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# Formalized classification of the class *Montio-Cardaminetea* in Europe: towards a consistent typology of spring vegetation

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**Abstract:** The class *Montio-Cardaminetea* includes vegetation of springs with constant water flow. These habitats, which function as islands for highly specialized and sensitive biota, are endangered by ongoing landscape and climatic changes. Although a harmonized classification into vegetation units is necessary for effective habitat conservation, there is currently no synthetic classification of the class *Montio-Cardaminetea*. Here a large set of vegetation-plot records was obtained from national and private databases. The aim was to validate the EuroVegChecklist classification scheme, search for additional ecologically meaningful vegetation types and develop an automatic system for classifying new plots from Europe. We formally defined the cores of eight of the ten EuroVegChecklist alliances: *Caricion remotae*, *Cratoneurion commutati*, *Lycopodo europaei-Cratoneurion commutati*, *Epilobio nutantis-Montion*, *Koenigio-Microjuncion*, *Mniobryo-Epilobion hornemanii*, *Philonotidion seriatae* (*Cardamino-Montion*) and *Swertio perennis-Anisothecion squarrosi*, which were also reproduced by unsupervised classifications. Both unsupervised and semi-supervised classifications further suggested two alliances not previously recognized in the EuroVegChecklist: *Anthelion julaceae* (liverwort-dominated subalpine to alpine springs in highly oceanic regions in Britain) and *Cratoneuro filicini-Calthion laetae* (mesotrophic herb-rich subalpine and alpine springs). The unsupervised classifications mainly reflected the base saturation gradient, distinguishing between calcareous and non-calcareous springs. Therefore, it is suggested the order *Montio-Cardaminetalia*, which is broadly delimited in the EuroVegChecklist, be divided into two separate orders and the following three orders should be distinguished within the class *Montio-Cardaminetea*: *Cardamino-Chrysosplenietalia* (non-calcareous forest springs; *Caricion remotae*), *Cardamino-Cratoneuretalia* (calcareous springs; *Cratoneurion commutati*, *Lycopodo europaei-Cratoneurion commutati*) and *Montio-Cardaminetalia* (non-calcareous non-forest springs; all other alliances).

**Keywords:** azonal habitat, expert classification system, phytosociology, plant community, supervised vegetation classification, unsupervised classification, vegetation survey, wetlands

## Introduction

The class *Montio-Cardaminetea* includes the vegetation of springs and spring-like habitats, such as flushes, seepages and the banks of mountain brooks. For simplicity, all of these habitats will be refered to as ‘springs’ in the following text. They are characterized by a more or less constant cold-water discharge, stable temperature and high oxygen saturation (Persson 1961, Zechmeister & Mucina 1994). Springs are an azonal vegetation type (Diekmann 1997, Joosten et al. 2017) and are also referred to as a hydrological subclimax (Hinterlang 1992). The low temporal variability of environmental conditions in situ favours the occurrence of a highly specialized biota (Cantonati et al. 2006, 2020b, Coufal et al. 2023).

Spring habitats are currently threatened in almost all parts of Europe, mostly due to the disruption of the hydrological regime by drainage for agricultural and forestry purposes or, in some areas, due to intensive trampling by cattle. Other threats include nutrient input, acidification and climate change (Cantonati et al. 2006, 2020a, Stevens et al. 2022). Environmental changes and site degradation can lead to a decline or loss of rare and sensitive spring biota. As a result, some spring types have recently been added to national Red Lists of habitats (e.g. Lindgaard & Henriksen 2011, Chytrý et al. 2019). Effective protection of selected habitats (including their monitoring and management, as well as the establishment of protected areas) generally requires a harmonized classification system based on clearly defined units. Since most terrestrial habitats can be successfully and unequivocally defined using vegetation science methods (Chytrý et al. 2020), it is essential to establish a consistent classification of spring vegetation that is useful for communication among scientists from different countries and for conservation management.

Variability in spring vegetation is determined by several ecological factors that are considered in previous vegetation classification schemes. Mineral richness, pH and conductivity, light and nutrient availability, elevation, and climate are repeatedly shown to be the most important determinants of species composition of spring vegetation (Beierkuhnlein & Gräsle 1998, Audorff et al. 2011, Hájková et al. 2011, Sekulová et al. 2011, Spitale et al. 2012, Schweiger et al. 2015a, b, Lyons & Kelly 2017, Miller et al. 2020).

Already in the early stages of phytosociological research, vegetation associated with springs was distinguished from other vegetation types (Samuelsson 1917, Allorge 1922). The first alliance was recognized in the pioneering works of Braun-Blanquet (1925, 1926), although his *Cardamino-Montion* was rather heterogeneous in terms of species composition and ecology. Research on spring vegetation has continued in numerous local and regional studies (e.g. Gams 1927, Nordhagen 1943, Dahl 1956, Hadač 1971, Dierssen 1973, Philippi 1975, Geissler 1976, Miserere & Buffa 2001, Sekulová et al. 2011, Lyons & Kelly 2017, Seiler et al. 2021). National overviews have been published for most Western and Central-European countries (Maas 1959, Hadač 1983, Rodwell 1991, Hinterlang 1992, 2017, Zechmeister 1993, Siebum et al. 1995, Valachovič 2001, Matuszkiewicz 2007, Hájková & Hájek 2011, Rivas-Martínez 2011, de Foucault 2018) and for some countries in south-eastern Europe (Horvat 1960, Coldea 1997, Tzonev et al. 2009). Although the classification schemes reflect similar sources of variation in species composition, including mineral richness, temperature, light and availability of macronutrients, the spring vegetation classification systems differ. The first synthesis of spring vegetation at a European scale based on a representative dataset (> 1,200 vegetation-plot records) was published by Zechmeister & Mucina (1994). An updated and modified scheme for *Montio-Cardaminetea*, not based on an analysis of data, was later published in the EuroVeg-Checklist (Mucina et al. 2016). The EuroVegChecklist distinguishes two orders within the class *Montio-Cardaminetea*: *Cardamino-Chrysosplenietalia* containing the *Caricion remotae* alliance, i.e. soft-water springs in forests and other shaded habitats (henceforth referred to as 'forest springs') and *Montio-Cardaminetalia*, which contains all the other alliances. Although the EuroVegChecklist is a broad consensus of experts on European vegetation, the majority of accepted syntaxa have not yet been critically revised based on the analysis of primary data (i.e. vegetation plots). Another classification system, originally produced as a national vegetation overview, but extended to the European level, was proposed by de Foucault (2018). Compared to the EuroVegChecklist, this system distinguishes other alliances of forest springs (*Wahlenbergio hederaceae-Sibthorpion europaeae*, *Lysimachio nemorum-Saxifragion hirsutae* and *Athyrio filicis-feminae-Chrysosplenion dubii*) and omits several alliances accepted in the EuroVegChecklist (e.g. *Epilobio nutantis-Montion*, *Lycopodo europaei-Cratoneurion commutati*).

The recent development of analytical software and computer expert systems that allow instant classification of thousands of plots, as well as the integration of vegetation databases into the European Vegetation Archive (EVA; Chytrý et al. 2016), has facilitated the production of vegetation syntheses across national boundaries dealing with different vegetation types (e.g. Eliáš et al. 2013, Aćić et al. 2015, Douda et al. 2016, Willner et al. 2017, 2019, Marcenò et al. 2018, Landucci et al. 2020, Novák et al. 2020, 2023, Bonari et al. 2021, Kalníková et al. 2021, Jiroušek et al. 2022). Such an analysis has not been conducted yet for spring vegetation of the class *Montio-Cardaminetea*.

The aims of this article are to: (i) validate or update the classification scheme of spring vegetation in the EuroVegChecklist using vegetation-plot data, (ii) delimit the main vegetation types (orders, alliances) of the class *Montio-Cardaminetea*, (iii) identify their diagnostic species, describe their species composition, and characterize the habitat and distribution of particular vegetation types, and (iv) develop an expert system for the automatic assignment of vegetation plots to class, orders and alliances.

## Methods

### *Data collection*

Vegetation plot records (relevés; henceforth referred to as 'vegetation plots' or 'plots') were obtained from the EVA database (Chytrý et al. 2016; for a list of the databases used see Supplementary Data S1), supplemented by private databases of some of the authors of this study. All vegetation plots were saved in a single file using Turboveg 3 software (Hennekens 2015) and subsequently imported into the JUICE 7.0 program (Tichý 2002). During the collection of data several hundred plots from northern Europe were digitized and stored in the European Mire Vegetation Database (Peterka et al. 2015).

The initial ("working") dataset of vegetation plots was prepared by including plots that contained at least one species that was considered to be a preliminary spring indicator (Supplementary Data S1). This dataset contained many plots with other vegetation types. Such a broad initial selection, however, was crucial for accurately testing the class definition. Pre-selection of vegetation plots is also necessary for practical reasons, as the EVA database currently contains nearly 2,000,000 vegetation-plot records.

**Fig. 1.** Distribution of vegetation plots of the class *Montio-Cardaminetea* in Europe.

### *Nomenclature*

Nomenclature was harmonized following Euro+Med (2006–2021) for vascular plants, Hill et al. (2006) for mosses and Söderström et al. (2016) for liverworts. Records of algae, fungi, lichens, and taxa identified only at the genus level (e.g. *Bryum* sp., *Carex* sp.) and at higher taxonomic levels (e.g. “hepatics”) were deleted. Subspecies were merged at the species level. Species with an unstable or ambiguous status (which were not differentiated in all data sources) were merged into aggregates (Supplementary Data S2) in order to minimise taxonomic bias (Jansen & Dengler 2010).

### *Formal definition of the class Montio-Cardaminetea*

To define the *Montio-Cardaminetea* class, the formal definition was developed for an automatic expert system using the principles outlined by Landucci et al. (2015), Tichý et al. (2019) and Chytrý et al. (2020). Because spring vegetation has a diverse species composition with varying species richness, the focus was on the proportion of species indicative of spring environments relative to species indicative of other habitats, rather than the absolute number of indicator species. Following the concept of Jiroušek et al. (2022) three species groups were defined:

(i) Spring-positive species (spring indicators): species that indicate springs and spring-like habitats.

(ii) Neutral species: species that are common in spring vegetation, but are also often found in other habitats. They are neither positive nor negative indicators of spring vegetation. Trees and shrubs are also included in this group because they often form a canopy layer above some types of spring vegetation. Thus, distinguishing spring vegetation from the vegetation of hygrophilous deciduous forests depends on the plot size used (Chytrý & Otýpková 2003). The mere presence of woody plants in a plot cannot be used as a criterion for classifying it as forest vegetation, since some scientists record the tree layer (shoot presence; Greig-Smith 1983, Dengler 2008) even when sampling true springs in plots of a few square meters.

(iii) Spring-negative species (other species): negative indicators of spring vegetation and corresponding environmental conditions. This group contains all other species present in the initial dataset of vegetation plots. These species are listed in the expert-system file; however, theoretically, this group could include all of the European flora.

The lists were compiled based on a collaborative effort of the authors. The class *Montio-Cardaminetea* was then formally defined based on the ratio of the summed percentage covers of spring-positive species to the summed percentage covers of spring-negative species. Thus, a vegetation plot was assigned to *Montio-Cardaminetea* if the group of spring-positive species in the plot had a higher total percentage cover than the group of spring-negative species. The ratio of these species groups was supplemented with negative criteria in order to exclude plots that contained species that occur in spring vegetation but belonged to other habitats, e.g. fens, wet cliffs or alpine tall-herb vegetation. For species lists and class definition, see Supplementary Data S3.

### *Data filtering*

After removing duplicates, 7,046 plots met the formal definition of the class *Montio-Cardaminetea* (Fig. 1). Initially, 87 plots with presence-absence-only data (i.e. 1.2% of plots classified in the class *Montio-Cardaminetea*) and 53 plots (0.8%) lacking coordinates, were deleted.

In the next step, the dataset was filtered based on plot size. Although a narrow (or equal) range of plot sizes is optimal from both statistical and methodological viewpoints (Dengler et al. 2009), restricting the data to a narrow size range could result in the exclusion of data from some regions due to differences in sampling traditions. Moreover, several studies (Forbes & Sumina 1999, Müllerová et al. 2020, Peterka et al. 2020) have shown that plots ranging in size from 1 $m^2$ to 16–25 $m^2$ are comparable in their richness of habitat specialist species and yield similar patterns in ordination analyses, at least when the focus is on aquatic, wetland or low-productive vegetation. Finally, 425 plots (6.0%) with sizes $< 0.25$ $m^2$ or $> 25$ $m^2$ were excluded. However, following the recommendation of Dengler et al. (2009), the ranges of plot sizes and median plot sizes for each cluster are presented in synoptic tables in order to allow for a post-hoc assessment of the potential effects of plot size. A lower limit of 0.25 $m^2$ was selected (rather than the more common value of 1 $m^2$; cf. Peterka et al. 2020) because of the data from Scandinavia, where some phytosociologists (e.g. Persson 1961) used this plot size. Therefore, excluding plots smaller than 1 $m^2$ would have resulted in a large gap in the data for northern Europe. The upper limit of 25 $m^2$ largely prevents the inclusion of heterogeneous stands with elements of spring vegetation and plots originally recorded during surveying alder forests, which are usually sampled using much larger plots (Chytrý & Otýpková 2003, Douda et al. 2016). In addition, 575 plots (8.2%) for which the size was not recorded were excluded, except for plots from France. Unlike other vegetation databases in EVA, plot sizes are not systematically reported in the French SOPHY database, but it is assumed that the size of most French plots is not smaller than 0.25 $m^2$ or larger than 25 $m^2$. Because trees are considered to be neutral species in the formal definition of class *Montio-Cardaminetea* and alder forests with an understory corresponding to the alliance *Caricion remotae* may fit this definition, French relevés originally assigned to forest syntaxa were excluded.

Although bryophytes are frequent and sometimes dominant in spring vegetation, they are not recorded by all phytosociologists. To avoid the bias caused by the omission of records of bryophytes in phytosociological samples, we selected (i) plots in which there was at least one bryophyte species and (ii) plots where the header data clearly indicated that the author systematically recorded bryophytes in the plots, and the absence of bryophytes in the record thus implies their absence in the vegetation sampled. Similarly, plots without vascular plants were omitted because they may have been selectively sampled bryophyte synusiae. The resulting dataset is referred to as the non-stratified dataset (4,979 plots).

Prior to unsupervised classifications, the definition of Cocktail groups and subsequent analyses, the dataset was geographically stratified to reduce potential bias associated with oversampling in some regions or at particular sites (Knollová et al. 2005). A maximum of five plots were selected for each grid cell of 1.25 min longitude × 0.75 min latitude (approximately 1.5 × 1.4 km). An heterogeneity-constrained random resampling (Lengyel et al. 2011), based on Bray-Curtis distance, was used. All records of tree and shrub species were omitted to avoid bias due to sampling inconsistencies. The resulting stratified dataset contained 4,038 plots. However, the non-stratified dataset was used for mapping the distribution of individual alliances (identified later by formal definitions in the expert system) and for testing the formal definitions of vegetation units.

### *Unsupervised classifications*

To identify the main types of spring vegetation, an unsupervised classification was carried out. Firstly, an agglomerative hierarchical cluster analysis using PC-ORD (McCune & Mefford 2006) connected to JUICE, with flexible beta linkage method (beta = –0.25; Legendre & Legendre 1998), the Bray-Curtis dissimilarity measure and square-root transformation of species covers was used. The number of clusters followed the recommendation of the OptimClass 1 algorithm (Tichý et al. 2010), which describes the relationship between the number of clusters and the total number of diagnostic species. The algorithm suggested an optimum between 28–30 clusters, and 28 clusters were used.

To evaluate whether the results of the cluster analysis reflected the main differences in spring vegetation or were instead affected by species spreading to the spring habitat islands from surrounding habitats, a parallel cluster analysis based on spring-positive species only was carried out. All settings were the same as for the cluster analysis based on total species composition.

To obtain a more robust phytosociological conclusion based on independent classifications, the dataset was also classified using the K-means method with Hellinger transformation of species percentage cover values, 50 algorithm starts and three plots to define the starting centroid. The number of resulting clusters was the same as in the previous classification. The analysis was again performed twice: based on the full species composition and only on the spring-positive species.

The clustering of the pan-European spring dataset was further supplemented by classifications of several regional subsets. The subsets were from the following geographically constrained and unequivocally defined regions: (i) Northern Europe (Fennoscandia and Iceland), (ii) Great Britain and Ireland, (iii) the Carpathians, (iv) the Alps, (v) the Balkan Peninsula and (vi) the Iberian Peninsula. We used (i) hierarchical cluster analysis with the same settings as in the analysis of the pan-European dataset and (ii) the unsupervised non-hierarchical classification algorithm Isopam (Schmidtlein et al. 2010) with the Bray-Curtis coefficient as the dissimilarity measure. Assuming that individual regions contain fewer vegetation types than all of Europe, the number of resulting clusters was set an order of magnitude lower. The number of clusters was, again, chosen based on the OptimClass method and varied between 5–8 per subset.

The results of the cluster analyses are presented in synoptic tables (Supplementary Data S4; clustering of pan-European dataset) and lists of diagnostic species for the resulting groups of vegetation plots (Supplementary Data S5; classification of regional subsets). The diagnostic species of each cluster were determined using the phi coefficient as a fidelity measure (Chytrý et al. 2002). Values of this coefficient range from –1 to +1. Positive values indicate that the species is more closely associated with the vegetation unit than would be expected by chance, with higher values indicating a greater degree of fidelity. The sizes of all groups were standardized to equal size, and the significance of fidelity was tested using Fisher's exact test ($P < 0.001$; Tichý & Chytrý 2006).

### *Supervised and semi-supervised classification*

To identify the cores of individual alliances, we defined sociological groups, i.e. species groups with a statistical tendency to co-occur in vegetation plots (Kočí et al. 2003), using the Cocktail method (Bruelheide & Chytrý 2000). The sociological groups were then combined into formal definitions using logical operators (AND, OR, NOT; Supplementary Data S6). The formal definitions of alliance cores were created considering the original material of a given alliance, tested on primary data (vegetation plots) and iteratively improved. For a general description of the process of creating formal definitions and their evaluation see Chytrý et al. (2020). As a baseline, we attempted to define all alliances listed in the EuroVegChecklist (Mucina et al. 2016). In addition, we considered other recently published high-rank syntaxa, e.g. the *Wahlenbergio-Sibthorpion*, *Lysimachio-Saxifragion* and *Athyrio-Chrysosplenion* alliances reported by de Foucault (2018). Then a semi-supervised classification was used to determine whether the unclassified plots formed new compositionally and ecologically meaningful vegetation types (groups). We considered varying numbers of resulting clusters (up to 30) to obtain robust arguments for the number of possible additional vegetation types. The semi-supervised K-means (Tichý et al. 2014) with Hellinger transformation of species percentage cover values, 50 algorithm starts and three randomly selected vegetation plots from each group to define the starting centroid was used. The resulting clusters were compared with alliances described in the literature but not separately distinguished in the EuroVegChecklist and with clusters produced by unsupervised classifications in terms of diagnostic species, overall species composition and geographic distribution.

For the core plots (i.e. plots matching the formal definition of an alliance), modelled values of groundwater calcium concentration were obtained from the map of European groundwater calcium (Hájek et al. 2021b), elevation was derived from the EU-DEM v. 1.1 model (European Environment Agency 2019), and mean annual temperature and annual precipitation were extracted from the WorldClim database (Fick & Hijmans 2017) using the ArcGIS 10 program (ESRI, Redlands, USA). Then the unweighted means of Ellenberg-type indicator values (hereafter ‘EIVs’) were calculated for light, temperature, moisture, soil reaction and nutrients. For moisture, we used EIVs available for European vascular plants and bryophytes occurring in peat-forming wetlands and related habitats (Hájek et al. 2020). Values for other factors were calculated using the new system of indicator values for European vascular plants (Dengler et al. 2023). Diagnostic species for each alliance were determined in the same way as for clusters (groups of plots) produced by unsupervised classifications (see previous chapter); they were determined separately for clusters consisting of core plots (Table 1, for full version see Supplementary Table S1) and for clusters consising of both core and non-core plots (Supplementary Table S2). In addition, the tables indicate the species identified as diagnostic for the orders (Supplementary Table S3). These were determined in a synoptic table resulting from the classification of the plots at the order level by the expert system (see the next chapter) using the stratified dataset.

The core plots of alliances were further subjected to non-metric multidimensional scaling (NMDS) of Bray-Curtis dissimilarities based on square-root transformed species percentage covers in the Canoco 5 program (Šmilauer & Lepš 2014). The NMDS solution was based on three main axes. In addition, (i) core and non-core plots of individual alliances and (ii) plots classified at the order level were subjected to ordination analyses with the same settings.

**Table 1.** Synoptic table of European spring vegetation alliances of the class *Montio-Cardaminetea*. The plots classified as cores of individual alliances by the expert system are included. The frequency values of species within each alliance are shown. Species are sorted by decreasing fidelity within alliances. Background shading indicates diagnostic species of alliances (phi > 0.35), asterisks (*) indicate highly diagnostic species (phi > 0.5). Other species are sorted by decreasing frequency within the dataset. A complete version of the table (with all species) can be found in Supplementary Table S1. For synoptic table with the core and non-core plots of the alliances, see Supplementary Table S2. For synoptic table of orders, see Supplementary Table S3. Diagnostic species of the orders are indicated by superscript letters: $^{\mathrm{CCh}}$ *Cardamino-Chrysosplenietalia*, $^{\mathrm{CCr}}$ *Cardamino-Cratoneuretalia*, $^{\mathrm{MCa}}$ *Montio-Cardaminetalia*. Ca_re: *Caricion remotae*, Cr_co *Cratoneurion commutati*, Ly-Cr: *Lycopodo europaei-Cratoneurion commutati*, E-Mo: *Epilobio nutantis-Montion*, K-Mj: *Koenigio-Microjuncion*, Cr-Ca: *Cratoneuro filicini-Calthion laetae*, An_ju: *Anthelion julaceae*, M-Ep: *Mniobryo-Epilobion hornemannii*, Ph_se: *Philonotidion seriatae*, Sw-A: *Swertio perennis-Anisothecion squarrosi*.

| Alliance | Ca_re | Cr_co | Ly-Cr | E-Mo | K-Mj | Cr-Ca | An_ju | M-Ep | Ph_se | Sw-A |
|---|---|---|---|---|---|---|---|---|---|---|
| Order | CCh | CCr | CCr | MCa | MCa | MCa | MCa | MCa | MCa | MCa |
| Number of plots | 293 | 101 | 160 | 74 | 27 | 99 | 20 | 41 | 165 | 21 |
| Range of plot sizes ($m^2$) | 0.4–25 | 1–25 | 0.25–25 | 0.25–16 | 1–20 | 1–25 | 0.25–4 | 0.25–16 | 0.25–25 | 1–25 |
| Median of plot size ($m^2$) | 9 | 4 | 4 | 2 | 1 | 10 | 4 | 1 | 4 | 4 |
| ***Caricion remotae*** | | | | | | | | | | |
| *Carex remota* $^{\mathrm{CCh}}$ | 72* | . | 6 | 1 | . | . | . | . | . | . |
| *Chrysosplenium alternifolium* $^{\mathrm{CCh}}$ | 62* | 1 | . | 11 | . | . | . | . | 1 | . |
| *Impatiens noli-tangere* $^{\mathrm{CCh}}$ | 52* | . | 1 | 1 | . | 2 | . | . | . | . |
| *Oxalis acetosella* $^{\mathrm{CCh}}$ | 50* | 2 | 6 | . | . | 2 | . | . | . | . |
| *Athyrium filix-femina* $^{\mathrm{CCh}}$ | 46* | . | 1 | 1 | . | 3 | . | . | 1 | . |
| *Carex sylvatica* $^{\mathrm{CCh}}$ | 40* | . | 1 | . | . | . | . | . | . | . |
| *Urtica dioica* $^{\mathrm{CCh}}$ | 39 | . | 1 | . | . | 1 | . | . | . | . |
| *Lamium galeobdolon* $^{\mathrm{CCh}}$ | 27 | . | 3 | . | . | . | . | . | . | . |
| *Veronica montana* $^{\mathrm{CCh}}$ | 22 | . | 1 | . | . | . | . | . | . | . |
| *Ranunculus repens* $^{\mathrm{CCh}}$ | 46 | . | 8 | 30 | . | 4 | . | 2 | 2 | . |
| *Stachys sylvatica* | 20 | . | 1 | . | . | . | . | . | . | . |
| *Lysimachia nemorum* $^{\mathrm{CCh}}$ | 28 | . | 2 | 8 | . | 1 | . | . | . | . |
| *Circaea lutetiana* $^{\mathrm{CCh}}$ | 21 | . | 1 | . | . | 1 | . | . | . | . |
| *Plagiomnium undulatum* $^{\mathrm{CCh}}$ | 37 | 3 | 13 | 5 | . | 4 | . | . | 2 | . |
| *Ajuga reptans* | 21 | . | 3 | 1 | . | . | . | . | . | . |
| *Schedonorus giganteus* | 17 | . | 1 | . | . | . | . | . | . | . |
| *Mnium hornum* | 16 | . | . | 1 | . | . | . | . | . | . |
| *Senecio nemorensis* agg. $^{\mathrm{CCh}}$ | 21 | 1 | 1 | 3 | . | 2 | . | . | . | . |
| *Chrysosplenium oppositifolium* $^{\mathrm{CCh}}$ | 28 | . | 4 | 14 | . | 1 | . | . | 1 | . |
| ***Cratoneurion commutati*** | | | | | | | | | | |
| *Bellidiastrum michelii* $^{\mathrm{CCr}}$ | . | 75* | 1 | . | . | 1 | . | . | . | . |
| *Arabis soyeri* $^{\mathrm{CCr}}$ | . | 65* | . | . | . | 2 | . | . | . | . |
| *Saxifraga aizoides* $^{\mathrm{CCr}}$ | . | 68* | . | . | . | 2 | . | . | 4 | . |
| *Pinguicula alpina* | . | 45* | . | . | . | . | . | . | . | . |
| *Tofieldia calyculata* | . | 39* | 2 | . | . | . | . | . | . | . |
| *Philonotis calcarea* $^{\mathrm{CCr}}$ | . | 39 | 10 | . | . | 5 | . | . | . | . |
| *Equisetum variegatum* | . | 25 | 1 | . | . | . | . | . | . | . |
| *Bryum pseudotriquetrum* agg. $^{\mathrm{CCr}}$ | 1 | 72 | 31 | 11 | 4 | 34 | . | 5 | 21 | 5 |
| *Tussilago farfara* | 4 | 33 | 10 | . | . | 2 | . | . | 1 | . |
| *Selaginella selaginoides* | . | 21 | 1 | 3 | . | 1 | . | . | . | . |
| *Soldanella alpina* | . | 18 | . | . | . | . | . | . | 1 | . |
| *Carex flacca* $^{\mathrm{CCr}}$ | 1 | 33 | 23 | . | . | 1 | . | . | . | . |
| *Carex frigida* | . | 21 | . | . | . | 1 | . | . | 4 | . |
| *Parnassia palustris* | . | 31 | 5 | . | 7 | 6 | . | . | 4 | . |
| *Sesleria caerulea* | . | 20 | 6 | . | . | . | . | . | . | . |

| Alliance | Ca_re | Cr_co | Ly-Cr | E-Mo | K-Mj | Cr-Ca | An_ju | M-Ep | Ph_se | Sw-A |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Lycopodo europaei-Cratoneurion commutati*** | | | | | | | | | | |
| *Pellia endiviifolia* $^{\mathrm{CCr}}$ | 2 | 2 | 82* | 1 | . | 1 | . | . | 2 | . |
| *Eucladium verticillatum* $^{\mathrm{CCr}}$ | 1 | 2 | 57* | . | . | . | . | . | . | . |
| *Hedera helix* agg. | 2 | . | 18 | . | . | . | . | . | . | . |
| *Didymodon tophaceus* | . | 1 | 17 | 1 | . | . | . | . | . | . |
| ***Epilobio nutantis-Montion*** | | | | | | | | | | |
| *Stellaria alsine* | 19 | 2 | 1 | 97* | . | 3 | . | . | 2 | . |
| *Montia fontana* $^{\mathrm{MCa}}$ | . | . | . | 99* | 30 | . | . | 20 | 8 | . |
| *Epilobium obscurum* | 2 | . | . | 53* | . | 1 | . | . | . | . |
| *Galium palustre* agg. | 25 | . | 3 | 45 | . | . | . | . | 1 | . |
| *Juncus effusus* | 15 | . | 3 | 32 | . | 2 | . | . | . | . |
| *Callitriche palustris* agg. | 1 | . | 1 | 19 | . | . | . | . | . | . |
| *Poa trivialis* | 15 | 1 | 5 | 34 | . | 1 | . | 2 | 3 | . |
| *Cardamine pratensis* agg. | 4 | 3 | 6 | 34 | . | 4 | . | 7 | 4 | . |
| *Philonotis fontana* agg. $^{\mathrm{MCa}}$ | 1 | 16 | 3 | 74 | 48 | 26 | 25 | 68 | 4 | 5 |
| *Trifolium repens* | . | . | 1 | 18 | . | 1 | . | . | 2 | . |
| ***Koenigio-Microjuncion*** | | | | | | | | | | |
| *Koenigia islandica* | . | . | . | . | 81* | . | . | . | . | . |
| *Sedum villosum* | . | . | . | 3 | 81* | . | . | 5 | 1 | . |
| *Juncus triglumis* | . | 13 | . | . | 89* | . | . | 5 | 1 | . |
| *Triglochin palustris* | . | 6 | 1 | 5 | 74* | . | . | . | . | . |
| *Juncus biglumis* | . | . | . | . | 48* | . | . | 5 | . | . |
| *Festuca vivipara* | . | . | . | . | 52* | . | 20 | . | . | . |
| *Luzula spicata* | . | . | . | . | 37* | . | . | . | . | . |
| *Cardamine nymanii* | . | . | . | . | 22 | . | . | . | . | . |
| *Cerastium fontanum* | . | 5 | 1 | 4 | 37 | 1 | 5 | 5 | 1 | . |
| *Sagina procumbens* | . | . | 1 | 20 | 33 | 1 | . | . | 1 | . |
| *Bryum archangelicum* | . | 2 | 1 | . | 19 | . | . | . | . | . |
| *Dicranella crispa* | . | . | . | . | 15 | . | . | . | . | . |
| *Pohlia filum* | . | . | . | . | 19 | . | . | 5 | . | . |
| ***Cratoneuro filicini-Calthion laetae*** | | | | | | | | | | |
| *Cardamine amara* $^{\mathrm{CCh}}$ | 56 | 4 | 4 | 16 | . | 85* | . | . | 18 | . |
| *Caltha palustris* | 24 | 12 | 4 | 19 | . | 83* | . | 5 | 30 | . |
| *Aconitum napellus* agg. | . | . | . | 1 | . | 56* | . | . | 2 | 38 |
| *Stellaria nemorum* | 29 | . | . | 3 | . | 42 | . | 5 | 4 | . |
| *Ligusticum mutellina* | . | 8 | . | . | . | 34 | . | . | 12 | 5 |
| *Silene pusilla* | . | 20 | . | . | . | 38 | . | . | 15 | . |
| *Palustriella decipiens* | . | 8 | 1 | . | . | 29 | . | 5 | 10 | . |
| ***Anthelion julaceae*** | | | | | | | | | | |
| *Anthelia julacea* | . | . | . | . | . | . | 100* | . | . | . |
| *Sphagnum auriculatum* agg. | 1 | . | . | 4 | 4 | . | 95* | . | 1 | . |
| *Racomitrium lanuginosum* | . | . | . | . | 7 | . | 75* | . | . | . |
| *Marsupella emarginata* | . | . | . | . | 4 | 1 | 70* | . | 1 | 5 |
| *Narthecium ossifragum* | . | . | 1 | . | . | . | 50* | . | . | . |
| *Agrostis vinealis* | . | . | . | . | . | . | 30* | . | . | . |
| *Scapania undulata* | 6 | 1 | . | 11 | 7 | 20 | 65 | . | 21 | 10 |
| *Campylopus atrovirens* | . | . | . | . | . | . | 20 | . | . | . |
| ***Mniobryo-Epilobion hornemannii*** | | | | | | | | | | |
| *Epilobium hornemannii* | . | . | . | . | . | . | . | 98* | . | . |
| *Scapania paludosa* | . | 1 | . | . | . | . | . | 61* | . | . |
| *Poa alpigena* | . | . | . | . | . | . | . | 41* | . | . |
| *Phleum alpinum* agg. | . | 1 | . | . | . | 2 | . | 44* | 2 | . |
| *Bryum weigelii* | . | . | . | 11 | . | 3 | . | 54* | 2 | 5 |

| Alliance | Ca_re | Cr_co | Ly-Cr | E-Mo | K-Mj | Cr-Ca | An_ju | M-Ep | Ph_se | Sw-A |
|---|---|---|---|---|---|---|---|---|---|---|
| *Carex lachenalii* | . | . | . | . | . | . | . | 27 | . | . |
| *Rumex lapponicus* | . | . | . | . | . | . | . | 24 | . | . |
| *Cerastium cerastoides* $^{MCa}$ | . | 1 | . | 3 | 7 | 7 | . | 49 | 22 | . |
| *Rhizomnium pseudopunctatum* | . | 6 | . | . | . | 4 | . | 29 | . | . |
| *Equisetum pratense* | 1 | 3 | . | . | . | . | . | 22 | . | . |
| *Hygrohypnum ochraceum* | . | . | . | . | . | . | . | 15 | . | . |
| ***Philonotidion seriatae*** | | | | | | | | | | |
| *Philonotis seriata* $^{MCa}$ | 1 | 4 | . | 3 | . | 38 | . | 10 | 94* | 10 |
| *Saxifraga stellaris* $^{MCa}$ | 1 | 29 | . | 14 | 41 | 18 | 30 | 37 | 89 | 5 |
| ***Swertio perennis-Anisothecion squarrosi*** | | | | | | | | | | |
| *Scapania uliginosa* | . | . | . | . | . | . | . | . | . | 95* |
| *Swertia perennis* | . | 18 | . | . | . | 7 | . | . | . | 86* |
| *Allium schoenoprasum* | . | 5 | . | . | . | 5 | . | . | . | 67* |
| *Sphagnum subsecundum* | . | . | . | . | . | . | . | . | . | 43* |
| *Pedicularis sudetica* | . | . | . | . | . | . | . | . | . | 33* |
| *Bryum schleicheri* | . | 10 | . | . | . | 1 | . | . | 8 | 48* |
| *Veratrum album* agg. | 1 | . | . | . | . | 9 | . | . | 2 | 38* |
| *Molinia caerulea* agg. | . | 3 | 9 | . | . | . | . | . | . | 38* |
| *Bistorta officinalis* | . | 3 | . | 1 | . | 8 | . | . | . | 38* |
| *Homogyne alpina* | . | 2 | . | . | . | 1 | . | . | 1 | 29 |
| *Sphagnum squarrosum* | 3 | . | . | 4 | . | 1 | . | . | 1 | 29 |
| *Potentilla erecta* | 1 | 12 | 3 | 4 | 4 | 2 | . | . | 4 | 38 |
| *Viola biflora* | . | 29 | . | 1 | . | 55 | . | . | 16 | 62 |
| *Crepis paludosa* | 15 | 31 | 8 | 9 | . | 9 | . | . | 1 | 52 |
| *Eriophorum angustifolium* | . | 4 | 1 | 1 | 15 | . | 20 | 7 | 4 | 48 |
| *Sphagnum girgensohnii* | 1 | . | . | . | . | 3 | . | . | 1 | 19 |
| *Epilobium anagallidifolium* | . | 2 | . | 14 | . | 17 | . | 7 | 7 | 38 |
| *Adenostyles alliariae* | 1 | 1 | . | . | . | 4 | . | . | 1 | 19 |
| **Diagnostis species for two alliances** | | | | | | | | | | |
| *Palustriella commutata* agg. $^{CCr}$ | 1 | 99* | 94* | 1 | . | 29 | . | 2 | 8 | . |
| *Bistorta vivipara* | . | 42 | . | . | 44 | . | . | 10 | 1 | . |
| **Other diagnostic species for orders** | | | | | | | | | | |
| *Brachythecium rivulare* $^{CCh}$ | 43 | 8 | 24 | 31 | 7 | 38 | . | 10 | 11 | 5 |
| *Rhizomnium punctatum* $^{CCh}$ | 44 | 15 | 4 | 5 | . | 10 | . | . | 7 | 38 |
| *Epilobium alsinifolium* $^{MCa}$ | . | 24 | . | 9 | 11 | 54 | . | 34 | 32 | 38 |
| *Myosotis scorpioides* agg. $^{CCh}$ | 34 | . | 1 | 36 | . | 16 | . | . | 6 | 5 |
| *Dichodontium palustre* $^{MCa}$ | 1 | 1 | 1 | 20 | 4 | 27 | . | 34 | 17 | 52 |
| *Alchemilla vulgaris* agg. $^{MCa}$ | 1 | 9 | 1 | 5 | . | 37 | . | 37 | 15 | 10 |
| *Warnstorfia exannulata* $^{MCa}$ | . | 1 | 1 | 4 | . | 7 | 5 | 29 | 35 | 5 |
| *Petasites albus* $^{CCh}$ | 21 | 2 | 4 | 3 | . | 2 | . | . | 1 | . |
| *Carex flava* agg. $^{CCr}$ | 1 | 21 | 13 | 4 | 15 | 5 | 15 | . | 1 | 5 |
| **Other species with higher frequency** | | | | | | | | | | |
| *Deschampsia cespitosa* | 17 | 45 | 8 | 35 | 30 | 65 | 55 | 39 | 50 | 76 |
| *Agrostis stolonifera* | 6 | 40 | 36 | 36 | 41 | 6 | 15 | . | 11 | . |
| *Chaerophyllum hirsutum* | 26 | 14 | 5 | 11 | . | 39 | . | . | 4 | 24 |
| *Geranium robertianum* | 29 | 7 | 32 | . | . | 1 | . | . | . | . |
| *Carex nigra* | 1 | 3 | 2 | 24 | 4 | 12 | 10 | 10 | 30 | 14 |
| *Pellia epiphylla* agg. | 21 | . | 1 | 14 | . | 3 | . | 20 | 2 | . |
| *Cratoneuron filicinum* | 7 | 15 | 27 | 5 | . | 5 | . | . | 1 | . |
| *Calliergonella cuspidata* | 6 | 1 | 17 | 31 | 33 | 7 | . | . | 1 | . |
| *Plagiomnium affine* agg. | 16 | 7 | 8 | 15 | 4 | 3 | . | 2 | 1 | . |
| *Pohlia wahlenbergii* | 1 | 9 | 6 | 1 | 22 | 11 | . | 51 | 4 | 43 |
| *Veronica beccabunga* | 16 | . | 8 | 18 | . | 1 | . | . | . | . |

| Alliance | Ca_re | Cr_co | Ly-Cr | E-Mo | K-Mj | Cr-Ca | An_ju | M-Ep | Ph_se | Sw-A |
|---|---|---|---|---|---|---|---|---|---|---|
| *Aneura pinguis* | 1 | 30 | 12 | . | 11 | 1 | 10 | 2 | 5 | 5 |
| *Festuca rubra* agg. | . | 7 | 19 | 16 | . | 1 | . | . | 11 | . |
| *Chiloscyphus polyanthos* agg. | 10 | 2 | 1 | 18 | . | 12 | . | 5 | 5 | . |
| *Conocephalum conicum* | 9 | 5 | 20 | 1 | . | 3 | . | . | . | . |
| *Epilobium nutans* | 1 | . | . | . | . | 13 | . | . | 27 | 29 |
| *Equisetum arvense* | 6 | 8 | 8 | 5 | 26 | 2 | . | 27 | 1 | . |
| *Poa alpina* | . | 20 | . | 1 | . | 18 | . | 7 | 8 | . |
| *Equisetum sylvaticum* | 12 | 2 | 1 | 11 | . | 1 | . | 12 | . | 5 |
| *Juncus articulatus* | 1 | 5 | 14 | 22 | 11 | 2 | . | . | 2 | . |
| *Brachythecium rutabulum* | 14 | . | 1 | 4 | . | 2 | . | . | 1 | . |
| *Epilobium palustre* | 3 | . | 2 | 27 | 30 | 4 | . | 7 | 1 | . |
| *Campylium stellatum* agg. | . | 28 | 6 | 1 | 4 | 2 | . | 5 | 3 | 5 |
| *Eupatorium cannabinum* | 6 | 3 | 17 | . | . | . | . | . | . | . |
| *Viola palustris* | 3 | 2 | . | 19 | 7 | 1 | 10 | 10 | 2 | 38 |

### *Classification of non-core plots and hierarchy of the expert system*

To enable classification of non-core plots, a hierarchical classification of spring vegetation in the expert system was developed (Supplementary Data S7; for practical recommendations on using the expert system, see Supplementary Data S8). The expert system file contains definitions at different priority levels. At the highest level, plots are classified by formal definitions based on the Cocktail method and sociological groups as described above. These definitions identify the core plots. Subsequently, the remaining unclassified plots are classified by definitions of lower priority. First, broader definitions of alliances are applied. In this step, the non-core plots of alliances are identified. In the final step, definitions of orders are applied so that the remaining unclassified plots, which often have a transitional composition between alliances, can be classified at the order level. However, the definitions of any priority level can be applied independently of the definitions of other priority levels (Supplementary Data S8).

Definitions of lower priority are based on discriminating species groups, which comprise a list of species that characterize a vegetation type. The list can be used to discriminate a particular vegetation type from other types of the same classification level (Willner 2011, Chytrý et al. 2020). The expert system then compares a quantitative representation of all discriminating species groups present in a plot. The plot is assigned to the vegetation type whose discriminating species groups has the highest representation. In this study, the analogous classification approach has already been used in the definition of the class *Montio-Cardaminetea*, where spring-positive species and spring-negative species act as discriminating species groups at the same level.

Before establishing discriminating species groups for orders and alliances, three informal ecological groups of alliances within the order *Montio-Cardaminetalia* were distinguished. The concept of ecological groups of alliances follows that of ecological groups of associations (Willner et al. 2019, Novák et al. 2020). Ecological groups of alliances constitute an additional hierarchical level between order and alliance, as some alliances are ecologically and compositionally closer to each other than the others within the same order.

The GRIMP algorithm (Tichý et al. 2019) was used to determine discriminating species groups for individual orders, ecological groups of alliances and alliances. GRIMP is a semi-automatic machine-learning method for optimizing species groups used to discriminate among vegetation types in expert systems. Plots identified as cores of each alliance were used as the training dataset. For determining discriminating species groups of orders, core plots of alliances belonging to the same order were grouped. For determining the discriminating species groups of ecological groups of alliances against other groups (if recognized), the core plots of alliances belonging to a particular group were combined. For determining the discriminating species groups of alliances (if not included into ecological group), only the cores of alliances of the same order were used. For determining the discriminating species groups of alliances falling into an ecological group of alliances (if recognized), only the cores of alliances of the same group were used. Quantitative representation of each discriminating species group in a plot was measured as the sum of the square-rooted percentage covers of individual species in the groups. All discriminating species groups determined by GRIMP were critically revised and iteratively improved using the non-stratified dataset.

## Results

### *Unsupervised classifications*

At the highest level of classification, hierarchical cluster analysis based on the overall species composition separated vegetation of calcareous springs (clusters 21–28) from all other types of spring vegetation (clusters 1–20; Supplementary Data S4). The group of non-calcareous (acidic and neutral) springs consists of two main branches: forest springs of the *Cardamino-Chrysosplenietalia* order (clusters 15–20) and non-forest spring vegetation (clusters 1–14). This pattern suggests the existence of three main high-rank syntaxa (~ orders) within the class *Montio-Cardaminetea*. Based on a literature search, the branch with calcareous springs was interpreted as the order *Cardamino-Cratoneuretalia* Maas 1959. All alliances listed in the EuroVegChecklist correspond to one or more clusters distinguished at lower levels of hierarchical classification, except for *Myosotidion stoloniferae* and *Pinguiculo balcanicae-Cardaminion acris*. On the other hand, some of the resulting clusters fit syntaxa not accepted in this syntaxonomical overview, but previously recognized in regional literature. These syntaxa were *Anthelion julaceae* Shimwell 1972 and *Cratoneuro filicini-Calthion laetae* Hadač 1983. The cluster analysis did not reveal the "additional" alliances described by de Foucault (2018) in the parallel survey of spring vegetation.

The hierarchical cluster analysis based only on spring-positive species yielded results that were fairly consistent with the cluster analysis based on the full species composition (Supplementary Data S4). The three main branches were identical, representing calcareous springs, non-calcareous forest springs and non-calcareous non-forest springs. The clusters generally matched those resulting from the previous analysis (with all species) and the alliances recognized in the EuroVegChecklist, except for a cluster unequivocally related to *Cratoneuro filicini-Calthion laetae*. This classification scheme was further reproduced by unsupervised K-means classifications (Supplementary Data S4).

Unsupervised classifications of regional data subsets using the Isopam algorithm and hierarchical cluster analysis (Supplementary Data S5) generally matched the results of the unsupervised classifications of the pan-European dataset described above. Although there were differences in diagnostic species and in the inter-regional variability of some alliances, the major vegetation types were consistently distinguished across regions by both classification methods. Clusters related to *Caricion remotae*, *Philonotidion seriatae* and *Cratoneurion commutati* occurred in the majority of the subsets analysed in different regions. Two alliances of calcareous springs, *Cratoneurion commutati* and *Lycopodo-Cratoneurion commutati*, were clearly separated in subsets from Great Britain and Ireland, Alps, Carpathians, Balkans and Iberian Peninsula (in the latter region only by cluster analysis). *Cratoneuro filicini-Calthion laetae* and *Caricion remotae* were separated from each other in the subsets from the Alps, Carpathians and Balkans; *Cratoneuro filicini-Calthion laetae* and *Philonotidion seriatae* were separated in the same three subsets. Vegetation corresponding to *Koenigio-Microjuncion* formed separate clusters in subsets from northern Europe, Great Britain and Ireland. Similarly, *Mniobryo-Epilobion hornemannii* was delimited in the subset from northern Europe and *Anthelion julaceae* in the subset from Great Britain and Ireland.

### *Supervised and semi-supervised classifications*

Formal definitions based on Cocktail-defined sociological groups were created for the alliances listed in the EuroVegChecklist, except for *Myosotidion stoloniferae* and *Pinguiculo balcanicae-Cardaminion acris*. Attempts were made to define these two alliances in the preliminary analyses, but were unsuccessful. We were also unable to delimit several alliances described in the survey of spring alliances by de Foucault (2018). Semi-supervised K-means, already with a small number of resulting clusters, revealed two additional vegetation types with clear ecological and syntaxonomical meaning. These types corresponded to *Anthelion julaceae* and *Cratoneuro filicini-Calthion laetae*. As these vegetation types were also independently distinguished in unsupervised classifications, their formal definitions were created as well. The formalized classification yielded diagnostic species for all alliances (Table 1, Supplementary Table S2), with the lowest number determined for *Philonotidion seriatae*. Likewise, three proposed orders are characterized by a sufficient number of diagnostic species (Table 1, Supplementary Table S3).

The Cocktail-based formal definitions identified 1001 vegetation plots (24.8%) in the stratified dataset and 1,257 plots (25.2%) in the non-stratified dataset as core plots of alliances. Within the non-stratified dataset, definitions at a lower priority level based on discriminating species groups enabled the assignment of 3,185 of the remaining plots. Thus, altogether 89.2% of the plots were classified at the alliance level. When the order definitions were applied independently to the non-stratified dataset, 4,781 plots (96.2%) were classified.

### *Ordination*

The NMDS analysis (Fig. 2) based on core plots of alliances distinguished the main types of spring vegetation corresponding to the proposed orders. Non-calcareous forest springs (*Caricion remotae*) were separated from non-calcareous non-forest springs along the first NMDS axis, while calcareous springs (*Cratoneuron commutati* and *Lycopodo-Cratoneurion*)

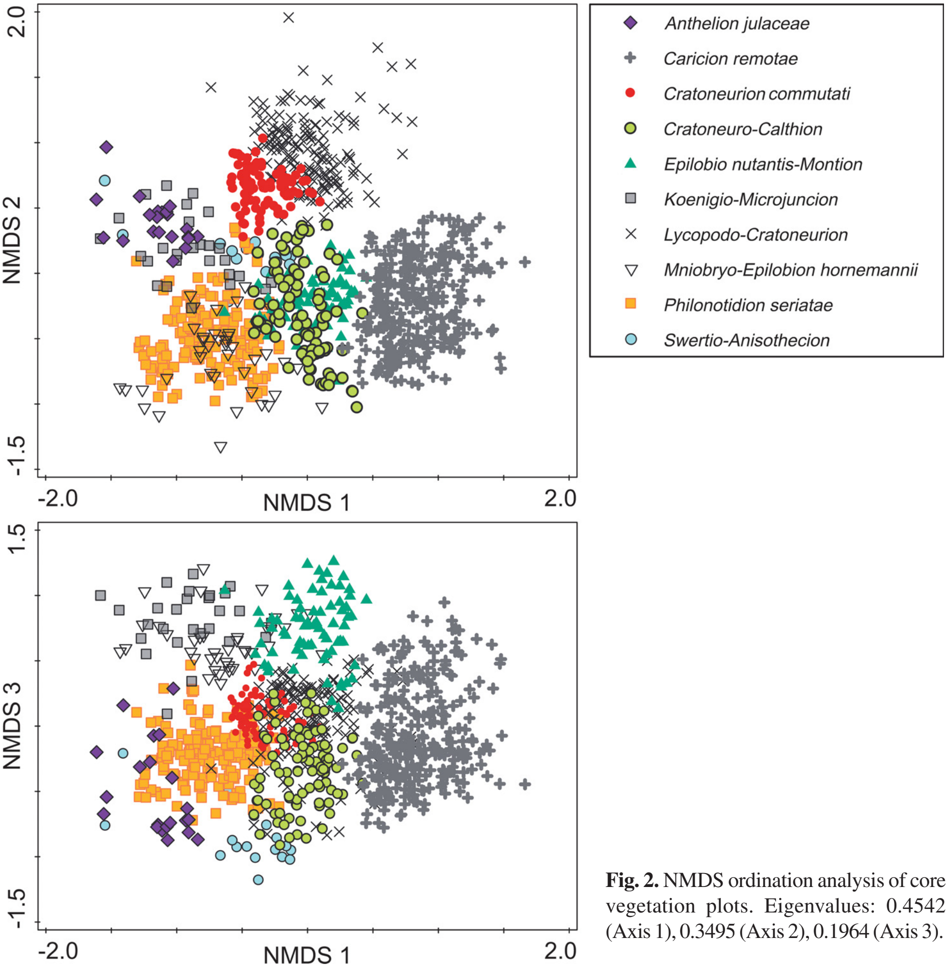

**Fig. 2.** NMDS ordination analysis of core vegetation plots. Eigenvalues: 0.4542 (Axis 1), 0.3495 (Axis 2), 0.1964 (Axis 3).

formed a distinct separate cluster along the second NMDS axis. Similarly, all individual alliances in the ordination space were well-differentiated. Some alliances overlapped along the first and second axes of the NMDS scatterplot, but were separated along the third axis. This concerned especially *Mniobryo-Epilobion hornemannii* versus *Philonotidion seriatae*, *Anthelion julaceae* versus *Koenigio-Microjuncion* and *Cratoneuro filicini-Calthion laetae* versus *Epilobio nutantis-Montion*. The same patterns were also observed in the joint NMDS ordination of core and non-core plots (Supplementary Fig. S1). Three proposed orders were separated by the NMDS analysis of plots classified at the order level (Supplementary Fig. S2).

## Synopsis and characteristics of the syntaxa

The distribution of core and non-core plots is displayed in maps in Fig. 3. A comparison of the main environmental characteristics is shown in Fig. 4. For a better interpretation and application of the proposed classification scheme, examples of subordinate associations for each alliance are listed in Supplementary Data S9.

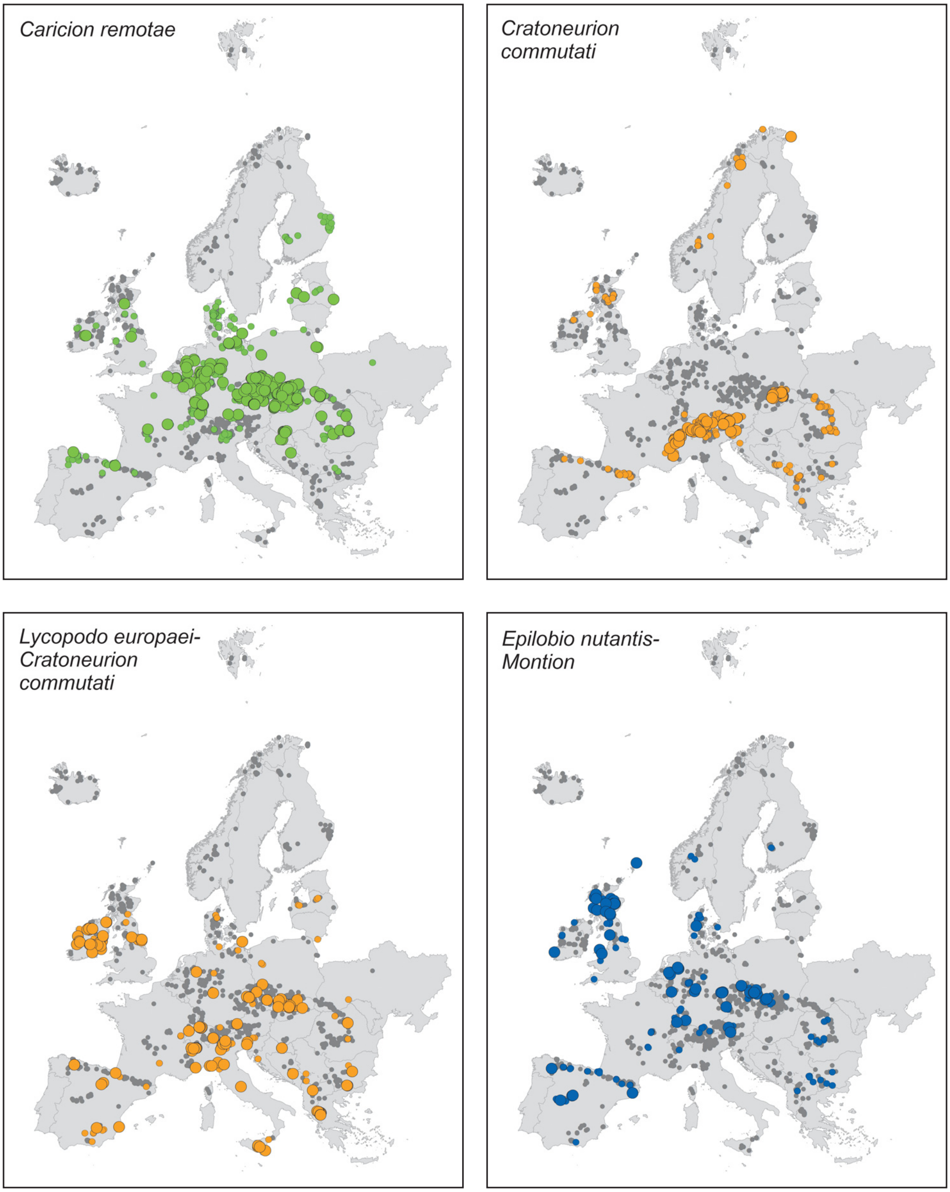

**Fig. 3**. Distribution of vegetation plots classified using the expert system into alliances of *Montio-Cardaminetea*. Big circles represent core plots (classified using Cocktail-based formal definitions), small circles non-core plots (classified using only GRIMP-based definitions). Grey circles in the background show all plots classified to the class *Montio-Cardaminetea*. Green colour: alliance of the *Cardamino-Chrysosplenietalia* order, yellow colour: alliances of the *Cardamino-Cratoneuretalia* order, blue colour: alliances of the *Montio-Cardaminetalia* order. (Continued on the next two pages).

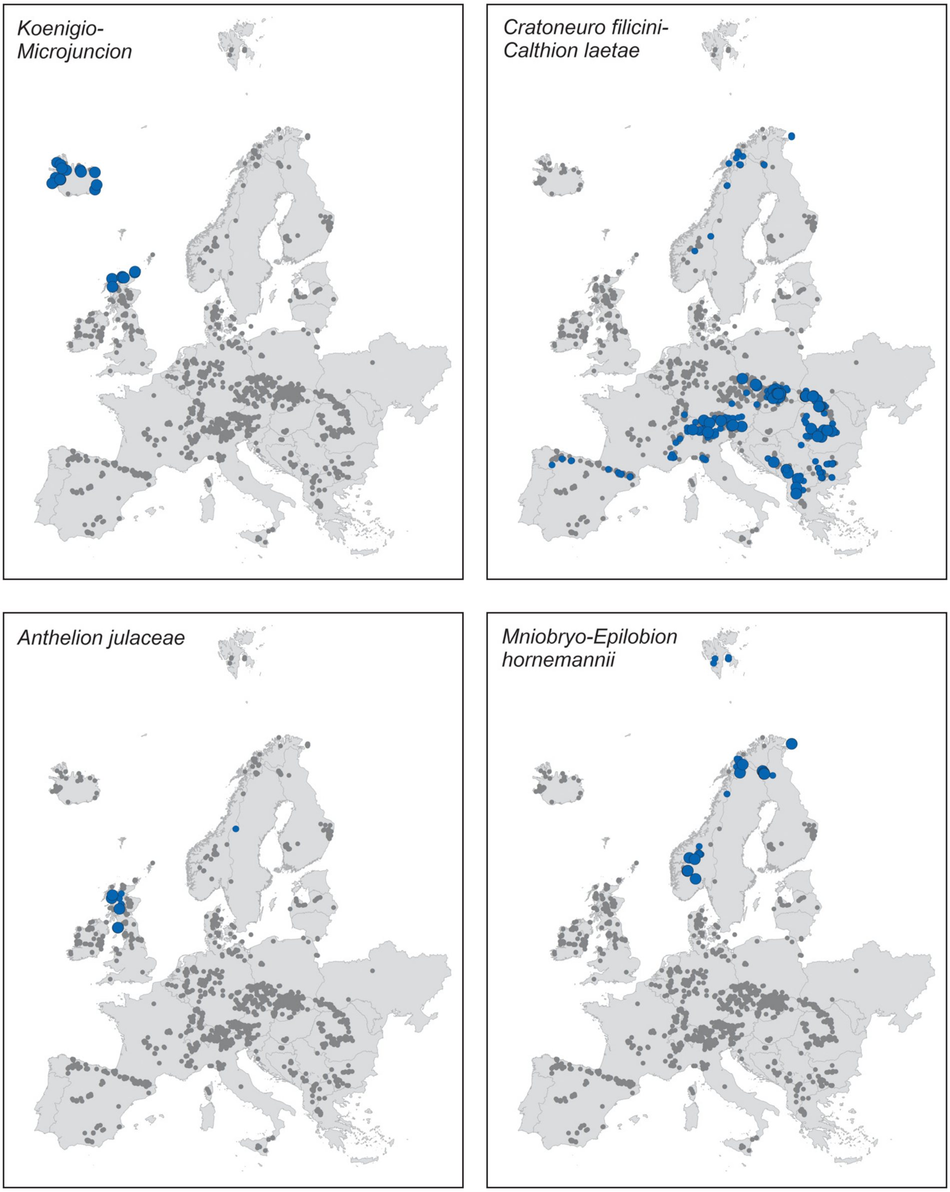

**Fig. 3.** Continued.

*Montio-Cardaminetea* Br.-Bl. et Tx. ex Klika et Hadač 1944

1. *Cardamino-Chrysosplenietalia* Hinterlang 1992
Vegetation of non-calcareous forest (shaded) springs. The most common characteristic taxa include *Carex remota*, *C. sylvatica*, *Chrysosplenium alternifolium*, and *Impatiens noli-tangere*.

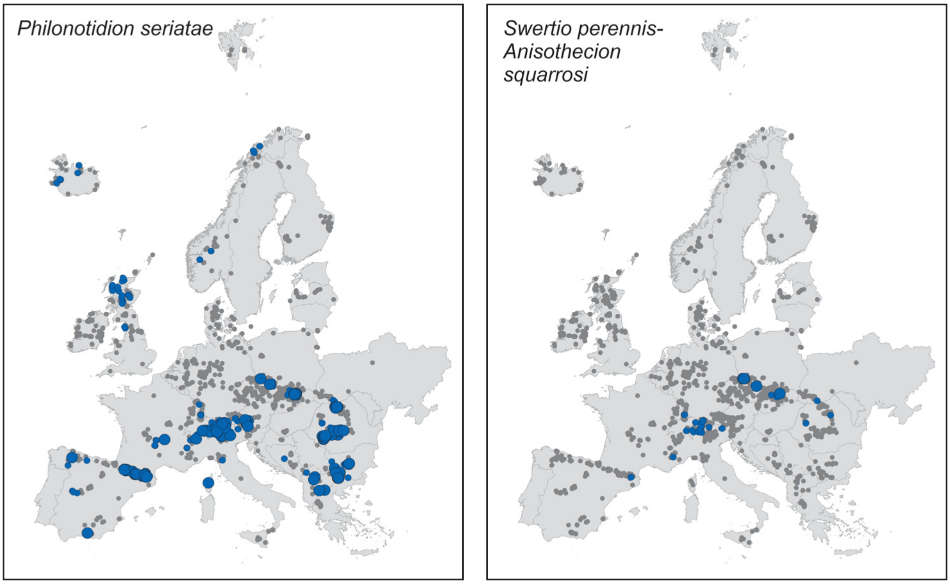

**Fig. 3.** Continued.

### 1.1 *Caricion remotae* Kästner 1941

Vegetation of non-calcareous forest springs. These springs are saturated with non-calcareous, slightly acidic to neutral water; they generally occur in submontane and montane areas of temperate Europe. Typical species include *Cardamine amara*, *Carex remota*, *Chrysosplenium alternifolium* and *C. oppositifolium* (the latter in Atlantic Europe). The bryophyte layer often consists of *Brachythecium rivulare*, *Plagiomnium affine* agg., *P. undulatum* and *Rhizomnium punctatum*. Within the class *Montio-Cardaminetea*, the alliance is also characterized by the irregular, albeit common, occurrence of forest species from the surrounding landscape (e.g. *Athyrium filix-femina*, *Impatiens noli-tangere*, *Stachys sylvatica* and *Veronica montana*). As shown by the indicator values, forest springs of the *Caricion remotae* occupy nutrient-rich, shaded sites in relatively warm regions (Fig. 4C).

### 2. *Cardamino-Cratoneuretalia* Maas 1959

Vegetation of calcareous springs, both in open landscapes and at shaded forest sites. The bryophyte layer is frequently well-developed and commonly dominated by *Palustriella commutata* agg.

### 2.1 *Cratoneurion commutati* Koch 1928

Vegetation of heliophilous plant communities in calcareous springs in the subalpine to alpine vegetation belts. This vegetation type can occasionally occur at lower elevations, where it contains subalpine and alpine species. The presence of alpine or arcto-alpine elements (*Arabis soyeri*, *Bellidiastrum michelii*, *Pinguicula alpina* and *Saxifraga aizoides*) differentiates *Cratoneurion commutati* from the second alliance in this order. Besides *Palustriella commutata* agg., other calcicole bryophytes (*Campylium stellatum* agg., *Philonotis calcarea*) may be present in the bryophyte layer. The high mineral richness of the groundwater is reflected in the high modelled values for calcium concentrations and indicator values for reaction, similar to *Lycopodo europaei-Cratoneurion commutati.* Indicator values for nutrients are relatively low, indicating oligotrophic conditions (Fig. 4C). This alliance is mostly distributed in the Alps, Carpathians and Scandinavian mountains. Stands in other mountain ranges (non-core plots recorded in the Pyrenees, Balkan Peninsula and Scottish Highlands) are characterized by a lower proportion of arcto-alpine species.

2.2 *Lycopodo europaei-Cratoneurion commutati* Hadač 1983
Vegetation of shaded to heliophilous calcareous springs, often with tufa formation. The *Lycopodo-Cratoneurion* communities lack the alpine species that characterize the *Cratoneurion commutati* alliance. The bryophytes *Eucladium verticillatum* and *Pellia endiviifolia* are the species with the highest frequency and fidelity in this vegetation type. These springs occur in the lowlands up to submontane vegetation belts. This alliance also occupies more nutrient-rich sites (high indicator values for nutrients) than the *Cratoneurion commutati* alliance. *Lycopodo-Cratoneurion* also shares species (especially bryophytes) with the class *Adiantetea*, which comprises chasmophytic vegetation at shaded or water-splashed sites in the Mediterranean area and Middle East (Mucina et al. 2016). However, the *Adiantetea* class also shares compositional and ecological features with the class *Asplenietea trichomanis* and hence has an intermediate character between *Montio-Cardaminetea* and *Asplenietea*. In contrast to *Lycopodo-Cratoneurion*, the class *Adiantetea* is characterized by chasmophytes (mostly ferns), which are often narrow-range endemics and relicts of presumably Tertiary origin (Deil 1995, 1996).

3. *Montio-Cardaminetalia* Pawłowski et al. 1928
Vegetation of heliophilous (i.e. non-forest) springs at sites with acidic to neutral water reaction and a low to moderate calcium concentration. The most frequent characteristic taxa in this order include *Cerastium cerastoides*, *Dichodontium palustre*, *Epilobium alsinifolium*, *Montia fontana*, *Philonotis fontana* agg., *P. seriata* and *Saxifraga stellaris.*

Group A: Oligotrophic to mesotrophic submontane and montane springs and flushes on silty to sandy sites

3.1 *Epilobio nutantis-Montion* Zechmeister in Zechmeister et Mucina 1994
Oligotrophic to mesotrophic springs in submontane and montane vegetation belts in Atlantic and sub-atlantic regions. The herb layer is typically formed by *Montia fontana*, accompanied, for example, by *Epilobium obscurum*, *Juncus articulatus*, *Philonotis fontana* agg., *Stellaria alsine* and *Veronica beccabunga*.

3.2 *Koenigio-Microjuncion* (Sørensen 1942) Hadač 1971
Vegetation of permanently wet, clayey or sandy flats near springs in Iceland and in the extreme north-west of Great Britain. Stands consist of spring therophytes (*Koenigia islandica*, *Montia fontana*), tiny graminoids (*Juncus alpinoarticulatus*, *J. biglumis*, *J. triglumis*, *Triglochin palustris*) and other species of oligotrophic but at least slightly disturbed wet sites (*Sagina nodosa*, *Saxifraga hirculus*, *Sedum villosum*). Mucina et al. (2016) speculated on the possible classification of this alliance in the class *Isoëto-Nanojuncetea*. However, unlike this vegetation type, *Koenigio-Microjuncion* lacks elements typical of periodically flooded habitats (*Eleocharis acicularis*, *Isoëtes* spp., *Limosella aquatica*, *Subularia aquatica*; compare with Sørensen 1942, Hadač 1971).

Group B: Mesotrophic and productive subalpine and alpine springs

3.3 *Cratoneuro filicini-Calthion laetae* Hadač 1983
Subalpine to alpine, herb-rich, mesotrophic springs with *Caltha palustris*, *Cardamine* spp. and an admixture of tall herbs. This vegetation occupies an intermediate position on the fertility (productivity) gradient between oligotrophic springs (*Philonotidion seriatae*, *Swertio perennis-Anisothecion squarrosi*) and productive tall-herb vegetation at moist sites (*Mulgedio-Aconitetea*). In contrast to the oligotrophic types of (sub)alpine spring vegetation, *Cratoneuro filicini-Calthion laetae* includes broad-leaved species. In contrast to the class *Mulgedio-Aconitetea*, this vegetation still consists of spring indicator species, and elements of tall-herb vegetation have generally a low cover (see e.g. Valachovič 2001, Hájek et al. 2005, Kliment et al. 2008). Thus, some stands are degraded phases of other spring alliances and form a transitional type between *Montio-Cardaminetea* and *Mulgedio-Aconitetea*. This alliance is distributed mainly in the Carpathians (Hadač 1983, Valachovič 2001) and Balkan Peninsula, e.g. in Bulgarian mountain ranges (Hájek et al. 2005, Hájková et al. 2006).

Group C: Cold oligotrophic subalpine and alpine springs

3.4 *Anthelion julaceae* Shimwell 1972
Vegetation of subalpine and alpine oligotrophic acidic springs in strongly oceanic areas in north-western Britain (mainly in the Scottish Highlands). The stands are dominated by the liverwort *Anthelia julacea*. The alliance differs from snow-flush communities in (i) the admixture of species that occur in soligenous mires and indicate the first stages of peat formation (e.g. *Carex demissa*, *Sphagnum auriculatum* agg., *Warnstorfia sarmentosa*) and (ii) the absence of species characteristic of snow-bed communities (e.g. *Anthelia juratzkana*, *Gnaphalium supinum*, *Salix herbacea*; Shimwell 1972). Among the other spring indicator species, *Scapania undulata* reaches high frequency. Indicator values shows that this vegetation occupies nutrient-poor sites (indicator values for nutrients are the lowest; Fig 4C).

3.5 *Mniobryo-Epilobion hornemanii* Nordhagen 1943
Vegetation of montane to alpine springs in boreal and arctic zones of Europe. This alliance is a geographical vicariant of *Swertio perennis-Anisothecion squarrosi* from central Europe. Both alliances include mountain springs with initial peat formation, sub-neutral pH and well-developed bryophyte and herb layers. *Mniobryo-Epilobion hornemanii* is differentiated by *Epilobium hornemannii* and other arctic and boreal species (*Agrostis mertensii*, *Cinclidium subrotundum*, *Poa alpigena*, *Rumex lapponicus*). Among the other spring indicator species, *Cerastium cerastoides* and *Scapania paludosa* reach high frequencies.

3.6 *Philonotidion seriatae* Hinterlang 1992
Early successional spring communities on crystalline bedrock in subalpine and alpine vegetation belts. Sites are characterized by a constant water flow, which (together with other factors such as snow slides, local microtopography, colder climate and short growing season) blocks peat formation. The lack of peat accumulation due to extreme habitat conditions differentiates *Philonotidion seriatae* from other alliances within this ecological group. Compared to *Mniobryo-Epilobion hornemanii* and *Swertio perennis-Anisothecion*

*squarrosi*, this alliance also differs in lower species richness and less-well developed herb layer. The early successional nature of these plant communities results in a low number of diagnostic species. Therefore, *Philonotidion seriatae* possibly matches the concept of a central alliance (Willner 2020), i.e. an alliance that has the diagnostic species of the next higher unit but differs only negatively from the other units of the same rank, as suggested by Hinterlang (1992).

Nomenclature note: The name *Philonotidion seriatae* is used here instead of *Cardamino-Montion* as in the EuroVegChecklist (Mucina et al. 2016). The alliance with the latter name, recognized and described by Braun-Blanquet (1925, 1926), was originally broadly delimited and comprised both subalpine springs (with e.g. *Bryum schleicheri*, *Philonotis seriata*, *Saxifraga stellaris*) and springs with *Cardamine amara*, *Chrysosplenium oppositifolium* and *Veronica beccabunga*. Hadač (1983) typified the alliance by the *Montio-Bryetum schleicheri* Br.-Bl. 1926 association, which contains species of subalpine non-forest springs. This narrower concept of *Cardamino-Montion* comprising non-calcareous springs in subalpine and alpine belts was adopted by Zechmeister & Mucina (1994), Tomaselli et al. (2011), and Mucina et al. (2016). Nevertheless, the name has been interpreted differently in the literature, including submontane to montane springs (with e.g. *Cardamine amara*, *Epilobium obscurum*, *Montia fontana*, *Philonotis fontana* agg., *Stellaria alsine*; Hinterlang 1992, Ranđelović & Zlatković 2010, Borhidi et al. 2012), all non-calcareous springs (Siebum et al. 1995, Coldea 1997, Diekmann 1997, Matuszkiewicz 2007) or forest springs (Tüxen 1937, Soó 1949, Raţiu et al. 1983, Laiviņš 1998). The latter interpretation fully excludes the type of *Cardamino-Montion*. According to the International Code of Phytosociological Nomenclature (Theurillat et al. 2021), a name must be rejected when, due to an earlier misinterpretation or various emendations or for any other reason, it has been so often used in a false sense that excludes its type that its re-introduction in its original correct sense would be a continual source of errors. Based on the previous examples, it is likely that this is the case for *Cardamino-Montion*. However, this solution has to be approved by the Committee for the Change and the Conservation of Names (CCCN). If this proposal is not accepted, *Cardamino-Montion* would remain a valid name for this vegetation, or another nomenclatorial solution would have to be found.

### 3.7 *Swertio perennis-Anisothecion squarrosi* Hadač 1983

Subalpine oligotrophic sub-neutral springs in central Europe. Unlike *Philonotidion seriatae*, this vegetation develops on soils with higher organic content. The herb layer is well-developed, richer in species and typically contains *Allium schoenoprasum*, *Bartsia alpina*, *Swertia perennis* and rarely *Pedicularis sudetica*. The initial stage of peat formation is indicated by the regular occurrence of mire elements, albeit with low cover (*Eriophorum angustifolium*, *Sphagnum subsecundum*, *Trichophorum cespitosum*, *Viola palustris*). Indicator values for moisture are slightly lower and modelled calcium concentration is slightly higher than for the related *Philonotidion seriatae* alliance (Fig. 4B, C).

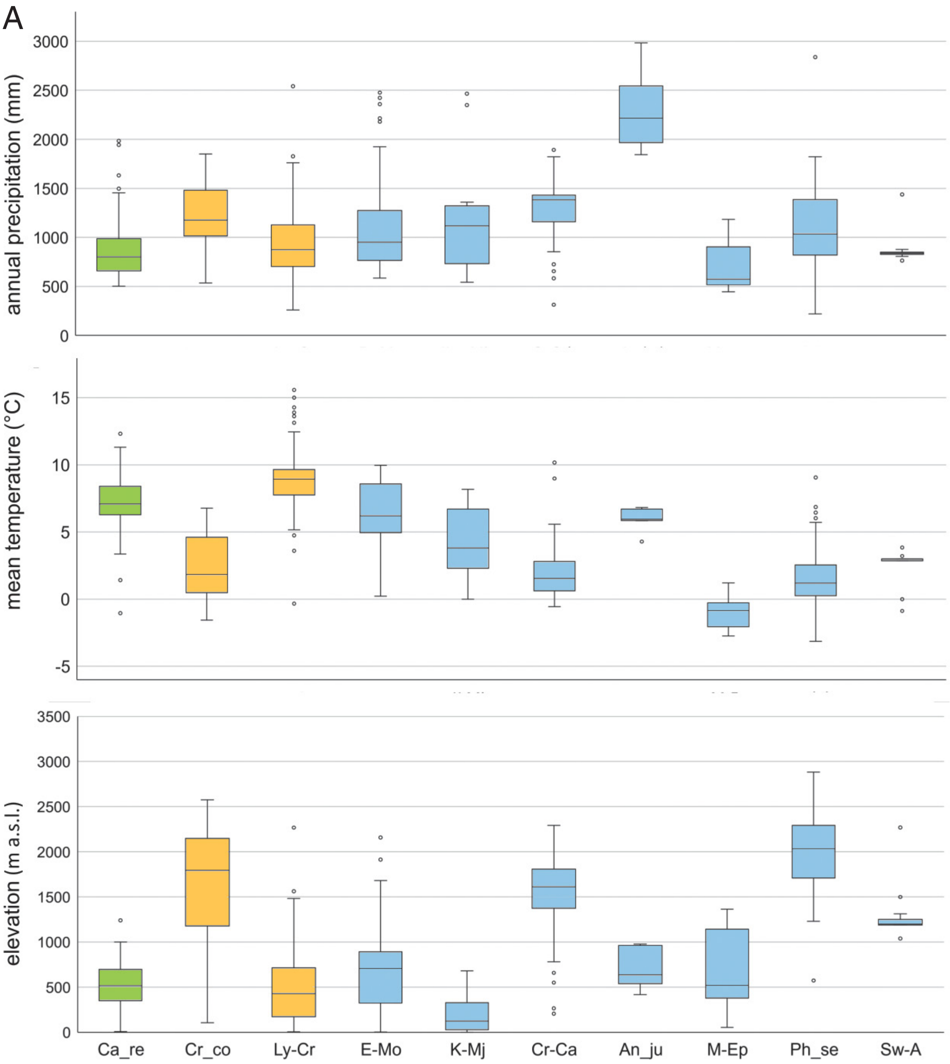

**Fig. 4.** (A) Annual precipitation (mm), mean annual temperature (°C) and elevation (m a.s.l.) for individual alliances. Boxes indicate the 25–75% interquartile range, whiskers indicate the range of values without outliers, circles are outliers. Abbreviations of alliances are explained in the heading of Table 1. Green: alliance of the *Cardamino-Chrysosplenietalia* order, yellow: alliances of the *Cardamino-Cratoneuretalia* order, blue: alliances of the *Montio-Cardaminetalia* order. (B) Comparison of modelled values of calcium (mg.l$^{-1}$) derived from the European map of groundwater Ca (Hájek et al. 2021b) and ecological indicator values (EIVs) for reaction (scale 0–10) for individual alliances. (C) Comparison of ecological indicator values (EIVs) for moisture (scale 1–12), light and nutrients (both scales 0–10) for individual alliances. (Continued on the next two pages).

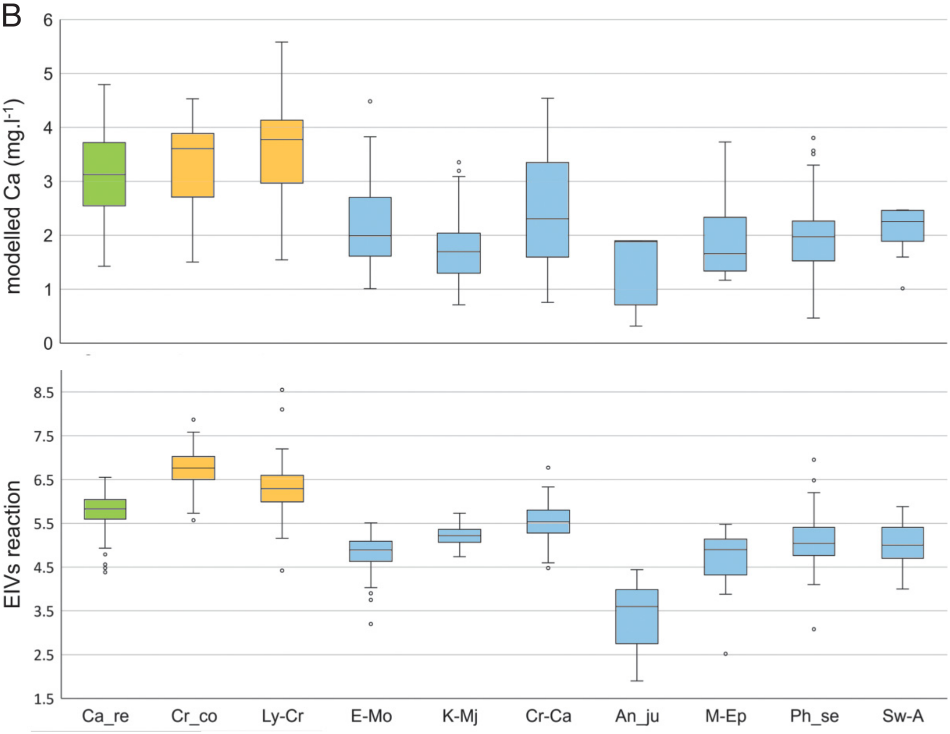

**Fig. 4.** Continued.

## Discussion

### *Validation and update of the EuroVegChecklist*

According to the EuroVegChecklist (Mucina et al. 2016), the class *Montio-Cardaminetea* includes two orders: *Cardamino-Chrysosplenietalia* (non-calcareous forest springs) and *Montio-Cardaminetalia* (all other springs). However, results presented here (especially the cluster analyses) support the existence of three orders, with the former order *Montio-Cardaminetalia* divided into (a) non-calcareous heliophilous springs (*Montio-Cardaminetalia* s. str.) and (b) calcareous shaded to heliophilous springs (*Cardamino-Cratoneuretalia*). Already in some previous studies (Maas 1959, Hadač 1983), calcareous springs were separated at the order level. The fact that both the availability of light, complex gradient of pH and mineral richness determine the main differences in spring vegetation (Beierkuhnlein & Gräsle 1998, Spitale et al. 2012, Cantonati et al. 2020b) supports the existence of three main high-rank syntaxa within the class *Montio-Cardaminetea*.

The alliances listed in the EuroVegChecklist were validated in terms of diagnostic species, differences in overall species composition and habitat conditions. Exceptions were the southern European *Myosotidion stoloniferae* and *Pinguiculo balcanicae-Cardaminion acris*. The former alliance was recognized as an endemic alliance of oligotrophic mountain springs on the western Iberian Peninsula (Rivas-Martínez et al. 1984, Molina 2001). In Spain, *Epilobium atlanticum*, *Myosotis stolonifera*, *Myosoton*

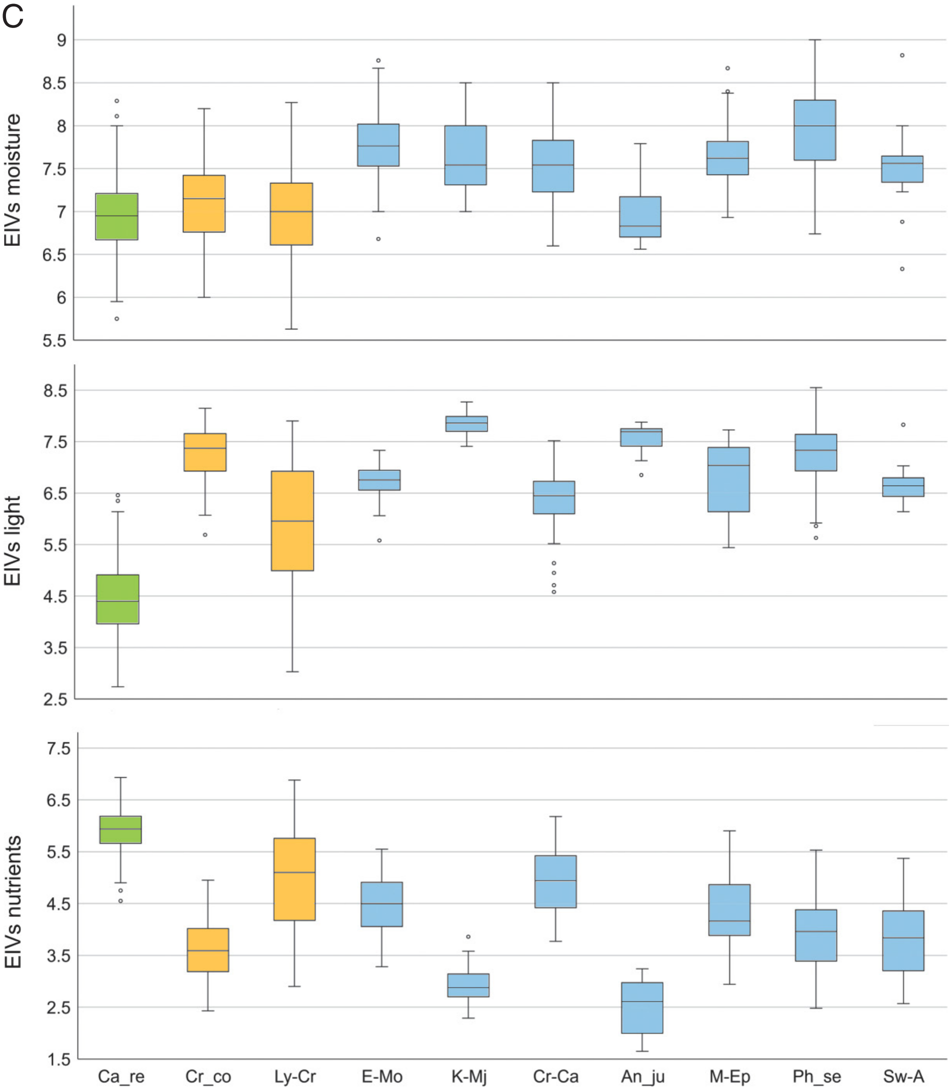

**Fig. 4.** Continued.

*aquaticum*, *Sedum lagascae*, and *Veronica nevadensis* were considered to be diagnostic of this alliance (some of these species are narrow-range endemics; Rivas-Martínez 2011). *Pinguiculo-Cardaminion* was described from the Pelister massif in North Macedonia (Čarni & Matevski 2010) based on the occurrence of Balkan endemics and the moss *Drepanocladus aduncus*, which is otherwise rare in springs (Dierssen 2001, Hedenäs 2003). After our visit to the locus classicus in 2022 (P. Hájková, M. Hájek), we suspect that *D. aduncus* was probably confused with *Warnstorfia exannulata*, a species of poor and intermediate fens and oligotrophic mountain springs. The material of Čarni & Matevski (2010) seems to be a heterogeneous set of relevés from soligenous fens, early successional oligotrophic springs and mesotrophic productive springs, all with a group of Balkan endemics with somewhat different habitat requirements (*Pedicularis limnogena* with an optimum in *Sphagnum* fens, *Pinguicula balcanica* with an affinity for brown-moss fens and *Silene asterias* for mesotrophic productive habitats; Hájková et al. 2006). Attempts to reproduce these two alliances (Iberian and Balkan) failed because we were unable to determine appropriate species groups using the Cocktail method and develop formal definitions. The likely reason for this is the relatively small number of available vegetation plots with identified bryophytes, which is underlined by the narrow geographic distribution of both vegetation types. Therefore, delimitation of *Myosotidion stoloniferae* and *Pinguiculo balcanicae-Cardaminion acris* is a topic for further research.

The Balkan springs are characterized, at least locally, by the occurrence of narrow-range taxa, the Balkan endemics. Hájková et al. (2006) report that the proportion of Balkan endemic species associated with Bulgarian high-mountain springs ranges from 13 to 22%. The number of endemics associated with calcareous subalpine springs (*Cratoneurion commutati*) and mesotrophic productive springs (*Cratoneuro filicini-Calthion laetae*) does not differ significantly from that of the fens assigned to the Balkan alliance *Narthecion scardici* (Lakušić 1968, Lakušić & Grgić 1971). Throughout southern Europe, there are still low numbers of vegetation plots documenting distinct types of spring vegetation with southern-European endemics that are related to those in the Balkans, e.g. *Pinguicula* taxa with a narrow range in the Apennines (Majeský et al. 2022), *Narthecium reverchonii* in Corsica (Deleuil 1974), or *Carex lepidocarpa* subsp. *nevadensis* in southern Spain (Jiménez-Mejías & Luceño 2009, Jiménez-Mejías et al. 2014). Further research in southern Europe is therefore needed.

Three alliances of forest (shaded) springs recently distinguished and described by de Foucault (2018) could not be defined by the Cocktail method and were not identified using cluster analyses. Of these units, *Athyrio filicis-feminae-Chrysosplenion dubii* and *Lysimachio-Saxifragion hirsutae* share several character species with *Caricion remotae* (e.g. *Athyrium filix-femina*, *Carex remota*, *Lysimachia nemorum*, *Stellaria nemorum* and *Veronica montana*; *Chrysosplenium oppositifolium* is only shared by *Caricion remotae* and *Lysimachio-Saxifragion hirsutae*). According to de Foucault's monograph, *Athyrio filicis-feminae-Chrysosplenion dubii* differs from *Caricion remotae* in the presence of *Chrysosplenium dubium* and *Lereschia thomasii*. The first species occurs in Italy, Turkey and Algeria, whereas the range of the second species is restricted to southern Italy (Tutin et al. 1968–1993, Euro+Med 2006–2021). Therefore, *Athyrio filicis-feminae-Chrysosplenion dubii* might be a Mediterranean vicariant of *Caricion remotae*, which occurs only marginally in Europe. However, to assess whether it is a suitable candidate for its own alliance, the analysis must be based on a larger dataset of spring vegetation plots with more data from the Mediterranean region (ideally supplemented by plots from Asia and Africa). Similarly, *Lysimachio-Saxifragion hirsutae* may be ecologically analogous vegetation to *Caricion remotae* in oceanic regions along the European Atlantic coast. The syntaxonomic position of *Wahlenbergio hederaceae-Sibthorpion europaeae* and its placement in class *Montio-Cardaminetea* are ambiguous, as mentioned already by de Foucault (2018). This unit includes vegetation growing on semi-shaded rocks and walls with *Sagina procumbens*, *Sibthorpia europaea* and *Wahlenbergia hederacea* (de Foucault 2018). However, the proper assessment of the validity of these three alliances was not possible because most of the vegetation plots in which their typical species (according to de Foucault 2018) are present lack identified bryophytes. Further research is needed to assess whether these syntaxa should be included in the variability of *Caricion remotae* or recognized as distinct units, either within class *Montio-Cardaminetea* or another class.

In addition to the units listed in EuroVegChecklist, we distinguish two other distinct types of spring vegetation corresponding to the previously described alliances *Anthelion julaceae* and *Cratoneuro filicini-Calthion laetae*, and propose to consider these types as separate alliances. Both types were unexpectedly identified by unsupervised and semi-supervised classifications and subsequently confirmed by supervised classification and ordination. In previous overviews of European spring vegetation, these vegetation types were treated as synonyms of accepted alliances. Zechmeister & Mucina (1994) merged *Cratoneuro filicini-Calthion laetae* with *Caricion remotae*. However, *Cratoneuro-Calthion* was described as a heliophilous subalpine to alpine community (Hadač 1983), while *Caricion remotae* was described as vegetation of shaded forest springs (Kästner 1941). Thus, both alliances clearly differ in terms of the elevations at which they occur (Valachovič & Janovicová 1999). Later, Mucina et al. (2016) synonymized *Cratoneuro filicini-Calthion laetae* with *Swertio perennis-Anisothecion squarrosi*, considering that both vegetation types occur near or above the timberline, and characterized the broadly delimited *Swertio perennis-Anisothecion squarrosi* as the vegetation of cold oligotrophic water springs. However, this description contradicts the original material of *Cratoneuro filicini-Calthion laetae* (Hadač 1983), which contains broad-leaved species, indicating increased macro-nutrient availability and the mesotrophic status of this vegetation type along the gradient of macro-nutrient availability between the oligotrophic (sub)alpine alliances and eutrophic vegetation of the class *Mulgedio-Aconitetea*. The high representation of neutral species is probably the reason why this alliance was not reproduced in the cluster analysis based on spring-positive species only. Unsupervised and semi-supervised classifications further discriminated communities of acidic springs that occur in the mountains in northern Britain and are characterized by the dominance of *Anthelia julacea*. This vegetation type corresponds to *Anthelion julaceae* (Shimwell 1972, Rodwell 1991). In the EuroVegChecklist, *Anthelion julaceae* was synonymized with *Mniobryo-Epilobion hornemannii*. However, we found no support for their merging.

Recently, Willner (2020) proposed that an alliance must be characterized by at least one absolute character taxon (species or subspecies) that has a global optimum in the syntaxon in question. This proposal and its general validity have not yet been discussed by the broader community of vegetation scientists. Nevertheless, when applied to spring vegetation, the concept supports the delimitation of the two above mentioned alliances. For the *Anthelion julaceae* alliance, *Anthelia julacea* appears to be an unequivocal absolute character taxon. Although this tiny liverwort is not exclusively restricted to true springs (Damsholt 2002), it occurs as a dominant species exclusively in oligotrophic mountain springs in the oceanic highlands of north-western Britain, at least according to the available vegetation-plot data. Candidate absolute character taxa for the *Cratoneuro filicini-Calthion laetae* alliance are montane subspecies of *Cardamine amara* (subsp. *opicii* and subsp. *balcanica*). Since these taxa are not consistently distinguished in all vegetation studies and databases, they were here combined at the species level. *Cardamine amara* subsp. *opicii* occurs in subalpine and alpine springs and on the banks of streams in the Carpathians and Sudetes (Marhold 1995). In the mountain ranges in western Bulgaria, the subspecies is replaced by the closely related *Cardamine amara* subsp. *balcanica* with a similar ecology (Marhold et al. 1996, 2002, Marhold & Valachovič 1998). Another potential absolute character taxon for *Cratoneuro filicini-Calthion laetae* could be *Caltha palustris* subsp. *laeta*. However, its taxonomic status remains unclear because its morphological characters overlap those of another subspecies of *Caltha palustris* (Chrtková & Jarolímová 1999, Valachovič & Janovicová 1999, but see Cieślak 2004).

### *Methodological aspects*

A key methodological step in broad-scale vegetation syntheses is the delimitation of the study object (the *Montio-Cardaminetea* class in our case). Following Jiroušek et al. (2022), the ratio of spring-positive to spring-negative species was used, supplemented by a negative criterion (percentage cover of selected species groups characterizing other habitats). The lists of species in all groups are the result of discussions within an international team of authors, which includes vegetation scientists and conservationists with experience from different European regions. Alternatively, the selection of vegetation plots could be based on the original author's assignment of vegetation plots to class *Montio-Cardaminetea* or subordinate syntaxa. However, syntaxonomic assignments are missing for many plots or are inconsistent due to varying personal opinions or different classification systems used in certain countries and at different periods of time. Another theoretical possibility for selecting plots would have been the simple presence of a species that occurs exclusively in springs. In general, however, there are few specialist species tightly associated with one habitat, as recently demonstrated by Dítě et al. (2023) for saline habitats or by Heinken et al. (2022) for forests. Moreover, such a simple criterion may lead to the selection of severely degraded springs, where the last individuals of a specialist species persist, but the vegetation already belongs to a different class due to successional shifts. This may be expected especially in soligenous fens, alder carrs and alpine grasslands, which develop after a decline of spring water flow due to climate change or local disruption of the hydrological regime.

Here we introduce an expert system that allows the hierarchical classification of spring vegetation based on formal definitions at different priority levels. Although traditional Cocktail-based formal definitions with sociological species groups (Kočí et al. 2003) are an appropriate means of identifying core plots, this approach typically allows the classification of about one third of all plots (e.g. Rodríguez-Rojo et al. 2014, Douda et al. 2016, Peterka et al. 2017, Kalníková et al. 2021) or, in some cases, slightly more than half (Novák et al. 2020, Hájek et al. 2021a). The formulas may also give a slightly higher chance to species-richer vegetation to be classified. However, classification of non-core (less-typical) plots may be important for habitat mapping. Definitions based on discriminating species groups would then be more applicable in practice.

## Conclusions and future perspectives

The first analysis and synthesis of European spring vegetation based on primary data (i.e. vegetation-plot records) was conducted by Zechmeister & Mucina (1994). The current study is the second attempt to produce a harmonized classification of the class *Montio-Cardaminetea* in the same geographical area, but using a much larger dataset and a broader range of analytical tools. Despite the quantity of vegetation-plot data compiled, there are still areas with a scarcity of plots belonging to class *Montio-Cardaminetea*, although a more frequent occurrence of spring vegetation is expected there (mainly in Fennoscandia, Balkan mountains, Apennines and other parts of southern Europe). Further sampling of vegetation in insufficiently studied areas and updates of vegetation databases are needed, especially for the future delimitation of *Myosotidion stoloniferae* and *Pinguiculo balcanicae-Cardaminion acris*. All other alliances listed in the EuroVegChecklist (Mucina et al. 2016) were formally reproduced and validated in terms of diagnostic species, species composition and ecological differences. In addition, we distinguished *Anthelion julaceae* and *Cratoneuro filicini-Calthion laetae* as separate alliances, both of which make ecological and compositional sense. We believe the results of this study could serve as a basis for further research on the classification of vegetation and typology of springs, as well as for developing conservation programmes.

## Supplementary materials

**Data S1.** Sources and preliminary data selection.
**Data S2.** List of aggregates.
**Data S3.** Formal definition of the *Montio-Cardaminetea* class and list of spring-positive species and neutral species.
**Data S4.** Results of unsupervised classifications of pan-European dataset.
**Data S5.** Results of unsupervised classification of regional subsets.
**Data S6.** Sociological species groups and formal definitions of cores of spring alliances.
**Data S7.** Expert system for identifying vegetation plots of *Montio-Cardaminetea* and for classifying plots into subordinate orders and alliances.
**Data S8.** Brief guide to the practical use of the expert system.
**Data S9.** Examples of associations for individual alliances.
**Table S1.** Full version of the synoptic table with the core plots of the alliances.
**Table S2.** Full version of the synoptic table with the core and non-core plots of the alliances.
**Table S3.** Synoptic table of orders of the class *Montio-Cardaminetea*.
**Fig. S1.** NMDS ordination analysis of core and non-core vegetation plots.
**Fig. S2.** NMDS analyses of plots classified at the order level.

Supplementary materials are available at www.preslia.cz

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# Formalizovaná klasifikace třídy *Montio-Cardaminetea* v Evropě: na cestě k jednotné typologii prameništní vegetace

Třída *Montio-Cardaminetea* zahrnuje vegetaci pramenišť a podobných biotopů ovlivněných stabilním prouděním vody. Jde o stanoviště ekologicky specializovaných a citlivých organismů. Současně jsou však prameniště ohrožená změnami v krajině i změnami klimatu. Přestože základem pro efektivní ochranu přírodních stanovišť je jednotná vegetační klasifikace, pro třídu *Montio-Cardaminetea* nebyl takový systém s využitím současných klasifikačních postupů dosud zpracován. V rámci této studie jsme shromáždili soubor evropských fytocenologických snímků z národních a soukromých databází. Našim cílem bylo ověřit klasifikační schéma prameništní vegetace z celoevropského přehledu vyšších syntaxonů (EuroVegChecklist), ověřit možnost přidání dalších vyhraněných rostlinných společenstev na úrovni svazů a vytvořit automatický systém pro klasifikaci fytocenologických snímků z pramenišť. Formálně jsme definovali jádra osmi z deseti svazů obsažených v přehledu EuroVegChecklist: *Caricion remotae*, *Cratoneurion commutati*, *Lycopodo europaei-Cratoneurion commutati*, *Epilobio nutantis-Montion*, *Koenigio-Microjuncion*, *Mniobryo-Epilobion hornemanii*, *Philonotidion seriatae* (*Cardamino- Montion*) a *Swertio perennis-Anisothecion squarrosi*. Tyto svazy byly rovněž rozlišeny neřízenými klasifikacemi. Neřízené i částečně řízené klasifikace odhalily existenci dvou dalších svazů, které v přehledu EuroVegChecklist chybí. Jedná se o *Anthelion julaceae* (subalpínská až alpínská prameniště s převahou játrovek ve Velké Británii) a *Cratoneuro filicini-Calthion laetae* (mezotrofní druhově bohatá subalpínská a alpínská prameniště). Neřízené klasifikace nejvíce odrážely gradient minerální bohatosti a rozlišovaly vápnitá a nevápnitá prameniště. Z toho důvodu navhujeme rozdělit dosavadní a široce vymezený řád *Montio-Cardaminetalia* na dva samostatné řády. V tomto pojetí by třída *Montio-Cardaminetea* zahrnovala tři řády: *Cardamino-Chrysosplenietalia* (lesní prameniště; svaz *Caricion remotae*), *Cardamino-Cratoneuretalia* (vápnitá lesní i nelesní prameniště; svazy *Cratoneurion commutati*, *Lycopodo europaei-Cratoneurion commutati*) a *Montio-Cardaminetalia* (nevápnitá nelesní prameniště; ostatní svazy).

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