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ORIGINAL ARTICLE

Floristic classification of *Geranion sanguinei* in South Moravia (Czech Republic)

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Abstract
Approaches to the classification of thermophilous fringe and tall-herb vegetation in Central Europe vary in many respects. In this study, we provide new vegetation-plot data from South Moravia (Czech Republic), develop a new classification based on differences in overall species composition and compare it with recently used classifications. A dataset of 169 relevés fulfilling the condition of at least 50% cover of tall herbs or lower broad-leaved herbs characteristic of fringe vegetation was classified into six informal vegetation types, four of which may be considered equivalent to phytosociological associations. The most mesophilous and species-rich type *Potentilla alba-Laserpitium latifolium* is distributed on deep loamy soils developed over the Carpathian flysh, mainly in the White Carpathians. *Potentilla argentea-Geranium sanguineum* is the most heliophilous type, including acidophilous species and occurring on siliceous rock outcrops along the eastern margin of the Bohemian Massif. Type *Vincetoxicum hirundinaria-Origanum vulgare* is confined to hard base-rich rocks and occurs mainly in the limestone areas of the Moravian Karst and the Pavlov Hills. Type *Geranium sanguineum-Peucedanum cervaria* occurs mainly on deep calcareous soils developed over loess and Tertiary claystones in the central part of the South Moravian forest-steppe. The floristic classification of the thermophilous fringe and tall-herb vegetation in South Moravia yielded ecologically and geographically well characterized units that simultaneously differ from dry grasslands by the dominance of herbs, mainly tall herbs. It may serve as a model for future revisions of the national syntaxonomic classification scheme of fringe and tall-herb vegetation in the Czech Republic.

Keywords Fringe vegetation · *Geranion sanguinei* · Syntaxonomy · Tall-herb vegetation · *Trifolio-Geranietea* · Vegetation classification

Introduction

Thermophilous fringe and tall-herb vegetation (alliance *Geranion sanguinei*) is an important component of forest-steppe mosaics. Stand dominated by broad-leaved herbs (e.g. *Clematis recta*, *Dictamnus albus*, *Geranium sanguineum*, *Laserpitium latifolium*, *Peucedanum cervaria*, *Trifolium alpestre*) often occur at the wettest and most productive places in dry grasslands, such as margins of thermophilous oak forests, north-oriented slopes or terrain depressions. They are usually relatively species-rich with one or more dominants and combinations of species typical for different habitats (dry-mesic steppe grasslands, meadows, thermophilous and mesophilous forests) are characteristic (Schneider-Binder 1984; Valachovič 2004; Roleček 2018; Roleček et al. 2022). This vegetation type occurs mostly on base-rich rocks (e.g. limestone, dolomite, calcareous claystone and sandstone, loess, basalt, andesite), where they are better developed and floristically better differentiated than on acidic substrates (Čarni 1997; Hoffmann 2007; Borhidi et al. 2012; Valachovič and Hegedüšová Vantarová 2014).

Opinions on the ecological drivers and convenient classification of *Geranion sanguinei* alliance, and herb-dominated vegetation in general, are far from unanimous since Müller's seminal paper (Müller 1962; Passarge 1967; Jakucs 1970; Dierschke 1974; van Gils 1978; Dengler and Krebs

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2003; Mucina et al. 2016). Among the issues debated are, for example, their link to forest fringe habitats, the assignment of herb-rich stands into high-rank syntaxa, or the use of physiognomic versus floristic criteria for their classification. In Central Europe, this inconsistency is reflected in different syntaxonomic treatments in national vegetation surveys. While in Germany (Schubert et al. 2001), Poland (Brzeg 2005; Matuszkiewicz 2007), Austria (Mucina and Kolbek 1993) and Slovakia (Valachovič and Hegedüšová Vantarová 2014), thermophilous, mesophilous and in some cases acidophilous fringes and tall-herb stands are classified in a separate class *Trifolio-Geranietea sanguinei* Müller 1962, in the Czech Republic (Chytrý 2007) and Hungary (Borhidi et al. 2012) they are classified together with dry grasslands in the class *Festuco-Brometea*. In the Czech national vegetation overview, the floristic criterion is not applied to distinguish associations within *Geranion sanguinei* alliance: these are defined on the basis of the dominance of individual species (Hoffmann 2007).

The main aims of this study are thus (i) to describe the diversity of thermophilous fringe and tall-herb vegetation in South Moravia; (ii) to develop a classification scheme based on differences in overall species composition; (iii) to investigate how floristic classification compares to recently used classifications.

Study area

The study area is located in South Moravia (Czech Republic) and is approximately delimited by the boundaries of the forest-steppe biome in this area (Chytrý 2012). Forest-steppe biome occurs here in the rain shadow of the Bohemian-Moravian Highlands. Long-term annual precipitation drops below 500 mm/year in places (Zíková 2009), while average annual temperatures exceed 8.25 °C (Chytrý 2012). The region represents a north-western tip of the zonal forest-steppe biome of the Pannonian Basin, adjacent to the forest-steppe of the eastern Austria and southern Slovakia and Hungary (Wendelberger 1954; Martinovský and Kolbek 1984; Chytrý et al. 2022). The geological substrate in South Moravia is relatively diverse. In the western part, the study area reaches the eastern margin of the Bohemian Massif, which is predominantly formed by acidic crystalline rocks of the Proterozoic and Paleozoic. In deep river valleys, base-rich rocks (amphibolites and marbles) are scattered, while Devonian limestones form the Moravian Karst. The remaining part of South Moravia consists mainly of calcareous rocks. Tertiary and Quaternary sediments, especially Neogene marine sediments and Pleistocene loess, are the main geological substrate in the lowlands of the Vienna Basin and adjacent hills. In the Outer Western Carpathians flysch claystones and sandstones prevail and Pavlov Hills are formed by Jurassic and Cretaceous limestones (Czech Geological Survey 2022).

Methods

Data acquisition

Vegetation plot data of *Geranion sanguinei* alliance were obtained from the Czech National Phytosociological Database (CNPD; Chytrý and Rafajová 2003; see the list of relevés in Supplement S1) stored in the database program Turboveg 2 (Hennekens and Schaminée 2001). These data were supplemented with 43 own relevés collected in the field in 2020 and 2021. Most new relevés came from squared plots of 16 m^2. Only relevés fulfilling the condition of at least 50% cover of tall herbs (average height 50 cm and more according to Kubát et al. 2002) or lower broad-leaved herbs characteristic of fringe vegetation (*Clinopodium vulgare*, *Euphorbia epithymoides*, *Geranium sanguineum*, *Melampyrum cristatum*, *M. nemorosum*, *Polygonatum odoratum*, *Trifolium alpestre*) were included the dataset.

Data analysis

The initial dataset consisted of 224 relevés. We unified the taxonomic concepts and nomenclature according to Danihelka et al. (2012). All records of woody species, bryophytes and hybrids were deleted. Also, the records of vascular plant species that were not identified at the species level were deleted unless considered informative at the genus level (*Alchemilla* sp.). We classified the dataset using the Modified Twinspan algorithm (Roleček et al. 2009) in the Juice program 7.1 (Tichý et al. 2011) with Total inertia as a dissimilarity measure and three pseudospecies cut levels corresponding to 0, 5 and 25% species cover. The minimum group size for the division was set to 2. To avoid classification bias due to a disproportionate number of similar relevés from some sites, we used geographical stratification. We divided the dataset using Modified Twinspan into 10 relatively homogeneous groups. The geographical grid spacing was set to 0.54' latitude and 0.84' longitude. In each stratum maximum of three relevés were retained. We also removed several outliers based on their remote position in the ordination plot: two relevés of forest clearing vegetation dominated by *Vicia sylvatica*, one relevé of ruderal vegetation, one relevé of rock outcrop vegetation and two relevés of dry grasslands. We also excluded relevés of mesophilous fringe and tall-herb vegetation corresponding to the alliance *Trifolion medii* based on the abundance of species considered diagnostic in Central Europe (Hoffmann 2007; Valachovič and Hegedüšová Vantarová 2014; Mucina and

Kolbek 1993). Groups with an average number of species diagnostic for *Trifolion medii* higher than for *Geranion sanguinei* were excluded. The final dataset thus contained 169 phytosociological relevés.

To choose the appropriate number of clusters in the final classification, we compared the number of diagnostic species when dividing the dataset into 2–10 groups based on Optimclass analysis (Tichý et al. 2010). The diagnostic species were determined based on Fisher's exact test with different values of p ($\leq 10^{-4} - 10^{-7}$).

Further analyses (ordination, comparison of ecological preferences and comparison of the classification with the syntaxonomic concepts used in the Czech Republic) were performed in R program version 4.1.2 (R Core Team 2021) using the functions of the package tidyverse (Wickham et al. 2019). For the multivariate analyses, we used the vegan package (Oksanen et al. 2020). Graphs were created using the package ggplot2 (Wickham 2016) and functions from packages stringr (Wickham 2019), ggrepel (Slowikowski 2021), ggfittext (Wilkins 2021) and gridExtra (Auguie 2017).

We used an unconstrained ordination DCA (detrended correspondence analysis) with logarithmic transformation and down-weighting of rare species to visualise the classification. We displayed sites and diagnostic species for each group using the envfit function. Species with fidelity phi ≥ 0.3 and the value of Fisher's exact test $p \leq 0.01$ were considered as diagnostic. In the ordination plot, only species occurring in at least five relevés were shown. Diagnostic (phi $\times$ 100 > 30, phi $\times$ 100 > 50 in bold), constant (frequency > 35%, frequency > 50% in bold) and dominant (cover > 15% with frequency > 10%, with frequency > 25% in bold) species of the individual vegetation types were listed in the text.

To compare the ecological demands of individual groups, we compared the average Ellenberg-type indicator values (EIVs) for individual relevés calculated on presence-absence data using the cwm function from the weimea package (Zelený 2020). We used EIVs for the Czech Republic (Chytrý et al. 2018). The distribution of vegetation types in South Moravia was displayed on a map using ArcGIS Desktop 10.7 (Esri Inc. 2018).

Using an alluvial plot, we compared the assignment of relevés in our classification with two classifications recently used in the Czech Republic: (i) the current national classification (Chytrý 2007), as implemented in the full version of the expert system for the vegetation of the Czech Republic (Chytrý et al. 2020), and (ii) the classification according to Moravec et al. (1995), to which the relevés are assigned in the Czech National Phytosociological Database (CNPD) based on the expert knowledge of the original author. The alluvial plot was created with the ggalluvial package (Brunson 2020). We also displayed the centroids of the relevés classified into the association level in the ordination diagram. Only centroids for associations represented by at least three relevés were displayed.

The syntaxonomic nomenclature used in this study follows Chytrý (2007). In the case of syntaxonomic units adopted from different sources, the author citation is mentioned by the first occurrence in the text.

Results

Classification and ordination

The dendrogram of the division of the dataset into six groups is shown in Fig. 1. The final number of six clusters in the classification was chosen based on the Optimclass analysis (Fig. 2). Because groups 4 to 6 were not well distinguished ecologically and geographically, we considered them as three subtypes of a single vegetation type. See the synoptic table of the classification in Supplement S2.

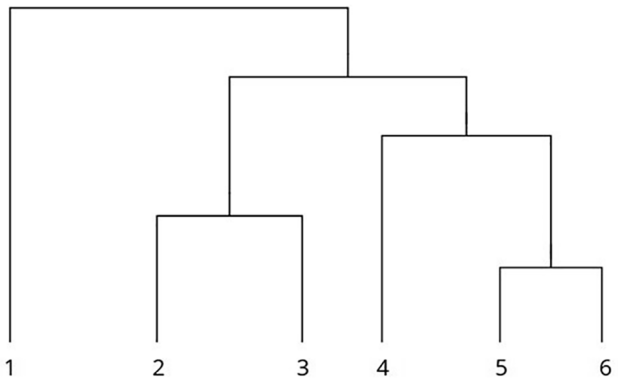

Fig. 1 Dendrogram of the division of the dataset using the Modified Twinspan algorithm into six groups. Legend: **1** – *Potentilla alba-Laserpitium latifolium*, **2** – *Potentilla argentea-Geranium sanguineum*, **3** – *Vincetoxicum hirundinaria-Origanum vulgare*, **4** – *Geranium sanguineum-Peucedanum cervaria*, variant *Inula insifolia*, **5** – *Geranium sanguineum-Peucedanum cervaria*, variant *Cytisus nigricans*, **6** – *Geranium sanguineum-Peucedanum cervaria*, variant *Dictamnus albus*

Detrended correspondence analysis was used to display the classification in the ordination plot (Fig. 3). The eigenvalues for the first ordination axis were 0.3750, for the second axis 0.2225 and for the third axis 0.1596. Along the first axis of the DCA, sites belonging to group 1 are separated from the other groups. Communities with higher moisture and nutrient demands are situated in the right part of the ordination diagram, while more thermophilous and heliophilous communities are separated in the left part. The group comprising subtypes 4–6 is distinguished from the other two along the second ordination axis; its subtypes are

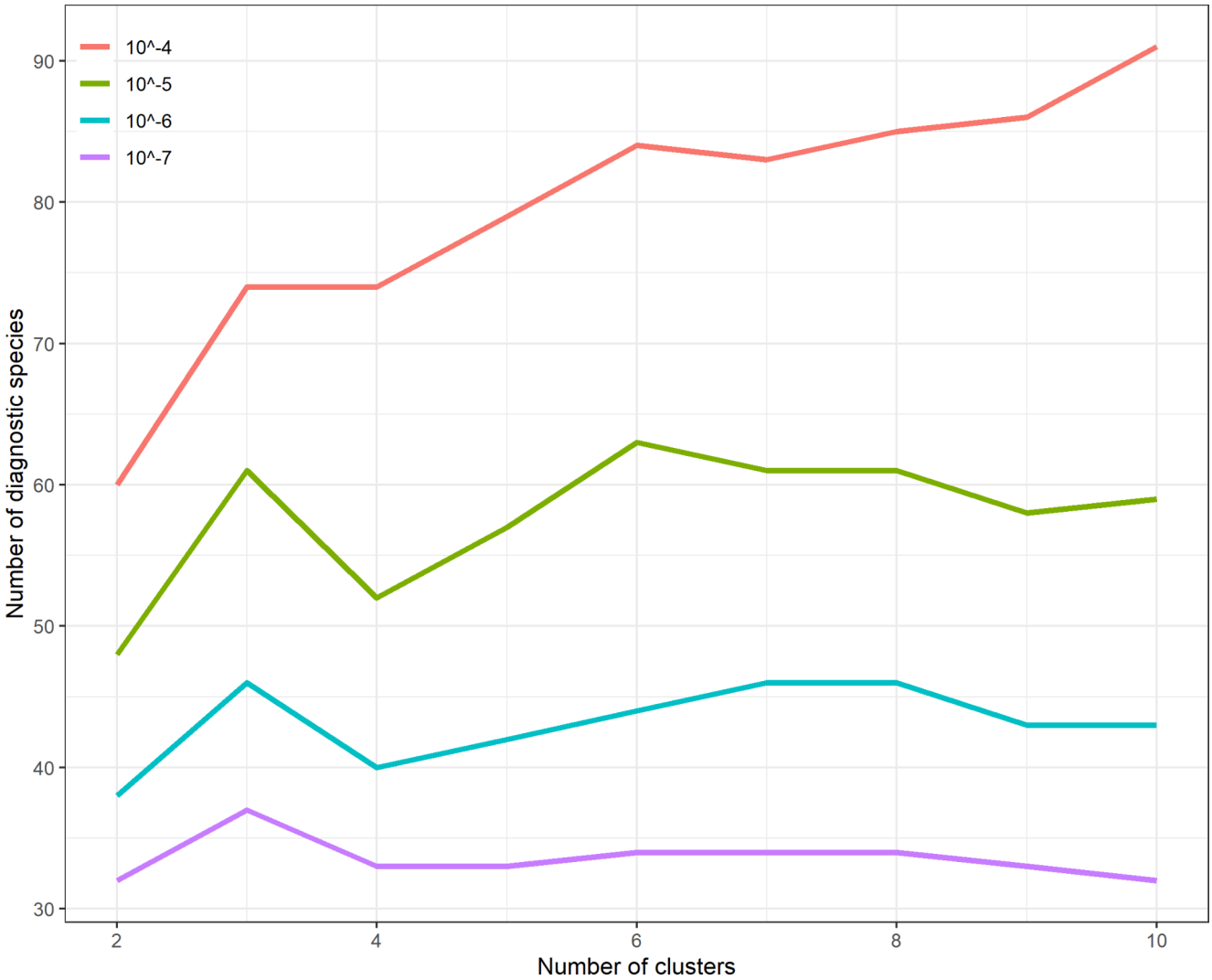

Fig. 2 Results of the Optimclass analysis when dividing the dataset into 2–10 clusters using different values of Fisher's exact test ($p \leq 10^{-4} - 10^{-7}$)

also separated by the second axis, which may be related to the gradient of pH and altitude. The third ordination axis distinguishes groups 2 and 3. This axis may be related to the gradient of nutrients and light. Differences in ecological requirements of the distinguished vegetation types are illustrated in Fig. 4.

Vegetation types

1 – White Carpathian type *Potentilla alba-Laserpitium latifolium*.

Diagnostic species

Potentilla alba, ***Trisetum flavescens***, ***Primula veris***, ***Cirsium pannonicum***, ***Betonica officinalis***, ***Sanguisorba officinalis***, ***Cruciata verna***, ***Serratula tinctoria***, ***Rumex acetosa***, ***Ranunculus polyanthemos***, ***Filipendula vulgaris***, ***Festuca rubra***, ***Bromus erectus***, ***Taraxacum* sect. *Taraxacum***, ***Campanula glomerata***, ***Lathyrus latifolius***, ***Carex montana***, ***Lathyrus niger***, ***Trifolium rubens***, ***Dactylis glomerata* agg.**, ***Valeriana officinalis* agg.**, ***Colchicum autumnale***, ***Clematis recta***, ***Symphytum tuberosum* agg.**, ***Trifolium montanum***, ***Stellaria graminea***, ***Ranunculus auricomus* agg.**, ***Centaurea jacea***, ***Agrostis capillaris***, *Pulmonaria angustifolia*, *Lathyrus pratensis*, *Laserpitium latifolium*, *Leucanthemum vulgare* agg., *Anthoxanthum odoratum* agg., *Heracleum sphondylium*, *Ajuga reptans*, *Pulmonaria mollis*, *Festuca pratensis* agg., *Plantago lanceolata*, *Centaurea phrygia* agg., *Knautia arvensis* agg., *Melampyrum nemorosum* agg., *Brachypodium pinnatum*, *Calamagrostis arundinacea*, *Astrantia major*, *Vicia cracca* agg., *Viola hirta*, *Molinia caerulea* agg., *Campanula patula*, *Prunella grandiflora*, *Allium scorodoprasum*, *Tanacetum corymbosum*, *Listera ovata*, *Leontodon hispidus*, *Carlina acaulis*, *Briza media*, *Veronica chamaedrys* agg.,

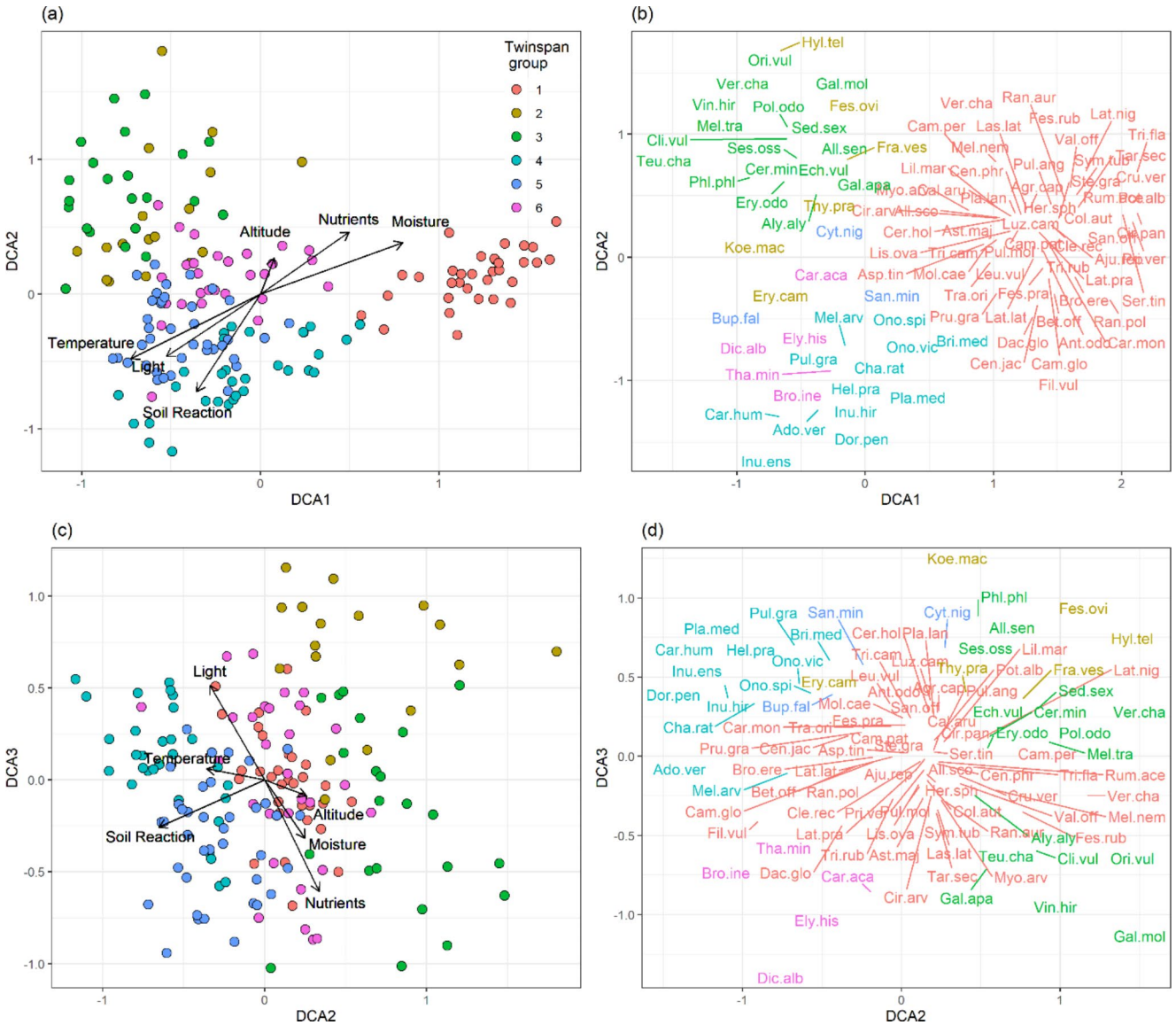

Fig. 3 Detrended correspondence analysis displaying sites and passively projected Ellenberg-type indicator values (a, c) and diagnostic species (b, d). The first two (a, b) or second and third (c, d) ordination axes are shown. Sites belonging to each cluster are displayed in different colours. Diagnostic species with fidelity phi × 100 ≥ 25 and Fisher's exact test $p \leq 0.01$ occurring in at least five relevés projected to DCA using the envfit function. The font colour corresponds to the colour of the group for which the species is diagnostic. Legend: **1** – *Potentilla alba-Laserpitium latifolium*, **2** – *Potentilla argentea-Geranium sanguineum*, **3** – *Vincetoxicum hirundinaria-Origanum vulgare*, **4** – *Geranium sanguineum-Peucedanum cervaria*, variant *Inula insifolia*, **5** – *Geranium sanguineum-Peucedanum cervaria*, variant *Cytisus nigricans*, **6** – *Geranium sanguineum-Peucedanum cervaria*, variant *Dictamnus albus*. Species names are abbreviated to the first three letters of the genus and species names (see Appendix S3 for full names)

Tragopogon orientalis, *Inula salicina*, *Cirsium arvense*, *Viola canina*, *Traunsteinera globosa*, *Chamaecytisus supinus*, *Luzula campestris* agg., *Trifolium campestre*, *Lilium martagon*, *Cerastium holosteoides*, *Galium boreale*, *Asperula tinctoria*, *Myosotis arvensis*, *Linum catharticum*, *Campanula persicifolia*, *Helianthemum grandiflorum*, *Scorzonera hispanica*, *Veronica officinalis*, *Trifolium ochroleucon*, *Chaerophyllum aromaticum*.

Constant species

Geranium sanguineum, ***Arrhenatherum elatius***, ***Poa pratensis* agg.**, ***Achillea millefolium* agg.**, ***Peucedanum cervaria***, ***Trifolium alpestre***, ***Salvia pratensis***, ***Galium verum* agg.**, ***Genista tinctoria***, *Festuca rupicola*.

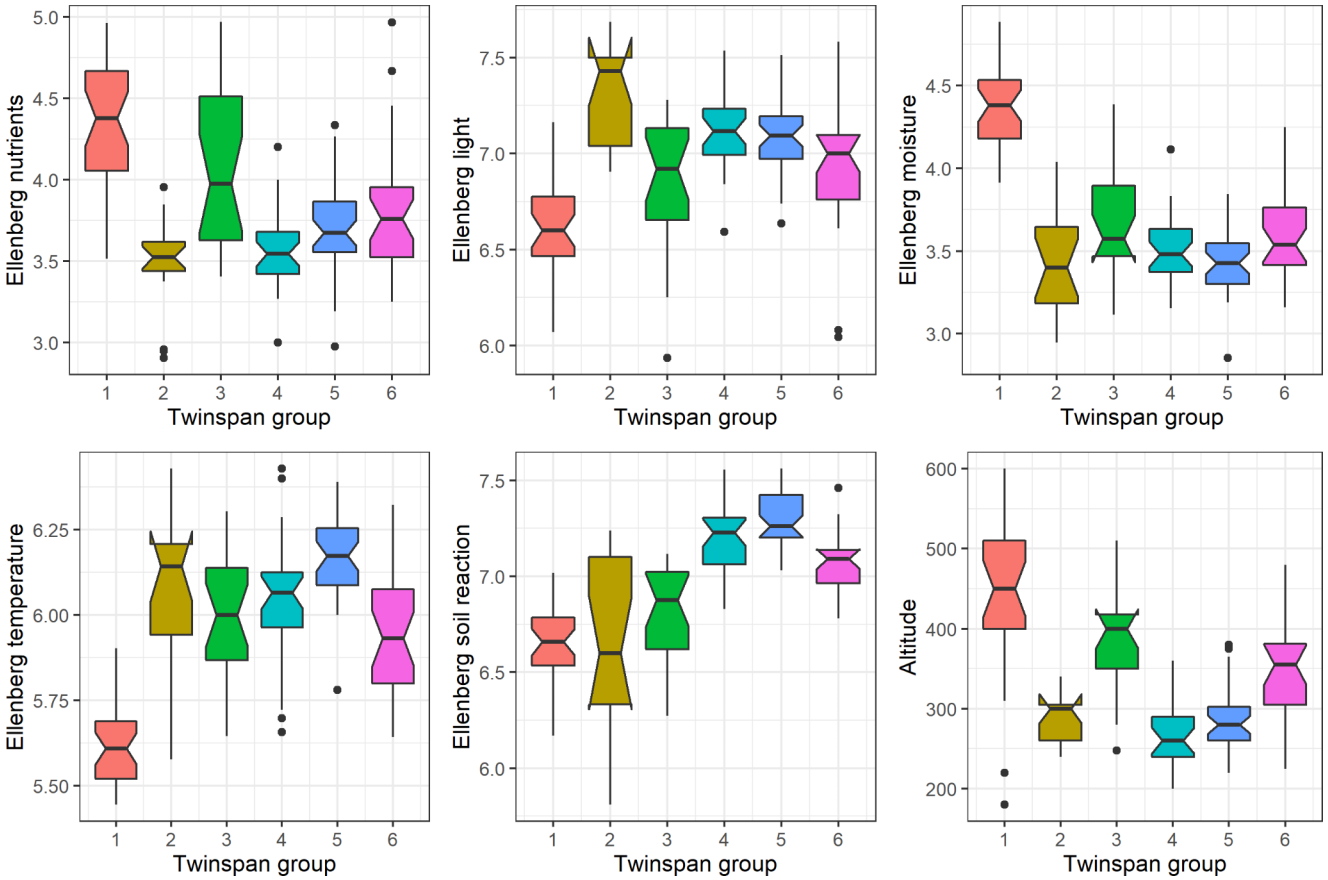

Fig. 4 Boxplots showing mean Ellenberg-type indicator values and altitude for individual vegetation types. Legend: **1** – *Potentilla alba-Laserpitium latifolium*, **2** – *Potentilla argentea-Geranium sanguineum*, **3** – *Vincetoxicum hirundinaria-Origanum vulgare*, **4** – *Geranium sanguineum-Peucedanum cervaria*, variant *Inula insifolia*, **5** – *Geranium sanguineum-Peucedanum cervaria*, variant *Cytisus nigricans*, **6** – *Geranium sanguineum-Peucedanum cervaria*, variant *Dictamnus albus*

Dominant species

Geranium sanguineum, *Brachypodium pinnatum*, *Vicia cracca* agg., *Potentilla alba*, *Melampyrum nemorosum* agg., *Laserpitium latifolium*, *Peucedanum cervaria*.

Brief characteristics This vegetation type (Fig. 5A) is the most mesophilous of all the communities distinguished. It shows the highest species richness and includes many species typical for the forest-steppe meadows of the White Carpathians (*Brachypodio pinnati-Molinietum arundinaceae*), with which it forms many transitions and mosaics. Here, it prefers more productive sites, such as fringes of forests and scrub, lower parts of slopes, terrain depressions, surroundings of solitary oaks or places affected by previous fertilization. It usually occurs at altitudes between 300 and 600 m, most often on flat terrain with an inclination up to 10° but may grow also on steeper west- to north-oriented slopes. The community occurs mainly in the southwest part of the White Carpathians (Fig. 6). Altogether 32 relevés were assigned to this vegetation type.

2 – Acidophilous rock type *Potentilla argentea-Geranium sanguineum*.

Diagnostic species

Eryngium campestre, *Hylotelephium telephium* agg., *Stachys germanica*, *Potentilla argentea*, *Linaria genistifolia*, *Koeleria macrantha*, *Artemisia campestris*, *Cytisus nigricans*, *Fragaria vesca*, *Trifolium arvense*, *Thymus praecox*, *Iris variegata*, *Verbascum phoeniceum*, *Silene otites*, *Festuca pulchra*, *Carex supina*.

Constant species *Geranium sanguineum*, *Arrhenatherum elatius*, *Trifolium alpestre*, *Achillea millefolium* agg., *Poa*

pratensis agg., *Festuca rupicola*, *Euphorbia cyparissias*, *Asperula cynanchica*.

Dominant species *Geranium sanguineum*, *Vincetoxicum hirundinaria*.

Brief characteristics This vegetation type (Fig. 5B) is the most acidophilous, heliophilous and least nutrient-demanding of all the communities distinguished. Also its species richness is the lowest. It occurs mainly over acidic bedrock with shallow soils and rock outcrops at the fringes of forests and scrub, mostly on east- to southwest-oriented slopes. It is distributed mainly along the eastern border of the Bohemian Massif (Fig. 6) at altitudes between 200 and 400 m. Altogether 17 relevés were assigned to this vegetation type.

3 – Basiphilous rock type *Vincetoxicum hirundinaria-Origanum vulgare*.

Diagnostic species

Vincetoxicum hirundinaria, ***Teucrium chamaedrys***, ***Origanum vulgare***, ***Verbascum chaixii* ssp. *austriacum***, ***Galium mollugo* agg.**, ***Erysimum odoratum***, *Cerinthe minor*, *Sedum sexangulare*, *Clinopodium vulgare*, *Echium vulgare*, *Viola tricolor*, *Seseli osseum*, *Melica transsilvanica*, *Alyssum alyssoides*, *Galium aparine*, *Polygonatum odoratum*, *Lamium maculatum*, *Brachypodium sylvaticum*, *Allium senescens*, *Fallopia convolvulus*, *Securigera varia*, *Carex muricata* agg., *Hesperis sylvestris*, *Asplenium trichomanes*, *Asplenium ruta-muraria*, *Arenaria serpyllifolia* agg., *Phleum phleoides*, *Viola odorata*, *Orobanche reticulata*, *Melica uniflora*, *Euphorbia cyparissias*.

Constant species

Poa pratensis* agg.**, ***Festuca rupicola, ***Hypericum perforatum***, ***Geranium sanguineum***, ***Hylotelephium telephium* agg.**, ***Bupleurum falcatum***, ***Achillea millefolium* agg.**, *Salvia pratensis*, *Genista tinctoria*, *Fragaria viridis*, *Veronica teucrium*, *Veronica chamaedrys* agg., *Tanacetum corymbosum*, *Stachys recta*, *Brachypodium pinnatum*.

Dominant species

Geranium sanguineum, ***Vincetoxicum hirundinaria***, *Origanum vulgare*, *Brachypodium pinnatum*.

Brief characteristics This vegetation type (Fig. 5C) is relatively heliophilous, basiphilous and has rather high nutrient demands compared to the other communities distinguished. It usually occurs over calcareous hard-rock bedrock, typically limestone. It prefers surroundings of rock outcrops and screes, fringes, and openings of the thermophilous oak forests, oak-hornbeam forests and scrub. It occurs mostly on steep east- to south-facing slopes with inclination often over 30°, at altitudes between 300 and 500 m. It is distributed mainly in the relatively mesic parts of limestone areas of the Moravian Karst and Pavlov Hills and scattered along the eastern margin of the Bohemian Massif (Fig. 6). Altogether 22 relevés were assigned to this vegetation type.

4–6 – Central South-Moravian type *Geranium sanguineum-Peucedanum cervaria*.

Diagnostic species

Inula ensifolia, ***Peucedanum cervaria***, *Centaurea scabiosa*, *Aster amellus*, *Thalictrum minus*, *Dorycnium pentaphyllum* agg., *Bromus inermis*, *Brachypodium pinnatum*, *Stachys recta*, *Bupleurum falcatum*, *Adonis vernalis*, *Salvia pratensis*, *Viola hirta*, *Festuca rupicola*, *Medicago falcata*, *Peucedanum alsaticum*.

Constant species

Achillea millefolium* agg.**, ***Euphorbia cyparissias, ***Teucrium chamaedrys***, ***Poa pratensis* agg.**, ***Fragaria viridis***, ***Anthericum ramosum***, *Elymus hispidus*, *Dactylis glomerata* agg., *Arrhenatherum elatius*, *Geranium sanguineum*, *Galium verum* agg., *Vincetoxicum hirundinaria*, *Tanacetum corymbosum*.

Dominant species

Peucedanum cervaria, *Geranium sanguineum*, *Brachypodium pinnatum*, *Dictamnus albus*.

Brief characteristics This vegetation type (Fig. 5D) includes drought-tolerant basiphilous communities of the core area of the south-Moravian forest-steppe. It includes typical stands of the alliance *Geranion sanguinei*, growing at the fringes of forests and scrub, in forest openings, and in steppe grassland mosaics (*Cirsio-Brachypodion pinnati*, *Festucion valesiacae*), particularly in the lower parts of the slopes, depressions and at abandoned sites. These stands occur mainly on base-rich calcareous sediments, often less consolidated, such as loess or claystones and sandstones of the Carpathian flysch or of Neogene age on deeper soils than the *Potentilla argentea-Geranium sanguineum* and *Vincetoxicum hirundinaria-Origanum vulgare* types. Altitude ranges between 180 and 420 m. Vegetation of this type is widespread from Pavlov Hills in the south to the southern foothills of the

Fig. 5 Photos of the four major types of thermophilous fringe and tall-herb vegetation in South Moravia: (**A**) *Potentilla alba-Laserpitium latifolium* (Zahrady pod Hájem, White Carpathians, July 6, 2020); (**B**) *Potentilla argentea-Geranium sanguineum* (Šobes, Podyjí National Park, July 20, 2021); (**C**) *Vincetoxicum hirundinaria-Origanum vulgare* (Říčka Valley, Moravian Karst, July 19, 2021); (**D**) *Geranium sanguineum-Peucedanum cervaria* (Danielsberg, Dunajovice Hills, June 6, 2020)

Ždánický les Hills and Litenčice Hills in the north; some relevés classified in this type were also recorded along the eastern margin of the Bohemian Massif, particularly in the southern outskirts of the Moravian Karst (Fig. 6). With 98 relevés, this is the largest unit in this classification.

The Central South-Moravian type can be further divided into three subtypes. The first of them, *Inula ensifolia* variant (4), consists of 30 relevés. It is a community with dominant *Peucedanum cervaria* and *Brachypodium pinnatum*, with the presence of species typical for dry grasslands of the *Cirsio-Brachypodion pinnati* alliance. Typical for this variant are e.g. *Carex humilis*, *Dorycnium pentaphyllum* agg., *Chamaecytisus ratisbonensis*, *Inula ensifolia*, *Pulsatilla grandis* and *Plantago media*.

The *Cytisus nigricans* variant (5) is represented by 26 relevés. These are communities mainly associated with the fringes of forests and shrubs. Typical species are *Buglossoides purpurocaerulea*, *Cytisus nigricans*, *Medicago minima*, *Melitis melissophyllum*, *Sanguisorba minor*, *Viola mirabilis* and others. Species such as *Brachypodium pinnatum*, *Geranium sanguineum*, *Peucedanum cervaria* or *Vicia cracca* agg. can dominate here.

The *Dictamnus albus* variant (6) includes 42 relevés of vegetation often appearing at forest fringes and openings or as successional stages of abandoned dry grasslands. Species of disturbed or nutrient-enriched sites such as *Carduus acanthoides* and *Bromus inermis* may occur here. Common dominants are *Dictamnus albus*, *Geranium sanguineum*, *Peucedanum cervaria* and *Vicia cracca* agg.

Comparison with previous classifications

The alluvial plot (Fig. 7) and the ordination plot with centroids of relevés classified into the association level (Fig. 8) illustrate the relationship of our classification to two classifications recently used in the Czech Republic. The most relevés of the *Potentilla alba-Laserpitium latifolium* type were previously not assigned to *Geranion sanguinei*, but rather to *Cirsio-Brachypodion* alliance (particularly the *Brachypodio pinnati-Molinietum arundinaceae* association) or to *Trifolion medii* alliance. Relevés of the *Potentilla*

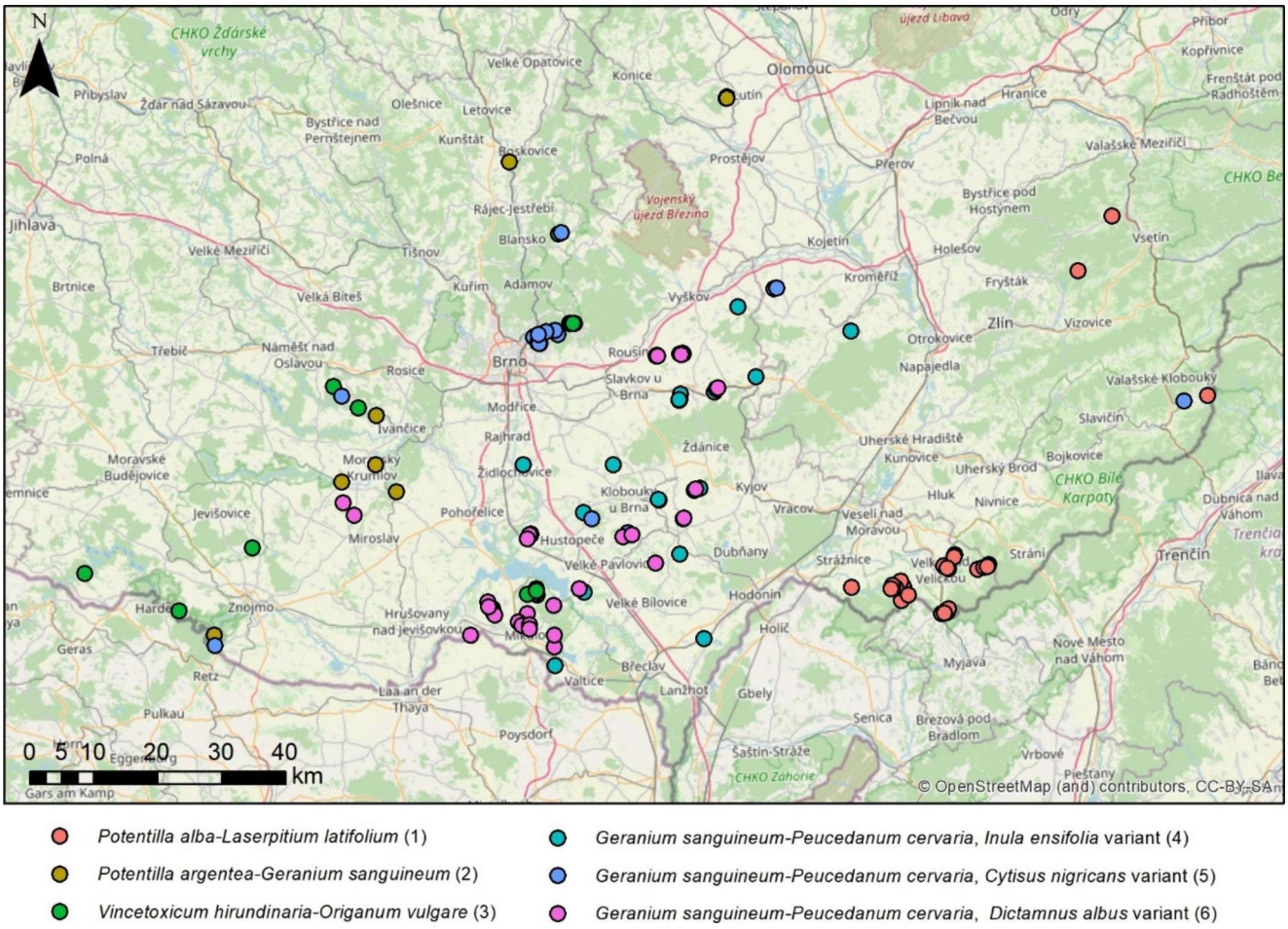

Fig. 6 Distribution of the tall-herb vegetation in South Moravia, sites belonging to each cluster are displayed in different colours

argentea-Geranium sanguineum type were previously mostly assigned to the *Trifolio alpestris-Geranietum sanguinei* association both by the current version of the expert system and in the CNPD. Relevés of the *Vincetoxicum hirundinaria-Origanum vulgare* type were previously also mostly assigned to *Trifolio alpestris-Geranietum sanguinei* by the expert system (if classified at the association level), while there was no consistent assignment in the CNPD (mostly *Vincetoxico hirundinariae-Origanetum vulgaris* Kolbek et Petříček 1979, *Geranio-Trifolietum alpestris* Müller 1962, or *Geranion sanguinei* Tüxen in Th. Müller 1961 with no association specified). Most relevés of the *Geranium sanguineum-Peucedanum cervaria* type, variant *Inula ensifolia*, were previously assigned either to *Geranio sanguinei-Peucedanetum cervariae*, or outside *Geranion sanguinei* (mostly to *Cirsio-Brachypodion* alliance) by the expert system, while they were mostly assigned to *Peucedanetum cervariae* Kaiser 1926 association in the CNPD. Relevés of the *Geranium sanguineum-Peucedanum cervaria* type, variant *Cytisus nigricans*, were previously mostly assigned either to *Geranion sanguinei* (then most often to *Geranio sanguinei-Peucedanetum cervariae*), or to *Cirsio-Brachypodion* alliance by the expert system, and either to *Peucedanetum cervariae* or *Geranio-Trifolietum alpestris* in the CNPD. Relevés of the *Geranium sanguineum-Peucedanum cervaria* type, variant *Dictamnus albus*, were previously split rather evenly among all three associations of the *Geranion sanguinei* alliance (*Trifolio alpestris-Geranietum sanguinei*, *Geranio sanguinei-Dictamnetum albae* and *Geranio sanguinei-Peucedanetum cervariae*) by the expert system, while they were often classified to *Geranio-Dictamnetum* Wendelberger ex Müller 1962 (or *Geranion sanguinei* with no association specified) in the CNPD.

Discussion

Variation of *Geranion sanguinei* in South Moravia

Our results show that the thermophilous fringe and tall herb vegetation is well differentiated ecologically and geographically in the South Moravian forest-steppe. In the warm and

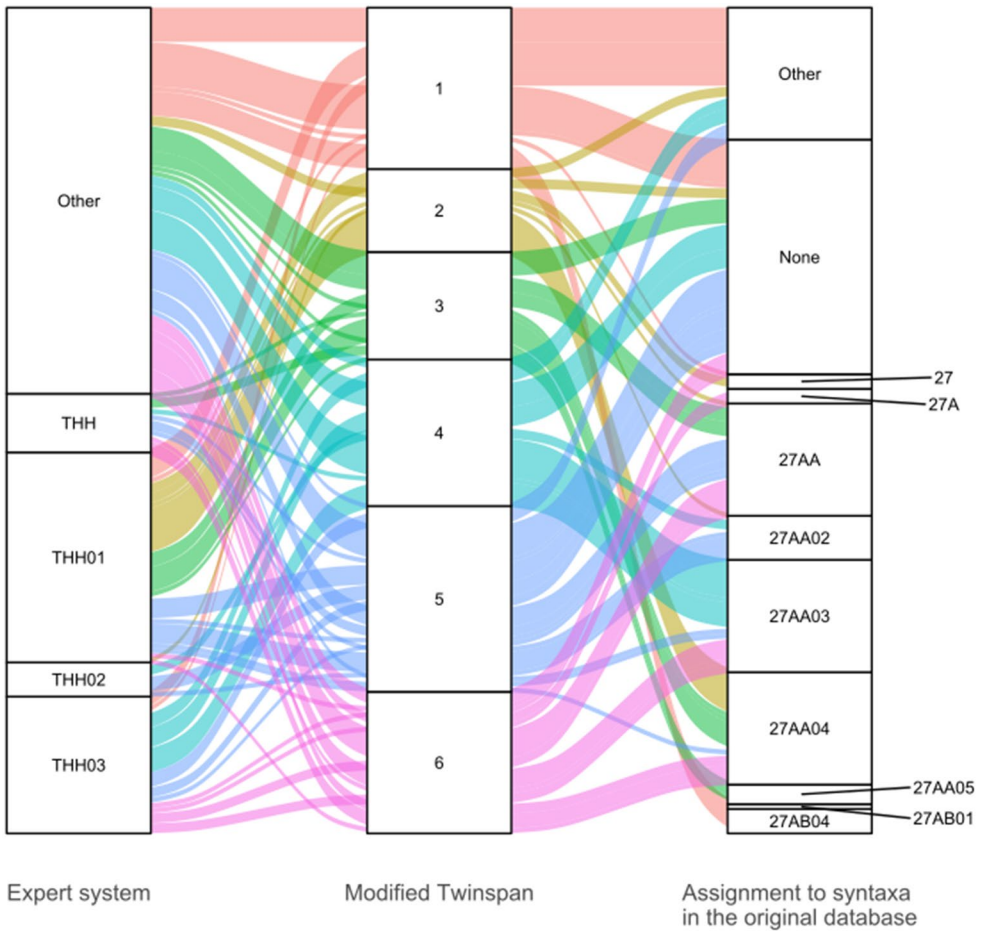

Fig. 7 Alluvial plot comparing the assignment of relevés to vegetation types presented in this paper (Modified Twinspan) with the current national classification (Hoffmann 2007) as implemented in the expert system for vegetation of the Czech Republic (Chytrý et al. 2020) and the original assignment to syntaxa of Moravec et al. (1995) in the CNPD. Groups created by the Modified Twinspan classification are plotted in different colours. Only syntaxa corresponding to the class *Trifolio-Geranietea sanguinei*, subclass *Origanetalia vulgaris*, alliance *Geranion sanguinei* and their subordinate units are displayed. Legend: THH – *Geranion sanguinei* Tüxen in Müller 1962, THH01 – *Trifolio alpestris-Geranietum sanguinei* Müller 1962, THH02 – *Geranio sanguinei-Dictamnetum albae* Wendelberger ex Müller 1962, THH03 – *Geranio sanguinei-Peucedanetum cervariae* Müller 1962, 1 – *Potentilla alba-Laserpitium latifolium*, 2 – *Potentilla argentea-Geranium sanguineum*, 3 – *Vincetoxicum hirundinaria-Origanum vulgare*, 4 – *Geranium sanguineum-Peucedanum cervaria*, variant *Inula insifolia*, 5 – *Geranium sanguineum-Peucedanum cervaria*, variant *Cytisus nigricans*, 6 – *Geranium sanguineum-Peucedanum cervaria*, variant *Dictamnus albus*, 27 – *Trifolio-Geranietea sanguinei* Th. Müller 1961, 27 A – *Origanetalia vulgaris* Th. Müller 1961, 27AA – *Geranion sanguinei* Tüxen in Th. Müller 1961, 27AA02 – *Geranio-Dictamnetum* Wendelberger ex Müller 1962, 27AA03 – *Peucedanetum cervariae* Kaiser 1926, 27AA04 – *Geranio-Trifolietum alpestris* Müller 1962, 27AA05 – *Vincetoxico hirundinariae-Origanetum vulgaris* Kolbek et Petříček 1979, 27AB01 – *Trifolio medii-Agrimonietum* Müller 1962, 27AB04 – *Trifolio medii-Melampyretum nemorosi* Dierschke 1973

dry central region of South Moravia, the type *Geranium sanguineum-Peucedanum cervaria* predominates, occurring on classic sites of xerothermic basiphilous vegetation in complexes with broad-leaved dry grasslands and thermophilous oak forests. Despite the considerable internal variability (shown e.g. by the classification dendrogram, Fig. 1), we suggest that, given the similar ecology and distribution of its variants, it is appropriate to conceive it as a single broad vegetation type. In the relatively mesic climate of the eastern edge of the Bohemian Massif and the higher elevations of the Pavlov Hills, two ecologically distinctive types of fringe and tall herb vegetation occur on the hard-rock bedrock: *Vincetoxicum hirundinaria-Origanum vulgare* on base-rich bedrock and *Potentilla argentea-Geranium sanguineum* on acidic bedrock. In the eastern part of South Moravia, where rainfall increases again on the windward slopes of the White Carpathians, the type *Potentilla alba-Laserpitium latifolium* occurs on calcareous claystones and sandstones, mainly at altitudes between 300 and 600 m. We suggest the four distinguished vegetation types are equivalent to phytosociological associations. Once verified at the national level, they can be used to rebuild the existing syntaxonomic system of the Czech Republic.

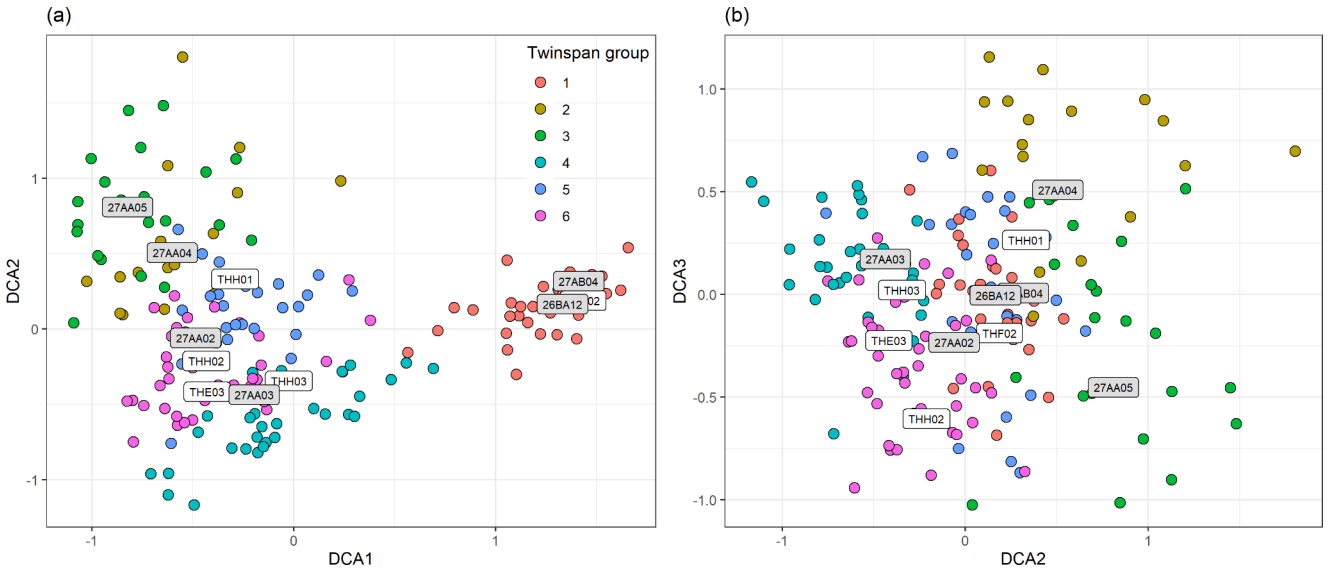

Fig. 8 Detrended correspondence analysis displaying sites. First two (**a**) or second and third (**b**) ordination axes are shown. Sites belonging to each cluster are displayed in different colours. Centroids for the relevés assigned by the expert system or in the original database to the association level are displayed. Only associations covered by more than three relevés are shown. **Legend: 1** – *Potentilla alba-Laserpitium latifolium*, **2** – *Potentilla argentea-Geranium sanguineum*, **3** – *Vincetoxicum hirundinaria-Origanum vulgare*, **4** – *Geranium sanguineum-Peucedanum cervaria*, variant *Inula insifolia*, **5** – *Geranium sanguineum-Peucedanum cervaria,* variant *Cytisus nigricans*, **6** – *Geranium sanguineum-Peucedanum cervaria*, variant *Dictamnus albus*, **THE03** – *Polygalo majoris-Brachypodietum pinnati* Wagner 1941, **THF02** – *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939, **THH01** – *Trifolio alpestris-Geranietum sanguinei* Müller 1962, **THH02** – *Geranio sanguinei-Dictamnetum albae* Wendelberger ex Müller 1962, **THH03** – *Geranio sanguinei-Peucedanetum cervariae* Müller 1962, **THI02** – *Trifolio-Melampyretum nemorosi* Dierschke 1973, **26BA12** – *Brachypodio-Molinietum* Klika 1939, **27AA02** – *Geranio-Dictamnetum* Wendelberger ex Müller 1962, **27AA03** – *Peucedanetum cervariae* Kaiser 1926, **27AA04** – *Geranio-Trifolietum alpestris* Müller 1962, **27AA05** – *Vincetoxico hirundinariae-Origanetum vulgaris* Kolbek et Petříček 1979, **27AB04** – *Trifolio medii-Melampyretum nemorosi* Dierschke 1973

In the phytosociological literature, the link of *Geranion sanguinei* to forest fringes is often emphasized (e.g. Müller 1977; Mucina and Kolbek 1993; Dengler and Boch 1997; Valachovič and Hegedüšová Vantarová 2014). In the study area, this vegetation indeed occurs on the fringes of forests and scrub, but also in other habitats, such as forest openings, surroundings of solitary trees and within complexes of broad-leaved steppe grasslands, particularly on north-oriented slopes, at lower parts of slopes and in terrain depressions. Compared to dry grasslands, their habitats are relatively moist, productive and less intensively managed (mowing, grazing). Too intensive management supports grasses and low herbs, while the tall herbs are often suppressed by removing aboveground biomass (Klimeš 1999; Čarni 2005; Roleček et al. 2019). In the absence of disturbance, these habitats are easily encroached by woody vegetation. Also their species composition is intermediate between dry grasslands and the herbaceous understorey of open woodlands and scrub.

Comparison with syntaxa recently used in the Czech Republic

The vegetation types distinguished in this study are delimited differently from those distinguished in the current national classification Vegetation in the Czech Republic (Hoffmann 2007) and also from those applied in the CNPD adopted from Moravec et al. (1995). These differences may be partly ascribed to the restriction of our study to South Moravia or to a different definition of the vegetation of the *Geranion sanguinei* alliance. Another reason could be that the individual associations in the Vegetation of the Czech Republic are defined by the dominance of *Dictamnus albus*, *Geranium sanguineum* and *Peucedanum cervaria*, which does not always correspond to patterns of variation in total species composition.

The vegetation classified as the type *Potentilla alba-Laserpitium latifolium* was previously assigned to the class *Trifolio-Geranietea* and its subordinate syntaxa only exceptionally. One of the reasons is that this vegetation type may have different dominants (besides *Geranium sanguineum* also e.g. *Betonica officinalis*, *Clematis recta*, *Laserpitium latifolium* or *Vicia cracca* agg.), so dominant-based classification may not work. This vegetation type is very rich in

species and due to the large representation of species of the White Carpathian forest-steppe meadows (e.g. *Cirsium pannonicum*, *Colchicum autumnale*, *Lathyrus latifolius*, *Potentilla alba*, *Sanguisorba officinalis*, *Serratula tinctoria*) was sometimes assigned to the association *Brachypodio pinnati-Molinietum arundinaceae* by the expert system. In contrast to this association, tall herbs prevail over grasses and mesophilous species (e.g. *Agrostis capillaris*, *Alchemilla* spp., *Astrantia major*, *Leucanthemum vulgare* agg., *Trisetum flavescens*) are highly represented in the type *Potentilla alba-Laserpitium latifolium*. The average cover of diagnostic species of the *Geranion sanguinei* alliance is only slightly higher than the average cover of species diagnostic for *Trifolion medii*; this may be the reason for the assignment of some relevés within the *Trifolion medii* alliance.

Relevés of the acidophilous type *Potentilla argentea-Geranium sanguineum* were previously usually assigned to the association *Trifolio alpestris-Geranietum sanguinei* by the expert system, corresponding to the association *Geranio-Trifolietum alpestris* in the CNPD. The reason probably is that *Geranium sanguineum* is the most frequent dominant here. On the other hand, *Geranium sanguineum* can dominate also in vegetation on the calcareous substrate and deeper soils, from which the vegetation type *Potentilla argentea-Geranium sanguineum* differs considerably in the representation of acidophilous species (e.g. *Festuca ovina*, *Potentilla argentea*, *Rumex acetosella*, *Viscaria vulgaris*) and species typical of dry rocky habitats with shallow soils (e.g. *Artemisia campestris*, *Koeleria macrantha*, *Linaria genistifolia*). In the monograph Vegetation of the Czech Republic (Hoffmann 2007), an acidophilous variant of the association *Trifolio alpestris-Geranietum sanguinei* is mentioned, with diagnostic species *Echium vulgare*, *Hylotelephium maximum*, *Viscaria vulgaris*, *Melica transsilvanica*, *Poa nemoralis* and *Trifolium alpestre* bound to rocky habitats at the nutrient-poor rocks, that may roughly correspond to this vegetation type.

Geranium sanguineum often dominates also in the *Vincetoxicum hirundinaria-Origanum vulgare* type, whose relevés were previously usually also assigned to *Trifolio alpestris-Geranietum sanguinei* by the expert system. In contrast to the other relevés classified into this association, species bound to limestone rocks (e.g. *Asplenium ruta-muraria*) can be found here. In the original database (CNPD), some relevés were classified into the association *Vincetoxico hirundinariae-Origanetum vulgaris* by their authors.

Phytosociological relevés of the type *Geranium sanguineum-Peucedanum cervaria* were previously assigned to all three associations of *Geranion sanguinei* recognized in the Vegetation of the Czech Republic (Hoffmann 2007) by the expert system. The *Inula ensifolia* variant, where *Peucedanum cervaria* dominates in most cases, was included almost exclusively in the association *Geranio sanguinei-Peucedanetum cervariae*. This vegetation corresponds to the variant *Festuca rupicola* with diagnostic species *Brachypodium pinnatum*, *Bupleurum falcatum*, *Medicago falcata* and *Salvia pratensis* (Hoffmann 2007). The most common species occurring in the *Inula ensifolia* variant are those typical for dry grasslands (*Aster amellus*, *Carex humilis*, *Dorycnium pentaphyllum* agg., *Festuca rupicola*, *Inula ensifolia* etc.), which explains the assignment of some relevés to the association *Polygalo majoris-Brachypodietum pinnati*. *Peucedanum cervaria* is also represented in broad-leaved steppe grasslands. The tall-herb vegetation with *Inula ensifolia* is at the beginning of the vegetation season very similar to the broad-leaved dry grasslands. However, in the summer, flowering *Peucedanum cervaria* reaches high cover and overgrows other species. In the older classification of the vegetation of the Czech Republic (Moravec et al. 1995), the stands were often classified into the association *Peucedanetum cervariae*. Relevés of the *Cytisus nigricans* variant were also in most cases assigned to the association *Geranio sanguinei-Peucedanetum cervariae* by the expert system, but compared to the previous variant, *Geranium sanguineum* often appears as a dominant in these stands, which is reflected in the assignment of some relevés to the association *Geranio-Trifolietum alpestris* in CNPD. Relevés of the *Dictamnus albus* variant were rather evenly distributed among all three associations of the alliance *Geranion sanguinei* by the expert system. In CNPD, most relevés of this variant were assigned to the association *Geranio-Dictamnetum* and several to the associations *Peucedanetum cervariae* and *Geranio-Trifolietum alpestris*. *Geranium sanguineum*, *Peucedanum cervaria* and *Dictamnus albus* may dominate these stands, sometimes together. In addition, *Vicia cracca* agg., *Phlomis tuberosa* and some other species may dominate here.

Comparison with syntaxa used in neighbouring countries

In other Central European countries, many different syntaxonomic units were used for the thermophilous fringe and tall herb vegetation. Vegetation similar to the type *Potentilla alba-Laserpitium latifolium* with a dominance of *Laserpitum latifolium* and co-occurrence of thermophilous and mesophilous, steppe and montane species, was recorded in several surrounding countries. Müller (1977) mentioned a montane variant of the *Geranio-Peucedanetum cervariae* (Kuhn 37) Th. Müller 62 association occurring in the Swabian and Franconian Jura. *Laserpitium latifolium* dominates here along with *Peucedanum cervaria*. The author further distinguishes a separate association *Bupleuro*

longifolii-Laserpitietum latifolii Th. Müller 77 in the higher parts of the Swabian Jura, which differs by a lower representation of thermophilous species (*Peucedanum cervaria*, *Aster amellus*) and the occurrence of montane and mesophilous species (e.g. *Bupleurum longifolium*, *Geranium sylvaticum*, *Phyteuma spicatum*). Mucina and Kolbek (1993) described a new association *Arabidi turritae-Laserpitietum asperi* Mucina in Mucina et Kolbek 1993 with the dominance of *Laserpitium latifolium*. There also occur species typical of thermophilous forest fringes (e.g. *Erysimum odoratum*, *Geranium sanguineum*, *Tanacetum corymbosum*, *Valeriana stolonifera* ssp. *angustifolia*, *Veronica vindobonensis*, *Vincetoxicum hirundinaria*). This association is known from the Hainburg Hills in Austria and from the surroundings of the Tematín Hills in Slovakia.

Potentilla argentea-Geranium sanguineum represents an acidophilous type of vegetation with a predominance of *Geranium sanguineum* and *Trifolium alpestre*, usually classified as the association *Geranio sanguinei-Trifolietum alpestris* Müller 1962. Besides the typical basiphilous variant of this association, Valachovič and Hegedüšová Vantarová (2014) mention the occurrence of an acidophilous type of this vegetation with *Viscaria vulgaris* on neovolcanic rocks, quartzites, granodiorites and flysch in Slovakia. Brzeg (2005) mentions among the typical species of the association *Geranio-Trifolietum alpestris* Th. Müller 1961 in Poland e.g. *Astragalus glycyphyllos*, *Festuca ovina*, *Hypericum perforatum*. In addition to the association *Geranio-Trifolietum alpestris* Th. Müller 61 with the acidophilous species *Agrostis capillaris* and *Melampyrum pratense*, Müller (1977) defines a separate association *Teucrio scorodoniae-Polygonatetum odorati* Korneck 74 em. Th. Müller for communities on acidic substrates in South Germany. This vegetation is reported from siliceous rocky slopes in the Regen and Danube valleys in the surroundings of Regensburg. The eastern variant of this association includes e.g. *Achillea millefolium* agg., *Artemisia campestris*, *Cytisus nigricans*, *Euphorbia cyparissias*, *Festuca ovina*, *Hylotelephium telephium*, *Potentilla argentea* and *Vincetoxicum hirundinaria*.

Basiphilous rock type *Vincetoxicum hirundinaria-Origanum vulgare* has a species composition similar to the association *Origano vulgaris-Vincetoxicetum hirundinariae*. This association was accepted by Moravec et al. (1995) for the Czech Republic and is reported also from neighbouring Slovakia (Valachovič and Hegedüšová Vantarová 2014) under the name *Origano vulgaris-Vincetoxicetum hirundinariae* Kolbek 2001 and from Poland (Brzeg 2005) under the name *Origano-Vincetoxicetum hirundinariae* Kolbek et Petříček 1979 ex M. Wojterska 2003. Stands in southern Moravia are more similar to those in Slovakia. *Galium mollugo* agg., *Polygonatum odoratum*, *Securigera varia* and *Teucrium chamaedrys* are among the typical species. The association occurs on steep slopes with shallow skeletal soils and screes and at the upper edges of limestone plateaus e.g. in Tribeč and Strážov Mts or in the Slovak Karst.

Inula ensifolia variant of the type *Geranium sanguineum-Peucedanum cervaria* with dominants *Peucedanum cervaria* and *Brachypodium pinnatum* and a large proportion of species typical for broad-leaved steppe grasslands is close to the association *Geranio sanguinei-Peucedanetum cervariae*. This association is distinguished in the Czech Republic and Slovakia (Hoffmann 2007; Valachovič and Hegedüšová Vantarová 2014), similar associations are distinguished in other central European countries: Müller (1977) reports *Geranio-Peucedanetum cervariae* (Kuhn 37) Th. Müller 61 from Germany, Mucina and Kolbek (1993) and Brzeg (2005) report *Peucedanetum cervariae* Kaiser 1926 from Austria and Poland, respectively.

Vicia cracca agg. (mostly *V. tenuifolia*) often dominates in relevés classified to the *Cytisus nigricans* variant of the type *Geranium sanguineum-Peucedanum cervaria*. Other species found in this association are for example *Arrhenatherum elatius*, *Bupleurum falcatum*, *Fragaria viridis*, *Medicago falcata* and *Viola hirta*. Similar stands are often classified as a separate association *Campanulo bononiensis-Vicietum tenuifoliae*: Müller (1977) reports *Campanulo-Vicietum tenuifoliae* Krausch 61 apud Th. Müller 62 em. Korneck 74 from Germany, Mucina and Kolbek (1993), Brzeg (2005) and Valachovič and Hegedüšová Vantarová (2014) report *Campanulo bononiensis-Vicietum tenuifoliae* Krausch in Müller 1962 from Austria, Poland and Slovakia, respectively.

Dictamnus albus variant of the type *Geranium sanguineum-Peucedanum cervaria* includes stands dominated by *Dictamnus albus* and *Geranium sanguineum* classified in most vegetation surveys into the association *Geranio sanguinei-Dictamnetum albae*: Müller (1977) reports *Geranio-Dictamnetum* Wendelberger 54 from Germany, Mucina and Kolbek (1993) report *Geranio-Dictamnetum* Wendelberger ex Müller 1962 from Brzeg (2005) reports *Geranio-Dictamnetum* Wendelberger 1954 ex Müller 1962 from Poland and Valachovič and Hegedüšová Vantarová (2014) reports *Geranio sanguinei-Dictamnetum albi* Wendelberger 1954 ex Müller 1962 from Slovakia. This vegetation type may be however dominated also by *Peucedanum cervaria*, *Vicia cracca* agg. and other species.

Methodological consequences

Our results confirm that when physiognomic criteria (e.g., the dominance of herbs, especially tall herbs) are used to define the vegetation of fringes and tall herbs, and a standard classification method based on the analysis of similarity in

species composition is applied, we can obtain an ecologically and geographically meaningful classification at the level of phytosociological associations. It is then up to our decision at which hierarchical level we include it in our classification scheme: whether as a separate unit at the highest hierarchical level (i.e., the *Trifolio-Geranietea* class in the case of the syntaxonomic classification) or as a subordinate unit of another high-level unit (e.g., *Festuco-Brometea* class). This decision depends on other circumstances, such as the purpose of the classification being prepared. However, the essential point is our finding that the structure of a variation of the fringe and tall herb vegetation does not require a dominance-based approach as recently used in the Vegetation of the Czech Republic (Hoffmann 2007) but allows for a meaningful application of floristic classification. New data from the field survey may need to be obtained before starting the syntaxonomic revision at the national level.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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