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Annual Vegetation of Saline Seasonal Wetlands (*Crypsietea aculeatae*) in Europe

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ABSTRACT

Aims: The class *Crypsietea aculeatae* comprises pioneer ephemeral dwarf-graminoid vegetation occurring in periodically flooded saline habitats. Although numerous regional studies have described this vegetation, a unified classification across Europe has been lacking. This study aims to establish a formalized, continent-wide classification at the association level, identify its biogeographical patterns, and assess relationships between species composition and environmental gradients.

Location: Europe (except Armenia, Azerbaijan, Georgia, and Russia).

Methods: We compiled a dataset of 2538 vegetation plots from the European Vegetation Archive (EVA), private databases, and literature. A hierarchical expert system was developed using formal definitions of syntaxa based on species cover. Nonmetric multidimensional scaling (NMDS) was applied to evaluate compositional differences and reveal biogeographical patterns. Distance-based redundancy analysis (db-RDA) and unweighted community means of Ellenberg-type indicator values (EIVs) were used to assess environmental drivers.

Results: We present a revised syntaxonomic framework for the class *Crypsietea aculeatae* and propose updates to the EuroVegChecklist. One alliance (*Cypero-Spergularion marinae*) and four associations (*Crypsietum aculeatae*, *Crypsietum schoenoidis*, *Cyperetum pannonicum*, and *Oxybasio chenopodioidis-Crypsietum aculeatae*) were formally defined, with basic descriptions of their species composition, ecological characteristics, and geographical distribution. The main gradients in

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vegetation variability within the class *Crypsietea aculeatae* are driven by climatic gradient and edaphic factors, including soil moisture, soil acidity, salinity, and nutrient availability.

Conclusions: We established the first formal classification of annual vegetation in European saline seasonal wetlands. The syntaxonomic nomenclature was revised, and modifications to the EuroVegChecklist were proposed. The resulting classification system, accompanied by an expert system, enables consistent application in nature conservation and ecological research.

1 | Introduction

Wetland habitats, including temporary wetlands, are important ecosystem types globally (Deil 2005; Calhoun et al. 2017; Boix et al. 2020; Ioannidou et al. 2021; Liu et al. 2023). Saline seasonal wetlands are a special type of temporary wetlands. They include periodically flooded, saline and muddy, nutrient-rich shores and dried-up bottoms of saline standing water bodies and occasional saline river banks (Janssen et al. 2016; Chytrý et al. 2020). These habitats are of high ecological value due to the services they provide (Geissler et al. 2013; Caçador et al. 2016; Atia et al. 2019; Boix et al. 2020; De Vicente 2021; Luković et al. 2021). They host unique flora (Deil 2005; Stenger-Kovács et al. 2014) and fauna (Horváth et al. 2014; Meland et al. 2020; Gajdoš et al. 2023) and contribute significantly to regional diversity (Lukács et al. 2015; Williams 2012; Boix et al. 2020; Felföldi 2020).

Compared to freshwater analogs, saline seasonal wetlands are more extreme habitats. Hydroperiod is a strong filter of species composition in these habitats by limiting the set of species to those that can grow rapidly and complete their life cycle in the short intervals of periodic droughts and floods (Colmer and Flowers 2008; Williams 2012). High salinity levels produce additional environmental stress, resulting in the dominance of a few tolerant species (Williams 2012; Lengyel et al. 2019; Márton et al. 2023; Päscht et al. 2024). Therefore, saline seasonal wetlands have relatively low, but highly distinctive and specialized biodiversity (Chauhan and Gopal 2016).

Saline seasonal wetlands are ecologically and socioeconomically significant ecosystems. Their unique hydroperiods and structural variability underpin a wide range of ecosystem services, including groundwater recharge (Schile et al. 2014), nutrient cycling (Blomqvist et al. 2004), carbon sequestration (Herbert et al. 2015), and biodiversity conservation (Boix et al. 2020). In addition to their ecological functions, they offer economic (e.g., food production, medicinal and ornamental plants, livestock grazing) (Dajić Stevanović et al. 2019), social (e.g., cultural and recreational uses) (Luković et al. 2021), and educational (Hails 2018) benefits. Despite their ecological importance and socioeconomic functions, saline seasonal wetlands are often considered as “wastelands” or land reserves by local communities (Williams 2012; Ioannidou et al. 2021). As a result, they are threatened by human population growth, urbanization, dumping, pollution, eutrophication, and increasing economic activities (Beja and Alcazar 2003; Euliss Jr. and Mushet 2004; Gedan et al. 2009; Ioannidou et al. 2021). Saline seasonal wetlands are also affected by climate change (Brock et al. 2005; Gonçalves et al. 2007; Ghosh et al. 2010; Junk et al. 2013; Renton et al. 2015) and invasive species (Zedler 2004; Deil 2005; Brundu 2015; Lázaro-Lobo and Ervin 2021).

The significant ecological and socioeconomic role of saline seasonal wetlands is recognized by the European Union's Habitats Directive (92/43/EEC) (Council of the European Communities 1992), which included them in the list of Habitats of Community Interest, as a part of habitat types 1530 (*Pannonic salt steppes and salt marshes) and 1310 (*Salicornia* and other annuals colonizing mud and sand). Saline seasonal wetlands are also in the European Red List of Habitats under the category “Endangered” (Janssen et al. 2016) and on the priority list of the EU's Biodiversity Strategy for 2030 (European Commission 2020).

Very specific vegetation is developed across saline seasonal wetlands. It has an ephemeral nature and includes mainly annual salt-adapted plant species, developing during the exposure phase, accompanied by some perennial plants tolerant to temporary total flooding and brackish conditions (Šumberová 2007; Janssen et al. 2016). From the phytosociological point of view, this vegetation belongs to the classes *Crypsietea aculeatae* Vicherek 1973, *Saginetea maritimae* Westhoff et al. 1962, and *Thero-Salicornietea* Tx. in Tx. et Oberd. 1958.

In this study, we focus on the class *Crypsietea aculeatae*. While the vegetation of this class, like that of the *Saginetea maritimae* and *Thero-Salicornietea*, is inherently pioneer and occupies periodically flooded saline habitats, it exhibits distinct characteristics that clearly differentiate the *Crypsietea aculeatae* as a separate unit:

- **Species composition and dominant life and growth forms:** The vegetation of the class *Crypsietea aculeatae* is characterized by the dominance of annual graminoids, primarily species from *Poaceae* and *Cyperaceae*. In contrast, *Saginetea maritimae* comprises vegetation dominated by small-sized annual non-graminoid herbs, while *Thero-Salicornietea* includes vegetation composed of annual succulents belonging to *Chenopodiaceae* (Tomaselli, Beccarisi, et al. 2020).
- **Ecology:** The class *Crypsietea aculeatae* typically occupies saline, mesotrophic soils with high concentrations of base cations (Ca^{2+} , Mg^{2+}) (Dítě et al. 2017). In contrast, *Thero-Salicornietea* is restricted to strongly saline, alkaline, and mesotrophic to eutrophic (less frequently oligotrophic) soils, while *Saginetea maritimae* develops on subsaline to saline soils, typically in habitats subject to frequent disturbances (Tomaselli, Veronico, et al. 2020; Salazar-Mendias and Lendínez 2021).
- **Biogeography:** The vegetation of *Crypsietea aculeatae* is most commonly associated with inland areas of sub-Mediterranean and subcontinental regions of Eurasia. In contrast, *Thero-Salicornietea* has a much broader Eurasian distribution, occurring in both coastal and inland areas, while *Saginetea maritimae* is restricted to the

Atlantic–Mediterranean region of Europe (Preislerová et al. 2022).

- **Phenology:** The phenological optimum of *Crypsietea aculeatae* is similar to that of *Thero-Salicornietea* vegetation and occurs from late summer to autumn, whereas *Saginetea maritimae* follows a winter–spring cycle.

Therefore, we define the class *Crypsietea aculeatae* as pioneer ephemeral dwarf-graminoid vegetation in periodically flooded saline habitats of Eurasia. Vegetation of the class mainly occurs in the semiarid climate of the Mediterranean, Continental, Pannonian, and Steppic biogeographical regions of Europe. Vegetation of *Crypsietea aculeatae* is also found across Southwest Asia and Northern Africa (Leredde 1954; Barbagallo et al. 1990; Léonard 2001), reaching the southernmost point in the Central Saharan Mountains (Quézel 1958).

The vegetation currently classified as *Crypsietea aculeatae* has been studied phytosociologically since the 1930s, with pioneering studies in some areas of central (Bojko 1932; Wenzl 1934; Wendelberger 1943) and southeastern Europe (Topa 1939). Subsequently, it was reported in local studies as a part of different vegetation classes or as a separate class (Slavnić 1948; Oberdorfer 1952; Rivas Goday et al. 1956; Rivas-Martínez et al. 1980; Golub and Mirkin 1986; Molero and Romo 1988; Korzhenevskiy and Klyukin 1990; Paradis and Lorenzoni 1994; Viciani and Lombardi 2001; Biondi and Bagella 2005; Farris et al. 2007; Lazu et al. 2012; Guitton and Terrisse 2015; Tomaselli, Beccarisi, et al. 2020; De Foucault 2021, 2022; Bertacchi et al. 2021; Brullo et al. 2022) and summarized in national surveys of Portugal (Costa et al. 2012), Spain (Rivas-Martínez et al. 2001), France (Roux et al. 2024), Austria (Mucina 1993), Czech Republic (Šumberová 2007), Slovakia (Dítě, Eliáš, and Melečková 2014), Hungary (Borhidi et al. 2012), Romania (Sanda et al. 2008), Bulgaria (Tzonev and Gushev 2021), and Ukraine (Dubyna et al. 2019). These contributions show discrepancies in the syntaxonomy of this vegetation across Europe, which can be related to diverse classification approaches and different viewpoints on the syntaxonomic position of the *Crypsietea aculeatae* in the system of phytosociological classes. Although Vicherek (1973) elevated this vegetation to a class level, some authors consider it a part of the *Isoëto-Nanojuncetea* (Rivas-Martínez et al. 2001; Costa et al. 2012; De Foucault 2013; Biondi et al. 2014; Brullo et al. 2022), *Saginetea maritimae* (Viciani and Lombardi 2001; Frondoni and Iberite 2002; Tomaselli et al. 2010; Bertacchi et al. 2021), *Thero-Salicornietea* (Borhidi et al. 2012), or *Festuco-Puccinellietea* (Mucina 1993; Sanda et al. 2008).

Critical pan-European syntaxonomic overviews based on extensive vegetation plot databases (Chytrý et al. 2016) have been produced for some vegetation types across Europe (e.g., Marcenò et al. 2018; Landucci et al. 2020; Kalníková et al. 2021; Jiroušek et al. 2022; Novák et al. 2023; Peterka et al. 2023). Such an overview has been lacking for the class *Crypsietea aculeatae*. To solve controversial issues and remove gaps in knowledge, this study aims to (i) revise critically the syntaxonomy of the *Crypsietea aculeatae* as proposed in the EuroVegChecklist (Mucina et al. 2016) by analyzing a large dataset of vegetation plots; (ii) identify the vegetation associations of the class *Crypsietea aculeatae* across Europe; (iii) outline the

biogeographical patterns of the defined vegetation units; (iv) develop an expert system for automatically classifying vegetation plots into the *Crypsietea aculeatae* class at the association level; (v) characterize the relationships between the species composition of this vegetation and the main environmental gradients.

2 | Methods

2.1 | Data Preparation

The vegetation plots from different phytosociological databases stored in the European Vegetation Archive (EVA) (Chytrý et al. 2016) were the basic data source for our analysis. The study area covers the whole of Europe; however, the territories of the Russian Federation, Armenia, Azerbaijan, and Georgia were excluded from the analysis due to their peripheral biogeographical position and the lack of comprehensive and spatially balanced vegetation-plot data in the EVA database. Given the aims of our study, we requested: (i) all plots with the presence of *Crypsis aculeata*, *C. schoenoides*, *Cyperus pannonicus*, *Lepidium latifolium*, and *Oxybasis chenopodioides*. The presence of at least one of these species, irrespective of its cover value, was considered a sufficient criterion for the selection of the vegetation plot. These specific species were selected because of their designation as characteristic species in the original diagnoses of the alliances (Slavnić 1948; Braun-Blanquet et al. 1952; Golub and Mirkin 1986) included in the *Crypsietea aculeatae*, according to the EuroVegChecklist (Mucina et al. 2016); (ii) all plots labeled in the EVA databases as belonging to the vegetation alliances included in *Crypsietea aculeatae* (i.e., *Cypero-Spergularion salinae*, *Heleochoilon schoenoidis*, and *Lepidion latifolium*) by Mucina et al. (2016). We also included data from some private unpublished sources not yet included in EVA and added some data from literature. The complete list of data sources can be found in Appendix S1. As a result, we compiled the initial (“working”) data set comprising 2538 vegetation plots, including 1714 plots from EVA, 535 plots from private unpublished sources, and 289 plots from literature. Then, we selected from this dataset only those plots in which the total cover of annual species was greater than the total cover of perennial plants and used these plots for further data filtering and data processing. All the vegetation plot records were stored in the TURBOVEG database software (Hennekens and Schaminée 2001) and imported into the JUICE 7.1 program (Tichý 2002).

We removed duplicates and non-georeferenced plots, except for those where it was possible to add geographical coordinates according to the description of localities in the original datasets. Having records from plots of variable size, which may affect the results (Otýpková and Chytrý 2006; Dengler et al. 2009), we kept only those with an area not smaller than 1 m² and not larger than 100 m². This size range was chosen to ensure broad representativeness and to avoid the exclusion of data collected under different regional sampling traditions, while still providing sufficient information on species composition and consistently capturing the main environmental gradients (Peterka et al. 2020). We did not exclude plots with missing information on the plot size because of concerns about losing data on some regions and assuming that nearly all such plots were sampled on an area between 1 and

100 m². The taxonomic concepts and nomenclature of vascular plants were unified according to the Euro+Med PlantBase (Euro+Med 2024). Taxonomically problematic species were merged into aggregates (Appendix S2). Records of the same species in different layers were merged to represent each species only once in the final data matrix. Taxa identified only to the genus or family level were omitted to ensure consistency and comparability across relevés. Subspecies were merged to the species level, but if a species was represented only by a single subspecies in the dataset, this subspecies was retained. All records of juvenile trees and shrubs in the herb layer were deleted from the dataset. Nonvascular plants were omitted because they were only recorded in a few plots.

2.2 | Classification

To build the classification protocol for the *Crypsitea aculeatae* class and choose the most appropriate approach, we had to consider specific features of this vegetation type: (i) distinct dominant species; (ii) a low number of species per plot; (iii) a limited number of species strictly associated with this vegetation type and, therefore, a limited set of diagnostic species of the class; (iv) a species composition that is often influenced by the adjacent vegetation and therefore enriched with species diagnostic for other vegetation classes. Therefore, to define the *Crypsitea aculeatae* class and the vegetation plots belonging to it, our classification protocol followed the protocol proposed by Landucci et al. (2015, 2020) for the phytosociological classification of species-poor vegetation. As in the case of species-rich vegetation, this approach applies formal logic to define vegetation units based on species cover while also relevantly considering physiology, dominance patterns, and functional species groups.

We created an expert system for automatic vegetation classification. We developed our expert systems in two steps. In the first stage of data processing, we provided formal definitions for vegetation alliances of the class *Crypsitea aculeatae* suggested in EuroVegChecklist (Mucina et al. 2016), except for the *Lepidion latifolii*. We excluded this vegetation from the *Crypsitea aculeatae* already at this stage of data analysis, since practically all plots with a high cover of the perennial *Lepidium latifolium*, as well as the plots originally assigned by the authors to the alliance *Lepidion latifolii*, were removed during the elimination of records dominated by perennial species. Considering that all such plots originated from Ukraine, while the distribution of the alliance extends further eastwards (see Preislerová et al. 2022), we critically analyzed the available phytosociological literature from Russia to support the validity of our decision to exclude *Lepidion latifolii* from the class *Crypsitea aculeatae*. This literature-based assessment focused on the species composition and life-form structure of the vegetation assigned to the *Lepidion latifolii* alliance. The formal definitions of the other two alliances of the *Crypsitea aculeatae* (i.e., *Cypero-Spergularion salinae* and *Heleochloion schoenoidis*), as accepted in the EuroVegChecklist (Mucina et al. 2016), are based on the threshold cover values of their characteristic species as listed in the original diagnoses (Slavnić 1948; Braun-Blanquet et al. 1952), characteristic species of the *Crypsitea aculeatae* class, and delimitation against other vegetation types using functional species groups. As characteristic species of the *Crypsitea aculeatae*, we considered: (i)

species listed as diagnostic for the class in the EuroVegChecklist (see Electronic appendix S6 in Mucina et al. 2016) and (ii) species that most frequently co-occur with diagnostic species, which we defined as those listed as constant species for EUNIS habitat type Q63 (Periodically exposed saline shore with pioneer or ephemeral vegetation) (Chytrý et al. 2020, 2024). Apart from defining the alliances of the *Crypsitea aculeatae*, we also developed the formal definitions for other classes of annual wetland vegetation (*Isoëto-Nanojuncetea*, *Bidentetea*, *Littorelletea uniflorae*, *Saginetetea maritima*, *Thero-Salicornietea*) to achieve a more precise classification of plots. To formally define the listed classes, we also relied on the list of diagnostic species provided in the EuroVegChecklist (see Electronic appendix S6 in Mucina et al. 2016).

The functional species groups also included lists of trees, shrubs, and a set of species characteristic of wetlands and vegetation often bordering wetlands, that is, ruderal, psammophilous, grassland, and halophilous vegetation. These species lists were compiled based on Mucina et al. (2016), other authoritative literature sources (i.e., Janssen et al. 2016; Chytrý et al. 2020), and our personal experience. The threshold values of percentage cover in the formal definitions were defined arbitrarily following our expert knowledge and the experience of authors who followed a similar classification approach before (Landucci et al. 2015, 2020; Kalníková et al. 2021). The definitions of *Cypero-Spergularion salinae* and *Heleochloion schoenoidis* we used comprise the following logical formulas (see Tichý et al. 2019 for syntax):

- (<#TC *Cypero-Spergularion salinae* GR 25> OR <#TC *Cypero-Spergularion salinae* GR #T\$>) NOT ((((((<#TC PSAMMOPHILOUS species GR 25> OR <#TC HALOPHILOUS species GR 50>) OR <#TC GRASSLAND species GR 25>) OR <#TC WETLAND species GR 25>) OR <#TC RUDERAL species GR 25>) OR <### Trees GR 20>) OR <### Shrubs GR 20>)
- (<#TC *Heleochloion schoenoidis* GR 25> OR <#TC *Heleochloion schoenoidis* GR #T\$>) NOT ((((((<#TC PSAMMOPHILOUS species GR 25> OR <#TC HALOPHILOUS species GR 50>) OR <#TC GRASSLAND species GR 25>) OR <#TC WETLAND species GR 25>) OR <#TC RUDERAL species GR 25>) OR <### Trees GR 20>) OR <### Shrubs GR 20>)

Thus, for a plot to be classified in one of the alliances, there had to be (i) the total cover of the characteristic species of a given alliance greater than 25% or (ii) the total cover of the characteristic species of a given alliance greater than the total cover of any other functional species group.

The second step of the data processing aimed to develop an expert system for the assignment of vegetation plots to the specific phytosociological association. For this purpose, we reviewed the concepts used in the literature to distinguish the associations within *Crypsitea aculeatae*. Since previously described associations were mostly based on the dominance of individual species, this concept was chosen as a baseline of the classification protocol for the whole class to the association level. We reviewed a large body of European phytosociological literature (e.g., Mucina 1993; Golub 1995; Rivas-Martínez et al. 2001;

Šumberová 2007; Sanda et al. 2008; Borhidi et al. 2012; Costa et al. 2012; Biondi et al. 2014; Dajić Stevanović et al. 2016; Dítě, Melečková, and Eliáš 2014; Dítě et al. 2017; Dubyna et al. 2019; Danihelka et al. 2022; Roux et al. 2024) and compiled the list of associations that were once classified as *Crypsitetea aculeatae* or where a name-giving taxon was a diagnostic species of the class (Appendix S3). First, we excluded from the list those associations in which perennials dominate. These associations were identified based on the results of the initial plot selection by dominant life-forms. Then, we eliminated those associations for which the majority of plots, including the nomenclatural type, met the criteria of the formal definitions of other annual wetland vegetation classes. Following this, we provisionally defined associations dominated by *Crypsis aculeata*, *C. schoenoides*, *Cyperus pannonicus*, and *Oxybasis chenopodioides*. To finalize the list of the *Crypsitetea aculeatae* associations and to assess the differences in species composition of previously described vegetation associations, we mapped all plots from their original diagnosis onto a nonmetric multidimensional scaling (NMDS) ordination diagram and conclusively determined the number of associations within the class *Crypsitetea aculeatae* (Appendix S4). For some associations, we had only synoptic tables available, so we could not select annual-dominated plots and map them in ordination space. Therefore, we first analyzed the life-form structure of these associations and excluded those with more than 50% perennial species. Then, we analyzed the species composition of such associations in terms of the proportions of species diagnostic for the *Crypsitetea aculeatae*, species that are frequent in the *Crypsitetea aculeatae* stands, and species that are typical of other vegetation types. If the total proportion of diagnostic and constant species of *Crypsitetea aculeatae*, which occurred with high constancy in a given association, was less than 50%, such associations were not considered part of the target vegetation.

In the final stage of classification, we developed the formal definitions for the phytosociological associations and supplemented our expert system (Appendix S5) with them to bring it in line with our final classification. In logical formulas, we combined all individual criteria using the logical operators AND, OR, and NOT (Bruehlheide 1997). Each formula contains a “dominant species,” the cover of which is either greater than the cover of any other species in the plot or has a cover value higher than or equal to 25%. The “dominant species” has the highest priority degree in the plot.

The assignment rules we used are as follows:

- If the cover of the dominant species is greater than that of any other species in the plot, the plot is assigned to the association characterized by that dominant species.
- If the cover of the dominant species is greater than or equal to 25%, the plot is assigned to the association characterized by that species.
- If two or more species have identical cover values, the plot is assigned based on further refinement using functional species groups.

Each of these rules operates if the previous one is not met. To apply such a sequence during the assignment process of

vegetation plots, we defined a hierarchy within the logical formulas directly. The expert system has three hierarchical levels (alliance, association, and class) and classifies in the bottom-up direction from the association to the class. The expert system for the automatic assigning of vegetation plots to the syntaxa within the class *Crypsitetea aculeatae* can be run in JUICE (Tichý 2002).

Diagnostic and constant species for each defined association are shown in a synoptic table that shows the percentage species frequency. In the table, species are sorted by decreasing fidelity (phi coefficient) measure (Chytrý et al. 2002). The threshold values for the phi coefficient were taken at the level of 0.2 for diagnostic species and 0.4 for highly diagnostic species. Species with a nonsignificant fidelity to the association according to Fisher's exact test ($P < 0.01$; Tichý and Chytrý 2006) were not considered diagnostic even though the phi value exceeded the above threshold. To determine the constant and highly constant species, we used constancy thresholds of 25% and 50%, respectively. Dominant species were defined as those occurring with cover value $> 20\%$ in at least 10% of the plots.

Syntaxonomic names were revised following the 4th edition of the International Code of Phytosociological Nomenclature (Theurillat et al. 2021).

2.3 | Ordination

The classification results were plotted using NMDS of Bray-Curtis dissimilarities based on square root-transformed species percentage covers. To assess differences in species composition between vegetation units, we applied a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. We also used NMDS to show how much the species composition of associations differed across the biogeographical regions. We tested the effects of climate variables on species composition and analyzed Ellenberg-type indicator values (EIVs) (Tichý et al. 2023). To test which climate predictors and environmental variables are significant for species composition, distance-based redundancy analysis (db-RDA ordination) with 999 unrestricted permutations and the same cover transformation and dissimilarity measure as in NMDS was used. The climate variables (BIO1–BIO19) were obtained from the CHELSA-BIOCLIM+ dataset (Brun et al. 2022). All significant climatic variables were presented as boxplots to compare the climatic affinity of vegetation units. To evaluate the differences in species composition between plant communities based on EIVs, we calculated unweighted means of species' values for each vegetation plot without considering the dominant species of associations (i.e., *Crypsis aculeata*, *C. schoenoides*, *Cyperus pannonicus*, and *Oxybasis chenopodioides*) to eliminate the overweighting effect of these species on the EIVs community means. To evaluate whether bioclimatic parameters and EIVs differed significantly among the vegetation groups, we performed statistical analyses tailored to the distributional properties of the data. Differences in bioclimatic variables among clusters were assessed using the nonparametric Kruskal–Wallis rank-sum test, as these variables did not meet assumptions of normality (verified via the Shapiro–Wilk test). To test for differences in EIVs among vegetation

associations, we applied a modified permutation test (Zelený and Schaffers 2012). In both cases, when the global test indicated significant differences ($p < 0.01$), we performed pairwise post hoc comparisons using Dunn's test with Bonferroni correction. Results of the pairwise comparisons were visualized using the Compact Letter Display method, where shared letters indicate statistically homogeneous groups.

All analyses were performed in R 4.3.2 (R Core Team 2023) using the *vegan* 2.6-4 (Oksanen et al. 2022), *weimea* (<https://github.com/zdealveindy/weimea>), *rstatix* (Kassambara 2023), *FSA* (Ogle et al. 2023), and *multcompView* packages (Graves et al. 2022). All visualizations were produced using the *ggplot2* package (Wickham 2016). Spatial data were managed in QGIS 3.34 (QGIS Development Team 2021).

3 | Results

3.1 | Vegetation Classification

The vegetation of the *Crypsietea aculeatae* class in Europe was classified into four vegetation associations, hierarchically grouped within a single alliance and a single order. Due to the lack of well-defined diagnostic species for most previously described associations, we defined only a single association per dominant species. Based on data analysis and a detailed syntaxonomic revision (see Section 4), we also accepted only one alliance within the *Crypsietea aculeatae*. We developed formal definitions for each recognized vegetation unit and designed an expert system to automatically classify vegetation plots into the *Crypsietea aculeatae* class. The proposed expert system (Appendix S5) includes not only formal definitions for the vegetation units of the *Crypsietea aculeatae* class but also species groups and formal definitions for other alliances and classes of annual wetland vegetation that are ecologically similar or toward which successional shifts are most likely to occur (i.e., *Isoëto-Nanojuncetea*, *Bidentetea*, *Saginetea maritimae*, and *Thero-Salicornietea*). We supplemented the expert system with the species groups of other vegetation types with which *Crypsietea aculeatae* communities often grow in conjunction (i.e., wetland, ruderal, and grassland). All of the abovementioned groups were incorporated to minimize the misclassification of plots to the target vegetation. The expert system we developed assigned 61.2% of the plots of the dataset to associations and 1.4% to alliances only. The unclassified plots amounted to 37.4% of the total dataset (Table 1). The unclassified plots were mostly affiliated with the classes not covered in this study. Of the plots, 1.9% were classified into more than one association. The results of the classification are presented in a synoptic table (Table 2). The geographic distribution of each association is presented in Figure 1. Photos of typical stands of each association are provided in Figure 2. The ordination diagrams are shown in Figure 3, and boxplots of environmental variables are given in Figures 4 and 5.

3.2 | Syntaxonomical Synopsis

We propose the following syntaxonomical synopsis of the class *Crypsietea aculeatae* in Europe:

TABLE 1 | Classification results with the number of plots assigned to each syntaxon defined in the expert system. The codes of the syntaxa follow the expert system.

Code	Syntaxon name	No of plots in the dataset
CRY01	<i>Crypsietum aculeatae</i>	201
CRY02	<i>Crypsietum schoenoidis</i>	119
CRY03	<i>Cyperetum pannonicum</i>	37
CRY04	<i>Oxybasio chenopodioidis-Crypsietum aculeatae</i>	54
CRY0	<i>Cypero-Spergularion marinae</i>	10
Additional plots in the dataset:		
	Double classification	13
	Unclassified	250

- *CRYSIETEA ACULEATAE* VICHEREK 1973
- *Crypsietalia aculeatae* Vicherek 1973
- *Cypero-Spergularion marinae* Slavnić 1948 nom. corr.
- *Crypsietum aculeatae* Wenzl 1934
- *Crypsietum schoenoidis* Topa 1939
- *Cyperetum pannonicum* Wendelberger 1943
- *Oxybasio chenopodioidis-Crypsietum aculeatae* Paradis et Lorenzoni 1994 mut. Iemelianova et al. 2025

3.3 | Description of Vegetation Units

CRYSIETEA ACULEATAE VICHEREK 1973

Original form: “Klasse *Crypsidetea aculeatae*” (Vicherek 1973, 42).

Name-giving taxon: *Crypsis aculeata* (L.) Ait.

Nomenclatural type (holotypus): *Crypsietalia aculeatae* Vicherek 1973.

Pioneer ephemeral dwarf-grass vegetation in periodically flooded saline habitats of Eurasia.

Crypsietalia aculeatae Vicherek 1973

Original form: “Ordnung *Crypsidetalia aculeatae*” (Vicherek 1973, 42).

Name-giving taxon: *Crypsis aculeata* (L.) Ait.

Nomenclatural type (holotypus): *Cypero-Spergularion marinae* Slavnić 1948.

Pioneer ephemeral dwarf-grass vegetation in periodically flooded saline habitats of Europe.

TABLE 2 | A shortened synoptic table of the associations of the *Crypsietea aculeatae* class: *Crypsietum aculeatae* (CRY01), *Crypsietum schoenoidis* (CRY02), *Cyperetum pannonicum* (CRY03), *Oxybasio chenopodioidis-Crypsietum aculeatae* (CRY04).

Association code	CRY01	CRY02	CRY03	CRY04
Number of plots	201	119	37	54
<i>Crypsietum aculeatae</i>				
<i>Crypsis aculeata</i>	100	30	38	59
<i>Cressa cretica</i>	29			
<i>Crypsietum schoenoidis</i>				
<i>Crypsis schoenoides</i>	6	100	8	25
<i>Polygonum aviculare</i> aggr.	3	30	5	
<i>Echinochloa crus-galli</i>	2	30	10	2
<i>Xanthium strumarium</i> aggr.	2	18	5	7
<i>Rorippa sylvestris</i>	1	10		
<i>Plantago major</i>	3	28	15	7
<i>Tripleurospermum maritimum</i> aggr.		10		2
<i>Cyperetum pannonicum</i>				
<i>Cyperus pannonicus</i>	1	2	100	3
<i>Spergularia marina</i>	7	19	49	5
<i>Tripolium pannonicum</i>	19	15	56	12
<i>Puccinellia distans</i> aggr.	18	14	57	7
<i>Cyperus flavescens</i>			15	
<i>Plantago maritima</i>	1		15	
<i>Taraxacum besarabicum</i>	1	2	18	
<i>Juncus articulatus</i>		1	10	
<i>Oxybasio chenopodioidis-Crypsietum aculeatae</i>				
<i>Oxybasis chenopodioides</i>	8	9	5	100
<i>Atriplex prostrata</i>	18	32	21	75
<i>Bolboschoenus maritimus</i> aggr.	21	21	38	57
Other frequent species (frequency > 15%)				
<i>Oxybasis glauca</i>	6	14	33	20
<i>Juncus compressus</i> aggr.	12	18	26	2
<i>Agrostis stolonifera</i>	3	14	26	13
<i>Suaeda maritima</i> aggr.	24	2	23	2
<i>Phragmites australis</i>	8	12	15	20

Note: The table is based on the expert system classification. The values are percentage frequencies. Species are sorted by their decreasing fidelity to a particular association: Dark shading indicates highly diagnostic species ($\phi_i \geq 0.4$) and light shading indicates diagnostic species ($\phi_i \geq 0.2$); nondiagnostic species are only shown if they reach a constancy of at least 15% in at least one association.

***Cypero-Spergularion marinae* Slavnić 1948 nom. corr**

Original form: "Sveza *Cypero-Spergularion salinae* Slavnić 1939" (Slavnić 1948, 84).

Original name-giving taxa: *Cyperus pannonicus* Jacq., *Spergularia salina* J. Presl & C. Presl.

Corrected name-giving taxa: *Cyperus pannonicus* Jacq., *Spergularia marina* (L.) Griseb.

Nomenclatural type (lectotypus hoc loco): *Cyperetum pannonicum* Wendelberger 1943.

Synonyms: *Crypsidion aculeatae* Pignatti 1953 (art. 3b); *Polygono salsuginei-Crypsion aculeatae* Korzhenevskiy et

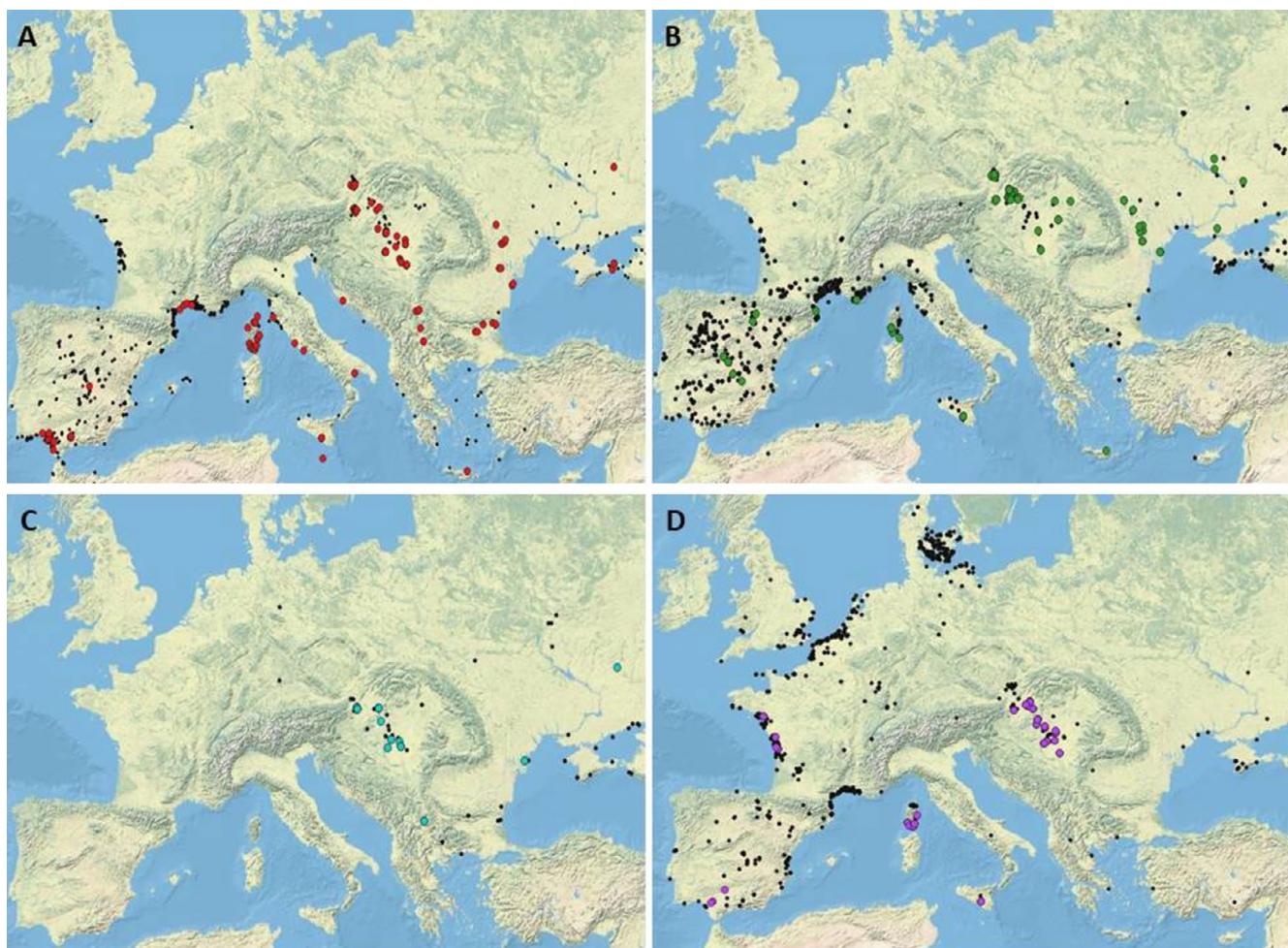


FIGURE 1 | Distribution of vegetation plots classified to associations by the expert system. Larger color circles represent plots assigned to each respective association of the *Crypsietea aculeatae*: (A) *Crypsietum aculeatae*; (B) *Crypsietum schoenoidis*; (C) *Cyperetum pannonicum*; (D) *Oxybasio chenopodioidis-Crypsietum aculeatae*. Small black points in the background show the distribution of the characteristic species of each association (i.e., *Crypsis aculeata*, *Crypsis schoenoides*, *Cyperus pannonicus*, and *Oxybasis chenopodioides*) according to the data extracted from GBIF (GBIF.org. 2024).

Klyukin 1990 (art. 1, 2a); *Polygono salsuginei-Crypsion aculeatae* Korzhenevsky et Klyukin 1991 (phantom); *Polygono salsuginei-Crypsion aculeatae* Korzhenevsky et Klyukin in Korzhenevsky et al. 1997 (syntax. syn.).

Pioneer ephemeral short-graminoid vegetation in periodically flooded saline habitats of Europe.

CRY01. *Crypsietum aculeatae* Wenzl 1934 (Figures 1A and 2A,B)

Original form “*Crypsidetum aculeatae*” (Wenzl 1934, 131).

Name-giving taxon: *Crypsis aculeata* (L.) Ait.

Nomenclatural type (lectotypus hoc loco): Wenzl (1934): table on page 124, relevé 37. H. Wenzl, Oberer Stinker See, Austria. Braun-Blanquet scale—*Crypsis aculeata* 3, *Suaeda maritima* = *S. pannonica* +.

Synonyms: *Damasonio alismatis-Crypsietum aculeatae* Rivas-Martínez et Costa in Rivas-Martínez et al. 1980 (syntax.

syn.); *Cresso creticae-Crypsietum aculeatae* Géhu et al. 1990 (syntax. syn.); *Polygono salsuginei-Crypsietum aculeatae typicum* Korzhenevsky et Klyukin 1990 (Art. 2a); *Atriplici prostratae-Crypsietum aculeatae* Paradis et Lorenzoni 1994 (syntax. syn.); *Samolo valerandi-Crypsietum aculeatae* Paradis et Lorenzoni 1994 (syntax. syn.); *Polypogono monspeliensis-Crypsietum aculeatae* Paradis et Lorenzoni 1994 (syntax. syn.); *Salicornio patulae-Crypsietum aculeatae* Paradis et Lorenzoni 1994 (syntax. syn.); *Polygono salsuginei-Crypsietum aculeatae* Korzhenevsky et Klyukin in Korzhenevsky et al. 1997 (syntax. syn.); *Salicornio patulae-Crypsietum aculeatae* Biondi et Bagella 2005 (Art. 31, syntax. syn.); *Damasonio bourgaei-Crypsietum aculeatae* Rivas-Martínez et Costa in Rivas-Martínez et al. 1980 corr. V. Silva & J.C. Costa in Costa et al. 2012 (syntax. syn.); *Salicornio ramosissimae-Crypsietum aculeatae* Guitton et Terrisse 2015 (syntax. syn.).

Diagnostic species: *Cressa cretica* ($\phi=0.26$), *Crypsis aculeata* (0.54).

Constant species: *Bolboschoenus maritimus* aggr., *Crypsis aculeata*, *Suaeda maritima* aggr.

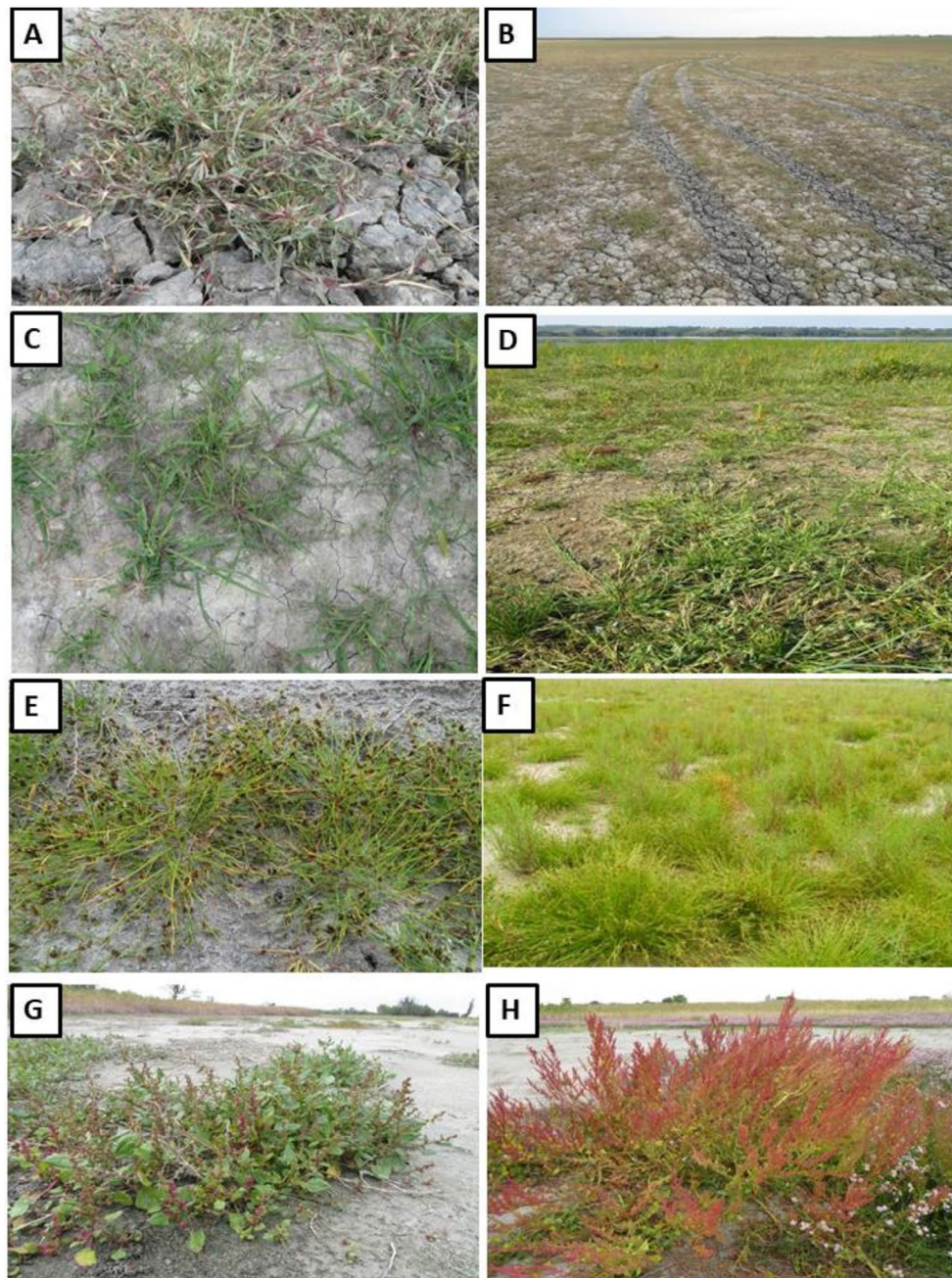


FIGURE 2 | Typical stands of each association of the class *Crypsietea aculeatae*. (A, B) *Crypsietum aculeatae* (Slano Kopovo, Novi Bečej, Serbia); (C, D) *Crypsietum schoenoidis* (Hlohovec, Southern Moravia, Czech Republic); (E) *Cyperetum pannonicum* (Neusiedler See, Illmitz, Austria); (F) *Cyperetum pannonicum* (Danube Delta, Odessa Region, Ukraine); (G, H) *Oxybasio chenopodioidis-Crypsietum aculeatae* (Neusiedler See, Illmitz, Austria). Photo credits: M. Chytrý (A, B, C, D, E, G, H), T. Dziuba (F).

Dominant species: *Crypsis aculeata*.

This association comprises species-poor vegetation dominated by the annual prostrate grass *Crypsis aculeata*. In optimal ecological conditions, this vegetation consists of low, one-layered stands where *C. aculeata* occurs together with a few obligate halophytes, in particular *Puccinellia distans* aggr., *Spergularia marina*, *S. media*, *Suaeda maritima* aggr., and *Tripolium pannonicum*. In places with lower salinity, the number of species increases due to the occurrence of facultative halophytes and plants with a broad ecological range that can withstand increased substrate salinity. This vegetation

occurs in periodically flooded saline habitats—exposed banks and bottoms of saline lakes, soda pans and periodic pools, saltmarsh depressions, fishpond shores, and periodically inundated depressions. The vegetation is less typical of the saline pastures and field margins. It is confined to areas with a continental or (sub-)Mediterranean climate where the water level drops in summer, exposing the mineral substrate on the bottom and causing salinization of the soil surface. The soil is sandy to clayey-loamy, tending to become strongly polygonal and fissured, with a high content of water-soluble salts and nutrients, alkaline reaction, and high pH (Pätsch et al. 2024). The *Crypsietum aculeatae* vegetation often

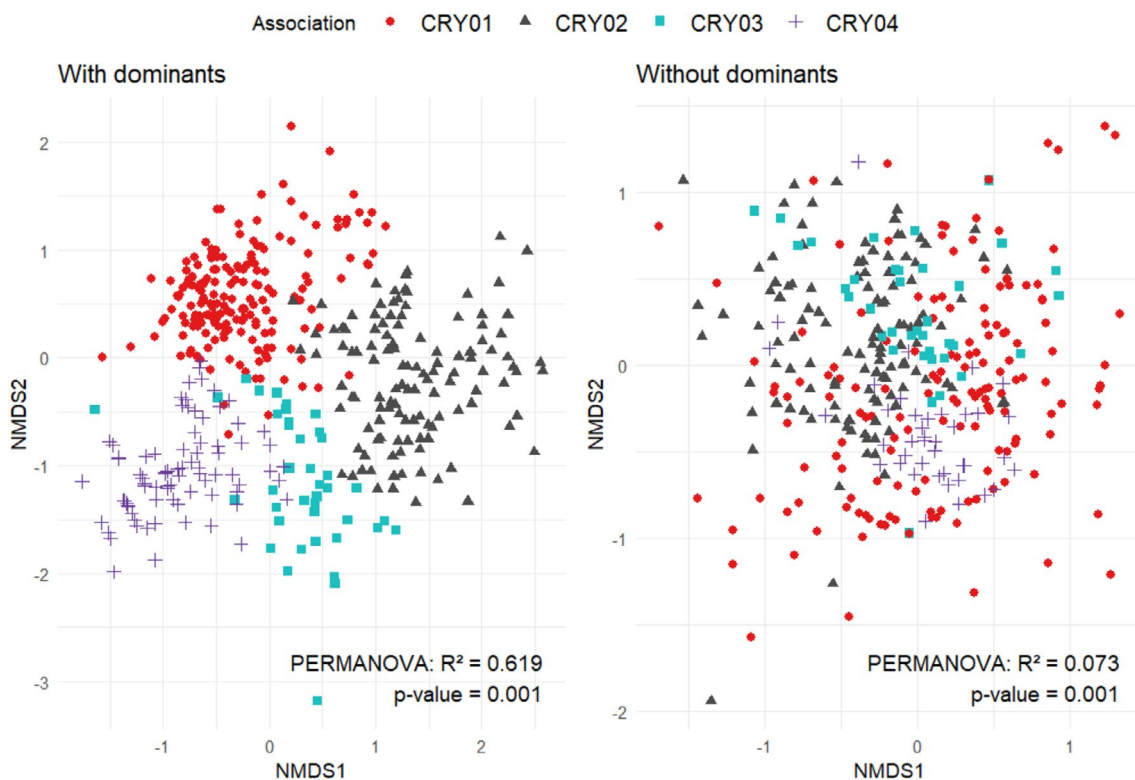


FIGURE 3 | NMDS ordination of vegetation plots classified by the expert system. Each association is indicated by a different symbol and color in the ordination diagrams. Associations are coded as follows: CRY01 = *Crypsietum aculeatae*, CRY02 = *Crypsietum schoenoidis*, CRY03 = *Cyperetum pannonicum*, CRY04 = *Oxybasio chenopodioidis-Crypsietum aculeatae*.

develops in complexes with halophilous grasslands or annual succulent stands and represents the initial stage of succession, which is blocked by substrate exposure for only a few months each year. The decrease in soil salinity contributes to a significant reduction in the number or total disappearance of obligate halophytes, to the gradual transition to the *Isoëto-Nanojuncetea* or *Bidentetea* vegetation, and colonization of the habitat by some reed species (*Bolboschoenus maritimus* aggr. and *Phragmites australis*). This vegetation type is distributed in continental regions of the Mediterranean, Central, and Eastern Europe (Figure 1A). According to our dataset, the vegetation of this association was sampled in Austria, Bulgaria, Croatia, the Czech Republic, France, Greece, Hungary, Italy, North Macedonia, Romania, Serbia, Slovakia, Spain, and Ukraine. According to the literature, vegetation associations with *C. aculeata* as a diagnostic species have also been reported from Portugal (Costa et al. 2012) and Russia (Golub and Mirkin 1986; Yuritsyna 2010).

CRY02. *Crypsietum schoenoidis* Țopa 1939 (Figures 1B and 2C,D).

Original form: “Asociația cu *Crypsis schoenoides* E. Țopa 1938” (Țopa 1939, 51).

Name-giving taxon: *Crypsis schoenoides* (L.) Lam.

Nomenclatural type (lectotypus hoc loco): Țopa (1939): table on page 51, relevé 1, E. Țopa, 1 September 1938, near Bălți city, Moldova, Braun-Blanquet scale with sociability—*Crypsis schoenoides* 3.5, *Plantago tenuiflora* 1.2, *Salicornia herbacea* = *S.*

europaea aggr. 1.1, *Spergularia salina* = *S. marina* 1.1, *Suaeda maritima* = *S. maritima* aggr. (*S. prostrata*) 1.1, *Juncus gerardi* = *J. compressus* aggr. +, *Polygonum aviculare* +, *Puccinellia limosa* = *P. distans* subsp. *limosa* +.

Synonyms: *Heleochoo-Spergularietum salinae* Slavnić 1948 (syntax. syn.); *Heliotropio supini-Crypsietum schoenoidis* Rivas Goday et al. 1956 (Art. 5); *Heleochoo schoenoidis-Fimbristyletum dichotomae* Br.-Bl. et Rivas Goday in Rivas Goday et al. 1956 (Art. 5); *Alismato-Salicornietum* Golub et Mirkin 1986 (syntax. syn.); *Argusio-Phragmitetum* Golub et Mirkin 1986 (syntax. syn.); *Juncus gerardi-Crypsietum schoenoidis* Molero et Romo 1988 (syntax. syn.); *Limonio-Crypsietum* Golub et Saveljeva in Golub 1995 (syntax. syn.); *Gnaphalio uliginosi-Crypsietum schoenoidis* Guitton et Terrisse 2015 (syntax. syn.).

Diagnostic species: *Crypsis schoenoides* (0.84), *Echinochloa crus-galli* (0.35), *Plantago major* (0.26), *Polygonum aviculare* aggr. (0.4), *Rorippa sylvestris* (0.26), *Tripleurospermum maritimum* aggr. (0.25), *Xanthium strumarium* aggr. (0.27).

Constant species: *Atriplex prostrata*, *Bolboschoenus maritimus* aggr., *Crypsis aculeata*, *Crypsis schoenoides*, *Echinochloa crus-galli*, *Plantago major*, *Polygonum aviculare* aggr.

Dominant species: *Crypsis schoenoides*.

This association includes open, low-growing wetland vegetation dominated by *Crypsis schoenoides*. The capacity of the community to occupy areas of lower salinity, in contrast to *Crypsietum aculeatae*, expands the spectrum of associated species. It

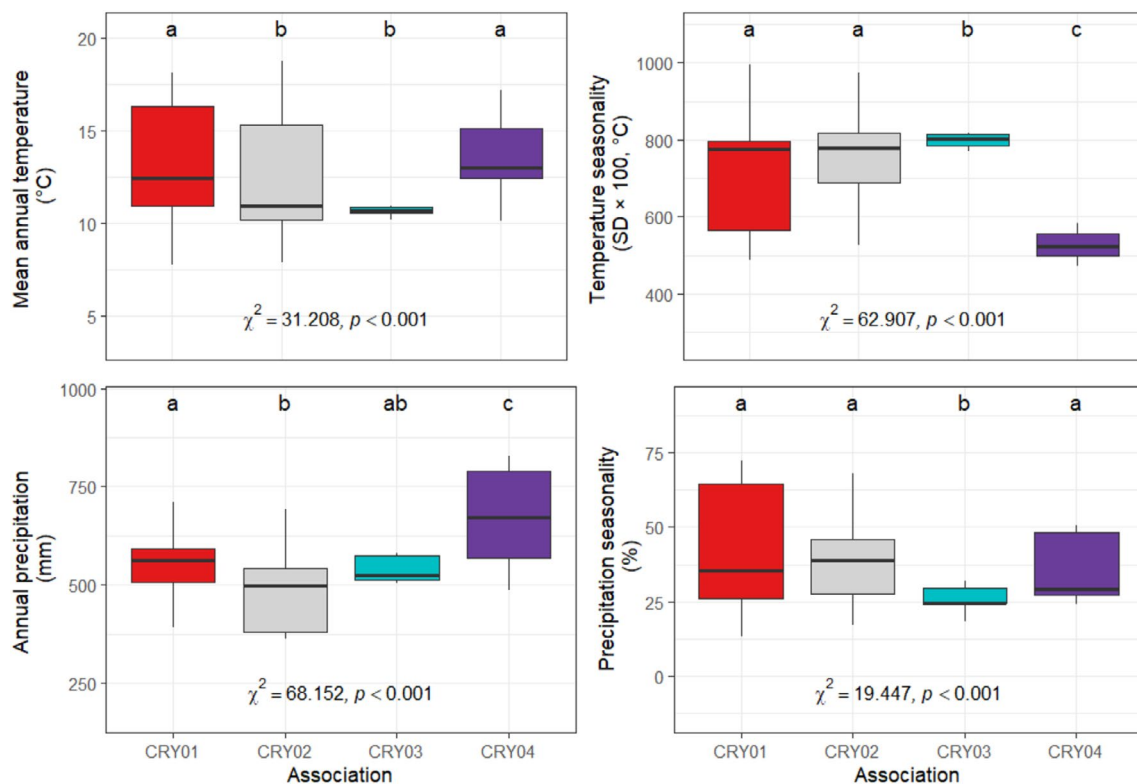


FIGURE 4 | Boxplots of mean annual temperature, temperature seasonality (standard deviation (SD) of the mean monthly temperature in °C multiplied by 100), annual precipitation, and precipitation seasonality (variation in monthly precipitation totals over the course of the year) for the plots assigned to each association. Boxes indicate the interquartile range, bold lines represent the median, and whiskers indicate the range of values. Kruskal–Wallis test statistics (χ^2) and p -values are indicated within each plot. Different letters above boxes indicate significant differences among associations ($p < 0.01$) based on Dunn's post hoc test with Bonferroni correction. Associations are coded as follows: CRY01 = *Crypsietum aculeatae*, CRY02 = *Crypsietum schoenoidis*, CRY03 = *Cyperetum pannonicum*, CRY04 = *Oxybasis chenopodioidis*-*Crypsietum aculeatae*.

contains various accessory plants (according to Dítě et al. 2023) occurring more or less frequently in saline habitats (*Agrostis stolonifera*, *Argentina anserina*, *Atriplex tatarica*, and *Eleocharis palustris*), sedges (*Carex melanostachya* and *C. vulpina*), reeds (*Bolboschoenus maritimus* aggr. and *Phragmites australis*) as well as ruderal herbs and grasses (*Chenopodium album*, *Cirsium arvense*, *Convolvulus arvensis*, *Cynodon dactylon*, *Echinochloa crus-galli*, *Elytrigia repens*, *Lepidium ruderales*, *Plantago major*).

This vegetation occupies regularly exposed bottoms and banks of periodically flooded saline pools and stream beds, as well as secondary habitats, such as ponds, field depressions, dirt roads, field margins, and wet fallows. The soils are mostly heavy, loamy to clayey, and dry out strongly in summer, becoming polygonal. *Crypsietum schoenoidis* is early successional vegetation that subsequently changes to *Puccinellion limosae* stands or, in areas with decreased soil salinity, to *Bidentetea* vegetation as a result of disturbances to the water regime and soil desalination. Occurrences of this vegetation were recorded in the Mediterranean regions of Spain and France, in Austria, the Czech Republic, Greece, Hungary, Italy, Slovakia, Romania, and Ukraine (Figure 1B). One locality is also known from Crete. It was also reported from Russia (Golub and Mirkin 1986) and mentioned in vegetation surveys of Portugal (Costa et al. 2012), Bulgaria (Tzonev et al. 2015), and Serbia (Dajić Stevanović et al. 2016).

CRY03. *Cyperetum pannonicum* Wendelberger 1943 (Figures 1C and 2E,F).

Original form “*Cyperetum pannonicum* (Soó 1933) Wendelberger 1943” (Wendelberger 1943, 126).

Name-giving taxon: *Cyperus pannonicus* Jacq.

Nomenclatural type (neotypus hoc loco): Wendelberger (1950): Table 2, relevé 1, G. Wendelberger, 18.09.1939, Obere Halbjochlacke, Austria, Braun-Blanquet scale with sociability—*Cyperus pannonicus* 5.5, *Aster pannonicus* = *Tripolium pannonicum* 1.2, *Crypsis aculeata* 1.1, *Bolboschoenus maritimus* +.

Synonym: *Acorelletum pannonicum* Soó 1947 (Art. 31).

Diagnostic species: *Cyperus flavescens* (0.36), *Cyperus pannonicus* (0.97), *Juncus articulatus* (0.26), *Plantago maritima* (0.34), *Puccinellia distans* aggr. (0.39), *Spergularia marina* (0.42), *Taraxacum besarabicum* (0.32), *Tripolium pannonicum* (0.41).

Constant species: *Agrostis stolonifera*, *Atriplex prostrata*, *Bolboschoenus maritimus* aggr., *Crypsis aculeata*, *Cyperus pannonicus*, *Juncus compressus* aggr., *Oxybasis glauca*, *Puccinellia*

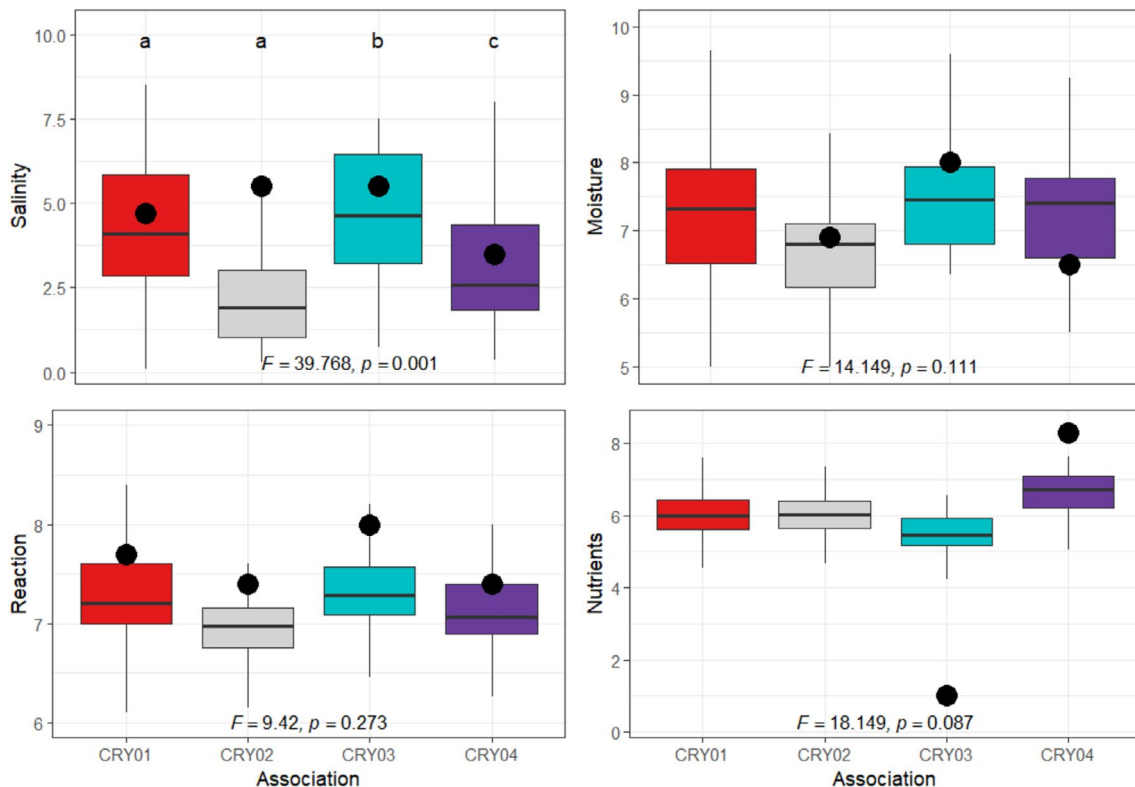


FIGURE 5 | Ellenberg-type indicator values for the salinity, moisture, reaction and nutrients for each association of the *Crypsietea aculeatae* class. Boxes indicate the interquartile range, bold lines represent the median, whiskers indicate the range of values, and black dots show indicator values for the dominant species of each association. *F*-values and associated significance levels from the modified permutation test are shown for each indicator. Different letters above the boxes indicate significant differences among associations ($p < 0.01$) based on Dunn's post hoc test with Bonferroni correction. Letters are shown only for the indicator with statistically significant differences according to the global test. Associations are coded as follows: CRY01 = *Crypsietum aculeatae*, CRY02 = *Crypsietum schoenoidis*, CRY03 = *Cyperetum pannonicum*, CRY04 = *Oxybasio chenopodioidis-Crypsietum aculeatae*.

distans aggr., *Spergularia marina*, *Suaeda maritima* aggr., *Tripolium pannonicum*.

Dominant species: *Cyperus pannonicus*.

This late-summer vegetation consists of stands dominated by *Cyperus pannonicus*. The herb layer includes species that are frequent in the vegetation of the class (*Crypsis aculeata*, *Spergularia marina*, *Suaeda maritima* aggr., *Tripolium pannonicum*) and other obligate halophytes (*Camphorosma annua*, *Carex extensa*, *Glaux maritima*, *Lepidium cartilagineum*, *Puccinellia distans* aggr.). The frequent occurrences of annual wetland species such as *Crypsis alopecuroides*, *Cyperus flavescens*, *C. fuscus*, *Pulicaria vulgaris*, and *Veronica anagalloides* are noted in the areas with lower salinity. As a result of disturbances of the flood regime, habitats are often colonized by competitively strong reeds such as *Phragmites australis* and *Bolboschoenus maritimus* aggr. The vegetation mainly occurs on periodically flooded shores of soda pans, brackish lakes, and in depressions on saline sandy, sandy-loamy, and gravel soils with an alkaline reaction.

The association is specific to the Ponto-Pannonian region and, according to our dataset, has been documented in Austria, Hungary, Romania, Serbia, Slovakia, and Ukraine (Figure 1C).

CRY04. *Oxybasio chenopodioidis-Crypsietum aculeatae* Paradis et Lorenzoni 1994 mut. Iemelianova et al. 2025 nom. mut. nov. (Figures 1D and 2G,H).

Original form “*Chenopodio chenopodioidis-Crypsidetum aculeatae*” (Paradis et Lorenzoni 1994, 25).

Name-giving taxa (original names): *Chenopodium chenopodioides* (L.) Aellen, *Crypsis aculeata* (L.) Ait.

Name-giving taxa (corrected names): *Oxybasis chenopodioides* (L.) S. Fuentes & al., *Crypsis aculeata* (L.) Ait.

Nomenclatural type (holotypus): (Paradis 1992) table 3, relevé Ta1, G. Paradis, Tanchiccia, Corsica, France, Braun-Blanquet scale—*Chenopodium chenopodioides* = *Oxybasis chenopodioides* 3, *Crypsis aculeata* 3, *Atriplex prostrata* 2, *Cotula coronopifolia* 1, *Scirpus maritimus compactus* = *Bolboschoenus maritimus* aggr. 1.

Synonyms: *Atriplici hastatae-Chenopodietum chenopodioides* Bouzillé, De Foucault et Lahondère 1984 (syntax. syn.); *Chenopodietum chenopodioidis* Paradis 1992 (syntax. syn.); *Salsolo sodae-Chenopodietum chenopodioidis* Martínez-Parras et Peinado 1993 (Art. 2b, syntax. syn.); *Chenopodio chenopodioidis-Crypsietum schoenoidis* Paradis et Lorenzoni 1994 (syntax. syn.); *Heleochoo schoenoidis-Chenopodietum botryos* Brullo et Sciandrello 2006 (syntax. syn.).

Diagnostic species: *Atriplex prostrata* (0.46), *Bolboschoenus maritimus* aggr. (0.23), *Oxybasis chenopodioides* (0.88).

Constant species: *Atriplex prostrata*, *Bolboschoenus maritimus* aggr., *Crypsis aculeata*, *Oxybasis chenopodioides*, *Oxybasis glauca*.

Dominant species: *Atriplex prostrata*, *Oxybasis chenopodioides*.

This association represents a halo-nitrophilous community that develops on the bottoms of inland salt lakes, in littoral zones of the coastal lakes, and field depressions subject to summer–autumn drying. It occurs on humid clayey-loamy soils with high concentrations of Na, Mg, and organic C (Dítě et al. 2017). Physiognomically, this vegetation is well differentiated by the dominance of the annual herb *Oxybasis chenopodioides*, which is typically accompanied by *Crypsis aculeata* and *Atriplex prostrata*. The community is composed of obligate halophytes (e.g., *Juncus maritimus*, *Puccinellia distans* aggr., *Salicornia europaea* aggr., and *Salsola soda*) with a prominent presence of *Bolboschoenus maritimus* aggr. and *Crypsis schoenoides*. Species with ruderal tendency (e.g., *Amaranthus retroflexus*, *Cirsium arvense*, *Cynodon dactylon*, *Plantago major*, and *Xanthium strumarium* aggr.) occur at sites affected by grazing. Occurrences of this vegetation were recorded from France, Hungary, Italy (Sicily), Serbia, Slovakia, and Spain (Figure 1D).

3.4 | Environmental Gradients

Compositional differentiation of the *Crypsietea aculeatae* vegetation is shown in NMDS ordination diagrams (Figure 3). While the vegetation was classified on the basis of species cover, the individual associations are well separated and do not overlap in ordination space. After the removal of the dominant species, the associations show substantial overlap in the ordination plot. However, differences between associations persist, as confirmed by PERMANOVA results, which, despite a notable decline in explained variance, remain statistically significant.

The *Crypsietea aculeatae* vegetation, except for *Cyperetum pannonicum* stands, which are restricted to the Ponto-Pannonian region, occurs across a broad range of mean annual temperatures, temperature seasonality, and precipitation seasonality (Figure 4). Statistical comparison using the Kruskal–Wallis test revealed significant differences among vegetation associations for all four significant bioclimatic parameters. The vegetation of *Crypsietum aculeatae* is affiliated with both oceanic and continental areas, while *Oxybasis chenopodioides*–*Crypsietum aculeatae* tends to occur in regions with relatively high annual precipitation, especially in western parts of its distribution range. The *Crypsietum schoenoides* stands were found to be more drought-tolerant. The main preferences regarding soil properties were reflected in the mean EIVs (Figure 5). Statistical comparisons using the modified permutation test showed significant differences among vegetation associations for salinity, while differences in moisture, reaction, and nutrients were not significant. The vegetation of the *Crypsietea aculeatae* class tends to occupy wet soils with basic conditions. Communities grow mostly within moderately

nutrient-rich sites. The slightly lower requirement for nutrients is characteristic of the *Cyperetum pannonicum* stands. The vegetation of the *Crypsietea aculeatae* is distributed across habitats with moderate and high salt concentrations, but indicator values show that *Crypsietum schoenoides* can occur on less saline soils than the other associations of the class.

3.5 | Geographical Distribution

The vegetation of the *Crypsietea aculeatae* class is distributed in different parts of Europe except for Northern Europe, where it is absent, and Northwestern Europe, where it is very rare. Only *Cyperetum pannonicum* stands have a clear correlation with one biogeographical region (Ponto-Pannonian), while the other associations occur in several biogeographical regions. Only a few species are confined to a single biogeographical region, typically with low constancy (Figures 6A–8A). In contrast, most diagnostic and frequent species occur across several regions, resulting in a high degree of floristic overlap among vegetation stands belonging to the same association throughout its distribution range (Figures 6B–8B). The physiognomic structure of the vegetation associations is quite similar as well: All the associations are represented by species-poor stands composed of annual halophytic species that can survive in extremely changeable conditions of soil moisture and excessive soil salinity, accompanied by some perennial herbs of broad ecological tolerance. This consistency suggests that despite regional environmental differences, the core floristic composition of *Crypsietea aculeatae* associations remains largely stable. Undoubtedly, the abundance of some Atlantic and Mediterranean species (*Corrigiola litoralis*, *Heliotropium supinum*, *Lythrum flexuosum*, *L. tribracteatum*, *Pulicaria arabica* subsp. *hispanica*, and *Polypogon maritimus*) is decreasing with increasing continentality, while the constancy of some continental floristic elements (*Alisma gramineum*, *Atriplex intracontinentalis*, *Polygonum salsugineum*, and *Suaeda acuminata*) is increasing.

In a biogeographical context, the *Crypsietum schoenoides* has the highest floristic diversity among all associations. In Western Europe, this vegetation is enriched with species typical of disturbed habitats, particularly those characteristic of the classes *Saginetum maritimae* and *Digitario sanguinalis*–*Eragrostietum minoris*. In Central and Southern Europe, where it occurs in patches within complexes of halophilous or subhalophilous grasslands, the most frequent species are from the *Festuco-Puccinellietea* and *Molinio-Arrhenatheretea* classes. Further eastward, the presence of typical halophytic species becomes increasingly pronounced.

4 | Discussion

4.1 | Geographical Distribution of the *Crypsietea aculeatae* Class in Europe

Our study shows that within Europe, the class *Crypsietea aculeatae* is distributed predominantly across the Mediterranean, Ponto-Pannonian, and Continental biogeographical regions. It occurs in areas with salt-affected soils in combination with dry climatic conditions. The western distribution limit reaches

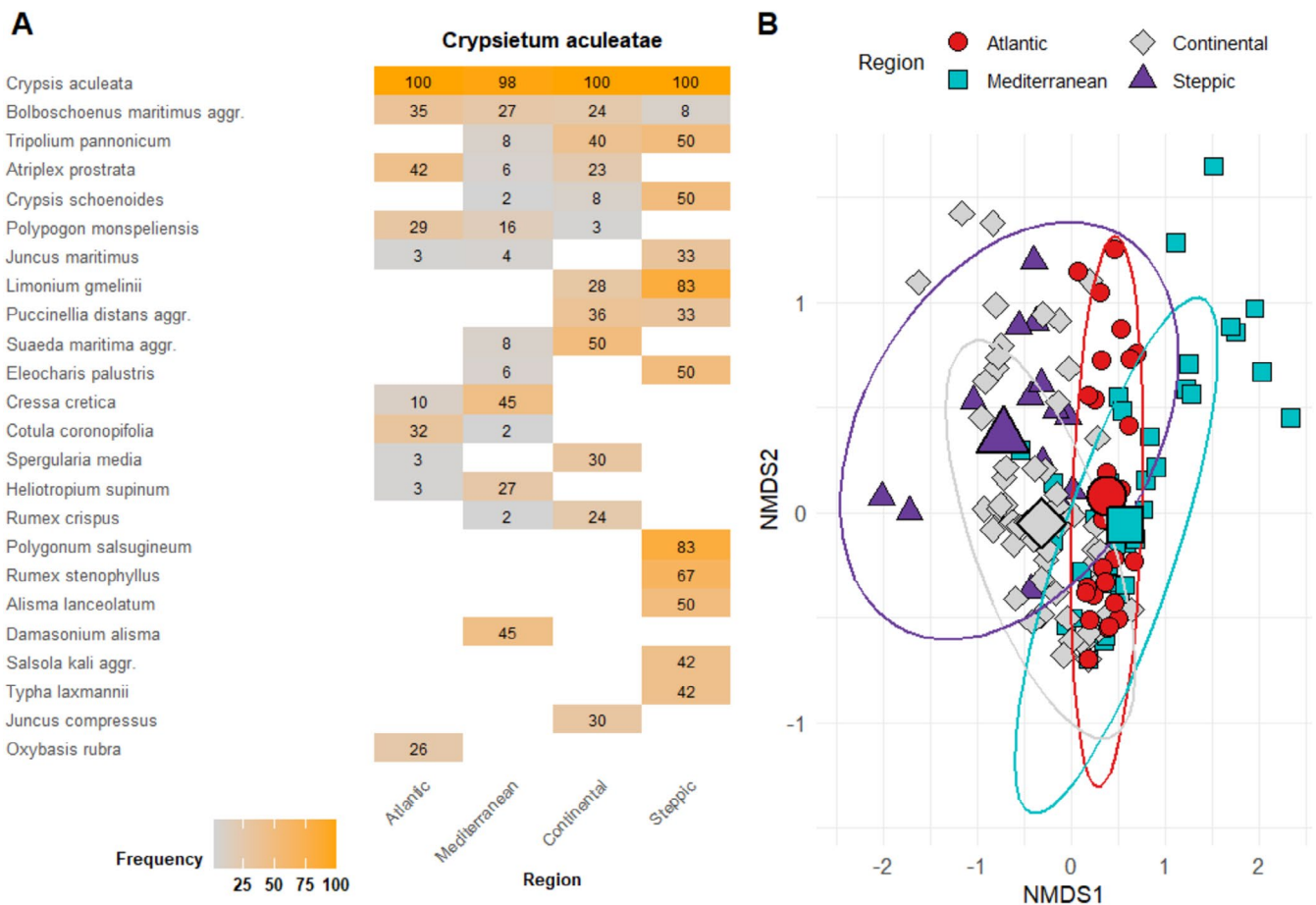


FIGURE 6 | Occurrences of the frequent species (A) and NMDS ordination of the plots (B) assigned to the *Crypsietum aculeatae* association in different biogeographical regions of Europe. Species with a frequency > 20% in at least one region are displayed. Colored symbols on the NMDS graph indicate plot affiliation to specific regions; large symbols represent group centroids. Colored ellipses represent 95% confidence intervals of the plot distribution within each region.

territories with long dry summers in the Iberian Peninsula. Costa et al. (2012) also reported the presence of the *Crypsietea aculeatae* vegetation in Portugal. However, no plot records from that territory were available, and additional research is needed to clarify the western distribution limit of the class. Toward the east, *Crypsietea aculeatae* extends to Ukraine and semiarid regions of Russia, specifically along the Lower Volga and western Caspian Sea coast (Golub 1995; Yuritsyna 2010). The southern range border of this vegetation in Europe reaches Malta, Sicily, and Crete. To the north, the geographical distribution of the *Crypsietea aculeatae* reaches its limits in eastern Austria, southern Moravia (Czech Republic), and southern Slovakia. The potential spread of this vegetation further north into the continental regions of Poland (Kujawy) and Germany (Thuringia, Saxony-Anhalt, and Brandenburg), where inland saline habitats are present, is not supported by recent phytosociological research (Piernik 2012; Dítě et al. 2022).

The biogeographical differentiation of the *Crypsietea aculeatae* communities depends mainly on climatic parameters that determine the duration of the flooding period, the intensity of water evaporation in the upper soil layers, and the increase in salinity with increasing climate continentality. Both *Crypsietum aculeatae* and *Cyperetum pannonicum* are more frequently associated with regions exhibiting pronounced continentality, whereas *Crypsietum schoenoides* and *Oxybasis*

chenopodioides-Crypsietum aculeatae are primarily distributed across Central and Mediterranean Europe. Eastward, climatic gradients become more pronounced: the annual temperature range increases, precipitation declines, and evaporation intensifies. These shifts result in markedly higher salt concentrations in the upper soil layers, favoring the development of *Crypsietum aculeatae* and *Cyperetum pannonicum*, both of which show a strong affinity for saline environments. Within these species-poor communities, the proportion of continental floristic elements—particularly obligate halophytes adapted to arid conditions—rises substantially in Eastern Europe. In contrast, *Crypsietum schoenoides* and *Oxybasis chenopodioides-Crypsietum aculeatae* are less dependent on high soil salinity and occur predominantly in temperate and Mediterranean climatic regions. Analyzing the current distribution of the class *Crypsietea aculeatae* in Europe, it is worth taking into account that some phytosociological data we analyzed are historical and may refer to vanished occurrences. Considering the strong correlation between *Crypsis aculeata* occurrences and soil salinity on the one hand and habitat desalination caused by draining and other human interventions on the other hand, it is likely that the distribution of the *Crypsietum aculeatae* today is more restricted than that of the *Crypsietum schoenoides*, which can grow in conditions of lower salinity. This is confirmed by recent studies that have documented a decrease in the number of localities with vegetation

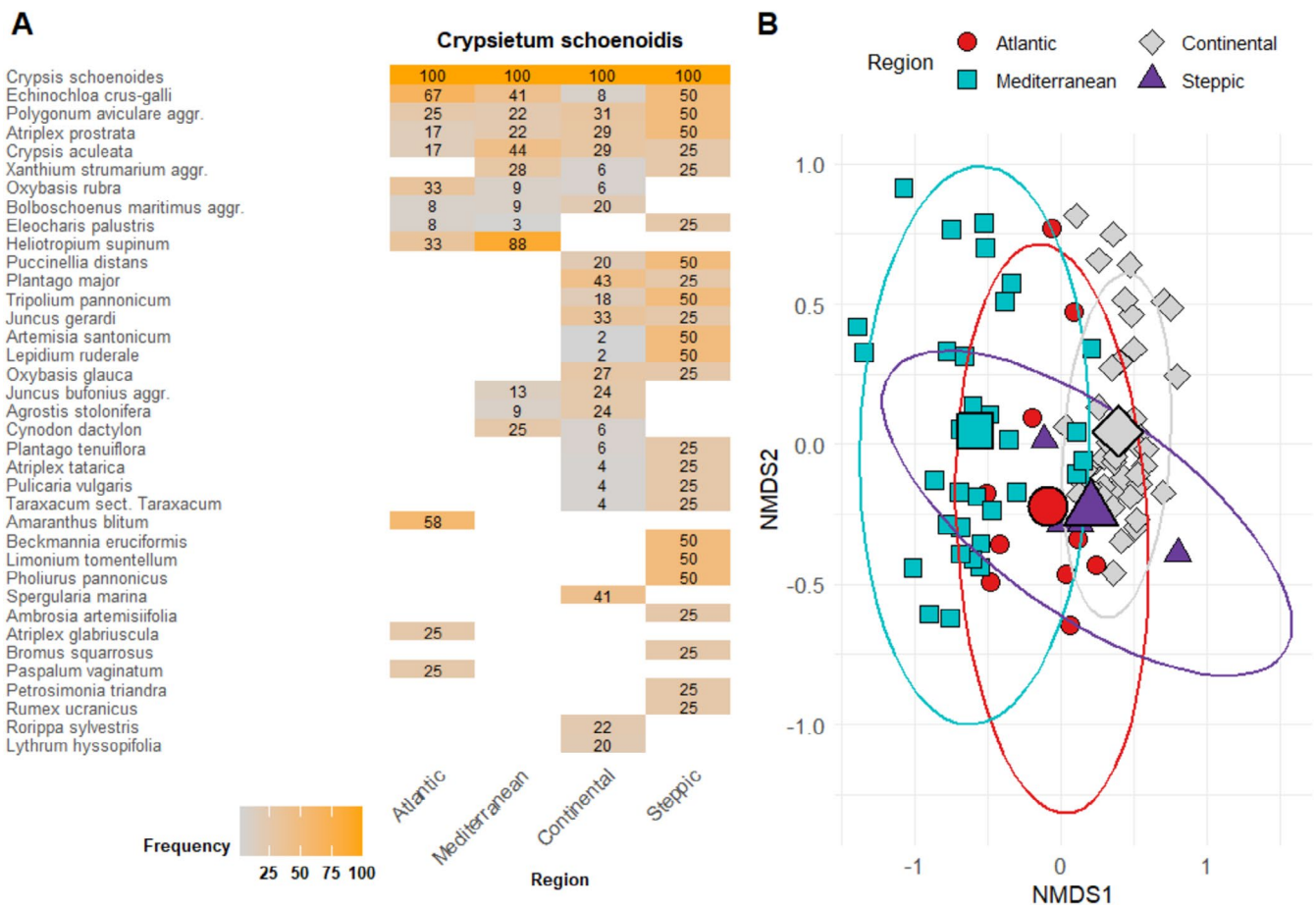


FIGURE 7 | Occurrences of the frequent species (A) and NMDS ordination of the plots (B) assigned to the *Crypsietum schoenoidis* association in different biogeographical regions of Europe. Species with a frequency >20% in at least one region are displayed. Colored symbols on the NMDS graph indicate plot affiliation to specific regions; large symbols represent group centroids. Colored ellipses represent 95% confidence intervals of the plot distribution within each region.

dominated by *C. aculeata* or their complete disappearance (Danihelka et al. 2022). There is also the probability of incorrect records of *Crypsietum aculeatae* due to possible mistakes in determining young individuals of *Crypsis schoenoides* as *C. aculeata*, as noticed by Eliáš Jun (2015).

Analyzing the density of phytosociological records in different regions, we can conclude that the *Crypsietea aculeatae* vegetation has been sampled in most parts of its distribution range in Europe. This vegetation has been sampled quite well in the Pannonian region and the Iberian Peninsula. However, there is still a lack of data from some countries, and further sampling efforts are needed in underrepresented areas to precisely map the geographical range of the *Crypsietea aculeatae* class.

4.2 | Phytosociological Framework and Amendment Proposals for the EuroVegChecklist

We provide the first continent-wide classification of the *Crypsietea aculeatae* class in Europe, developed at the association level. This classification is derived from a large vegetation plot database and applies a consistent formal protocol that prioritizes species dominance while also accounting for

other diagnostic taxa. Previous national and regional studies frequently described multiple associations dominated by the same species; for example, stands of *Crypsis aculeata* were often separated based on a single codominant or regionally frequent species (Korzhenevskiy and Klyukin 1990; Paradis 1992; Paradis and Lorenzoni 1994; Guitton and Terrisse 2015; Dubyna et al. 2020). However, the ecological conditions of these communities—particularly soil moisture and salinity—were generally similar across regions, supporting their consolidation into a single association. Our pan-European analysis further showed that, because only a few diagnostic species are well-defined at the continental scale, reliable classification is possible only at the level of one association per dominant species. Geographic variation in species composition does occur among geographically distant plots but is better addressed in regional studies and may be expressed at the subassociation or variant level.

In addition to defining associations, we propose critical adjustments at higher hierarchical levels of the classification, especially regarding the interpretation and delimitation of alliances. Thus, according to EuroVegChecklist (Mucina et al. 2016), the pioneer ephemeral dwarf-grass vegetation in periodically flooded saline habitats is represented by one phytosociological order (*Crypsietalia aculeatae*) and three alliances, which are mainly divided by the biogeographical principle. The alliance

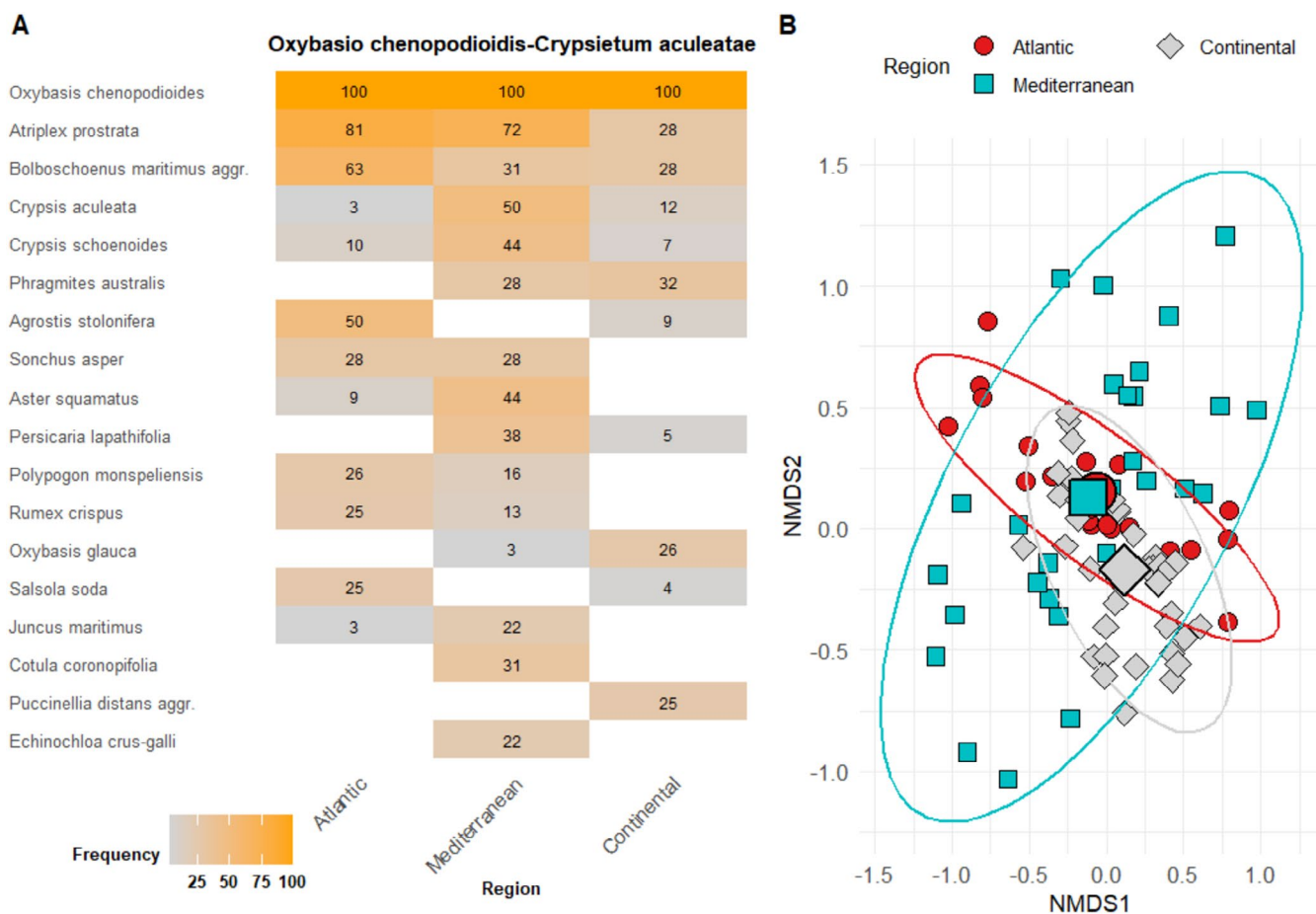


FIGURE 8 | Occurrences of the frequent species (A) and NMDS ordination of the plots (B) assigned to the *Oxybasis chenopodioidis-Crypsietum aculeatae* association in different biogeographical regions of Europe. Species with a frequency >20% in at least one region are displayed. Colored symbols on the NMDS graph indicate plot affiliation to specific regions; large symbols represent group centroids. Colored ellipses represent 95% confidence intervals of the plot distribution within each region.

Cyero-Spergularion marinae unites pioneer ephemeral dwarf-grass vegetation in periodically flooded saline habitats of subcontinental Central and Eastern Europe; *Heleochloion schoenoides* represents analogous vegetation in the (sub-) Mediterranean regions of Southern Europe and Northern Africa. In continental Eastern Europe, pioneer ephemeral vegetation dominated by halophytes has been classified as *Lepidion latifolii*.

Based on our study, we propose to reject the alliance *Heleochloion schoenoides*, both its name due to nomenclature reasons and its concept due to the lack of diagnostic species and the lack of biogeographical uniqueness. This alliance was described from southern France by Braun-Blanquet (Braun-Blanquet et al. 1952) as part of ruderal vegetation, specifically within the class *Chenopodietae* and subordinated to the order *Paspalo-Heleochloetalia*. However, the name *Heleochloion* Br.-Bl. in Braun-Blanquet et al. 1952 was published invalidly since it was proposed as a provisional name (see Art. 3b of ICPN). It was not validated by Rivas Goday et al. (1956) as cited in many syntaxonomic studies. Rivas Goday considered the vegetation described under the name *Heleochloion* to be part of the ruderal vegetation, specifically within the class *Ruderali-Secalietea* Br.-Bl. et al. 1936—a broad class that included all anthropogenic vegetation known at the time. Among the subordinate units of the mentioned class, the author listed the *Paspalo-Heleochloetalia*,

noting that Braun-Blanquet had proposed two alliances within it: *Paspalo-Agrostidion* and *Heleochloion*. However, due to the weak floristic differentiation of plant communities within these alliances, Rivas Goday refrained from dividing the order into alliances and instead directly subordinated associations to the *Paspalo-Heleochloetalia*. Therefore, the name *Heleochloion schoenoides* Br.-Bl. ex Rivas Goday 1956 cannot be considered validly published, and all subsequent citations in later syntaxonomic studies, including the EuroVegChecklist (Mucina et al. 2016), should be regarded as incorrect. Instead, the valid name that should be accepted is *Heleochloion schoenoides* Br.-Bl. ex Rivas Goday 1970. In any case, it is important to emphasize that the plant communities originally described by Braun-Blanquet (Braun-Blanquet et al. 1952) and later validly published by Rivas Goday (1970) under the name *Heleochloion schoenoides* differ significantly from the vegetation currently classified within the class *Crypsietea aculeatae*. Among the characteristic species of the vegetation previously referred to as *Heleochloion schoenoides*, species from *Isoëto-Nanojuncetea* were the most prominent (Braun-Blanquet et al. 1952; Rivas Goday et al. 1956). Among the diagnostic species of the *Crypsietea aculeatae* class, only *Crypsis schoenoides* showed high cover and abundance, while others (specifically *Crypsis aculeata* and *Polygomon monspeliensis*) were only sporadically recorded. This may explain why the syntaxonomic position of this alliance has often

changed over time. Different authors classified the *Heleochloion schoenoidis* within different classes of halophytic vegetation (Sanda et al. 2008; Borhidi et al. 2012) or *Isoëto-Nanojuncetea* (Rivas-Martínez et al. 1999; De Foucault 2013; Biondi et al. 2014; Guitton and Terrisse 2015). In some recent syntaxonomic surveys (Rivas-Martínez et al. 2001; Costa et al. 2012; Brullo et al. 2022), the authors considered *Heleochloion schoenoidis* a syntaxonomic synonym of the *Verbenion supinae* alliance belonging to *Isoëto-Nanojuncetea*. Considering the original diagnosis of *Heleochloion schoenoidis*, this interpretation is completely reasonable. The vegetation described and classified by Braun-Blanquet et al. (1952) within this alliance corresponds entirely to the vegetation currently classified as *Verbenion supinae*. Among the species that make these two alliances highly similar, the most notable ones are *Centaureum pulchellum*, *Veronica anagalloides*, as well as other typical species of *Isoëto-Nanojuncetea*. Another reason for such discrepancies in interpreting the syntaxonomic position of the *Heleochloion schoenoidis* lies in the high heterogeneity of its species composition. Due to not-so-harsh environmental conditions in terms of soil salinity, *Crypsis schoenoides* stands are rich in widespread, (sub)halophilous wetland and grassland species associated with different habitat types. The ability to adapt to anthropogenic disturbances (Eliáš Jun 2015), as a result of land reclamation and grazing, and co-occurrence with other halophytic vegetation also affect the species composition of *C. schoenoides* stands. Our study shows that there are no reasons to consider this vegetation as a separate phytosociological alliance in terms of floristic composition and biogeographical distinction. It is obvious that the *C. schoenoides* stands include some floristic elements specific to particular biogeographical regions, but they are not directly related to the class *Crypsietea aculeatae* as a specific phytosociological unit. This is rather an effect of the complex influence of climatic factors, the surrounding zonal vegetation types, and succession relationships rather than the biogeographical specificity of the studied vegetation.

We also suggest that there are no reasons to differentiate the alliance *Lepidion latifolii* for continental Eastern Europe. It was first mentioned by Golub and Mirkin (1986), but was not supported with sufficient diagnosis. Dubyna et al. (1994) validated this alliance by designating the association *Cynancho acuti-Lepidietum latifolii* as its nomenclatural type. The name-forming and often dominant species *Lepidion latifolium* is a perennial plant, which occurs in different vegetation types, ranging from soft sea-cliffs (Géhu and Géhu 1969) to grasslands (association *Poo pratensis-Lepidietum latifolii* Lysenko et al. 2003) (Lysenko et al. 2003) and anthropogenic habitats (association *Lepidietum latifolii* Diaconescu 1978) (Diaconescu 1978; Sanda et al. 2008). In the EuroVegChecklist (Mucina et al. 2016), the alliance *Lepidion latifolii* was accepted as a part of the *Crypsietea aculeatae* class under the name *Lepidion latifolii* Golub et Mirkin in Golub 1995 with incorrect author citation. Golub and Mirkin (1986) described two associations within the *Lepidion latifolii* alliance from the Lower Volga valley in Russia: *Argusio-Phragmitetum* and *Alismato-Salicornietum*. Since our study did not cover the territory of Russia, vegetation plots from this region were not included in our analysis. However, an examination of these associations in terms of species composition, as published in the scientific literature, strongly suggests that *Alismato-Salicornietum* and *Argusio-Phragmitetum* can be

considered synonyms of *Crypsietum schoenoidis*. Other vegetation types classified by some authors (Golub and Mirkin 1986; Golub and Yuritsyna 2001; Yuritsyna 2010; Dubyna et al. 2020) in the *Lepidion latifolii* alliance should be excluded from the *Crypsietea aculeatae*, in particular, the associations *Bolboschoeno maritimi-Salicornietum*, *Salicornio-Chenopodietum rubri*, and *Spergulario salinae-Eleocharitetum parvulae* proposed by Golub and Yuritsyna (2001), as well as *Cynancho acuti-Lepidietum latifolii* suggested by Dubyna et al. (1994). All of these associations are dominated by perennials, thus not fitting the definition of the class *Crypsietea aculeatae*, which is characterized by annual species.

In this study, within the class *Crypsietea aculeatae*, we consider vegetation stands dominated by *Oxybasis chenopodioides* that are floristically distinct from other *O. chenopodioides* communities by the consistent presence of annual graminoids. Vegetation dominated by *O. chenopodioides* has typically been classified within the *Bidentetea* (Martínez Parras et al. 1988; Rivas-Martínez et al. 2001; Šumberová 2007), disregarding the clearly halophytic nature of these communities (Bouzillé et al. 1984; Paradis and Lorenzoni 1994). Slavnić (1948) was the first to classify *O. chenopodioides* stands as a separate association with the name *Chenopodio chenopodioidis-Atriplicetum prostratae*. The floristic composition of the association he described was quite heterogeneous, as it included nitrophilous annual herbs and species from saline habitats with both groups being equally represented. This could be the reason why later authors have tended to consider all vegetation dominated by *O. chenopodioides* within the association *Chenopodio chenopodioidis-Atriplicetum prostratae*. However, a comprehensive analysis of previously described syntaxa, together with more recent studies, suggests that stands dominated by *O. chenopodioides* should be classified within different vegetation associations, depending on the specific habitat conditions of individual sites. Due to its ecological range, *O. chenopodioides* can colonize different habitats along the salinity gradient, ranging from solonchaks and moderately saline areas to secondary ruderalized habitats. The vegetation that develops in anthropogenically disturbed (secondary) habitats, where soil desalination has occurred, should be classified within the association *Chenopodio chenopodioidis-Atriplicetum prostratae* Slavnić 1948 corr. Gutermann et Mucina in Mucina et al. 1993. A distinctive feature of this vegetation is the presence of nitrophilous species and weeds. Vegetation that develops under conditions of high substrate salinity should be assigned to the class *Thero-Salicornietea*, specifically to the association *Chenopodietum chenopodioidis* proposed by Dítě et al. (2017). This vegetation is characterized by very low species richness, a high (>90%) cover of *O. chenopodioides*, the frequent absence of *Atriplex prostrata*, and a significant contribution of annual succulent halophytes. However, the name *Chenopodietum chenopodioides* Dítě et al. 2017 requires correction, as it is a later homonym of *Chenopodietum chenopodioidis* Paradis 1992, and therefore, according to Art. 31 of the ICPN (Theurillat et al. 2021), it is illegitimate. A third vegetation type dominated by *O. chenopodioides* develops in moderately saline habitats and is distinguished by the presence of annual graminoids and a significant proportion of facultative halophytes. We consider the latter type to be part of the class *Crypsietea aculeatae* and propose that it should be included within this class as the association *Oxybasio chenopodioidis-Crypsietum aculeatae*.

However, there is a line of argumentation that supports an alternative perspective on the syntaxonomic placement of all *O. chenopodioides* communities, specifically favoring their classification within the *Bidentetea* class. This viewpoint is supported by several key considerations: (i) the frequent co-occurrence of *O. chenopodioides* with typical species of the *Chenopodion rubri* alliance; (ii) the ecological overlap between *O. chenopodioides* and species of the *Chenopodion rubri* alliance, as both commonly occur in nitrogen-enriched, subhalophytic environments; (iii) a distinct physiognomy, with *O. chenopodioides* representing a chenopod life-form, in contrast to the annual graminoids that dominate *Crypsietea aculeatae* vegetation. Taken together, these factors provide grounds for a broader syntaxonomic interpretation, suggesting that all *O. chenopodioides* stands could be treated as a single association within the *Bidentetea* class, with ecological and floristic variation reflected at the subassociation level. Although this interpretation is well-founded, we argue that the consistently prominent presence of annual graminoids in certain *O. chenopodioides* stands, combined with their specific floristic composition, and supports their placement within *Crypsietea aculeatae*. These communities occupy a distinct ecological niche along the salinity gradient, setting them apart from the more ruderal or nitrophilous vegetation typical of *Bidentetea*. Nonetheless, we recognize the complexity of this issue and the need to address these contrasting perspectives within the broader discussion on the classification of vegetation across periodically flooded habitats.

Some authors have also considered the vegetation formed by *Crypsis alopecuroides* to be a part of the *Crypsietea aculeatae* class. This vegetation occupies periodically exposed bottoms and banks of water reservoirs and watercourses on occasionally flooded, alkaline, and clayey, sometimes, salty soils (Dítě, Eliáš, and Melečková 2014). It has been reported from Hungary (Borhidi et al. 2012), Romania (Sanda et al. 2008), and Bulgaria (Tzonev and Gussev 2021). Recent studies of *C. alopecuroides* plant communities in the Pannonian Basin and adjacent regions (Dítě, Eliáš, and Melečková 2014; Eliáš et al. 2021) suggest that these stands do not represent halophytic vegetation. Due to its broad ecological amplitude, *C. alopecuroides* is frequently found on both nonsaline and slightly saline soils. Literature data (Dítě, Eliáš, and Melečková 2014) and vegetation plots stored in the databases accessible to us indicate that stands dominated by *C. alopecuroides* typically include species such as *Cyperus michelianus*, *Gnaphalium uliginosum*, *Juncus bufonius* aggr., *Lythrum hyssopifolia*, and *Pulicaria vulgaris*, and are most likely affiliated with the *Isoëto-Nanojuncetea* class, particularly the *Verbenion supinae* alliance. However, further detailed studies are needed to draw definitive conclusions regarding the placement of *C. alopecuroides* vegetation, particularly within the *Crypsietea aculeatae* class.

It is also worthwhile to discuss the placement of continental (Pannonian) *Salicornia*- and *Suaeda*-dominated communities in the alliance *Cypero-Spergularion marinae*, which is suggested in some vegetation surveys (Mucina 1993). The justification for this decision was primarily rooted in the consistently high floristic similarity among all types of annual halophytic vegetation occurring in continental regions, in comparison with analogous vegetation across coastal areas. According to this approach, the

differentiation of associations within alliances and other higher rank syntaxa reflects ecological variability driven by soil moisture, salinity, and the degree of habitat disturbance. However, such a classification is largely topological, as it joins communities that differ significantly in physiognomic, ecological, and floristic characteristics within a single high-rank syntaxonomic unit. While the physiognomic differences between the annual halophytic communities are evident, their ecological and floristic differences have been demonstrated by recent studies employing numerical methods (Dítě et al. 2017).

5 | Conclusions

We present the first pan-European synthesis of the *Crypsietea aculeatae* class, based on a comprehensive analysis of extensive vegetation plot data combined with a critical revision of syntaxonomical concepts. Our results demonstrate that the current subdivision into three alliances, as presented in the EuroVegChecklist (Mucina et al. 2016), lacks floristic and ecological support. We therefore propose a revised syntaxonomic framework that unites all European vegetation of this class within a single alliance, *Cypero-Spergularion marinae*, comprising four well-delimited associations: *Crypsietum aculeatae*, *Crypsietum schoenoidis*, *Cyperetum pannonicum*, and *Oxybasio chenopodioidis-Crypsietum aculeatae*. This framework highlights the key role of climatic and edaphic gradients, rather than biogeographical boundaries, in shaping these communities. We developed formal definitions for all vegetation units within *Crypsietea aculeatae*, summarized in an expert system that ensures reproducible classification and provides a robust baseline for future vegetation surveys, long-term monitoring, and conservation strategies targeting inland saline habitats.

Author Contributions

S.I. and M.C. conceived the idea; S.I. prepared the dataset, expert system, performed the analyses, and prepared the classification under the supervision of M.C.; S.I. led the writing; M.C., D.D., Z.D., W.W., E.B., and A.P.-H. participated in the manuscript improvements; all authors reviewed the results and critically revised the manuscript.

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Conflicts of Interest

Milan Chytrý is an Associate Editor of Applied Vegetation Science and a coauthor of this article. To minimize bias, he was excluded from all editorial decision-making related to the acceptance of this article for publication.

Data Availability Statement

Vegetation plot data used in this study are available in the European Vegetation Archive (EVA, Chytrý et al. 2016). They can be obtained upon request from the database administrators with reference to EVA project no. 151.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Databases from which vegetation plots were used for the analysis and the number of plots used in this study. **Appendix S2:** List of species merged to aggregates (aggr.). **Appendix S3:** List of associations cited in the literature as part of the *Crypsidetea aculeatae* or with the diagnostic species of the class in the association's name. **Appendix S4:** Supplementary analysis to support the justification for merging different names within associations defined within *Crypsidetea aculeatae*. **Appendix S5:** Expert system for classification of *Crypsidetea aculeatae* vegetation plots.