vulgaris</i>									
<i>Chara vulgaris</i>	100 ⁵	.	.	.	.	.	.	.	.
Cluster 2: <i>Lemnetea</i>									
<i>Utricularia vulgaris</i> agg.	.	78 ^{a-4}	.	.	4 ¹	15 ^{+a}	.	25 ¹	.
<i>Spirodela polyrrhiza</i>	.	44 ⁺¹	12 ¹	.	8 ⁺	.	.	.	.
<i>Aldrovanda vesiculosa</i>	.	33 ⁺³	.	.	.	.	.	.	.
<i>Ricciocarpos natans</i> (E ₀)	.	33 ^{+a}	.	.	.	.	.	.	.
<i>Lemna trisulca</i>	.	67 ¹⁻³	19 ^{r-1}	50 ⁺	4 ¹	11 ^{+a}	.	.	.
<i>Stratiotes aloides</i>	.	67 ⁴⁻⁵	44 ⁺³	25 ¹	20 ^{+a}	7 ¹⁻³	.	.	.
<i>Hydrocharis morsus-ranae</i>	.	67 ^{a-4}	50 ^{1-b}	.	40 ^{r-4}	22 ⁺³	.	.	.
<i>Riccia fluitans</i> (E ₀)	.	11 ⁴	.	.	.	.	.	.	.
Cluster 3: <i>Phragmito-Magnocaricetea</i>, <i>Carici-Rumicion hydrolapathi</i>									
<i>Cicuta virosa</i>	.	44 ^{+a}	94 ⁺³	.	24 ^{+b}	4 ⁺	.	.	.
<i>Thelypteris palustris</i>	.	.	25 ³⁻⁴	.	4 ^b	.	.	.	.
Cluster 4: <i>Phragmito-Magnocaricetea</i>, <i>Eleocharito palustris-Sagittarion sagittifoliae</i>									
<i>Phellandrium aquaticum</i>	.	.	50 ⁺⁵	75 ^{a-4}	36 ^{r-a}	.	67 ^a	25 ⁺	.
<i>Leersia oryzoides</i>	.	.	.	25 ⁵	4 ^r	.	33 ⁺	25 ⁺	.
Cluster 5: <i>Phragmito-Magnocaricetea</i>, <i>Phragmiton communis</i>									
<i>Phragmites australis</i>	.	.	.	.	40 ⁺⁵	33 ⁺³	33 ³	25 ⁺	.
<i>Typha angustifolia</i>	.	11 ⁺	19 ^{1-a}	.	24 ⁺⁵	33 ^{r-3}	.	25 ⁺	.
<i>Equisetum fluviatile</i>	.	.	12 ^{a-3}	.	20 ^{b-4}	19 ¹⁻³	.	.	.
Cluster 6: <i>Phragmito-Magnocaricetea</i>, <i>Magnocaricion elatae</i> and <i>Magnocaricion gracilis</i>									
<i>Carex elata</i>	.	.	6 ^a	.	20 ^{1-b}	56 ⁺⁵	33 ⁴	.	.
<i>Carex rostrata</i>	.	.	.	.	.	19 ¹⁻³	.	25 ¹	.
<i>Carex acutiformis</i>	.	.	.	.	.	15 ¹⁻⁵	.	.	.
<i>Carex paniculata</i>	.	.	31 ¹⁻⁴	.	4 ¹	4 ⁵	.	.	.
Cluster 7: <i>Bidentetea</i>, <i>Bidention tripartitae</i>									
<i>Bidens cernuus</i>	.	.	25 ⁺³	75 ⁺¹	20 ^{r-3}	15 ^{r+}	67 ³⁻⁴	.	.
<i>Bidens tripartita</i>	.	.	.	.	4 ³	7 ⁺	33 ³	.	.
Cluster 8: <i>Isoëto-Nanojuncetea</i>, <i>Nanocyperetalia</i>									
<i>Cyperus fuscus</i>	.	.	.	.	.	.	.	50 ^{b-3}	.
<i>Juncus articulatus</i>	100 ¹	.	.	25 ⁺	.	11 ⁺	.	100 ¹⁻⁵	50 ^b
Cluster 9: <i>Molinio-Arrhenatheretea</i>, <i>Molinion caeruleae</i>									
<i>Molinia caerulea</i> agg.	.	.	.	.	.	.	.	.	100 ^{+a}
<i>Juncus effusus</i>	.	.	.	25 ⁺	8 ¹	11 ⁺¹	.	50 ^{+b}	100 ^{b-4}
Other species with occurrence at least 10% of all relevés									
<i>Carex pseudocyperus</i>	100 ⁺	100 ⁺	100 ⁺⁴	100 ¹⁻⁴	100 ^{r-4}	100 ^{r-5}	100 ^{r-a}	100 ^{r-3}	100 ⁺
<i>Lycopus europaeus</i>	.	44 ^{r+}	38 ^{+a}	100 ⁺³	64 ^{r-3}	63 ^{r-a}	100 ⁺³	75 ^{r-a}	100 ¹
<i>Lythrum salicaria</i>	.	.	12 ⁺¹	25 ⁺	60 ^{r-3}	78 ⁺³	67 ¹⁻³	100 ^{+b}	50 ⁺
<i>Lysimachia vulgaris</i>	.	11 ^r	44 ^{+a}	25 ⁺	36 ^{+a}	63 ⁺³	33 ¹	.	100 ^{+a}
<i>Lemna minor</i>	.	100 ¹⁻⁵	69 ⁺³	50 ⁺³	40 ⁺⁵	19 ^{+a}	.	.	.
<i>Rumex hydrolapathum</i>	.	44 ^{r+}	50 ¹⁻³	75 ^{+a}	28 ⁺³	26 ^{r-b}	.	.	.
<i>Glyceria maxima</i>	.	44 ^{r+}	12 ¹⁻³	50 ⁺¹	52 ¹⁻⁵	30 ^{r-b}	.	.	.
<i>Alisma plantago-aquatica</i>	.	.	19 ¹	25 ⁺	40 ^{r-a}	33 ^{r-a}	100 ^{+a}	75 ^{r+}	.
<i>Galium palustre</i>	.	.	38 ^{1-a}	.	40 ^{+a}	37 ^{+a}	33 ¹	25 ¹	50 ^a
<i>Typha latifolia</i>	.	.	19 ^{1-b}	.	52 ⁺⁵	26 ⁺¹	67 ⁺¹	25 ¹	.
<i>Persicaria amphibia</i>	.	.	19 ^{+a}	50 ⁺	24 ^{+a}	44 ^{+b}	33 ^a	25 ⁺	.
<i>Salvinia natans</i>	.	56 ¹⁻³	44 ⁺³	75 ⁺¹	28 ⁺³	7 ⁺¹	.	.	.
<i>Solanum dulcamara</i>	.	.	50 ^{+a}	.	36 ^{r-3}	19 ^{+a}	33 ¹	.	.
<i>Sparganium erectum</i>	.	22 ⁺	25 ⁺¹	50 ⁺¹	32 ^{r-5}	11 ^{r+}	33 ^r	25 ^r	.

Table 2 (continued)

Cluster	1	2	3	4	5	6	7	8	9
No. of relevés	1	9	16	4	25	27	3	4	2
<i>Scutellaria galericulata</i>	.	.	44 ⁺	50 ⁺	32 ^{r-a}	7 ⁺¹	33 ¹	.	.
<i>Iris pseudacorus</i>	.	.	12 ^{+a}	.	24 ⁺⁵	37 ^{+a}	.	25 ⁺	.
<i>Carex riparia</i>	.	.	.	.	36 ⁺³	33 ⁺⁵	.	.	50 ⁺
<i>Carex vesicaria</i>	.	.	6 ^b	.	20 ^{+b}	30 ⁺⁴	.	50 ⁺¹	50 ¹
<i>Mentha aquatica</i>	.	.	19 ^{1-a}	.	28 ⁺⁴	19 ⁺¹	.	.	.
<i>Salix cinerea</i> (E ₁)	.	.	12 ^{r+}	25 ⁺	20 ¹⁻³	19 ^{r-3}	.	.	.
<i>Agrostis stolonifera</i> agg.	.	.	.	25 ⁺	8 ^{a-3}	22 ^{+a}	.	25 ¹	100 ⁺
<i>Ranunculus repens</i>	.	.	.	25 ⁺	8 ¹	33 ^{r-a}	.	.	.
<i>Symphytum officinale</i>	.	.	.	.	4 ^a	41 ⁺³	.	.	.
<i>Ranunculus lingua</i>	.	.	12 ^{1-b}	.	24 ⁺³	7 ^{a-b}	.	.	.
<i>Sium latifolium</i>	.	.	6 ⁺	.	16 ^{r-1}	19 ^{+b}	.	.	.
<i>Lysimachia nummularia</i>	.	.	.	25 ⁺	8 ^a	26 ^{+a}	.	.	.
<i>Rorippa amphibia</i>	.	11 ⁺	.	50 ⁺¹	20 ^{r-1}	4 ⁺	.	.	.
<i>Calamagrostis canescens</i>	.	.	19 ⁺	.	12 ^{1-b}	7 ^{a-a}	.	25 ⁺	.
<i>Eleocharis palustris</i>	.	.	.	.	12 ⁺³	19 ⁺¹	33 ⁺	.	.

habitat preferences, and potential threats to *Carex pseudocyperus* in Slovakia, revealing notable geographical differences. This sedge species forms loose to dense clumps with ornamental bright yellow-to-green leaves and lowest bract exceeding the inflorescence (Koopman et al. 2025). It is easily determined by its robust, pendulous female spikes (Fig. 1a, b), consisting of dense utricles that gradually taper into a long beak with slightly spreading teeth (Dostál and Červenka 1992; Grulich et al. 2024). This species was confused with some tall sedges of eutrophic sites in the studied herbaria, but in a few cases, we could not exclude that this was due to a labelling mistake. Published records without any support of herbarium specimens can therefore be considered almost exclusively correct, which highlights the high relevance of the present distribution pattern (Fig. 2).

Most of the stable occurrences with numerous localities of the species were documented in lowlands of south-western and eastern Slovakia (especially in Záhorská nížina and Východoslovenská nížina lowlands), where its distribution continuously extends to Pannonian localities in Hungary (Bartha et al. 2015). In other regions of Slovakia, this sedge species is considered relatively rare or even absent and is, thus, listed among regionally threatened vascular plants (e.g. in the Muránska planina Mts; Kochjarová et al. 2004). The distribution pattern also underlines the ecological optimum of the species along the elevational gradient. It is widespread from lowland to mountainous areas, although most occurrences have been recorded at low and middle elevations (Appendix 1). A similar pattern has been observed in the neighbouring Czech Republic, where the lowest elevation is around 150 m in Lanžhot and the highest reaches 870 m in Šumava (České Žleby) (Grulich et al. 2024). This elevation range also overlaps with that of Mediterranean European

countries, where *C. pseudocyperus* is mostly found at elevations from sea level to 1000 m a.s.l. (Italy; Laghi et al. 2015) or up to 1200 m a.s.l. (Spain, Portugal; Muñoz-Secilla and Sánchez-García 2013).

Our results suggest that some past localities of the species have completely disappeared, and many other populations have been reduced in abundance. For example, the oldest records of *C. pseudocyperus* in Slovakia (Reuss 1853) comprised ditches near the town of Kežmarok, but there is a lack of current chorological data for this locality. Although this species is almost absent from this cold region of northern Slovakia (Fig. 2), it was confirmed at a nearby locality in gravel pits in the village of Batizovce (Spišské kotliny Basins) and newly discovered near the village of Plaveč (Čergov Mts; Appendix 1). Among the oldest records of *C. pseudocyperus* are those associated with the city of Bratislava and the Danube River, where the species was reported to be abundant (Reuss 1853). Since the author did not provide a precise localisation or further site description, it cannot be ruled out that this record is the historically known locality of Šúr, situated near the city of Bratislava (south-western Slovakia). Here, *C. pseudocyperus* still grows today in the forest understorey of well-preserved alder swamps (Fig. 1c; Appendix 1). The Slovak inland Danube Delta region has experienced strong human-induced changes over recent decades. The negative effects of river regulation and channelisation were amplified by intensive land use and increasing population density (Schindler et al. 2016), which generally have serious ecological consequences for the biodiversity value of riparian areas (Poff et al. 2007; Slezák et al. 2022; Havrdová et al. 2023). In this case, they led to extensive landscape degradation with a loss of numerous wetland habitats and species over the years

(Petrášová-Šibíková et al. 2017). Although the abundance of this sedge species may suffer under succession due to rapid spread and dominance of tall herb or graminoid competitors, it was recorded at several localities along the Danube River (e.g. open gravel deposits in the city of Bratislava) and in its surroundings. Paleobotanical research on an extinct branch of the Danube River near the village of Vrakúň also demonstrated the long-term presence of *C. pseudocyperus* in the Danube region, although its occurrence at this location has not been recently confirmed (Pišút and Procházka 2012).

Many localities situated outside the national network of protected areas showed high levels of naturalness and ecological functions in the landscape, such as wetland and floodplain ecosystems along the Laborec and Latorica Rivers (eastern Slovakia). Species populations also thrive on sandy soils typical of the Záhorská nížina lowlands, which are less affected by human activities than the Podunajská nížina lowlands due to the less suitable environment for intensive agriculture (Hrivnák et al. 2024). This species is shade tolerant but can readily colonise exposed substrates of various quality (e.g. sandy and gravelly substrates with different organic mud thicknesses), which developed either by natural floods as new depositional bars in rivers or by removal of riparian vegetation due to gravel mining in active river channels or floodplains. This is consistent with our recent observations of an increasing number of occurrences in anthropogenically influenced habitats. These include gravel ditches, pits, muddy margins and littoral zones of artificial water bodies, and drainage channels (e.g. gravel pits in Batizovce; Kochjarová and Hrivnák 2017). Similar findings with relation to the artificial habitats has already been observed in other regions of Slovakia and other countries (e.g. Nikolin et al. 2016; Dančák and Kocián 2018).

The dynamics of species distribution records are also worth discussing, as we observed a significant increase in the number of recent records (since 2000), which almost equalled the total findings for the previous half-century. Our results suggest that *C. pseudocyperus* tolerates fluctuations in resource availability and inhabits novel riparian sites or temporarily persists in degraded ones, which may facilitate its rising occurrence data. This positive trend should be interpreted carefully, as raising awareness and ecological knowledge about the importance of wetland and floodplain ecosystems may encourage more intensive biodiversity research and plant species monitoring in the modern era. The increase in new species records was mainly associated with literature sources and herbaria. We expected a similar positive trend in species occurrence data from online citizen science platforms, such as iNaturalist. However, these records have not increased as rapidly as those for other vascular plants (i.e. only 7 observations of *C. pseudocyperus* in Slovakia on iNaturalist, accessed on 24th January 2025), which could be explained by the well-established low level of public interest in

graminoid species and by less attractive and accessible habitats for this species.

Our vegetation analysis showed that *C. pseudocyperus* in Slovakia prefers wetland and riparian habitats, with a scattered occurrence in other plant communities, such as aquatic vegetation, wet meadows, pioneer vegetation of periodically flooded or exposed bottoms of freshwater habitats. The high frequency and cover values in alder swamp forests (*Alnion glutinosae* alliance) and marshy vegetation of the *Phragmito-Magnocaricetea* class coincide with the vegetation affinity of this species reported throughout Europe (Appendix S3 in Doua et al. 2016; Appendix S7 in Landucci et al. 2020). Vegetation syntheses performed on continental or regional scales identified *C. pseudocyperus* as a diagnostic species of the alliance *Carici-Rumicion hydrolapathi* (*Phragmito-Magnocaricetea*), which was manifested in Europe (Landucci et al. 2020) and in some Central European countries (Austria – Grabherr and Mucina 1993; Poland – Matuszkiewicz 2008; Czech Republic – Šumberová et al. 2011; Hungary – Borhidi et al. 2012). Plant communities of this alliance are extremely rare in Slovakia because many suitable sites vanished in the last few decades due to habitat destruction, river regulation and associated changes in water regime (Hrivnák and Oľahelová 2023). Specifically, this species occurred mainly in the association *Cicuto-Caricetum pseudocyperi* (Valachovič 2001), but there are no recent phytosociological relevés documenting its species composition. All available vegetation records were confined to a small geographic area in eastern Slovakia and were sampled in the period 1957–1984. The vegetation preference of *C. pseudocyperus* for alder swamps and non-forest wetland habitats partially overlaps with that of some other marshy tall sedges, namely *Carex acuta*, *C. acutiformis*, *C. paniculata* and *C. riparia* (Appendix S3 in Doua et al. 2016; Appendix S7 in Landucci et al. 2020). In contrast to these tall sedges, *C. pseudocyperus* showed a broader ecological niche and exclusive position in unique habitats of the alliance *Carici-Rumicion hydrolapathi* in Central Europe.

The distribution pattern of the species showed geographical discrepancies in Slovakia. Although the frequency of its new records increased, the abundance of several populations was reduced, or localities disappeared. Its vulnerability seems to be closely linked to the susceptibility of wetland and floodplain habitats to changes in the water regime, land use and climate, which may severely negatively modify environmental conditions for this species. These habitat threats suggest that *C. pseudocyperus* deserves more attention.

Appendix 1

List of localities for each phytogeographical district with *Carex pseudocyperus* occurrence in Slovakia. The name of the city, town, or village is listed first, followed by a more

detailed specification of the location and the altitude, if this data was available. The municipalities are sorted alphabetically within the phytogeographical units. Herbarium specimens, unpublished records, literature sources and online database data are provided in the brackets

Pannonicum

2. Ipeľsko-rimavská brázda Region: Chanava, northeast of the village, Veľká hať, oxbow of the Slaná River, 157 m (Hrivnák, Reussia 3/1, Table 1, rel. 3, 2006). – Poltár, south edge of the town, 233 m (Hrivnák 1999 SAV; Bednár F., iNat ID 181278956, 2023). – Zelené, fishpond NNE of the village, 220 m (Hrivnák 2018–2019 ined.). **4. Záhorská nížina Lowland:** Borský Peter, Special Areas of Conservation Bahno (Hegedúšová & Škodová, Bull. Slov. Bot. Spoločn. 28, p. 254, 2006). – Borský Svätý Jur, Tomky settlement, 180 m (Dvořák 1971 BRNM). – Cerová, edge of the military area (Kollár et al., Phytopedon 4/2, Table 3, rels 1, 16–17, 21, 2005). – Cerová, Pustý mlyn (s. coll. ex herb. Špaček 1949 BRNU; Šmarda 1950 BRNM; Součková 1950 BRNM). – Jablonica (Šmarda, Čas. Mor. Mus. 36, Table 7, rel. 1, 1951). – Jablonica, Na Šranku, peat meadows (Šmarda 1949 BRNM). – Kátov, Baráky fishpond west of the village (Hrivnák, Oťaheľová & Valachovič 2008 ined.). – Kostolište, northwest of the village (Malovcová-Staníková, Diss. Thesis (msc.) depon. in Bot. ústav SAV Bratislava, Table 2, rels 1, 2, 2001; Malovcová-Staníková, Acta Rer. Natur. Mus. Nat. Slov. 49, Table 1, rel. 1, 2003). – Kúty, near the railway station, 160 m (Staněk 1947 BRNM). – between Kúty and Gbely (Domin 1931 PRC). – between Kúty and Čáry (Domin 1931 PRC). – Lakšárska Nová Ves, west of the village, Červený rybník, 195–200 m (Valenta 1937, 1938 BRA; Šmarda 1950 BRNM; Ružička 1952 SAV). – Lakšárska Nová Ves, Husársky rybník, 200 m (Malovcová-Staníková, Bull. Slov. Bot. Spoločn. 22, p. 189–190, 2000). – Lakšárska Nová Ves, southeast of the village, 232 m (Oťaheľová 1984 ined.). – between Lakšárska Nová Ves and Studienka, 230 m (Staněk 1946 BRNM). – Lozorno, Water reservoir Lozorno I, ESE of the village and south of the Kopanička hill (Hrivnák, Oťaheľová & Valachovič 2008 ined.). – Malacky (Futák 1948 SLO; s. coll. ex herb. Špaček 1948 BRNU). – Malacky, the edge of a pond (Opluštilová 1947 SLO). – Malacky, depression Bahno, 180 m (Valachovič 1998 ined.). – Malacky, Orlovské vršky (Hegedúšová & Škodová, Bull. Slov. Bot. Spoločn. 28, p. 246, 2006). – Malacky, Marheček rybníky, 143–170 m (Řepka 1985 BRNM; Suja 2023 MBU; Valachovič 1998 ined.; Hrivnák, Oťaheľová & Valachovič 2008 ined.; Malovcová-Staníková, Diss. Thesis (msc.) depon. in Bot. ústav SAV Bratislava, Table 2, rels 1, 2, 2001; Malovcová-Staníková, Acta Rer. Natur. Mus. Nat. Slov. 49, Table 1, rel. 2, 2003; Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013). – between Malacky and

Studienka, 170–172 m (Valenta 1939 BRA; Stanová, Dipl. Thesis (msc.) depon. in PriF UK Bratislava, Table 2, rel. 6, 1991). – Plavecké Podhradie, the left bank of the Rudava River, 185 m (Stanová, Dipl. Thesis (msc.) depon. in PriF UK Bratislava, Table 2, rel. 14, 1991). – Plavecký Peter, Hanšpíle field on the left bank of the Rudava River (Eliáš jun. 2004 NI). – Plavecký Peter, peatland on the right bank of the Rudava River opposite the inflow of the Hrudky Stream, 230 m (David 1987 LTM). – Plavecký Štvrtok, Nature Reserve Bezodné, lake (Feráková & Rácová 1985 SLO). – Prievaly, northwest of the village, lakes (Somogyi & Hodálová, Bull. Slov. Bot. Spoločn. 24, p. 144, 2002). – Rohožník, northwest of the village, alluvium of the Rudávka River (Valachovič 1997 SAV). – Rohožník, water reservoir Vývrat, 234 m (Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013; Kochjarová et al., Bull. Slov. Bot. Spoločn. 36/1, p. 86, 2014). – Sekule, west of the village, anabranč near Malolevářský channel (Malovcová-Staníková, Acta Rer. Natur. Mus. Slov. 50, Table 3, rel. 17, 2004). – Šajdíkové Humence, Horniačka (Kollár et al., Phytopedon 4/2, Table 3, rel. 13, 2005). – Šajdíkové Humence, 180–187 m (Dvořák 1963 BRA; Bottlíková 1965 BRA; Kollár et al., Phytopedon 4/2, Table 3, rels 16–17, 21, 2005). – Šaštín-Stráže, Special Areas of Conservation Vanišovec (Hegedúšová & Škodová, Bull. Slov. Bot. Spoločn. 28, p. 258, 2006). – Studienka (Holzknecht 1946 BRNU). – Studienka, in the Rudava River valley south of the village, 180 m (Chrtek & Křísa 1964 PRC). – Studienka, confluence of the Rudava and Rudávka Rivers, 175 m (Stanová, Dipl. Thesis (msc.) depon. in PriF UK Bratislava, Table 2, rel. 15, 1991). – Veľké Leváre, Nature Reserve Abrod, 200 m (Posltová, Dipl. Thesis (msc.) depon. in PriF UK Bratislava, Table 3, rel. 5, 1997). – Veľké Leváre, alluvium of the Rudava River, between village and the tributary of Rudávka River (Stanová, Bull. Slov. Bot. Spoločn. 15, p. 65, 1993). – Vysoká pri Morave, Bezedné Lake, 139 m (Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013). – Závod, northwest of the village, 150–160 m (Řepka 1986 BRNM; Barta 2017 W; Balátová-Tuláčeková, Veg. ČSSR, B3, Table 7, rels 2–3, 1976). **5. Devínska Kobyla Mts:** Bratislava-Karlova Ves (Rapoš P., iNat ID 3949195304, 2021). **6. Podunajská nížina Lowland:** Bratislava-Petržalka, Chorvátske rameno Anabranč near Technopol (Valenta 2000 BRA). – Bratislava-Petržalka, former island Pečňa, at deposited gravel of the Dunube River (Letz 2018 ined.). – Bratislava-Podunajské Biskupice, Biskupické rameno, littoral area, 146 m (Slezák 2025 ined.). – Bratislava-Vajnory, gravel pit Vajnorka (Feráková 1972 SLO). – Dolný Bar, Hroboňovské rybníky (Eliáš jun. 2017 NI). – Gabčíkovo, oxbow Dekan (Šuchová 1972, 1973 SAV). – Jahodná, south of the village (tommy501, iNat ID 54763235, 2020). – Kalná nad Hronom, elevation point 161 (Šomšák, Diss. Thesis (msc.) depon. in PriF UK Bratislava, p. 300, rel. 1, 1967). – Kľúčovec,

National Nature Reserve Čičovské mŕtve rameno (Hrivnák & Oťaheľová 2021 ined.). – Koplastovce, muddy and gravelly edges of the gravel pits, 141–143 m (Slezák 2022 ined.). – Lúka, north of the Lúčanské rameno, 170–171 m (Slezák 2022 ined.; Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013). – Martovce, alluvium of Žitava River, SSE of the village, 113 m (Slezák 2025 ined.). – Nové Mesto nad Váhom, eastern edge of the town, edge of the gravel pit in inundation area of the Váh River, 181 m (Hrivnák & Oťaheľová 2008; Slezák 2022 ined.). – Pezinok (Holuby 1921 PRC). – Pusté Úľany, Tarnocký (ut Trnavský) channel, south of the Veľkogrobský rybník, 130 m (Šípošová & Komárová 1996 SAV). – Pusté Úľany, between two channels (Mráz 1996 SAV). – Svätý Jur, Nature Reserve Šúr, 129–130 m (Wiesbauer 1865 W; Holuby 1911, 1913, 1914, 1922 PRC, 1914 BRA; Zigmundík 1913, 1914 BRA; Mikuláš 1922 PRC; Ptačovský 1922 SAV; Dlabáčová 1934 PRC; Krist 1937 BRNU; Májovský 1941 SLO; Futák & Juričková 1942 SLO; Berta 1955, 1956 SLO; Mérgl 1989 SAV; s. coll. s. dat. PRC; Slezák 2022 ined.; Kornhuber, Verh. Ver. Naturkunde Pres., Vol. 3/2, p. 33, 1858; Berta, Dipl. Thesis (msc.) depon. in PriF UK Bratislava, p. 67, rels 1, 8–9, 11, 14, 1957). – between Svätý Jur and Grinava, wet ditch by the road, 135 m (Staněk 1946 BRNM). – Topoľníky, northern edge of the village, muddy bank of the Klátovské rameno, near the road bridge, 110 m (Slezák 2023 ined.). – Trhová Hradská, east of the village, Klátovské rameno, muddy bank, 118 m (Slezák 2023 ined.). – Veľké Bielice, at the mineral spring (Eliáš jun. 2001 NI). **8. Východoslovenská nížina Lowland:** Boľ (Berta, Veg. ČSSR, B1, Table 45, rel. 2, 1970). – Boľ, east of the village (Hejný 1957 ined.). – Boľ, Guttmanov dvorec, 105 m (Černoch 1963 BRNM; Hejný 1961 ined.; Berta, Veg. ČSSR, B1, p. 153, Table 44, rel. 6, Table 45, rel. 1, Table 47, rels 12, 15–19, 21–22, 1970). – Boľ, oxbow Tice, north of the village (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 11, rel. 9, Table 13, rel. 1, 1963). – between Boľ and Zatín (Hejný 1957, 1961 ined.). – between Boľ and Vojka (Hejný 1957 ined.). – Hraň, oxbow, 103 m (Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013). – Hrušov, west of the settlement Keresztúr, interdune depression, 100 m (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 1, rels 2, 5, Table 3, rel. 5, Table 5, rel. 17, Table 9, rels 1–3, 6, 1963; Fraňo, Acta Fac. Rer. Natur. Univ. Comen. 19, p. 22, 1971). – Hrušov, depression, west of the agriculture buildings (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 2, rels 2–3, 9, 1963). – Ižkovce (Fraňo, Acta Fac. Rer. Natur. Univ. Comen. 19, p. 21, 1971). – Kráľovský Chlmec (Hejný 1961 ined.). – Kráľovský Chlmec, eastern edge of the pheasantry Erés (Hejný 1961 ined.; Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 11, rel. 7, 1963). – Kráľovský Chlmec, Fejséš settlement, 100 m (Oťaheľová 1979 ined.; Berta, Veg. ČSSR, B1, Table 44, rel. 7, Table 47,

rels 13, 20, 1970). – Kráľovský Chlmec, towards Leles (Hejný 1948, 1951 ined.; Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 11, rels 1–2, Table 13, rel. 3, 1963). – Kráľovský Chlmec, swamp under Pupoš Hill (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 2, rels 1, 10, Table 9, rel. 9, 1963). – Kráľovský Chlmec, towards Svätušie, grounded oxbow of the Tice'Dalmoš'(Berta, Veg. ČSSR, B1, Table 47, rels 9, 14, 1970). – Kusín, east of the village, swampy pastures, 120 m (Staněk 1949 BRNM). – Leles, oxbow of the Latorica River, 100 m (Hrivnák, <http://sbs.sav.sk/atlas/detail.php?rowid=852>, 2019). – Leles, oxbow Tice (Hrivnák 2019 ined.; Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 11, rels 3–4, 1963; Berta, Veg. ČSSR, B1, Table 44, rel. 4, 1970). – Leles, swampy channel, 100 m (Staněk 1947 BRNM). – Malý Horeš, interdune depression eastern and western of point Planina (ut Homók-pusztá) (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 6, rels 5–6, Table 9, rel. 10, 1963). – Oborín, Kucany, oxbow of the Laborec River (s. coll. 1981 SAV). – Pavlovce nad Uhom, SSE of the village, oxbow Ortov, 105 m (Staněk 1949 BRNM; Mikoláš 1984 KO). – Poľany, anabranch of the Latorica River (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 2, rel. 8, 1963). – Poľany, oxbow Tice, 100 m (Staněk 1947 BRNM; Berta, Veg. ČSSR, B1, Table 47, rels 10–11, 1970). – Sírnik, oxbow on Laborec River, 101 m (Oťaheľová 1981 ined.). – Soľníčka, oxbow Tice, west of the village (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 11, rel. 6, 1963). – Somotor, west of the village, oxbow of the Bodrog River (Grulich 1979 BRNU). – Somotor, Somotorský channel south of the village (Hrivnák 2022 ined.; Dudáš M., iNat ID 220951863, 2024). – Strážne, swamp northwest of the sand mine (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 6, rel. 10, 1963). – Strážne, in the middle of a wet meadow, 100 m (Staněk 1947 BRNM). – Streda nad Bodrogom, oxbow Tajba, 101 m (Margittai 1928 BP; Staněk 1947 BRNM; Malý 1992 BRNU; Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 2, rel. 7, Table 3, rel. 6, Table 4, rel. 3, Table 12, rels 7–8, 1963). – Streda nad Bodrogom, oxbow of the Bodrog River, between the andesite hill and the railway station (Marvan & Marvanová 1958 BRNU). – Streda nad Bodrogom, oxbow Starý Bodrog and surroundings, 100 m (Mártonfi et al., Bull. Slov. Bot. Spoločn. 36, Suppl. 1, p. 49, 2014). – Svätá Mária, Severný Radešský channel near the bridge, about 0.4 km NNE of the church, 100 m (Mártonfi et al., Bull. Slov. Bot. Spoločn. 36, Suppl. 1, p. 49, 2014). – Svätušie, towards Boľ, interdune depression, 100 m (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 1, rel. 11, Table 2, rel. 4, 1963). – Svätušie, southwest of the village (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 2, rels 5–6, 1963). – Svätušie, Veľké jazero Lake, 105 m (Šomšák, Acta Fac. Rer. Natur. Univ. Comen.

Bot. 8, Table 1, rels 7, 9, Table 10, rels 1, 4–5, 1963). – Svinice, interdune depression southeast of the village (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 6, rel. 8, 1963). – Veľký Horeš, oxbow Malá Krčava (ut Karča) (Šomšák, Acta Fac. Rer. Natur. Univ. Comen. Bot. 8, Table 3, rel. 4, Table 4, rel. 10, 1963). – Veľký Kamenec, Veľká Krčava, north edge of the oxbow, east of the road to Pácin, 101 m (Hrivnák 2022 ined.; Mártonfi et al., Bull. Slov. Bot. Spoločn. 36, Suppl. 1, p. 49, 2014). – Veľký Kamenec, oxbow 0.8 km to the east of the eastern edge of the village (Mártonfi et al., Bull. Slov. Bot. Spoločn. 36, Suppl. 1, p. 49, 2014). – Vojka, Zelené jazero Lake (Berta, Veg. ČSSR, B1, Table 45, rel. 5, 1970). – Vojka, near the village, in the swamp of the Tice (Margittai 1928 BP). – Zátin (Hejný 1961 ined.). – between Zátin and Vojka (Hejný 1957 ined.). – Zemplínske Jastrabie, 1 km southwest of the village, depression (Berta, Veg. ČSSR, B1, Table 47, rel. 7, 1970).

Carpaticum occidentale

9. Južné Biele Karpaty Mts: Štvrtok, swampy ditches and railway pits (Holuby 1880 PRC, 1885, 1899 BRA, 1899 BRNU). – between Trenčianske Bohuslavice and Štvrtok, ditches (Andrasovszky 1915 BP). – Zemianske Podhradie (Holuby 1879 BRNU). **10. Malé Karpaty Mts:** Bratislava-Lamač, area of the former hospital Rázsochy, drainage channel, 225 m (Májeková & Klačanová 2024 SAV). **13. Strážovské and Súľovské vrchy Mts:** Dubnica nad Váhom, gravel pits Dubnické štrkoviská, 218 m, 225 m, 235 m (Mertanová & Smatanová, Bull. Slov. Bot. Spoločn. 28, Suppl. 1, p. 68, 2006; Rydlo & Smatanová, Řada Přír. 26, Table 1, rel. 10, Table 8, rels 123, 126, 2011). – Trenčín, Sihoľ, swamp (Schidlay 1927 BRA). **14c. Kremnické vrchy Mts:** Kľačany, northeast of the village, Flochovský chrbát, depression, 589 m (Slezák & Hrivnák 2013 ined.; Vlčko, Dipl. Thesis (msc.) depon. in LF TU Zvolen, 1986). **14d. Poľana Mts:** Banská Bystrica, near Pod Rybou (Ondrejová 1993 SMBB; Peregrym M., iNat ID 143062067, 2022). **15. Slovenské rudohorie Mts:** Bacúch, Nature Reserve Bacúšska jelšina (Šomšák, Acta Fac. Rer. Natur. Univ. Comen., Ser. Bot. 15, rel. 1, 1967). – Mokrý Lúka, oxbow of the Muránka River, 286 m (Hrivnák et al., Muzeum a Současnost 24, Table 2, rels 28–29, 2009). – Muránska Lehota, ponds, 373–375 m (Hrivnák 2003 ined.; Kochjarová et al., Bull. Slov. Bot. Spoločn. 23, p. 80, 2001; Hrivnák et al., Reussia 1, Table 3, rels 13–14, p. 45, rel. B, 2004; Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013). – Pohorelá, southwest of the village, Nižný Bor, alluvium of the Hron River, 655–660 m (Blanár 2020 ined.). – Revúca, pond east of the town (Blanár, Dipl. Thesis (msc.) depon. in LF TU Zvolen, p. 22, 1993). **16. Muránska planina Mts:** Muránska Huta, Nature Reserve Mokrý Poľana, 885 m (Blanár &

Hrivnák in Šibík (ed.), Bull. Slov. Bot. Spoločn. 40/1, p. 99, 2018). **19. Slanské vrchy Mts:** Bystré (ut Bystré nad Topľou) (Hazslinszky s. dat. SLO). – Slanská Huta, Malá Izra lake, 525–531 m (Mikoláš 1985 W; Slezák 2012 ined.; Berta, Biologia 48, Table 1, rels 1–5, 7, 10, Table 2, rels 3–7, 1993). – Slanská Huta, Izra lake, 445–448 m (Staněk 1949 BRNM; Dudáš 2021 BRNU; Dudáš M., iNat ID 216840079, 2024). **20. Vihorlatské vrchy Mts:** Jovsa, in the valley of the Jovsiansky potok Stream, 550 m (Vorel 1970 BRNU). **22. Nízke Tatry Mts:** between Predajná and Lopej, wet meadows near the Hron River, 400 m (Dvořák 1966 BRA). – Šalková, oxbow of the Hron River (Rybaříková 2003 SMBB). **25. Turčianska kotlina Basin:** Horná Štubňa, left tributary of the Mútnik Stream (Bernátová 2006 BRA). – between Ivančiná and Jazernica, pond edge (Bernátová & Obuch 2005 BRA; Hrivnák 2019 ined.). – Nolčovo, west of the village, oxbow near the gardening settlement, 404–410 m (Škovirová 1994 TM; Hrivnák 2018 ined.; Slezák 2022 ined.; Hrivnák & Kochjarová, Bull. Slov. Bot. Spoločn. 30/2, Table 1, rels 8, 37, 2008; Kliment et al., Bull. Slov. Bot. Spoločn. 39/1, p. 23, 2017). – Nolčovo, west of the village, oxbow on the right bank of the Váh River, near road (Hrivnák 2021 ined.). – Sučany, Biele brehy, Ontário lake, 387–400 m (Škovirová 2003 TM; Hrivnák & Kochjarová, Bull. Slov. Bot. Spoločn. 30/2, 1, rel. 9, 2008). – Turany, ca 1 km SSE of the village, muddy edge of the gravel pit near the Váh River (Hrivnák 2021 ined.; Slezák 2023 ined.). – Turčianska Štiavnička, Vojtovo, north of the railway near the railway bridge, gravel pit bank, 395 m (Očka 2012 TM). **26a. Liptovská kotlina Basin:** Kvačany, Dlhá Lúka (ut Luka pod Proseckou dolinou) (s. coll. ex herb. Žofák 1931 PRC). **26b. Spišské kotliny Basins:** Bati-zovce, gravel pits, 750–765 m (Slezák & Hrivnák 2019 POP; Kochjarová & Hrivnák, Bull. Slov. Bot. Spoločn. 39/1, p. 93, 2017). – Kežmarok, ditches (Reuss, Května Slovenska, p. 451, 1853). **27a. Severné Biele Karpaty Mts:** Horenická Hôrka, gravel pit, 0.9 km SSE of the village, 249 m (Rydlo & Smatanová, Řada Přír. 26, Table 8, rel. 133, 2011). – Kameničany, eastern edge of the village, muddy bank of a gravel pit currently without water surface, 228 m (Slezák 2022 ined.). – Lednické Rovne, buried gravel pit, 246 m (Rydlo & Smatanová, Muz. Souč. Řada Přír. 26, Table 8, rel. 124, 2011). **28. Západné Beskydy Mts:** Hruštín, reservoir northeast of the village, 669 m (Kochjarová et al., Bull. Slov. Bot. Spoločn. 35/2, p. 110, 2013). – Párnica, Orava River, gravel ditches, 450 m (Hrivnák et al., Biologia 66, Table 3, rels 5, 38, 2011). – Párnica, abandoned fishponds, 450 m (Hrivnák et al., Biologia 66, Table 3, rel. 23, 2011; Bednár F., iNat ID 83315526, 2021). – Zubrohlava, Poľanový Kriváň Stream, 650 m (Migra 1996 NI). **30a. Šarišská vrchovina Mts:** Uzovský Šalgov, Šalgovské rybníky Ponds (Kochjarová et al., Bull. Slov. Bot. Spoločn. 34/2, p. 198, 2012). **30b. Čergov Mts:** Plaveč, protected area Plavečské

štrkoviská, easternmost pond between Ľubotínka River and railway to Orlov, 479 m (Dudáš 2024 KO; Dudáš M., iNat ID 225379304, 2024).

General data

Bratislava (Reuss, Května Slovenska, p. 451, 1853). – Danube River, riverbeds (Reuss, Května Slovenska, p. 451, 1853). – Rudava River, oxbow (Krippelová 1979 SAV). – Slaná River and Rimava River, riverbeds, oxbows and alluvial floodplains (Kochjarová & Kliment, Bull. Slov. Bot. Spoločn. 32, Suppl. 1, p. 7, 2010). – Tisa River, riverbeds (Reuss, Května Slovenska, p. 451, 1853). – Veľká Fatra (Májovský s. dat. SLO).

Appendix 2

List of the literature sources (author, abbreviated reference, number of relevés) for the relevés used in the numerical classification Table 1.

Cluster 1: Šomšák (1967, Acta Fac. Rer. Natur. Univ. Comen., Botanica 15: 1–11) – 1 rel.; Blanár in Šibík (2018, Bull. Slov. Bot. Spoločn. 40: 98–103) – 1 rel. **Cluster 2:** Stanová (1991, Dipl. Thesis) – 1 rel.; Kollár et al. (2005, Phytopedon 4 (2005/2): 1–11) – 2 rels; Slezák M. (unpublished) – 1 rel. **Cluster 3:** Šmarda (1951, Mor. Mus., Brno, 36: 38–68) – 1 rel.; Berta (1957, Dipl. Thesis) – 4 rels; Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 2 rels; Šomšák (1967, Diss. Thesis) – 1 rel.; Berta (1970, Vegetácia ČSSR, B1, Vyd. SAV) – 16 rels; Berta (1993, Biológia, Bratislava, 48: 53–59) – 7 rels; Kollár et al. (2005, Phytopedon 4 (2005/2): 1–11) – 3 rels; Stanová (1991, Dipl. Thesis) – 2 rels; Hejný S. (unpublished) – 2 rels; Slezák M. (unpublished) – 1 rel.; Valachovič M. (unpublished) – 1 rel. **Cluster 4:** Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 18 rels; Berta (1970, Vegetácia ČSSR, B1, Vyd. SAV) – 6 rels.

Table 2.

Cluster 1: Rydlo & Smatanová (2011, Muz. Souč., řada Přír. 26: 177–186) – 1 rel. **Cluster 2:** Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 6 rels; Hrivnák (2006, Reussia 3: 1–11) – 1 rel.; Hrivnák & Kochjarová (2008, Bull. Slov. Bot. Spoločn., 30/2: 261–278) – 2 rels. **Cluster 3:** Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 6 rels; Berta (1993, Biológia 48: 53–59) – 5 rels; Hejný S. (unpublished) – 4 rels; Oťaheľová H. (unpublished) – 1 rel. **Cluster 4:** Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 3 rels; Hrivnák et al. (2011, Biologia 66: 626–637) – 1 rel. **Cluster 5:** Berta J. (1957, Dipl. Thesis) – 1 rel.; Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 6 rels; Malovcová-Staníková (2000, Bull. Slov. Bot. Spoločn. 22: 187–193) – 2 rels;

Hrivnák et al. (2009, Muz. Souč., řada Přír., 24: 77–90) – 2 rels; Hrivnák et al. (2011, Biologia 66: 626–637) – 1 rel.; Hejný S. (unpublished) – 10 rels; Hrivnák R. (unpublished) – 1 rel.; Malovcová-Staníková M. (unpublished) – 1 rel.; Šomšák L. (unpublished) – 1 rel. **Cluster 6:** Šomšák (1963, Acta Fac. Rer. Nat. Univ. Comen. 8: 229–302) – 4 rels; Fraňo (1971, Acta Fac. Rer. Natur. Univ. Comen. 19: 3–193) – 2 rels; Balátová-Tuláčková (1976, Vegetácia ČSSR ser. B 3: 1–258) – 2 rels; Malovcová-Staníková (2003, Acta Rer. Natur. Mus. Nat. Slov. 49, 40–51) – 2 rels; Hrivnák et al. (2004, Reussia 1: 33–54) – 3 rels; Malovcová-Staníková (2004, Acta Rer. Natur. Mus. Slov. 50: 31–43) – 1 rel.; Hrivnák & Kochjarová (2008, Bull. Slov. Bot. Spoločn. 30/2: 261–278) – 1 rel.; Hrivnák et al. (2011, Biologia 66: 626–637) – 1 rel.; Rydlo & Smatanová (2011, Muz. Souč., řada Přír. 26: 177–186) – 3 rels; Hejný S. (unpublished) – 4 rels; Malovcová-Staníková (unpublished) – 2 rels; Oťaheľová H. (unpublished) – 1 rel.; Posltová A. (1997, Dipl. Thesis) – 1 rel. **Cluster 7:** Rydlo & Smatanová (2011, Muz. Souč., řada Přír. 26: 177–186) – 1 rel.; Hejný S. (unpublished) – 1 rel.; Oťaheľová H. (unpublished) – 1 rel. **Cluster 8:** Hrivnák R. (unpublished) – 1 rel.; Oťaheľová H. (unpublished) – 1 rel.; Valachovič M. (unpublished) – 2 rels. **Cluster 9:** Malovcová-Staníková (unpublished) – 1 rel.; Valachovič M. (unpublished) – 1 rel.

Appendix 3

List of plant species merged to aggregates (agg.) in the data set

Agrostis stolonifera agg. (incl. *A. gigantea*, *A. stolonifera*), *Carex flava* agg. (*C. demissa*, *C. flava*), *Dryopteris carthusiana* agg. (*D. carthusiana*, *D. dilatata*), *Molinia caerulea* agg. (*M. arundinacea*, *M. caerulea*), *Mysosotis palustris* agg. (*M. laxiflora*, *M. scorpioides*), *Poa pratensis* agg. (*P. angustifolia*, *P. pratensis*), *Utricularia vulgaris* agg. (*U. australis*, *U. vulgaris*), *Valeriana dioica* agg. (*V. dioica*, *V. simplicifolia*).

Acknowledgements This work was supported by the Science Grant Agency of the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences under Grant VEGA 2/0053/23. We would like to thank all contributors to the Slovak Vegetation Database, namely S. Hejný (†), M. Malovcová-Staníková, H. Oťaheľová, L. Šomšák (†) and M. Valachovič for providing unpublished data. We also thank all curators of herbaria that allowed us to study specimens and Bruno Wallnöfer and Lajos Somlyay for their help with finding and providing herbarium items from Wien and Budapest. Dominik Roman Letz helped us to decipher some old herbarium labels and to identify localities. We would also like to thank the two anonymous reviewers for their detailed and thoughtful comments on this manuscript.

Author's contribution Study conception and design were performed by R. Hrivnák and M. Slezák. Material preparation and data collection were carried out by R. Hrivnák, J. Májeková, M. Majerová, and

M. Slezák. Data analysis was performed by R. Hrivnák. M. Majerová led the writing, but all co-authors commented the original and revised version of the manuscript.

Funding Open access funding provided by The Ministry of Education, Science, Research and Sport of the Slovak Republic in cooperation with Centre for Scientific and Technical Information of the Slovak Republic. This work was supported by the Science Grant Agency of the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences under Grant VEGA 2/0053/23.

Data Availability Chorological data are provided in the appendices of this paper. Published vegetation data, stored in the Slovak Vegetation Database, are available upon request from the database administrators.

Declarations

Conflict of interest The authors declare there is no conflict of interest.

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