

# Retrodunal dry grassland vegetation in the hinterland of Velika Plaža (Montenegro)

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**Abstract** – The article presents the results of a study on retrodunal dry grassland communities in the hinterland of Velika Plaža (town of Ulcinj, Montenegro). They are documented with 47 relevés, which were compared with 177 dry grassland and 107 sand dune vegetation plots. Using hierarchical cluster analysis (flexible Beta method), and ordination (non-metric multidimensional scaling), the dry grasslands from the hinterland of Velika Plaža were grouped into three clusters, representing three new associations: *Junco bufonii-Vulpium ligusticae*, *Tuberario guttatae-Avellinietum festuroidis*, *Helinathemo jonii-Artemisietum campestris*. The first association develops at the transition from wet grassland on gleyic soil to xerophilous grassland over sands. It is characterized by relatively high biomass production and is thus regularly mowed. The second association develops on somewhat higher and better drained sands, and due to very low biomass production, it is used exclusively as pasture. The *Helinathemo jonii-Artemisietum campestris* is also a pasture, evolved as a result of progressive natural succession of dune sands on the highest part of the dune system. It is represented by two sub-associations, one of which is characterized by the extremely high coverage of *Asphodelus ramosus*. Stands with *A. ramosus* primarily grow in the form of narrow strips along roads and around fences, sheltered from the wind, and on more developed and humus-rich soils. This suggests that *Asphodeletosum ramosi* present the terminal stage of the dune community *Helianthemo jonii-Artemisietum campestris*. The latter association is classified within the *Crucianellion maritimae* (Ammophiletea arundinaceae), whereas the other two belong to the *Vulpio-Lotion* (*Helianthemetea guttati*).

**Keywords:** dry grasslands, *Crucianellion maritimae*, *Helinathemo jonii-Artemisietum campestris*, *Junco bufonii-Vulpium ligusticae*, retrodunal grasslands, syntaxonomy, *Tuberario guttatae-Avellinietum festuroidis*, *Vulpio-Lotion*

## Introduction

In the last decade, when the mapping of NATURA 2000 habitats in Montenegro began, the research on vegetation was intensified, especially regarding rare and endangered communities. The wider area of Ulcinj, specifically the Velika Plaža dunes, stands out in terms of the number of vegetation relevés in the coastal region (Stanišić-Vujačić et al. 2023). This is the largest sandy beach on the eastern Adriatic and though it is a very popular tourist destination it still has well-developed dune vegetation (Šilc et al. 2016, Stešević et al. 2020, Milanović et al. 2021). The main focus of vegeta-

tion research has been on the narrow coastal zone, embryonic dunes, and shifting sand dunes (Mijović 1994, 2006, 2012, Stešević et al. 2020). Part of the area was declared a natural monument in 1968 (Official Gazette of the Republic of Montenegro 30/1968). However, the accompanying documentation did not specify the boundaries of the protected area, so a review was later proposed (CGIS 2017). According to the IUCN categorization of protected areas, Velika Plaža belongs to category III (CGIS 2017).

Recent new findings of rare, endangered and important plant species in the hinterland of Velika Plaža (e.g. *Isoetes histrix*, *I. gymnocarpa*, *Solenopsis aurentia*, *Avellinia festuroides*,

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*Corynephorus divaricatus*, Stešević et al. 2025) and its habitats (Mediterranean temporary ponds, *Brachypodietalia* dune grasslands with annual plants) indicate its biological value and provide an argument for extending the boundaries of the protected area deeper inland. In the hinterland, dry and wet grasslands alternate with wet forests, shrubs, and bodies of water, forming a unique mosaic (Šilc et al. 2020, Milanović et al. 2021). In terms of species diversity, Mediterranean dry grasslands are particularly notable (Apostolova et al. 2014) and are listed in the European Union Council Directive 92/43/EEC, as well as on the European Red List of Habitats (Jansen et al. 2016). These are important from the perspectives of synecology, distribution, and classification, as the delimitation of some dry grassland syntaxa is not always clear. Certain plant communities show intermediate characteristics between two syntaxa, such as *Vulpio-Lotion* and *Psammo-Vulpion* (Mucina et al. 2016). The literature on dry grassland communities in the coastal part of Montenegro lists the following associations: *Holoschoeno-Scabiosetum albae* Hodak 1974, *Laguro-Corynephorum divaricatae* Horvatić 1974, *Lupino-Laguretum ovati* Lakušić 1965 (Blečić and Lakušić 1976), *Onobrychido caput-galli-Vulpium fasciculatae* Stešević et al. 2020 (Stešević et al. 2020) and *Artemisietum campestris* prov. (Milanović et al. 2021). The first three associations, which are not documented with relevés, were originally classified in the *Vulpio-Lotion* alliance; the fourth in *Laguro ovati-Vulpion fasciculatae*, while the fifth association is considered a vegetation equivalent of the NATURA 2000 habitat type 2240 *Brachypodietalia* dune grasslands.

It is a major challenge for phytosociologists to understand the regularity of occurrence and spatial variation of plant communities that have evolved over more or less stabilized dune sands, their syntaxonomic position and ecological characterization. Addressing this challenge requires sufficient information on numerous natural phenomena: origin and age of the sand, pH reaction, depth and moisture of the sand, humus and clay content in the upper soil layers where most plants develop their roots, degree of sand stabilization (especially in the upper soil layers), exceptional seasonal dynamics with pronounced change of phenophases, pathways of natural succession and regression, impact of different human activities on the floristic composition of communities, etc. (Marcenò et al. 2018). This is particularly true for sandy deposits, which are well drained and rich in organic matter and therefore unsuitable for many plant species. They are often only colonized by a small number of highly specialized taxa that have adapted to be able to thrive in these unfavorable natural conditions (Iserman 2011). In these environments, the appearance of only one new plant species on the surface may reflect important evolutionary processes in the soil and within plant communities. Such changes may require a revision of the syntaxonomic position of the community within higher classification units.

Although this phenomenon is clearly recognizable ecologically and explainable in the field, it often presents challenges for objective classification based on statistical parameters. Moreover, it is often the case that many species considered diagnostic of some more widespread alliances

and higher vegetation units that have developed over sands do not occur in certain geographical localities. This ultimately drives the need to classify the studied plant associations into appropriate syntaxonomic schemes based more on ecology and physiognomy than on floristic composition (Pignatti et al. 1995, Mucina et al. 2016, Marcenò et al. 2018). This problem is further exacerbated by the frequent and diverse influences of humans, who have used sand for various purposes since the earliest epochs (EEA 1999).

In this paper, we present 3 new dry grassland associations from the hinterland of Velika Plaža and describe them in detail. We discuss different approaches to the classification of Mediterranean dry grassland communities and propose a syntaxonomic classification.

## Material and methods

The wider area of the hinterland of Velika Ulcinjska Plaža is an alluvial plain in a flysch zone that extends in a WNW-SSE direction from the mouth of the Port Milena channel to the Bojana River and its mouth into the Adriatic Sea (Fig. 1).

Immediately behind the sea coast, up to 3.5 m high drifting sand deposits, known as Breg mora, have formed due to the constant impact of sea waves and wind. Various dry dune communities on the mild southern slopes and wetlands in dune slacks, sporadically overgrown with scattered willow trees or well-developed floodplain riparian ash and oak forests, develop in this belt just after the open dunes. After this swamp area, on the highest part of the dunes, various retrodunal grasslands emerge. These areas are protected from the direct influence of the winds from the sea, and the dune sands are almost fixed with closed communities, though they still experience some shifting sand, mainly due to direct or indirect human impact. Often, they are fenced, used for grazing and mowing, or partly converted into agricultural land. Behind this zone there is a depression running parallel to the seashore with a bottom about 2.2 meters above sea level, containing fragmented remnants of floodplain riparian ash and oak forests. Alongside these forests, wet grasslands have developed in a narrower or wider zone, gradually transitioning into more xerophytic grasslands as the terrain rises, eventually forming a sand deposit up to 5.5 meters high called Štojska Greda. On its embankment, the main road to Ada Bojana was built. Between the settlements in Gornji Štoj and the road, the terrain is almost flat, yet interspersed with shallow depressions and gentle, barely perceptible rises where grassy vegetation develops, ranging from temporary ponds to low therophyte meadows. In the far east, along the course of the Bojana River, the sandy clayey soils rise again (sometimes with deep loam and peat), and extensive forest complexes develop on them, although these have been cleared in places and converted into hay meadows.

The phytosociological relevés were made according to the Braun-Blanquet (1964) approach, using plots of 25 m<sup>2</sup>, a plot size commonly employed for sampling grassland communities (Chytrý and Otýpková 2003). The plots were



**Fig. 1.** Geographic position of Velika Plaža in Montenegro. The circle on the map in the lower left corner indicates the research area in the SE European context.

located in the retrodunal sand deposits, within stands displaying various physiognomies of dry grasslands in the hinterland of Velika Plaža. The plant material was deposited in the Herbarium collection of the University of Montenegro (TGU) and the Herbarium of the Faculty of Forestry of the University of Banja Luka (BALU). All relevés were entered into the Turboveg database (Hennekens and Schaminée 2001). The original relevés are stored in the Vegetation database of Montenegro (GIVD EU-ME-001, Stanišić-Vujačić et al. 2023).

The entire data collection consisted of 331 relevés: 47 original ones (sandy soils), 177 relevés of dry grassland associations in Montenegro and Croatia (on different substrata), and 107 to the sand dune vegetation on Velika Plaža (On-line Suppl. Tab. 1).

Species cover was estimated using the seven-degree cover-abundance scale of Braun-Blanquet (1964) and converted to the percentage midpoints of the estimated cover classes ( $r - 0.1\%$ ,  $+$   $- 2\%$ ,  $1 - 3\%$ ,  $2 - 13\%$ ,  $3 - 38\%$ ,  $4 - 63\%$ ,  $5 - 88\%$ ). The hierarchical cluster analysis was performed on a dataset comprising 224 relevés (47 original ones and 177 from the literature or unpublished of dry grassland communities (different substrata) from Montenegro and Croatia), by PC-ORD 4 (McCune and Mefford 1999) incorporated in JUICE 7.0 software package (Tichý 2002). Relative Sørensen was used as distance measure (McCune and Grace 2002) and the flexible Beta ( $-0.25$ ) as a linkage method. The species cover values were square-root transformed. Diagnostic species were identified according to their fidelity values (Chytrý et al. 2002). All groups were standardized to equal sizes (Tichý and Chytrý 2006), and Fisher's exact test ( $P < 0.01$ ) was applied. To identify constant and dominant species, a frequency threshold of 50% and a coverage threshold of 25% were applied, respectively.

Diagnostic, constant, and dominant species of the retrodunal communities from Velika Plaža were identified on the smaller dataset (47 relevés), while diagnostic species of the major Clusters (I-V) of dry grassland communities (different substrata) from Montenegro and Croatia and dry ret-

rodunal communities (on sandy soil) from Velika Plaža were identified on the large dataset (224 relevés).

A three-letter code (e.g., BUL = *Poetea bulbosae* Rivas Goday et Rivas-Mart. in Rivas-Mart. 1978) in brackets after a taxon name indicates the vegetation class of which the taxon is a diagnostic species, as reported in the FloraVeg.EU database (<https://floraveg.eu/>, Chytrý et al. 2024).

NMDS ordination analyses were conducted using the R 4.3.2 programming environment (R Core Team 2023), using the *vegan* package on different datasets: (i) 224 relevés (47 original ones and 182 from the literature or unpublished), (ii) 154 relevés of dune and retrodune dry grassland vegetation. The ecological indicator values of the relevés (Pignatti 2005) were calculated in JUICE (Tichý 2002) and passively projected onto a non-metric multidimensional scaling (NMDS) diagram (using Bray-Curtis distance measures) to illustrate the ecological relationships between the relevés in these three datasets and to explain the environmental gradients underlying the main ordination axes. Percentage cover data were transformed using the Hellinger transformation.

Life forms according to Raunkiaer (Pignatti 1982) were obtained for each species, and the proportion of particular life forms was calculated for each relevé. The nomenclature of taxa follows POWO (2024). Syntaxonomical concepts and nomenclature of higher syntaxa follow the Database of European Vegetation (Chytrý et al. 2024).

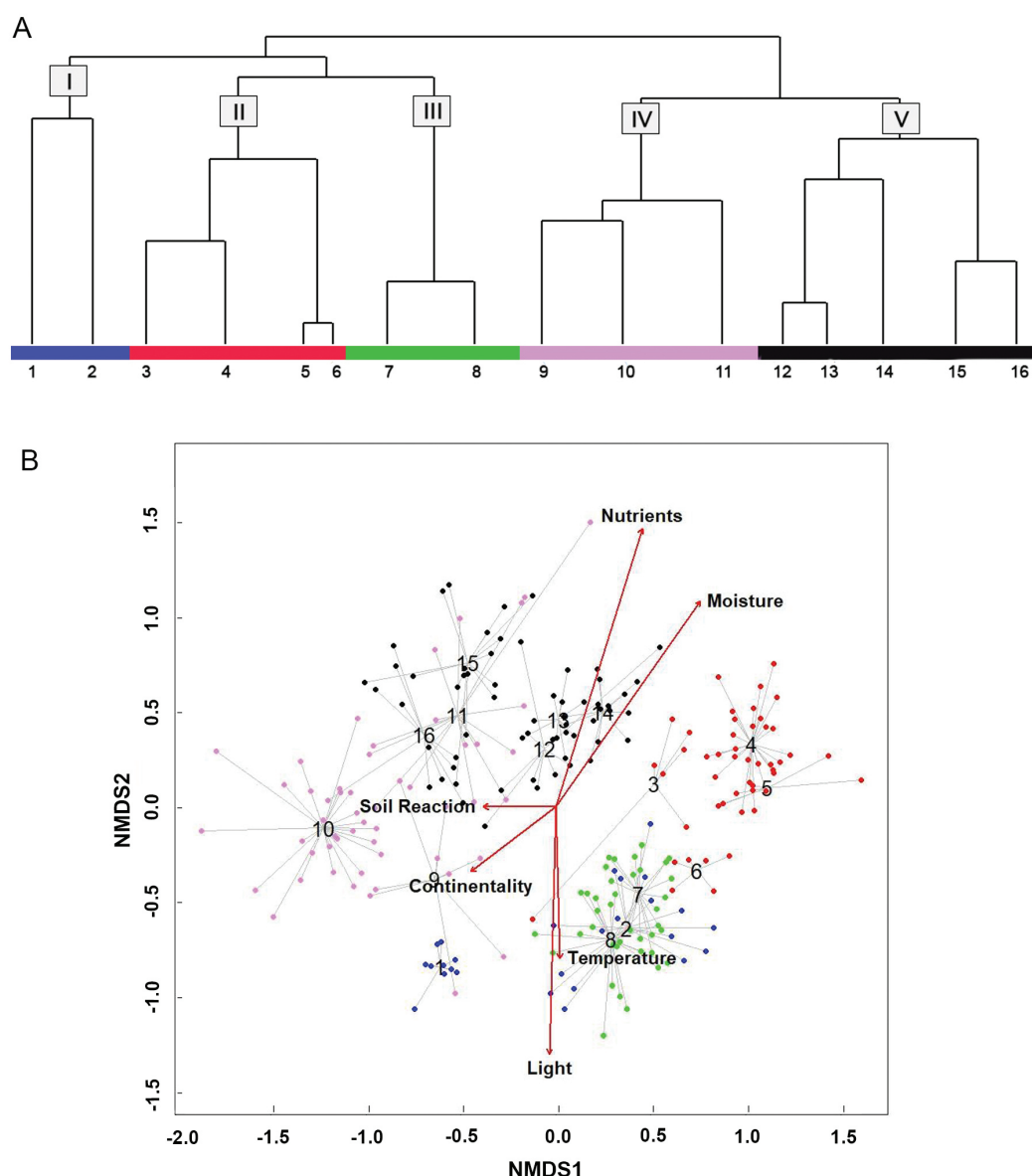
## Results

In the hierarchical cluster analyses, performed on the dataset of 224 relevés the dry grassland communities (on different substrata) from Montenegro and Croatia and retrodunal grasslands from Velika Plaža were differentiated into five main clusters (I-V) and 16 subclusters (1-16), which corresponds to 13 associations (Fig. 2A).

Cluster I is characterized by perennials *Chrysopogon gryllus*, *Centaurea deusta*, *Eryngium amethystinum* and includes 2 associations: *Chrysopogoni-Airetum capillaris* (MNE), and *Bromo-Chrysopogonetum grylli* (MNE); Cluster II by annuals *Bromus hordeaceus*, *Bunias erucago*, *Vulpia ligustica*, *Trifolium nigrescens*, and three plant communities: *Dasypyrum villosum* comm. (MNE), *Bunio erucagi-Vulpium ligusticae* (MNE), and *Junco bufonii-Vulpium ligusticae* ass. nova (Velika Plaža hinterland, MNE); Cluster III by psammophytes *Onobrychis caput-galli*, *Helianthemum jonium*, *Lagurus ovatus*, *Artemisia campestris*, *Hedypnois rhagadioloides*, and *Helianthemum jonii-Artemisietum campestris* ass. nova from the Velika Plaža hinterland, MNE; Cluster IV by perennials *Bromus erectus*, *Phleum bertolonii*, and *Helichrysum italicum*, and four associations: *Chrysopogoni-Airetum* (HRV), *Psiluro-Trifolietum* (HRV), *Agrostietum maritimae arenosum* (HRV), *Haynaldio-Phleum* (HRV), Cluster V by *Trifolium stellatum*, *Ornithopus compressus*, *Anthyllis circinnata* and three associations: *Ornithopodo-Vulpium* (HRV), *Trifolio-Brachypodietum rupestris* (HRV), and *Gastridio-Brachypodietum retusii* (HRV).

NMDS ordination of the relevés shows that along the first axis, clusters are divided into two big groups that cor-





**Fig. 2.** Hierarchical cluster analysis (A), and ordination analysis: NMDS (B) of the dataset with 224 relevés of dry grassland communities (different substrata) from Montenegro and Croatia and retrodunal communities (on sandy soil) from Velika Plaža; Cluster I (blue): 1 – *Chrysopogoni-Airetum capillaris* (MNE), 2 – *Bromo-Chrysopogonetum grylli* (MNE), Cluster II (red): 3 – *Dasypyrum villosum* comm. (MNE), 4 – *Bunio erucagi-Vulpium ligusticae* (MNE), 5 – *Junco bufonii-Vulpium ligusticae* (Velika Plaža hinterland, MNE), 6 – *Tuberario guttatae-Avellinetum festuoidis* (Velika Plaža hinterland, MNE), Cluster III (green): 7 – *Helianthemo jonii-Artemisietum campestris asphodeletosum ramosi* (Velika Plaža hinterland, MNE), 8 – *Helianthemo jonii-Artemisietum campestris typicum* (Velika Plaža hinterland, MNE), Cluster IV (pink): 9 – *Chrysopogoni-Airetum* (HRV), 10 – *Psiluro-Trifolietum* (HRV), 11 – *Agrostietum maritimae arenosum* and *Haynaldio-Phleetum* (HRV), Cluster V (black): 12, 13, 14 – *Ornithopodo-Vulpium* (HRV), 15 – *Trifolio-Brachypodietum rupestris* (HRV), 16 – *Gastridio-Brachypodietum retusii* (HRV). Stress value: 0.23.

respond to the classification in Fig. 2A and the first axis is correlated with soil reaction. The second axis strongly correlates with nutrients, moisture, light, and temperature (Fig. 2B). The retrodunal communities of Cluster II are placed in the right part of the diagram, as more nitrophilous and moist, while on the left are communities of Clusters IV and V, which grow on nutrient poorer and less humid substrates. Communities of Clusters I and III are discriminated on the gradients of light and temperature.

NMDS ordination analysis was performed on the 154 relevés of sand dune communities and retrodunal dry com-

munities documented at Velika Plaža (On-line Suppl. Fig. 1). The first axis is also correlated with soil reaction, and the second with light, continentality, moisture and temperature. Retrodunal communities are discriminated along the gradient of continentality, and placed in the right of the diagram (On-line Suppl. Fig. 1, clusters 7-10). Retrodunal grasslands from the hinterland of Velika Plaža were grouped into Clusters II and III, subclusters 5-8 (Fig. 2A), Clusters 5-8 (Fig. 2B), and Clusters 7-10 (On-line Suppl. Fig. 1) which correspond to the newly reported associations: therophyte-dominated grasslands *Junco bufonii-Vulpium*

*ligusticae* ass. nova and *Tuberario guttatae-Avellinietum festucoidis* ass. nova, and perennial grasslands *Helianthemum jonii*-*Artemisietum campestris* ass. nova (On-line Suppl. Fig. 2).

***Junco bufonii-Vulpium ligusticae*** ass. nova  
(relevés 1-7 in Tab. 1, holotypus: relevé 6, hinterland of Velika Plaža, subcluster 5 in Fig. 2A; On-line Suppl. Fig. 3A)

**Diagnostic species:** *Vulpia ligustica*, *Plantago lanceolata*, *Lotus corniculatus*, *Juncus bufonius*, *Anthoxanthum odoratum*, *Ranunculus marginatus*

**Constant species:** *Vulpia ligustica*

**Dominant species:** *Vulpia ligustica*, *Vulpia ciliata*

**Ecology, distribution and use:** This association represents the hygro-xerophilous type of grassland, whose stands occur under extremely hygrophilous conditions in winter and spring, and extremely xerophilous conditions in summer (Fig. 2B, cluster 5; On-line Suppl. Fig. 1, cluster 7). This type of vegetation thrives on flat terrain, covering nearly 100% of the soil and reaching a height of approximately 30 cm. Due to the relatively high biomass production, these are the only xerophilous retrodunal grasslands in the Velika Plaža hinterland that are regularly mowed. They usually develop at the transition from wet grassland on gley soil (*Alopecuro-Ranunculetum marginati* Zeidler 1954) to xerophilous grasslands on sandy soils, in the zone of primary distribution of *Quercus robur*. The soils in these areas have a higher clay and humus content due to the persistent moisture resulting from the influence of groundwater or a high water table in spring. As a result, the soils dry out more slowly, allowing a dense vegetation cover to develop, with a combination of mesohygrophilous and xerophilous plants. It is optimally developed in May and is characterized by a very high cover and the nearly absolute dominance of the annual grass *Vulpia ligustica* (TUB).

Anthropogenic floristic elements also have absolute or high frequency in this association, including *Trifolium nigrescens* (BUL, CHE), *Anthemis arvensis* (PAR), *Avena barbata* (CHE), *Bromus hordeaceus* (SIS). Species of *Stipo-Trachynietea distachyae* and *Helianthemetea guttati* are also present, such as *Hypochaeris glabra*, *Vulpia myuros*, *Trifolium campestre*, *Cerastium pumilum* var. *glutinosum*, and *Petrorrhagia dubia*. Due to its transitional nature, many species of hygrophilous grasslands (mainly of *Alopecuro-Ranunculetum marginati*) are also present, including *Alopecurus rendlei*, *Ranunculus marginatus*, *Juncus bufonius*, *Linum bienne*, *Trifolium subterraneum*, and *Briza minor*. Therophytes dominate the biological spectrum (On-line Suppl. Fig. 2).

Recently, the spatial continuity of these grasslands has been interrupted by the conversion of land into construction sites or arable land.

In the study area, this spring and early summer ephemeral association forms narrow or wider strips along wet grasslands in the central depression of the hinterland, and in favorable spots on slight elevations on the terrace of the

Bojana River. According to current knowledge, the distribution of this association is limited to the hinterland of Velika Plaža in Ulcinj (On-line Suppl. Fig. 4). However, given the ecological similarity with Velipoja in Albania, it is possible that *Junco bufonii-Vulpium ligusticae* also occurs there.

***Tuberario guttatae-Avellinietum festucoidis*** ass. nova  
(relevés 8-13 in Tab. 1, holotypus: relevé 12, hinterland of Velika Plaža, subcluster 6 in Fig. 2A, On-line Suppl. Fig. 3B)

**Diagnostic species:** *Tuberaria guttata*, *Lotus angustissimus*, *Filago gallica*, *Aira elegans*, *Trifolium nigrescens*, *Avellinia festucoides*, *Crepis neglecta*

**Constant species:** *Sherardia arvensis*, *Linum bienne*, *Lagurus ovatus*, *Cynodon dactylon*, *Arenaria leptoclados*, *Anthemis arvensis*

**Dominant species:** *Vulpia ciliata*, *Trifolium nigrescens*, *Anthemis arvensis*, *Poa bulbosa*, *Medicago minima*, *Bromus hordeaceus*

**Ecology, distribution and use:** This association develops on slightly higher and better-drained sands in the zone of built-up areas and in their immediate vicinity, on flat terrain, covering 100% of the soil and reaching a height of 15-20 cm. Compared to the *Junco bufonii-Vulpium ligusticae*, it is xerophilous (Fig. 2B, cluster 6; On-line Suppl. Fig. 1, cluster 8). It is characterized by a marked change in phenology of plant community and very low biomass production, which is why it is used exclusively as pasture.

Due to the low biomass production and the grazing, the surface sands are weakly bound, brownish-grey, with little humus and almost no carbonates. They develop at the highest points of the seemingly flat terrain, where they are replaced in slightly deeper depressions by the vegetation of temporary ponds and the *Scirpoides holoschoenus* community. Depending on the intensity of trampling and grazing and the humus content of the surface layer, these communities can range from poorer to richer in the total species number and participation of ruderal elements. Consequently, they exhibit numerous transitions to ruderal Mediterranean ephemeral communities.

In early spring, *Poa bulbosa*, *Avellinia festucoides* and *Tuberaria guttata* typically dominate, and are later replaced by *Crepis neglecta*, *Aira elegans*, *Vulpia ciliata*, *Trifolium nigrescens* or *Anthemis arvensis*. They are optimally developed in May during and after the frequent spring rains, in the summer they are completely dry, and in autumn some characteristic geophytes and late-flowering annual introduced grasses appear.

Among the elements of anthropogenic vegetation, the following species are particularly common: *Erodium cicutarium* (BUL, SIS), *Silene gallica* (CHE, TRA), *Bromus hordeaceus* (SIS), as well as species of *Helianthemetea guttati* and *Stipo-Trachynietea distachyae*: *Tuberaria guttata*, *Filago gallica*, *Aira elegans*, *Corynephorus divaricatus*, *Lagurus ovatus*, *Vulpia ciliata*, *Crepis neglecta*, *Hypochaeris glabra*,

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*Cuscuta australis* ssp. *cesatiana*

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**Tab. 1. Continued**

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**Tab. 1. Continued**

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*Petrorhagia dubia*, *Trifolium campestre*s, *Cerastium pumilum* var. *glutinosum*. In some stands, extremely high moss coverage (70%) was observed, while in others it was completely absent. Therophytes dominate the biological spectrum (On-line Suppl. Fig. 2).

According to current knowledge, the distribution area of this association is limited to the hinterland of Velika Plaža in Ulcinj (On-line Suppl. Fig. 4). However, fragments are expected in Velipoja, Albania.

***Helinathemo jonii-Artemisietum campestris* ass. nov.** (relevés 14–47 in Tab. 1, holotype: relevé 42, cluster III (subclusters 7 and 8) in Fig. 2A; On-line Suppl. Fig. 3C–E).

**Diagnostic species:** *Artemisia campestris*, *Onobrychis caput-galli*, *Helianthemum jonium*

**Constant species:** *Artemisia campestris*

**Dominant species:** *Artemisia campestris*, *Asphodelus ramosus*, *Helianthemum jonium*, *Onobrychis caput-galli*

**Ecology, distribution and use:** It is a pasture-like retrodunal xerophilous association that has developed as a result of the progressive natural succession of the highest part of the dune system and the regression stage on artificially destabilized sands in the hinterland of Velika Plaža. The terrain is mostly flat, only occasionally sloping 15–20° and facing north. Due to the dynamics of the relief and the conversion of land and infrastructure works, it is often fragmented and interspersed in a mosaic with dune depressions, mown meadows or anthropogenic habitats. The stands are characterized by a total plant cover of (50–)70 to 90(–95)%, with the proportion of mosses ranging from 0 to 30%. The June aspect of the association is dominated by *Helianthemum jonium* and the July–August aspect by *Artemisia campestris*. In addition to species of *Helianthemetea guttati*, *Helichryso-Crucianielletea maritimae* and *Stipo-Trachynietea distachyae* (e.g. TRA, TUB – *Medicago littoralis*, *Lagurus ovatus*, *Vulpia ciliata*, TRA – *Linum strictum*, TUB – *Onobrychis caput-galli*, *Corynephorus divaricatus*), elements of the anthropogenic vegetation of *Chenopodietea* (*Avena barbata*, *Catapodium rigidum*, *Dasyphyrum villosum*), *Poetea bulbosae* (*Poa bulbosa*, *Trifolium scabrum*) and *Sisymbrietea* (*Crepis foetida*), are common and a sign of strong zoo-anthropogenic pressure. In the spectrum of life forms, annual species have the largest share, but perennials dominate in the physiognomy of this community.

As with *Junco bufonii-Vulpietum ligusticae*, the fragmentation of these communities has recently become apparent due to the conversion of land into construction sites or arable land.

The range of the association is restricted to the hinterland of Velika Plaža, but its fragments may be expected in the Velipoja reserve (Albania), although Fanelli et al. (2015) did not mention psammophytic communities dominated by the eponymous species *Artemisia campestris* and *Helianthemum jonium*.

The association is represented by two subassociations.

***Helinathemo jonii-Artemisietum campestris typicum* subass. nova**

(relevés 35–47 in Tab. 1, holotypus: relevé 42, Hinterland of Velika Plaža, subcluster 8 in Fig. 2A, On-line Suppl. Fig. 3C)

**Diagnostic species:** *Helianthemum jonium*, *Artemisia campestris*, *Erigeron canadensis*

**Constant species:** *Artemisia campestris*

**Dominant species:** *Artemisia campestris*, *Helianthemum jonium*, *Onobrychis caput-galli*, *Dasyphyrum villosum*, *Chrysopogon gryllus*

**Ecology, distribution and use:** This subassociation has developed primarily as a result of progressive natural succession of dune sands on the highest part of the dune system (Breg Mora) which is usually protected by a windbreak belt of floodplain riparian ash and oak forest fragments or pine plantations, and mostly situated in fenced areas. It is also found in degraded areas in the highest parts of the sand deposits in the hinterland (Štojska Greda) as a regression stage on artificially destabilized sands, reaching a height of 15–20 cm. Community is characterized by a total cover of (50–)70–90(–95)%, reaching a height of 35–40 cm, with mosses accounting for (1–)3–15(–20)%. The invasive species *Erigeron canadensis* was frequently found in these stands, which is expected given the zoo-anthropogenic pressure, grazing, increased traffic and visits during the tourist season, and infrastructure works. In the physiognomy of this community, the chamaephyte form dominates (On-line Suppl. Fig. 3C), while in the spectrum of life forms, annual species have the largest share (On-line Suppl. Fig. 2).

***Helinathemo jonii-Artemisietum campestris asphodeletosum ramosi* subass. nova**

(relevés 14–34 in Tab. 1, holotypus: relevé 20, Hinterland of Velika Plaža, subcluster 7 in Fig. 2A, On-line Suppl. Fig. 3D, E)

**Diagnostic species:** *Asphodelus ramosus*, *Crepis sancta*

**Constant species:** *Asphodelus ramosus*

**Dominant species:** *Asphodelus ramosus*, *Artemisia campestris*

**Ecology, distribution and use:** This subassociation represents the final stage of development of the association during the progressive natural overgrowth of dune sands, driven by sand stabilization and the accumulation of humus in the upper soil layers. It typically occurs as linear strips in wind-protected areas along forest edges, roads, or fences, mostly on flat terrain, occasionally sloped 15–20°, with a northern exposure. It is characterized by a high total vegetation cover of (75–)80(–90%), reaching a height of 95–100 cm, and a moss cover ranging from 0 to 30%. *Asphodelus ramosus* dominates the spring aspect, and *Artemisia campestris* dominates the summer aspect.

Compared to the *typicum* subassociation, grazing intensity is low, and the increased humus in the surface layer leads to sand stabilization. This is reflected in the colonization by more geophytes and species that do not typically inhabit the sand, as exemplified by the spread of *Asphodelus ramosus*. The ecological ambience in these stands is more

mesophilous (Fig. 2B, Clusters 7, 8; On-line Suppl. Fig. 2, Clusters 9, 10). Species of contact habitats, such as forest species, are found in these stands: *Anemone hortensis* (PUB), *Arum italicum* (PUB, POP, QUI). Anthropogenic and dry species include: *Avena barbata*, *Dasypyrum villosum*, *Crepis sancta* (CHE), *Sherardia arvensis*, *Euphorbia helioscopia*, and *E. peplus* (PAR). Moist habitat species include: *Linum bienne* (MOL). Elements of *Stipo-Trachynietea distachyae* and *Helianthemetea guttati* are common: *Lagurus ovatus*, *Vulpia ciliata*, *Briza maxima*, *Linum strictum*, *Onobrychis caput-galli*.

The physiognomy of this community is dominated by the perennial forms of geophytes and chamaephytes (On-line Suppl. Fig. 3D, E), while in the overall spectrum of life forms, annual species have the largest share (On-line Suppl. Fig. 2).

According to current knowledge, the distribution of this subassociation is also limited to the hinterland of Velika Plaža (On-line Suppl. Fig. 4). Its fragments might also occur in the Velipoja Reserve (Albania), although Fanelli et al. (2015) did not mention psammophytic communities dominated by *Asphodelus ramosus*.

## Discussion

### Relation of the *Junco bufonii-Vulpietum ligusticae* to other therophyte dry grassland communities

A recent study of sub-Mediterranean dry grassland communities in the sub-Mediterranean parts of Montenegro documented a novel association dominated by *Vulpia ligustica*, provisionally named *Bunio erucagi-Vulpietum ligusticae* (Stanišić-Vujačić 2023, Fig. 2A). This community is ecologically and syntaxonomically similar to mown meadows that have developed on former nutrient-rich arable land. It exhibits two phenological aspects: early spring, characterized by species such as *Bunias erucago*, *Calepina irregularis*, *Erodium cicutarium*, *Sherardia arvensis*, *Tordylium apulum*; and late spring, dominated by *Vulpia ligustica*. The community is widespread in the area of the Zeta Plain at altitudes of 25-73 m a.s.l. and is associated with the *Vulpio-Lotion*.

*Calepina irregularis* and *Tordylium apulum* are completely absent in the newly described retrodunal community *Junco bufonii-Vulpietum ligusticae* from the hinterland of Velika Plaža, while *Bunias erucago* occurs only sporadically. The community has a rather mesophilic character, as indicated by the presence of species such as *Alopecurus rendlei*, *Ranunculus marginatus* and *Linum bienne* in addition to *Juncus bufonius* (Tab. 1). Typical psammophytic elements common in the surroundings of the Velika Plaža hinterland, such as *Lagurus ovatus*, *Onobrychis caput-galli*, and *Medicago littoralis* (Stešević et al. 2020) are almost completely absent. This absence may be related to the complete stabilization of the sand and the competitive dominance of dry grasslands and exclusively non-psammophytic species. This floristic feature differentiates *Junco bufonii-Vulpietum*

*ligusticae* from the nearby dune grasslands *Onobrychis caput-galli-Vulpietum fasciculatae*, part of the *Laguro ovati-Vulpion fasciculatae* alliance (On-line Suppl. Fig. 1).

According to the *Prodromus of Plant Communities of Montenegro* (Blečić and Lakušić 1976), Mediterranean grasslands in the coastal region include three associations: *Holoschoeno-Scabiosetum albae*, *Laguro-Corynephorum divaricatae* and *Lupino-Laguretum ovati*. However, these associations are known only by name, and data on their floristic composition and structure are unavailable. They were classified into *Vulpio-Lotion*, *Thero-Brachypodietalia* and *Thero-Brachypodietea*. In modern syntaxonomy, the order *Thero-Brachypodietalia* is considered synonymous with *Cymbopogono-Brachypodietalia ramosi*, and the position of *Vulpio-Lotion* has been reclassified into *Vulpietalia* and *Helianthemetea guttati* (Chytrý et al. 2024). Because of the aforementioned lack of relevés or textual descriptions of the mentioned communities, it was not possible to perform a critical revision of the classification or a comparison of the floristic composition or its ecology with *Junco bufonii-Vulpietum ligusticae*.

In Croatia and Albania, no communities are known where *Vulpia ligustica* is a dominant, name-giving or differential species (Dring et al. 2002, Trinajstić 2008, Fanelli et al. 2015).

In Italy, *Vulpia ligusticae-Dasypyretum villosii* (Fanelli 1998) is characterized as a non-littoral pseudosteppe grassland dominated by therophytes growing on acid sands located more than 5 km inland from the coast (Fanelli 1998, 2011). *Dasypyrum villosum* and *Hordeum bulbosum* dominate, while *Vulpia ligustica* as a characteristic species has low coverage. As in the community on the retrodunal sands of Velika Plaža, *Molinio-Arrhenatheretea* elements are represented in a considerable number of stands (Fanelli 1998), but this community also contains ecologically drier variants and is variable. It is classified in the order *Brometalia rubentictectorum* and the class *Thero-Brachypodietea* and not in the class *Chenopodietea*, which is thought to be floristically more similar (Fanelli 1998). In the modern classification (Chytrý et al. 2024), *Thero-Brachypodietea* is synonymous with *Lygeo sparti-Stipetea tenacissimae*, while the order *Brometalia rubentictectorum* retains its position in the class *Chenopodietea*.

Also, in Italy, De Pace et al. (2011) documented a low-density *Dasypyrum villosum-Lagurus ovatus-Vulpia ligustica* association in a pine forest near sand dunes on the Ionian Sea coast in the Apulia region. However, the classification of this community was not discussed.

In northwestern Sardinia, Farris et al. (2013) described an agro-pastoral, semi-nitrophilous, therophytic community dominated by *Vulpia ligustica: Cynosuro polybracteati-Vulpietum ligusticae*. It is a ploughed pasture divided into 4 ecological variants distributed across the altitudinal range from 250-1000 m a.s.l. The association is classified into the anthropogenic vegetation *Stellarietea mediae*, *Thero-Brometalia*, and *Echio plantaginei-Galactition tomentosae*.



In the recent classification, *Stellarietea mediae* is synonymous with *Papaveretea rhoeadis* and *Thero-Brometalia* with *Brometalia rubenti-tectorum* (Chytrý et al. 2024).

Mainly due to the affiliation of the dominant and characteristic species *Vulpia ligustica* with the class *Helianthemetea guttati*, the newly described retrodunal association *Junco bufonii-Vulpietum ligusticae* from the hinterland of Velika Plaže is included in *Helianthemetea guttati*, *Vulpietalia* and *Vulpio-Lotion*, whereby the specificity of this community is emphasized by the proportion of anthropogenic vegetation elements (*Poetea bulbosae* and *Chenopodietea*) and anthropogenically managed pastures and meadows (*Molinio-Arrhenatheretea*).

#### Relation of the *Tuberario guttatae-Avellinietum festuroidis* to other therophyte dry grassland communities

*Avellinia festuroides*, the differential and name-giving species of this community, was recently recorded as new in the flora of Montenegro (Stešević et al. 2025). Although it prefers dry, open, sandy habitats, usually near the sea (Tutin 1980, Pignatti 1982), in the hinterland it has also been observed in occasional wet habitats, such as Mediterranean temporary ponds, wet dune slacks and wooded dunes with *Pinus pinea* and/or *Pinus pinaster* (Stešević et al. 2025). In hierarchical cluster analysis and ordination analyses of selected grassland and dune communities, the association *Tuberario guttatae-Avellinietum festuroidis* is clearly distinguished (Fig. 2A, B, On-line Suppl. 1).

With *Avellinia festuroides* (syn. *Avellinia michelii* (Savi) Parl.), the endemic community *Sileno conicae-Avellinietum michelii* part of the alliance *Laguro ovati-Vulpion membranaceae* (Géhu and Biondi 1994), *Malcomietalia*, *Tuberarietea guttatae*, were described in the inner north Adriatic fixed dunes (Sbrulino et al. 2013). Similar to our community, its physiognomy is partly determined by perennial plants from anthropogenic vegetation, *Poa bulbosa* and *Cynodon dactylon*, as well as by typically psammophytic elements such as *Lagurus ovatus* (Sbrulino et al. 2013).

Given these findings and considering the basic ecological and floristic principles that compare our association with others outside the southeastern Adriatic, the *Laguro ovati-Vulpion membranaceae* and *Vulpio-Lotion* should be vicarious alliances that share a considerable number of common species. The proposed solution that *Laguro ovati-Vulpion membranaceae* belongs to segetal and ruderal vegetation (*Brometalia rubenti-tectorum*, *Chenopodietea*) and that *Vulpio-Lotion* belongs to Mediterranean and sub-Mediterranean-Atlantic annual low-growing ephemeral herbaceous and grass-rich vegetation on acidic substrates, sometimes developed over sands in dunes (*Vulpietalia*, *Helianthemetea guttati*), seems to be unfounded. Rather than classifying them into completely different orders and classes, we are of the opinion that *Laguro ovati-Vulpion membranaceae* should find its place among the dune ephemeral grasses of the order *Vulpietalia*.

The retrodunal association *Tuberario guttatae-Avellinietum festuroidis* is quite distant from all associated communities of the *Vulpio-Lotion* from Croatia (*Agrostetum maritimae arenosum*, *Chrysopogoni-Airetum capillaris*, *Ornithopodi-Vulpietum myuri*, *Gastridio-Brachypodietum retusi*, *Psiluro-Trifolietum cherleri*, *Haynaldio-Phleetum* and *Trifolio cherleri-Brachypodietum rupestris*) and is much more closely related to *Junco bufonii-Vulpietum ligusticae*, despite significant ecological, floristic, and physiognomical differences (Fig. 2A, B). In addition to the markedly different floristic composition of the Croatian associations, they are separated by a significantly lower number of perennial plants characteristic of the *Cymbopogono-Brachypodietalia ramosi*, into which this alliance was originally classified (Horvatić 1963), and also by the absence of species that prefer slightly moist habitats traditionally understood as characteristic of the alliance (*Linaria pelisseriana*, *Trifolium subterraneum*). This is to be expected as the dune systems in Croatia are very limited, and typical psammophytic decalcified low Mediterranean grasslands are very rare.

The above characteristics define our association as a terrophytic-geophytic and a dry association with washed-out carbonate sands. This makes it similar to some dry alliances of the classes *Koelerio-Corynephoretea canescentis* and *Stipo-Trachynietea distachyae*. Despite the significant participation of elements of anthropogenic vegetation, we classify this community within *Helianthemetea guttati*, *Vulpietalia* and *Vulpio-Lotion*.

The community develops on retrodunal sands (Štojska Greda), at higher positions which are well drained and very dry in summer. Settlements have been founded in these areas, and stands are now greatly diminished in extent. Due to these unfavorable hydrological conditions, these areas have been used as pastureland, primarily for small livestock (sheep and goats). This usage has led to the appearance of species that can tolerate trampling and grazing, but at the same time do not allow further pedogenesis and natural succession.

#### Relation of the *Helianthemo jonii-Artemisietum campestris* to other dry grassland communities

In view of the physiognomic similarity between the spring aspect of *Helianthemo jonii-Artemisietum campestris asphodeletosum ramosi* from the retrodunal sands of Velika Plaža and the stands of the *Bromo-Chrysopogonetum grylli* pasture community dominated by *Asphodelus ramosus* from Čemovsko Polje near Podgorica, a comparison of these communities was conducted. Both are heliophilous and thermophilous, with a pronounced dominance of perennials (Stanišić-Vujačić et al. 2022, Fig. 2A, B). They are pasture-type and spatially alternate with mown meadows dominated by *Vulpia ligustica*. These communities are also linked by their syntaxonomy, while *Artemisia campestris* is considered a diagnostic species of the *Festuco-Brometea* class (Mucina 1997), to which *Bromo-Chrysopogonetum grylli* also belongs. However, due to its extensive ecological niche, *Artemisia campestris* is also included in the *Sedo-Scleranthetea* and *Koelerio-Corynephoretea canescentis*

(Chytrý et al. 2024), while its communities developed on shifting and stabilized dunes are classified as *Ammophiletea* (Babalónas et al. 1995, Šykora 2003, Tzonev et al. 2005, Mahdavi 2017) and *Helichryso-Crucianelletea maritimae* (Mahdavi 2017, Marcenò et al. 2018) as well as the psammophilous garrigues community in *Ononido-Rosmarinetea* (Choisnet et al. 2014). The ordination analysis revealed no significant similarity between *Helianthemo jonii-Artemisietum campestris* and *Bromo-Chrysopogonetum grylli* (Fig. 2B) and assigned the first community to other grasslands developed on sandy substrates. The second name-giving taxon of this community, *Helianthemum jonium*, which Brullo et al. (2001) considered as one of the characteristic species of the order *Helianthemo ionici-Scabiosetalia albae* Brullo et al. 2001 (from the class *Helichryso-Crucianelletea maritimae*). This order includes chamaephytic-hemicryptophytic communities of mesophytic character colonizing the inner, weakly mobile parts of the dunes of the Adriatic and Ionian coasts of the Italian Peninsula.

Tomaselli et al. (2024) identified *Helianthemum jonium* as a characteristic species of garrigue vegetation in the Apulia region, within the following syntaxa: order *Cisto-Micromerietalia julianae* (class *Ononido-Rosmarinetea*) and associations *Helianthemo jonii-Thymetum capitati*, *Vicio giacominiianae-Helianthemetum jonii*, and *Helianthemo jonii-Fumanetum thymifoliae*. Data on the synecology of this species are also available for Albania (Hamallaj, north of Durrës), where it grows on sandy dunes in open areas between *Juniperus macrocarpa*, *Cistus salviifolius*, *Medicago marina*, *Alkanna tinctoria*, *Juncus acutus* and others. In addition, there are data from Croatia (Dalmatia), where it grows on sandy soils of abandoned vineyards within garrigues of *Cisto-Micromerietalia julianae*, then along roads and abandoned vineyards, on calcareous rocks in open grasslands mixed with garrigues, on sandy slopes of abandoned excavations under *Alkanna tinctoria*, *Ononis natrix*, *Foeniculum vulgare*, *Brachypodium retusum*, *Helichrysum italicum* and others (Bogdanović et al. 2020). As this species was discovered relatively recently in the eastern Adriatic (Bogdanović et al. 2020), communities with this species have not yet been documented.

The *Helianthemo jonii-Artemisietum campestris* from the retrodunal sands of Velike Plaža could be classified into *Helianthemo ionici-Scabiosetalia albae* (Brullo et al. 2001), but in FloraVeg.EU (Chytrý et al. 2024) this order is not mentioned, even as a synonym.

As part of mapping habitat types of community interest according to the 92/43 EEC Directive in Montenegro, stands of communities with *Artemisia campestris* and *Helianthemum jonium* from the hinterland of Velika Plaža are listed as a vegetation equivalent of the habitat type 2240 *Brachypodietalia* dune grasslands with annuals (Milanović et al. 2021), although according to the syntaxonomic classification they cannot be classified in *Lygeo sparti-Stipetea tenacissimae*. The analysis of the syntaxonomic affiliation of species to vegetation classes (Pignatti et al. 1995, Mucina 1997, FloraVeg.EU 2024) revealed a relatively low proportion of dune species from the class *Ammophiletea arundinaceae*

(Tab. 1), instead containing species of *Chenopodietea*, *Helianthemetea guttati* and *Stipo-Trachynietea distachyae*. Nevertheless, referring to the evaluation of physiognomic and ecological criteria for syntaxonomy (Pignatti et al. 1995), we consider that it belongs to the class *Ammophiletea arundinaceae*, the order *Crucianelletalia maritimae*, and the alliance *Crucianellion maritimae*. The same approach was followed by Šilc et al. (2016) when classifying the *Scabiosa argentea-Ephedra distachya* community from Albania. Although the community has several diagnostic species of *Ammophiletea arundinaceae* and only one – the name-giving taxon *Ephedra distachya* of *Crucianellion maritimae* – is classified in *Crucianelletalia maritimae* based on its ecology and physiognomy.

Regarding grazing intensity, *Helianthemo jonii-Artemisietum campestris* is represented by two sub-associations. One is characterized by an extremely high coverage of *Asphodelus ramosus* (On-line Suppl. Fig. 3D, E), the other by its almost complete absence (On-line Suppl. Fig. 3C). It is known that this species is unpalatable to most domestic animals and that it can be a sign of overgrazing (Stanišić-Vujačić et al. 2022, Terzi 2023), and its presence can also be indicative of underuse or abandonment of agro-pastoral activities (Biondi et al. 2016). The fact that stands with *Asphodelus ramosus* grow mainly in the form of narrow strips along roads and around fences, sheltered from the wind, on better developed and more humus-rich soil, suggests that they represent the final stage of the *Helianthemo jonii-Artemisietum campestris* dune community. In this stage, the vitality and coverage of the name-giving species decline due to natural succession followed by soil development on stabilized dunes. Therefore, this syntaxon should be considered a developmental stage (sub-association) of the previous association, leading to further natural succession.

In recent years, decreasing engagement in agriculture and livestock farming has led to the overgrowth of pastures and arable land. Meanwhile, the transformation of land into construction sites poses a serious threat to the continuity of this association.

## Syntaxonomical classification

TUB *Helianthemetea guttati* Rivas Goday et Rivas-Mart. 1963

TUB-02 *Vulpietalia* Pignatti 1953

TUB-02D *Vulpio-Lotion* Horvatić 1963

*Junco bufonii-Vulpietum ligusticae* ass. nov.,  
Holotypus: rel. 6, Tab. 1

*Tuberario guttatae-Avellinietum festucoidis* ass.  
nov.; Holotypus: rel. 12, Tab. 1

AMM *Ammophiletea arundinaceae* Br.-Bl. et Tx. ex Westhoff et al. 1946

AMM-02 *Crucianelletalia maritimae* Sissingh 1974

CRU-02A *Crucianellion maritimae* Rivas Goday et Rivas-Mart. 1958

***Helianthemo jonii-Artemisietum campestris* ass. nov.**; Holotypus: rel. 42, Tab. 1

**subass. *typicum***

**subass. *asphodeletosum ramosi***; Holotypus: rel. 20, Tab. 1

## Acknowledgements

This paper was published on the occasion of the 100<sup>th</sup> anniversary of Acta Botanica Croatica.

The authors would like to thank Ioannis Tsiripidis for assistance with the literature and unpublished data on *Artemisia campestris* communities in Greece; Željko Škvorc and Nenad Jasprica for help with the literature about dry grassland communities in Croatia; Dejan Medojević and Iztok Sajko for preparing the maps; Eduardo Pagliere for checking English language.

D.S. was supported by the Ministry of Science and Technological Development (Project No.04-082/23-2533/1). U.Š. was supported by the Slovenian Research and Innovation Agency (Research Core Funding No. P1-0236).

## Author contribution statement

D.S. – conceptualization, conducted the relevés, funding acquisition, M.S.V., Đ.M. – conducted the relevés, writing, U.Š. – funding acquisition, methodology validation, writing. All authors reviewed the paper and agreed to the published version of the manuscript.

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