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A formal classification of the *Lygeum spartum* vegetation of the Mediterranean Region

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Abstract

Aims: We examined local and regional contribution on the grasslands dominated by *Lygeum spartum* from Southern Europe and North Africa to produce a formalised classification of this vegetation and to identify main factors driving its plant species composition.

Location: Mediterranean Basin and Iberian Peninsula.

Methods: We used a dataset of 728 relevés, which were resampled to reduce unbalanced sampling effort, resulting in a dataset of 568 relevés and 846 taxa. We classified the plots by TWINSPAN, interpreted the resulting pools, and used them to develop formal definitions of phytosociological alliances characterised by *L. spartum* vegetation. The definitions were included in an expert system to assist automatic vegetation classification. We related the alliances to climatic factors and described their biogeographical features and ecological preferences. The floristic relationships between these alliances were analysed and visualised using distance-based redundancy analysis.

Results: We defined eleven alliances of *L. spartum* vegetation, including the newly described *Launaeo laniferae-Lygeion sparti* from SW Morocco and the *Noaeo mucronatae-Lygeion sparti* from the Algerian highlands and NE Morocco. Biogeographical, climatic, and edaphic factors were revealed as putatively driving the differentiation between the alliances. The vegetation of clayey slopes and inland salt basins displayed higher variability in comparison with those of coastal salt marshes.

Main conclusions: The most comprehensive formal classification, accompanied by an expert system, of the *L. spartum* vegetation was formulated. The expert system, containing the formal definitions of the phytosociological alliances, will assist in identification of syntaxonomic position of new datasets.

Key words: badlands, dry grassland, expert system, *Lygeo-Stipetea*, *Lygeum spartum*, Mediterranean Region, phytosociology, *Salicornietea fruticosae*, salt marsh, vegetation classification

Introduction

Lygeum spartum is a robust rhizomatous grass, widely distributed in the Mediterranean Region. It belongs to the subfam. *Pooideae* and it is the only representative of the tribe *Lygeeae* (Soreng et al., 2015). *L. spartum* occurs from the sea level up to an elevation of 2260 m, mainly in the Western Mediterranean (Iberian Peninsula, NW Africa), with some scattered, isolated populations found in Southern Italy, Sardinia, Sicily, Malta, SE Crete, Cyrenaica, and Northern Egypt. Besides its resistance to drought, *L. spartum* is a moderately salt-tolerant species and can be considered a typical stress tolerant *sensu* Grime (1977), even if it occasionally behaved as a competitive species under optimal ecological conditions, where it becomes locally dominant.

The grasslands dominated by *L. spartum* are supported by three kinds of habitats, including (1) salt-rich clayey outcrops (locally called ‘calanchi’ or ‘badlands’; see Caraballo-Arias & Ferro, 2016), (2) edges of salt marshes, and (3) inland salt pans. These habitats are found in regions experiencing different climatic conditions, and they span montane semi-deserts of Morocco and Algeria, the Mediterranean coastal wetlands and seasonally-arid inland depressions characterised by cold winters of the Ebro Valley in Northern Spain (Pugnaire & Haase, 1996). In each habitat type, *L. spartum* largely contributes to rainfall intercept and reduces the runoff associated with erosion of fine, clayey sediments. (García-Fayos, Recatalá, Cerdá, & Calvo, 1995; Solé-Benet et al., 1997; Pueyo et al., 2016; Hooke & Sandercock, 2017).

All the habitat types supporting *L. spartum* are now recognised as Sites of Community Importance by the European Commission (Habitat Directive 92/43/EEC, habitat codes: 1420, 1510*, 6220*). They are highlighted as habitats that contribute significantly to the maintenance and preservation of biological diversity (European Commission, 2013).

In a new classification scheme of the European vegetation (EuroVegChecklist: Mucina et al., 2016; henceforth EVC), the grasslands dominated by *L. spartum* are assigned either to the phytosociological order *Lygeo-Stipetalia tenacissimae* (class *Lygeo sparti-Stipetea tenacissimae*), comprising the circum-Mediterranean grasslands on deep clayey soils, and to the *Limonietalia* and

Limoniastretalia guyoniani (class *Salicornietea fruticosae*), comprising the Western and Central Mediterranean vegetation of inland salt pans (*Limonietalia*) and saline, rarely flooded coastal retrodune depressions (*Limoniastretalia guyoniani*). Based on substantial floristic and phytogeographic differences, several plant associations have been described in the phytosociological literature, and these were classified into several alliances (see Peltier, 1982; Aidoud-Lounis, 1984; Brullo, De Marco, & Signorello, 1990; Djebaili, 1990; Brullo, Giusso del Galdo, & Guarino, 2002; Brullo et al., 2010; Rivas-Martínez et al., 2011), further classified into the orders and classes listed above.

Since a data-driven classification of the communities dominated by *L. spartum* is still missing, we set off to: (1) test the robustness of the classification of *L. spartum* grasslands proposed in the EVC; (2) test whether, involving also the extra-European regions of the distribution of these communities, the EVC classification might also be expanded onto regions originally not covered by it; and (3) to define phytosociological alliances dominated by *L. spartum,* using the formal language of a vegetation classification expert system (Bruelheide, 1997; Mucina et al., 2016).

We hypothesise that the pools of the diagnostic species of the alliances might be strongly under control of regional species pools (incl. numerous endemics), i.e. by the phytogeographic patterns of the disjunct Mediterranean-North African distribution of *L. spartum,* while both climatic and edaphic drivers might influence the ecological niche specialization of *L. spartum*. Based on these assumptions, we also aimed at (4) delineating the distribution areas of the phytosociological alliances with dominating *L. spartum*, and (5) exploring the relationships of these alliances with selected, putatively relevant, climatic gradients.

Material and methods

Study area

L. spartum has a fragmentary geographical distribution pattern, due to its edaphic specialisation to clayey outcrops and salt marshes. Our study area ranges from the sea level to the north-facing slopes of the Siroua Massif (SW Morocco) reaching elevations up to 2060 m. The study area is part of the Mediterranean Basin (in a broad sense) and has an approximately quadrilateral shape, with corners at 30°28' N, 8°52' W (Taroudant Province, SW Morocco), 42°42' N, 1°40' W (Navarra, N Spain), 31°21' N, 27°14' E (Wadi Habis, Marsa Matrouth, NW Egypt), 40°44' N, 16°14' E (Irsina, S Italy). Following Rivas-Martínez (2004), this area encompasses the Mediterranean bioclimatic units from the Mediterranean pluvi-seasonal oceanic to desertic oceanic belt.

Clayey outcrops colonised by *L. spartum* are characterised by banded or discontinuous vegetation patterns that experience high rates of erosion. Water and wind sculpt the soft sedimentary materials into intricate mazes of narrow ravines, V-shaped gullies, knife-sharp ridges, buttes, and colourful pinnacles (Nadal-Romero, Martínez-Murillo, & Kuhn, 2018). In this habitat context, *L. spartum* occupies patches at the feet of the outcrops or in locations where the soil has endured superficial runoff.

Saltmarshes, on the other hand, are flat or gently sloping sites colonised by halophytic vegetation in areas influenced by the tidal action and/or by the seasonality of rainfall. Species distribution in salt marshes is controlled by the presence, frequency, and duration of flooding (tidal action), as well as salt content in the soil. Few centimetres of variation in relative elevation can result in different vegetation physiognomies (Adam, 1990), determined by different dominants. In the salt marsh system, *L. spartum* colonizes supratidal habitats, exposed only to occasional flooding, yet showing high ambient salinity (Àlvarez, Ortiz, & Alcaraz, 2001). Rarely, the *L. spartum* dominated vegetation is also found along fringes in inland salt pans, such as those found in NW Africa and the Iberian Peninsula (DGOH, 1991; Le Houérou, 2001). In several locations, both clayey outcrops and inland salt pans co-occur in small patches distributed according to soil salt content and humidity (Peralta et al., 2013).

Dataset

We compiled a database comprising 1838 relevés following as storing criteria occurrences of *L. spartum*. A section of these data (496 relevés) came from the European Vegetation Archive (EVA; Chytrý et al., 2016). Other 1272 relevés were harvested from literature and 70 unpublished relevés have been provided by the authors. All data were stored using Turboveg (Hennekens &

Schaminée, 2001). The data harvested from literature and 70 unpublished relevés are accessible in the Mediterranean *Ammophiletea* database (Global Index of Vegetation-Plot Databases, GIVD code: EU-00-016).

As the first step of the data collection, we selected only data from plots with *L. spartum* showing cover values > 13% (the Braun-Blanquet scale was transformed automatically by the JUICE software to cover percentage as follows: 5=88%, 4=68%, 3=38%, 2=13%, 1=3% and +=2%). In this way, we filtered 728 plots from nine countries. The information about data sources, country, sampling, decades, and plot sizes is reported in Appendix S1. The selected relevés provided by EVA (168 plots) included latitude and longitude information, the other 560 plots were georeferenced according to the locality descriptions reported in the original publications or by the authors of the unpublished relevés. The accuracy of our georeferencing can be estimated in ≤ 1 km^2 for 488 plots and ≤ 144 m^2 for 72 plots in which latitude and longitude were provided by the authors, corresponding to a 12 m maximum standard error of GPS measurements in the open air.

Taxonomic nomenclature was standardised according to the Euro+Med PlantBase (accessed in January 2019; www.emplantbase.org). Whenever possible, reference was made to more analytical taxonomy (Castroviejo, 1986–2015; Pignatti, Guarino, & La Rosa, 2017–2019). The adoption of a very analytical taxonomy helped in enforcing the resolution of our analyses. However, we ignored the recent taxonomical splitting whenever infraspecific taxa displayed overlapping geographical distributions. Records identified only to genus level, hybrids, and the few available records of bryophytes and lichens (i.e. *Cladonia foliacea*, *Fulgensia fulgens, Pleurochaete squarrosa*) were removed from the dataset. The species aggregations and nomenclatural discrepancies from the Euro+Med PlantBase taxonomy are listed in section 1 of the expert system (Appendix S2).

To reduce the complexity of the dataset (Roleček, Tichý, Zelený, & Chytrý, 2009), we used only relevés sampled between 10 m^2 to 100 m^2. An exception was made for plots from NE Spain, Morocco and southern Tunisia, since the only available data were sampled in plots of 1000 m^2. The exclusion of these plots would have resulted in a critical loss of data relevant to our purposes.

Since some of the available relevés were sampled too close to the borders of arable lands (hard wheat cultivations), all relevés in which the number of species typical of the *Papaveretalia* *rhoeadis* (segetal vegetation) was comparable to the number of species typical of the *L. spartum* grasslands (according to the EVC) were discarded.

The dataset was resampled with JUICE (Tichý, 2002) as follows: All vegetation plots were stratified by their habitat (tool: habitat stratification by associations). In this step, the plots were assigned to the phytosociological associations proposed by their authors (Knollová, Chytrý, Tichý, & Hájek, 2005). The habitat strata were geographically resampled, retaining a maximum of 5 relevés for each quadrat of a geographical grid of 2.5 longitudinal and 1.5 latitudinal minutes. Afterwards, the data set was geographically stratified, considering the previous grid position, and resampled by the Heterogeneity-Constrained Random Resampling Algorithm (Lengyel, Chytrý, & Tichý, 2011). In this way, we retained 5 additional relevés per each stratum using Bray-Curtis dissimilarity as resemblance criterion. This resampling procedure guaranteed that the set of resampled plots was representative of the variation in species composition within each grid cell (Knollová, Chytrý, Tichý, & Hájek, 2005). The resampled data set contained 568 relevés and 846 taxa.

Classification

Since our dataset displayed a relatively low heterogeneity and textural (in term of species composition) complexity, as measured by Whittaker's beta diversity, we opted for a modified TWINSPAN (Roleček et al., 2009) as an appropriate (divisive) classification strategy. By means of the JUICE software (Tichý, 2002), we ran the modified TWINSPAN classification (pseudo cut levels 0, 5, 25) starting from 30 initial divisions and we identified the Diagnostic, Constant, and Dominant species of each of the resulting *pools* (group of relevés created by a divisive classification procedure; Pielou, 1984; Mucina & van der Maarel, 1989).

The Diagnostic species were formally defined as those for which the *phi* coefficient of association (Tichý & Chytrý, 2006), measuring the concentration of species occurrences in a given pool, was > 0.2. In the calculations, we assumed an equal number of relevés per pool, and we disregarded those species whose concentration in the group was not significant at $p < 0.01$, based on Fisher's exact test (Tichý & Chytrý, 2006). The Constant species were defined as those with percentage frequency > 30%, while the Dominant species were defined as those occurring in at least 10% of relevés with cover values > 30%.

We interpreted pools in syntaxonomic terms by comparing the pool composition (diagnostic and constant species) and geographical distribution with the information reported in phytosociological literature (Long, 1954; Le Houérou, 1969; Peltier, 1982; Aidoud-Lounis, 1984; Djebaili, 1990; Brullo et al., 1990, 2002, 2010; Rivas-Martínez et al., 2011). In this way we progressively grouped and decreased the number of pools until we reached a configuration of 13 divisions, which resulted to be relatively coherent with the alliances recognised in the consulted literature and, as for the higher syntaxonomic ranks, with the framework adopted in the EVC. Nine of these 13 divisions were matching quite precisely the alliances known from the literature, two of them were interpreted as new alliances, and two residual pools (in total: 74 out of 568 relevés) were interpreted as therophyte-rich stages of vegetation floristically close to examined alliances (Appendix S3).

Basing on the eleven pools interpreted as alliances, we created an expert system (henceforth: ES) for the automatic classification of the *L. spartum*-dominated communities. The expert system aims to formalise the floristic and geographic boundaries of the recognised alliances and to enable the application of our classification scheme to new datasets. The Diagnostic, Constant, and Dominant species of the eleven pools corresponding to alliances were used to define the indicator species groups in the formal definitions of each alliance (see Appendix S2). The formal definition was based on the comparison of square-rooted percentage covers of the species characterising different alliances (Schaminée et al., 2016; Marcenò et al., 2018) and it was implemented according to recommendations by Bruelheide (1997). The ES was prepared as a script readable by JUICE (Tichý, 2002) and by TURBOVEG 3 (https://www.synbiosys.alterra.nl/turboveg3/help/en/index.html, accessed in February 2019).

To check how close the ES was able to approximate the hierarchical classification, a confusion matrix (Appendix S4) was created between all the 13 TWINSPAN pools and the formally defined alliances. Then the ES was tested on the whole data set before data stratification (728 relevés), and the diagnostic species of each alliance were re-calculated following the same procedure used for the pools. The percentage of relevés classified by the ES in the whole data set was used as a measure of its performance.

Since the *phi* coefficient allows the recognition of diagnostic species only for a declared number of pools (the alliances, in our case), we checked for the occurrence of species having good diagnostic value at higher hierarchical level (groups). The criterion used to recognise the diagnostic species was very conservative, i.e. only species with the exclusive occurrence, hence not occurring in other groups, were considered diagnostic. This rule was broken only in few cases when a given species was linked to a group (in terms of high percentage constancy) but had sporadic occurrences in one or few other units of the same rank. Depending on the hierarchical level of exclusive occurrence, the species were considered as diagnostic of, either phytosociological orders or classes (Matevski, Čarni, Ćušterevska, Kostadinovski, & Mucina, 2018). These are identified and labelled in Table 1 and Appendix S5.

Ordination analyses

To explore the major environmental gradients determining the species composition of the *L. spartum*-dominated communities and the position of the alliances along these gradients, we used the distance-based redundancy analysis (db-RDA; Legendre & Anderson, 1999) because of low compositional heterogeneity and its versatility to accommodate distance metrics. Due to lack of soil data, yet very clear habitat differences between the plots assigned to the class *Lygeo-Stipetea* and the class *Salicornietea fruticosae,* the RDA analyses were performed separately for each class. The db-RDA was also chosen for its superiority to CCA in terms of explaining higher proportion of compositional variance (see also Tsakalos et al., 2018). The analyses were performed in CANOCO 5 (ter Braak & Šmilauer, 2012). We essayed as potential drivers of *L. spartum* vegetation patterns 19 climatic variables obtained through the overlay of the individual plot coordinates with CHELSA climate data set (Karger et al., 2017) in ArcGIS 10 (ESRI, Redlands, CA, USA). Climatic data were harvested in high-resolution raster of 30 arc-sec, corresponding to a spatial resolution of ~1 km.

The db-RDA allows for the flexible selection of many resemblance functions to analyse the relationship between environmental and composition data (Legendre & Gallagher, 2001). We used

Bray-Curtis dissimilarity because of its ability to explain a high proportion of the compositional variance during *a priori* data exploration (Legendre & Gallagher, 2001). We tested and explored the predictor effect of all constrained axes, by running an unrestricted permutation test of 499 permutations. The number of explanatory variables was progressively reduced through the forward selections step with Bonferroni correction of P values. A variable was included in the db-RDA if it explained a significant portion <0.05 of the variance and if the overall model did not exceed the adjusted R^2.

Results

Classification

The first TWINSPAN division (Fig. 1) separates the Western Mediterranean (the Iberian Peninsula and the Maghreb) from the Central and Eastern Mediterranean communities (Southern Italy, Sardinia, Sicily and Crete). The second division for the Western Mediterranean separates the communities of Maghreb (pools 1–3) from those of the Iberian Peninsula (pools 4–9). The same applies for the Central and Eastern Mediterranean community group, in which the second division separates the Eastern Mediterranean communities (Crete, pool 10) from those of Southern Italy and Sicily (pools 11–13). The third division in the Maghrebian pool differentiates coastal salt marshes (pool 1) from inland communities (pools 2, 3). The same applies for the Iberian unit, in which salt marshes and salt basins (pools 4, 5) of central-southern and SE Spain (Mancha and Murcian-Almerian regions, respectively) are separated from clayey slopes communities (pools 8, 9). Two exceptions are represented by the pool 6, including inland mountain grasslands of Morocco, in which the elevation compensates for latitude, making the Moroccan communities relatively similar with the Iberian ones, and the pool 7 which includes the *L. spartum* grasslands of the inland salt pans of Northern Spain.

Of the 13 pools recognised by the classification, eleven can be attributed to phytosociological alliances while the other two are interpreted as therophyte-rich vegetation of the *Agropyro pectinati-Lygeion sparti* + *Limonion catalaunico-viciosoi* (pool 9) and the *Moricandio-Lygeion* *sparti* (pool 12), respectively. Distribution maps and lists of Diagnostic, Constant and Dominant species of each TWINSPAN pool are provided in Appendix S3.

Expert system

Formal definitions were developed for eleven syntaxa of *L. spartum* dominated communities. The ES (Appendix S2) was applied to the whole data set (728 relevés), of which 689 relevés (94.6%) were classified. The relevés not classified by the ES at the alliance level were classified at the order level, in particular: ten as the *Limoniastretalia guyoniani*, seven as the *Limonietalia,* and 22 as the *Lygeo-Stipetalia tenacissimae*. The missing alliance assignments are due to the methodology adopted here, which is based on the comparison of square-rooted percentage covers of the species characterising different alliances. Extremely species-poor relevés will remained unclassified. The consensus between the pools obtained by the TWINSPAN analysis and the alliances classified by our ES is shown in the confusion matrix reported in Appendix S4.

As we did not analyse the entire variability within the *Salicornietea fruticosae* and *Lygeo-Stipetea*, in the ES the name of indicator species groups is followed by "p.p." (*pro parte*) when deemed necessary. More specifically, this is the case of *Lygeo-Lepidion cardamines* p.p., *Lygeo sparti-Limonion furfuracei* p.p., *Limonion catalaunico-viciosoi* p.p., and *Limoniastrion monopetali* p.p. This is because associations not dominated by *L. spartum,* and hence not considered in the survey, are also ascribed to these syntaxa, and this may lead to some misclassifications, especially when the ES is applied to data sets containing different dry grassland types or inland salt pans or saline retrodune vegetation. In such cases, we have added to our formula the command “AND *Lygeum spartum* GR 15”, helping to overcome misclassification problems.

Syntaxonomic interpretation

Here we present the result of the classification and the syntaxonomic interpretation thereof. Distribution maps and lists of diagnostic and constant species of classes, orders and alliances are reported in Figs. 2 and 3, Table 1 and in Appendix S5. The bibliographic references of all the relevés classified in this survey are listed in Appendix S6. The most representative communities dominated by *L. spartum* are shown in Fig. 4.

1. Lygeo sparti-Stipetea tenacissimae Rivas-Mart. 1978

(Mediterranean and Saharo-Arabian dry grasslands on rocky substrates and clayey soils)

1.1 Lygeo-Stipetalia tenacissimae Br.-Bl. et O. de Bolòs 1958

(Edaphic and climatic dry grasslands on clayey soils)

1.1.1 Agropyro pectinati-Lygeion sparti Br.-Bl. et O. de Bolòs 1958 corr. Rivas-Mart. et al. 1999; Fig. 2, *Ag-Ly*

This alliance comprises vegetation supported by clayey substrates in the eastern regions of the Iberian Peninsula (bajoaragonés, manchego, bético and murciano-almeriense subprovinces) over siltite, gypsum or sandstones. This vegetation develops at the feet of slopes receiving regular downslope input of fine materials (silt, clay) and it can tolerate short periods of hydromorphy (Berastegi, 2013). It is dominated by *Lygeo-Stipetea* elements, such as *Brachypodium retusum*, *Dactylis glomerata* subsp. *hispanica*, and characterised by the co-occurrence of many annual species (*Asterolinum linum-stellatum, Filago pyramidata, Linum strictum, Trachynia distachya*) and subshrubs and shrubs such as *Artemisia herba-alba, Camphorosma monspeliaca, Caroxylon vermiculatum, Salvia rosmarinus* and *Thymus vulgaris*.

1.1.2 *Launaeo laniferae-Lygeion sparti all. nova hoc loco;* Fig. 2, *Lla-Ly*

Holotypus of the alliance: *Convolvulo trabutiani-Lygeetum sparti ass. nova hoc loco*

Synonym: ‘Association à *Armoise blanche* et *Erodium jahandiezianum’* Peltier 1982, ineffectively published (ICPN, Art. 1)

Type relevé (holotypus of the association): Peltier (1982: Table 19, rel. 1129), *Carlina involucrata* 3, *Convolvulus trabutianus* 3, *Launaea lanifera* 3, *Lygeum spartum* 3, *Stipa barbata* 2, *S. parviflora* 2, *Artemisia herba-alba* 1, *Carthamus pinnatus* 1, *Centaurea resupinata* s.l. 1, *Chamaerops humilis* 1, *Dactylis glomerata* subsp. *hispanica* 1, *Petrorhagia illyrica* 1, *Bombycilaena discolor* +, *Callipeltis cucullaris* +, *Erodium jahandiezianum* +, *Filago germanica* +, *Helianthemum croceum* +, *Helianthemum ledifolium* +, *Lomelosia stellata* +, *Neatostema apulum* +, *Plantago afra* +, *Paronychia chlorothyrsa* +, *Polycnemum fontanesi* +, *Teucrium aureum* +, *Thymus willdenowii* +, *Trachynia distachya* +, *Triticum ovatum* +.

This is vegetation is colonising clayey and silty depositions at the base of sandstone slopes, and it is distributed from Northern Morocco to the High Atlas, the Siroua Massif and from the slopes of the Antiatlas to the Souss Basin (SW Morocco), between elevations of 1600 and 2060 m. It experiences meso- to supramediterranean dry bioclimate. The relevés dominated by *L. spartum* had been interpreted by Peltier (1982) as *facies* of "steppes ligneuses", described by the same author as the *Artemisio incultae-Erodietum jahandieziani* and the *Artemisio incultae-Thymetum satureioidis*. These associations are ecologically and floristically somewhat different from the stands dominated by *L. spartum*, because they group vegetation dominated by cushion scrubs colonising stony slopes and windy plateaus classified into the *Stipo-Launeion acanthocladae* (Kaabeche, 1990, 1996). For this reason, a new alliance for the NW African montane *L. spartum* vegetation is proposed here. This new alliance is characterised by the dominance of *L. spartum, Carlina hispanica, Chamaerops humilis, Convolvulus trabutianus,* and by the recurrent occurrence of *Erodium jahandiezianum, Launaea lanifera* and *Leysera leyseroides*. Peltier (1982) used the taxonomic concept of *Artemisia inculta* s.str., which is; however, a SE Mediterranean species reaching westwards as far as Libya (according to Euro+Med PlantBase). In the Moroccan Highland Plateau, it is replaced by *A. herba-alba*, belonging to the same taxonomical aggregate.

1.1.3 *Noaeo mucronatae-Lygeion sparti all. nova hoc loco;* Fig. 2, *No-Ly*

Holotypus of the alliance*: Noaeo mucronatae-Lygeetum sparti ass. nova hoc loco*

Synonym: *Noaeo mucronatae-Artemisietum herbae-albae* Aidoud-Lounis 1984, ineffectively published (ICPN, Art. 1)

Type relevé (holotypus of the association): Aidoud-Lounis (1984: Tab. 49, rel. 104): *Artemisia* cf. *saharae* 2, *Lygeum spartum* 2, *Macrochloa tenacissima* 1, *Plantago albicans* 1, *Rostraria pubescens* 1, *Atractylis pheolepis* +, *Caroxylon vermiculatum* +, *Echium humile* +, *Euphorbia falcata* +, *Herniaria fontanesii* +, *Malva aegyptia* +, *Noaea mucronata* +, *Scorzoneroides hispidula* +, *Stipa parviflora* +.

This alliance comprises vegetation of the Algerian highlands, colonising initial soils rich in clay and silt, and experiencing seasonal dryness. The periodical drought leads to the emergence of alkaline, calcium-rich soil-surface crusts (Aidoud-Lounis, 1984). This vegetation is marginally occurring also on calcareous outcrops and sandy soils with high concentrations of sulphates (Djebaili, Djellouli, & Daget, 1989). It is also present in NE Morocco (Eastern High Plateau), at elevations ranging from 650 to 1400 m. (Ben El Mostafa, Haloui, & Berrichi, 2001). The habitat experiences both summer drought and cold winter stress (Djebaili, 1978). The vegetation physiognomy is characterised by the dominance of *L. spartum* and *Stipa parviflora*, along with some chamaephytes (*Artemisia campestris, Atractylis serratuloides* and *Noaea mucronata* subsp. *mucronata*). The original name, ineffectively published, of this alliance was *Noaeo mucronatae-Artemision herbae-albae.* However, *Artemisia herba-alba* s.str. is a Western Mediterranean species, limited to Morocco, Spain and Southern France (according to Euro+Med PlantBase), whereas in Algeria and Tunisia it is replaced by the taxonomically close relative *A. saharae*. In our tables, following the Euro+Med, we replaced *Artemisia herba-alba* with *A. saharae* in all relevés from Algeria, provided that an exhaustive analysis of the North African distribution of the many taxa belonging to the critical group of *Artemisia herba-alba* s.l. is still missing. The alliance *Noaeo mucronatae-Lygeion sparti* is floristically similar with the *Launaeo laniferae-Lygeion sparti.* Also, the human influence in both units is similar as the vegetation of both units is traditionally used as a spring and early summer pasture. In both alliances, overgrazing leads to an increase of cover of therophytes and unpalatable species, such as *Atractylis serratuloides* and *Caroxylon vermiculatum.*

1.1.4 *Launaeo angustifoliae-Lygeion sparti* Le Houérou 1969; Fig. 2, *Lan-Ly*

Original form of the name: 'Alliance à *Launaea angustifolia* et *Lygeum spartum'* (Le Houérou, 1969)

These are open-canopy grasslands colonising flat or gently sloping soils rich in sulphates, resulting from the degradation of gypsum outcrops. They are found at elevations spanning the sea level and 600 m, distributed in central and southern Tunisia, reaching westwards as far as Libya (Maire & Weiller, 1947) and Egypt (Tadros, 1953; Tadros & Atta, 1958). This vegetation is sometimes utilised as marginal rangeland (Le Houérou, 1969). The soil texture ranges from sandy-loamy to loamy-clayey, and the concentration of sulphates ranges from 45% to 90% (Le Houérou, *l.c.*). Besides *L. spartum*, this vegetation is dominated by Southern Mediterranean and Saharan elements, mainly *Atractylis serratuloides, Echiochilon fruticosum, Erodium glaucophyllum, Gymnocarpos decander, Helianthemum kahiricum,* and *Reamuria vermiculata*.

1.1.5 Moricandio-Lygeion sparti Brullo, De Marco & Signorello 1990; Fig. 2, *Mo-Ly*

The *Moricandio-Lygeion sparti* comprises the *L. spartum*-dominated grasslands of the Central Mediterranean. These communities are usually confined on steep slopes of badlands strongly affected by gully erosion, experiencing thermomediterranean dry bioclimate, and spanning elevations from the sea level up to 400 m. The occurrence of a pool of edaphic specialists (such as *Capparis sicula, Eryngium dichotomum, Moricandia arvensis*) is an important floristic feature of this alliance, endemic to Southern Calabria, Sicily, Sardinia, and Malta.

1.1.6 *Polygonion tenorei* Brullo, De Marco & Signorello 1990; Fig. 2, *Pol*

This alliance was described to accommodate relict *L. spartum*-dominated grasslands occurring on deep clayey soils of Basilicata and Northern Calabria (Southern Italy). It can be considered a more mesic variant of the previous alliance, experiencing mesomediterranean subhumid bioclimate and floristically characterised by *Camphorosma monspeliaca*, *Cardopatium corymbosum, Polygonum tenorei, Puccinellia distans* and *Scorzonera hispanica.*

1.1.7 *Scorzonero creticae-Lygeion sparti* Brullo, Giusso & Guarino 2002; Fig. 2, *Sc-Ly*

The *Scorzonero creticae-Lygeion sparti* comprises the *L. spartum*-dominated grasslands supported on halo-morphic clayey vertisols in SE Crete and experiencing thermo- to inframediterranean dry bioclimate conditions. These communities are characterised by some Eastern Mediterranean taxa such as *Carlina graeca, Limonium graecum, Phagnalon rupestre* subsp. *graecum* and *Scorzonera cretica*.

2 *Salicornietea fruticosae* Br.-Bl. et Tx. ex A. Bolòs y Vayreda et O. de Bolòs in A. Bolòs y Vayreda 1950

(Mediterranean and- thermoatlantic perennial salt-marsh herblands and scrub)

2.1 *Limonietalia* Br.-Bl. et O. de Bolòs 1958

(Western and Central Mediterranean, sea-lavender herblands of saline rarely flooded coastal depressions and on elevated edges of inland salt pans)

2.1.1 *Lygeo-Lepidion cardamines* Rivas Goday et Rivas-Mart. in Rivas-Mart. et M. Costa 1984; Fig. 3, *Ly-Le*

This vegetation is colonising seasonally flooded edges of inland salt pans, of Central Spain (La Mancha), experiencing mesomediterranean dry bioclimate. It is characterised by *Elytrigia* *curvifolia, Gypsophila tomentosa*, *Jacobaea auricula*, *Lepidium cardamines* and by several endemic *Limonium* species.

2.1.2 *Lygeo sparti-Limonion furfuracei* Rigual 1972; Fig. 3, *Ly-Li*

This alliance, restricted to the semiarid SE areas in Spain (Murcian-Almerian districts), can be considered as a southern analogon of the previous one. It is characterised by *Atriplex glauca*, *Frankenia corymbosa* and *Salicornia fruticosa*, along with several endemic *Limonium* species.

2.1.3 *Limonion catalaunico-viciosoi* Rivas-Mart. et M. Costa 1984; Fig. 3, *Lca-vi*

This alliance, restricted to the Ebro Basin, can be considered a northern analogon of the *Lygeo-Lepidion cardamines* and it is floristically poorer than the previous two. Nevertheless, the floristic differentiation is also ensured by the occurrence of some endemic *Limonium* species and by the high frequency of *Bupleurum tenuissimum* and *Plantago maritima* subsp. *serpentina,* which do not occur in the other two alliances.

2.2 *Limoniastretalia guyoniani* Guinochet 1951

(Sea-lavender hypersaline scrub in supratidal, rarely inundated sandy habitats of the semi-desert regions of the southern Mediterranean)

2.2.1 *Limoniastrion monopetali* Pignatti 1952; Fig. 3, *Lmo*

This alliance comprises vegetation colonizing edges of coastal salt marshes having sandy-loamy soils. It occurs in southern regions of the Mediterranean Basin and its distribution range overlaps with that of *Limoniastrum monopetalum*, which is restricted to coastal hypersaline sediments, in regions experiencing thermomediterranean bioclimate.

Ordination

Considering all available environmental variables, the variance partitioning suggests that isothermality, mean temperature of the warmest quarter, annual precipitation, and precipitation of the driest quarter have significant influence on the compositional differentiation of the *L. spartum* vegetation (Fig. 5 and 6). The explained variation of these four climatic variables is shown in

Table 2. The variance explained by the considered climatic variables is reported in Table 3. The cumulative explained variation resulted to be 15.1% in the case of *Lygeo-Stipetea* and 13.1% in the case of *Salicornietea fruticosae*.

The gradient of annual precipitation shown in the db-RDA, reveals that South European communities benefit from higher annual rainfall than those of North Africa and the Iberian Peninsula. The communities of the North African Highlands are the most influenced by the gradient of isothermality.

Discussion

Syntaxonomic considerations

The formal classification yielded eleven phytosociological alliances and documents a well-defined floristic differentiation between the Western Mediterranean (North Africa and the Iberian Peninsula) and the Central-Eastern Mediterranean (Southern Italy, Sicily, Sardinia and Crete) communities (Fig. 1). Our results also highlight a clear separation between the pan-Mediterranean edaphic pseudo-steppes and the vegetation of inland salt pans and saline coastal depressions, when focusing on *L. spartum* dominated vegetation only. The important ecological and biogeographical differences translate into two phytosociological classes, namely the *Lygeo-Stipetea* and the *Salicornietea fruticosae*, as proposed by Pignatti (1952), Rivas-Martínez (1977) and EVC (Mucina et al., 2016), among others. Importantly, this syntaxonomic partition is valid not only for the region of the EVC, but also for the North African vegetation.

All seven alliances of the *L. spartum*-dominated edaphic pseudo-steppes recognised in our study are classified into the order *Lygeo-Stipetalia tenacissimae*. Among these alliances, the *Launaeo angustifoliae-Lygeion sparti* is showing the most remarkable floristic originality. Indeed, the profound drought period experienced yearly by these communities (Fig. 5) might be the major reason why several Saharo-Arabian elements (typical of the so-called ‘pre-desert shrub-steppes’; better perhaps to be defined as 'semidesert low scrub'), such as *Argyrolobium uniflorum, Atractylis serratuloides, Deverra tortuosa, Echiochilon fruticosum, Erodium glaucophyllum, Gymnocarpos* *decander, Linaria aegyptiaca* subsp. *fruticosa* and *Stipagrostis ciliata*, occur profusely in this unit. At the same time, the occurrence of *Anarrhinum brevifolium, Anabasis oropediorum, Diplotaxis harra, Helianthemum lippii* and *Matthiola capiomontana* points upon gypsum-rich substrates (Le Houréou, 1969; Musarella et al., 2018; Pérez-García et al., 2018).

The *L. spartum* vegetation of the NW African Highlands also displays a remarkable floristic originality. From the floristic point of view, both the *Launaeo laniferae-Lygeion sparti* and the *Noaeo mucronatae-Lygeion sparti* are characterised by the occurrence of low shrubs of Saharo-Arabian, Irano-Turanian and Western Mediterranean provenience, such as *Artemisia saharae, Echiochilon fruticosum, Noaea mucronata*, *Reaumuria vermiculata* and the like. These species are absent from the *L. spartum* vegetation found in Europe. The Algerian *L. spartum* vegetation was classified into two alliances, namely the *Noaeo mucronatae-Lygeion sparti* and the *Astragalo cruciati-Muricarion prostratae* (Aidoud-Lounis, 1984). The former alliance is widely distributed on shallow soils and stony/rocky outcrops, whereas the latter is related to deeper, more sandy soils. The floristic difference between the two alliances is, however, related to the abundance of segetal and ruderal species, highlighting the intensive use of the *Astragalo cruciati-Muricarion prostratae* as pasture (Celles, 1975). Because of the abundant annual species considered diagnostic of the latter alliance, we concur with Djebaili (1990) that the *Astragalo cruciati-Muricarion prostratae* should instead be classified into the order *Brachypodietalia distachyi*. A step in the same direction was also taken by Kaabeche (1990) who classified the 'Association à *Medicago truncatula* et *Astragalus cruciatus'* in the order *Brachypodietalia distachyi.*

In a recent phytosociological survey of the vegetation of Morocco (Taleb & Fennane, 2019), the *L. spartum* vegetation of Moroccan Highlands is classified in the Algerian alliance *Noaeo mucronatae-Artemision herbae-albae* (here renamed as *Noaeo mucronatae-Lygeion sparti*) although the authors admit that further studies are needed to clarify the matter. Our results support the classification of the *L. spartum* vegetation of the high plateaus of the Western Antiatlas of Morocco to an alliance described here as the *Launaeo laniferae-Lygeion sparti.*

As far as the Central and Eastern Mediterranean vegetation is concerned, the *Moricandio-Lygeion sparti* and *Scorzonero creticae-Lygeion sparti* were recognised by Mucina et al. (2016), while the *Polygonion tenorei* was considered a synonym of the *Moricandio-Lygeion sparti*. Our results support the reinstatement of the *Polygonion tenorei* as a different alliance, following the suggestions by Brullo et al. (1990, 2010) and Biondi et al. (2014).

On the Iberian Peninsula, our results confirm the recognition of the alliance *Agropyro pectinati-Lygeion sparti*, showing a scattered distribution pattern in the eastern regions of the Iberian Peninsula (bajoaragonés, manchego, bético and murciano-almeriense subprovinces; according to Rivas-Martínez et al., 2011). The vegetation ascribed to this alliance colonises the slopes of the inland depressions, whereas the floristically well-differentiated vegetation of the *Salicornietea fruticosae* occupies the inland salt pans where seasonal ponds occur due to the accumulation of rainwater in wintertime (Braun-Blanquet & de Bolòs, 1958). In general, as already noted by Braun-Blanquet & de Bolòs (*l.c.*), the vegetation ascribed to the *Agropyro pectinati-Lygeion sparti* is related to the Moroccan *L. spartum* communities (Figs. 1 & 5), as they share *Artemisia herba-alba*, *Stipa parviflora* and some Southern Mediterranean therophytes (*Arabis parvula, Malva aegyptia*, *Nonea micrantha,* etc.).

The *L. spartum* communities of the class *Salicornietea fruticosae* are classified into four alliances and two orders (*Limonietalia* and *Limoniastretalia guyoniani).* The communities of three of the alliances classified in the *Limonietalia* occur in endoreic depressions of the Iberian Peninsula: the *Lygeo-Lepidion cardamines* in the La Mancha region (Central Spain), the *Lygeo sparti-Limonion furfuracei* in Murcia and Almeria (SE Spain), and the *Limonion catalaunico-viciosoi* in the Ebro Basin of Northern Spain (Rigual-Magallón, 1968; Costa & Boira, 1981; García-Fuentes, Salazar, Torres, Cano, & Valle, 2001; Molina, Pertíñez, & De La Cruz, 2001; Rivas-Martínez et al., 2011). Within the Iberian inland salt marshes, the floristic-sociological recognition of three different alliances is underpinned by the occurrence of apomictic species of the genus *Limonium*. Our analyses (see Fig. 3) revealed close affinity of the *Agropyro pectinati-Lygeion sparti* and the *Limonion catalaunico-viciosoi* (Biurrun, 1999). Both alliances have been described for the same area, and a salinity gradient is likely to drive the difference between these units from the periphery of salt pans to the surrounding clayey hills.

The species composition of the *L. spartum* vegetation in the coastal depressions appears to be much more homogeneous throughout the Mediterranean Basin. The vegetation of these habitats is classified in the *Limoniastrion monopetali,* found in Egypt (Tadros, 1953), Libya (Brullo &

Furnari, 1988), Sicily (Brullo & Di Martino, 1974), Spain (Rivas-Martínez et al., 2011) and Tunisia (Pignatti, 1952; Barbagallo, Brullo, & Furnari, 1990; Géhu & Géhu-Frank, 1992). This type of vegetation is still poorly known, and we envisage that new data may bring new insights, especially in recognition of an Eastern Mediterranean alliance. Many authors (see above) prefer to keep the *Limoniastrion monopetali* within the order *Limonietalia.* The proposal by Mucina et al. (2016), followed here, to classify the *Limoniastrion monopetali* into the order *Limoniastretalia guyoniani,* deserves further investigation to be taken for granted.

On the origin of the Lygeum spartum communities

The communities dominated by *L. spartum* are most commonly distributed in Maghreb (Tunisia, Algeria and Morocco) and are becoming progressively more scattered in the northward and eastward directions. In Crete, Sardinia, Libya, and Egypt they become restricted to the coastal areas only (Aidoud, Le Floc'h, & Le Houérou, 2006). According to several authors (see Olago, 2001 for a review), the distribution area of these communities experienced expansions and contractions in response to climatic fluctuations typical of Pleistocene. Palynological data support expansive phases of *L. spartum* vegetation during cooler and drier periods (Lamb, Eeicher, & Switsur, 1989). It is likely that the maximum of expansion took place during the Messinian Salinity Crisis (MSC; 5.96–5.33 Ma), when several xerophilous species migrated from North Africa to Europe (Bocquet, Widler, & Kiefer, 1978; Fauquette et al., 2006; Guarino, 2006). During the MSC, the climatic continentality increased all over the Mediterranean Basin (Murphy, Kirk-Davidoff, Mahowald, & Otto-Bliesner, 2009; Jiménez-Moreno et al., 2013). During that period, the Mediterranean Basin might have been characterised by many continental elements, including a typical continental genus such as *Artemisia* (Coetzee, 1967). This element began to disappear from the Mediterranean when the Strait of Gibraltar re-opened at the end of the MSC, and the climatic condition returned to benign (Guarino, Giusso del Galdo, & Pignatti, 2006). This hypothetical sequence of events is suggestive of coherence with our results: the ordination shows a clear gradient from the Central and Eastern Mediterranean communities to the Western Mediterranean and this gradient is positively correlated with the isothermality.

Isothermality quantifies how extensive is the daily temperature range in comparison with the summer-to-winter temperature range. That means that the *L. spartum* communities of North Africa experience daily temperature significantly greater than those of the Iberian Peninsula and Central and Eastern Mediterranean. From the West to the East, across the Mediterranean Basin, a gradual impoverishment in character species of the order *Lygeo-Stipetalia* occurs; the latter tend to be replaced by more broadly-distributed thermomediterranean elements of the class *Lygeo-Stipetea* or floristic elements characteristic of the class *Pegano-Salsoletea* (*Atriplex halimus, Salsola oppositifolia, Suaeda vera* etc.). In the Eastern Mediterranean, the only representative of the order is *L. spartum* itself, whereas in the Iberian Peninsula *Artemisia herba-alba* and *Stipa parviflora* do also occur, probably due to the higher daily temperature ranges of the Iberian Meseta (Fátima, Garcia, Ruiz, Morla, & Sainz, 2001). The karyotype analyses provided a strong support for the *L. spartum* migration scenario (Fauquette et al., 2006), showing that the so far known diploid populations (2n = 16) of *L. spartum* occur in the Algerian Highlands (Benmansour & Harche-Kaid, 2001), whereas in the coastal areas of Oranais (Algeria; Benmansour, & Harche-Kaid *l.c.*), Egypt (Amin, 1972) and Spain (Aragón, Lorenzo-Andreu & García-Sanz, 1950; Granada, Reeder & Singh, 1967) only polyploid populations (2n = 40) have been recorded. The concentration of the diploid populations of *L. spartum* on the NW African Highlands agrees with the general gradients of polyploid frequency shown by Rice et al. (2019).

Conservation notes

The *L. spartum*-dominated communities exhibit always a remarkable occurrence of short-lived annual species. The most typical case is the floristic overlap between the perennial dry grasslands of the *Lygeo-Stipetalia tenacissimae* and the ephemeral communities of the *Stipo-Trachynietea distachyae* (Aidoud-Lounis, 1997). However, the incidence of short-lived (annual) species often increases due to human action. Until recent times, in the Iberian Peninsula, *L. spartum* was used as an indicator of good soil quality for crops (Braun-Blanquet & de Bolòs, 1958), which caused the disappearance of *L. spartum* grasslands from many areas, currently reduced to the fringe of cultivated areas (Ochoa, 1982). The same processes were typical in the inland regions of Sicily and Southern Italy where most of the *L. spartum* grasslands have been transformed into cereal fields, and their remnants are currently restricted to the steepest clayey slopes.

L. spartum is still a significant economic resource in the arid zones from Morocco, Algeria, and Tunisia, especially for nomadic people (Cope & Nesbitt, 2002). It is an important food item for livestock during wintertime and, until a recent past, its leaf fibres were used for paper making, weaving works, shoes, ropes and baskets (Cope & Nesbitt, *l.c.*). According to Aidoud et al. (2006), the occupancy area of *L. spartum* grasslands has been progressively reduced during the last decades, along with the increase of human populations and the intensification of land use. The gain in livestock and cereal fields caused a consequent decline and trivialization of the *L. spartum* grasslands, especially due to the over-grazing, which became a severe problem in the late twentieth century (Puigdefábregas & Mendizabal, 1998). In Europe, the vegetation at issue is protected by the Natura 2000 network (Directive 92/43 EEC) and has been included in the European Red List of Habitats (Janssen et al., 2016), but this tool does not apply to those North African countries, where the *L. spartum* grasslands have not been considered a conservation target so far.

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Data accessibility

The plots for re-analyses are available upon request in an internal repository in the European Vegetation Archive (EVA). The name of the internal repository is "35 – 2016-05-02".

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Supporting Information

Appendix S1 (Basic data on the vegetation plot sources, their origin and associated information on sampling period and plot size).

Appendix S2. (Expert system for classification of phytosociological alliances and classes of *Lygeum spartum* communities).

Appendix S3. (Characteristics of the pools revealed by the TWINSPAN classification).

Appendix S4. (Confusion matrix between the TWINSPAN pools and the alliances for which formal definitions were developed in our expert system).

Appendix S5. (Full synoptic sorted table of Ls dominated communities of the Mediterranean).

Appendix S6. Bibliographic references for all the plots classified using an expert system in this study.

Tab. 1. Simplified synoptic sorted table of *L. spartum* dominated communities of the Mediterranean. For the full version of the table see Appendix S5. Each column represents an alliance. Classes: L: *Lygeo-Stipetea*, S: *Salicornietea fruticosae*. Orders: A: *Lygeo-Stipetalia tenacissimae*, B: *Limonietalia*, C: *Limoniastretalia guyoniani*. Informal groups of alliances: a and b. Alliances: 1: *Agropyro pectinati-Lygeion sparti*, 2: *Launaeo laniferae-Lygeion sparti*, 3: *Noaeo mucronatae-Lygeion sparti*, 4: *Launaeo angustifoliae-Lygeion sparti*, 5: *Moricandio-Lygeion sparti*, 6: *Polygonion tenorei*, 7: *Scorzonero creticae-Lygeion sparti*, 8: *Lygeo-Lepidion cardamines*, 9: *Lygeo sparti-Limonion furfuracei*, 10: *Limonion catalaunico-viciosoi*, 11: *Limoniastrion monopetali*. The column identified as D features the diagnostic value of species in the recognised syntaxa: 1: diag. for the alliance 1, etc.; a or b: diag. for the groups of alliances of the Western and Eastern Mediterranean, resp.; A, B, or C: diag. for the orders A, B, or C, resp.; L and S: diag. species of the classes *Lygeo-Stipetea* and *Salicornietea*, resp.; o: other species not having particular diagnostic value. The grey shading within the body of the table indicates the diagnostic species as identified by the Fisher's exact test, with dark grey shading indicating phi> 0.6 and the light grey shading indicating phi > 0.3. The values in the body of the table are constancy values (% of occurrence in a set of relevés) of species per alliance. The nomenclature of the taxa indicated by asterisk follows other nomenclature sources than the Euro+Med PlantBase.

Classes		L	L	L	L	L	L	L	S	S	S	S
Orders		A	A	A	A	A	A	A	B	B	B	C
Informal groups of alliances		a	a	a	a	b	b	b				
Alliances		1	2	3	4	5	6	7	8	9	10	11
Number relevés per alliance		150	15	34	24	172	43	63	37	95	11	45
	D											
Linum strictum s.l.	1	49	-	-	-	13	2	8	3	-	-	-
Trachynia distachya	1	41	47	3	-	23	-	3	-	-	-	2
Catapodium rigidum s.l.	1	40	-	-	-	5	2	2	5	-	-	-
Launaea lanifera	2	-	73	-	-	-	-	-	-	-	-	-
Carlina hispanica subsp. *hispanica*	2	3	67	-	-	-	-	-	-	-	-	-
Stipa barbata	2	5	60	-	-	-	-	-	-	-	-	-
Leysera leyseroides	2	-	53	-	-	-	-	-	-	-	-	-
Erodium jahandiezianum	2	-	53	-	-	-	-	-	-	-	-	-
Schismus barbatus	3	1	7	85	25	-	-	-	-	2	-	16
Noaea mucronata subsp. *mucronata*	3	-	-	41	-	-	-	-	-	-	-	2
Cutandia divaricata	3	-	-	38	-	-	-	-	-	-	-	-
Gymnocarpos decander	4	-	-	-	75	-	-	-	-	-	-	16
Reamuria vermiculata	4	-	-	-	54	1	-	-	-	-	-	9
Atractylis serratuloides	4	-	-	41	79	1	-	-	-	-	-	11
Echiochilon fruticosum	4	-	-	-	50	-	-	-	-	-	-	9
Helianthemum kahiricum	4	-	-	3	67	-	-	-	-	-	-	33
Moricandia arvensis	5	2	-	-	-	34	-	-	-	2	-	-

Salsola oppositifolia	5	-	-	-	-	27	-	-	-	1	-	2
Allium paniculatum	6	3	-	-	-	1	58	-	-	1	-	-
Scorzonera hispanica	6	1	-	-	-	1	49	-	-	-	-	-
*Polygonum tenorei**	6	-	-	-	-	1	47	-	-	-	-	-
Phagnalon rupestre subsp. *graecum*	7	-	-	-	-	2	-	81	-	-	-	-
Scorzonera cretica	7	-	-	-	-	-	-	76	-	-	-	-
Helichrysum stoechas subsp. *barrelieri*	7	-	-	-	13	-	-	63	-	-	-	11
Limonium dichotomum	8	-	-	-	-	-	-	-	54	-	-	-
Lepidium cardamines	8	-	-	-	-	-	-	-	54	1	-	-
Limonium caesium	9	2	-	-	-	-	-	-	-	44	-	-
Limonium cossonianum	9	1	-	-	-	-	-	-	-	39	-	-
Limonium viciosoi	10	-	-	-	-	-	-	-	-	-	100	-
Dorycnium pentaphyllum s.l.	10	9	-	-	-	1	-	-	-	12	82	-
Atriplex prostrata	10	-	-	-	-	-	-	-	-	-	36	-
Plantago maritima subsp. *serpentina*	10	7	-	-	-	-	-	-	27	5	36	-
Herniaria hemistemon	11	-	-	-	4	-	-	-	-	-	-	51
Limonium alleizettei	11	-	-	-	13	-	-	-	-	-	-	58
Limoniastrum monopetalum	11	-	-	-	-	2	-	-	-	-	-	44
Lotus creticus	11	-	-	-	-	-	-	-	-	-	-	40
Stipa parviflora	a	22	73	53	21	-	-	-	-	1	-	-
Plantago albicans	a	41	-	62	71	16	2	14	-	-	-	2
Filago pyramidata	a	43	13	50	-	9	2	-	-	8	-	-
Artemisia herba-alba	a	52	100	-	-	-	-	-	-	12	9	-

Table 2. Results of the db-RDA step-wise forward selection.

Lygeo-Stipetea	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues*	0,0711	0,041	0,0226	0,0164
Explained variation (cumulative)	7,11	11,21	13,47	15,1
Pseudo-canonical correlation	0,8715	0,8608	0,7665	0,6763
Salicornietea fruticosae				
Eigenvalues**	0,0661	0,0329	0,0194	0,0118
Explained variation (cumulative)	6,61	9,9	11,84	13,02
Pseudo-canonical correlation	0,7531	0,5894	0,6947	0,6506

*Axis 1 (Pseudo-F= 35.3) and all axes (Psedudo-F= 17) combined were significant at P=0.002

**Axis 1 (Pseudo-F= 11.3) and all axes (Psedudo-F= 5.3) combined were significant at P=0.002

Table 3. Explanatory values of the considered climatic variables.

Lygeo-Stipetea	Explains %	Contribution %	pseudo-F	P	P(adj)
Isothermality [ºC]	6,2	38,4	26,2	0,002	0,01
Annual Precipitation [mm/year]	4,2	25,9	18,5	0,002	0,01
Mean Temperature of Warmest Quarter [°C]	2,7	16,5	12,1	0,002	0,01
Precipitation of Driest Quarter [mm/quarter]	2,1	12,8	9,6	0,002	0,01
Salicornietea fruticosae					
Mean Temperature of Warmest Quarter [°C]	4,8	34,9	8,4	0,002	0,01
Annual Precipitation [mm/year]	3,4	24,5	6	0,002	0,01
Isothermality [ºC]	2,7	19,1	4,8	0,002	0,01
Mean Temperature of Driest Quarter [°C]	1,5	10,8	2,8	0,002	0,01
Precipitation of Driest Quarter [mm/quarter]	1,5	10,7	2,8	0,002	0,01

Fig. 1 A diagram of the modified TWINSPAN classification of the 568 resampled relevés into 13 pools. The axis Y reports Whittaker's beta diversity heterogeneity measure.

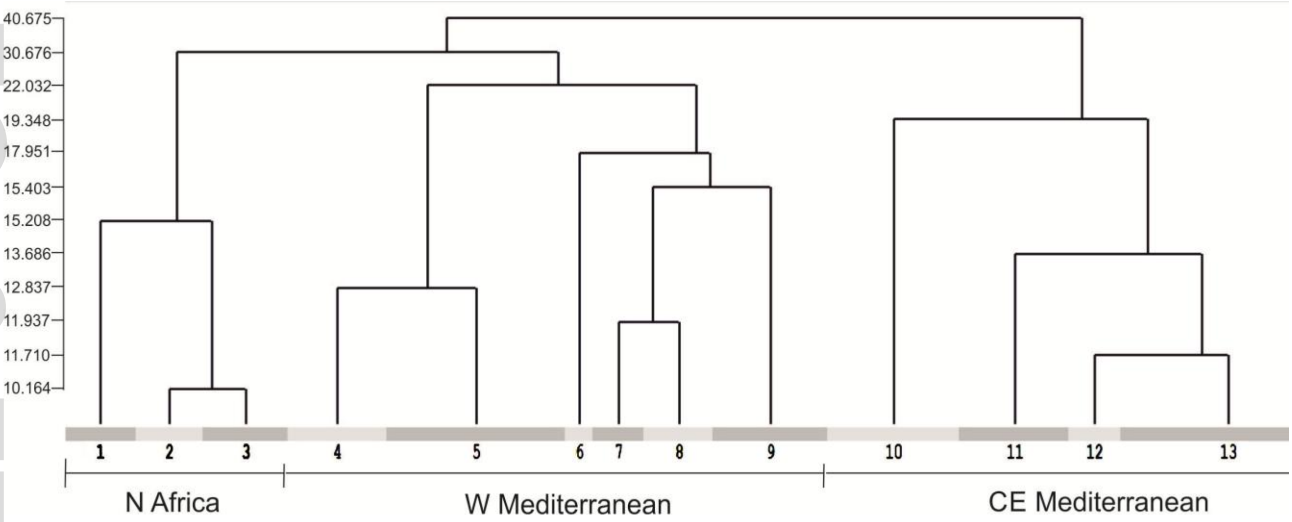

Fig. 2 Distribution map of the vegetation plot data classified to the class *Lygeo sparti-Stipetea tenacissimae*. Abbreviations: *Agropyro pectinati-Lygeion sparti* (Ag-Ly); *Launaeo laniferae-Lygeion sparti* (Lla-Ly); *Noaeo mucronatae-Lygeion sparti* (No-Ly); *Launaeo angustifoliae-Lygeion sparti* (Lan-Ly); *Moricandio-Lygeion sparti* (Mo-Ly); *Polygonion tenorei* (Pol); *Scorzonero creticae-Lygeion sparti* (Sc-Ly). The base map of the Mediitterranean comes from the public source downloaded from https://www.naturalearthdata.com/ website (accessed in April 2019).

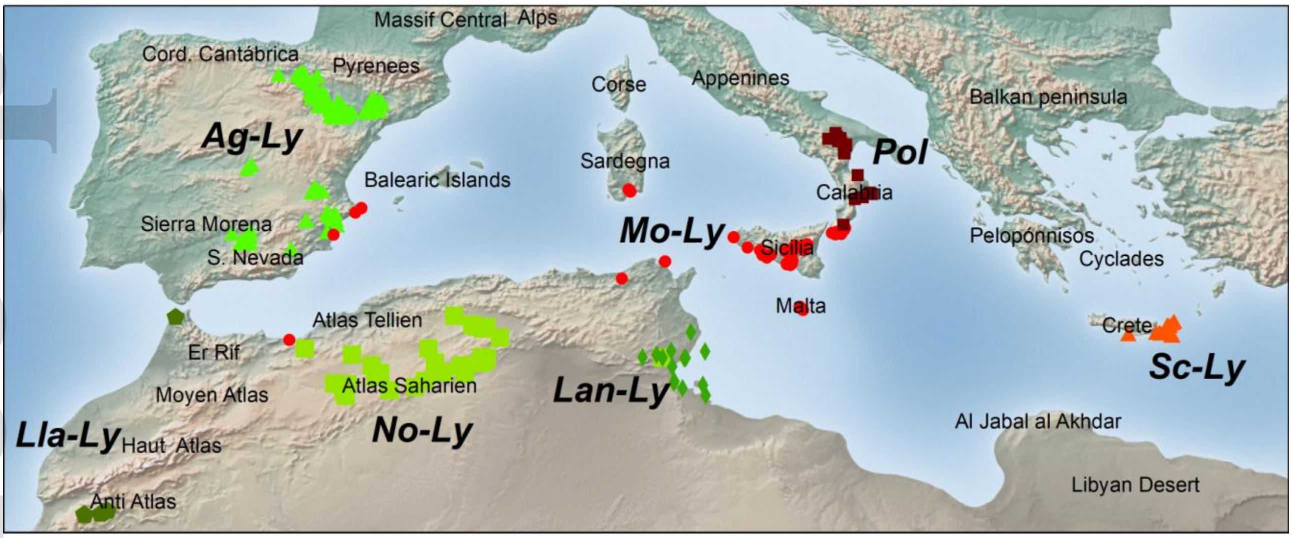

Fig. 3 Distribution map of the selected (ES homogenization) vegetation plot data ascribed to the class *Salicornietea fruticosae*. Abbreviations: *Lygeo-Lepidion cardamines* (Ly-Le); *Lygeo sparti-Limonion furfuracei* (Ly-Li); *Limonion catalaunico-viciosoi* (Lca-vi); *Limoniastrion monopetali* (Lmo). The base map of the Meditterranean comes from the public source downloaded from https://www.naturalearthdata.com/ website (accessed in April 2019).

Fig. 4 The Mediterranean vegetation dominated by *Lygeum spartum*. A: Extensive stands of the *Limonio dubii-Lygeetum spartii* (*Limoniastrion monopetali*) at Saline di Trapani e Paceco near Trapani (Sicily, Italy). B: A stand of the *Sarcocornio fruticosae-Limonietum ferulacei* (*Limoniastrion monopetali*), with prominent *Limoniastrum monopetalum* (pink) at the edge of coastal saline pan (the same locality as A). C: Clayey landscapes of the Bardenas Reales, Navarra, Spain, featuring sparse stands of the *Stipo parviflorae-Lygeetum sparti* (*Agropyro pectinati-Lygeion sparti*). D: A stand of the *Noaeo mucronatae-Lygeion sparti*, with *Noaea mucronata* subsp. *mucronata*, *Lygeum spartum*, *Artemisia saharae*, *Thymus munbyanus* subsp. *ciliatus*, *Helianthemum ruficomum*, *Stipa parviflora*, *Atractylis serratuloides* and *Psychine stylosa*) from the surroundings of the Sacred Natural Site Sidi Atmane-Tichniouine, near Ait Zora, Basse Moulouya, Province Nador, NE Morocco. E: Monte San Nicola near Gela (Sicily), geologically important locality serving as the GSSP reference point for the beginning of Quaternary, supporting vegetation of the *Phagnalo annotici-Lygeetum sparti* (*Moricandio-Lygeion sparti*). F: Vegetation of the *Limonion catalaunico-viciosoi* (saline bottomlands) and the *Agropyro pectinati-Lygeion sparti* (piedmonts) at Los Monegros near Zaragoza (Aragón, NE Spain), in the central Ebro Basin. G: Stands of the *Lygeo sparti-Limonion furfuracei* in saladares of the Murcia-Almeria region, southern Spain. H:

Pleistocene (Blue Clay) badlands in the ancient intra-Apennine marine Paleobacino di Sant’Arcangelo at Ferrandina (Basilicata, Southern Italy), supporting the *Camphorosmo monspeliacae-Lygeetum sparti* (*Polygonion tenorei*). Photo credits: A, B, E: L. Mucina; C: M. Janišová; D: U. Deil; F: J. Loidi; G: F. Alcaraz; H: R. Guarino.

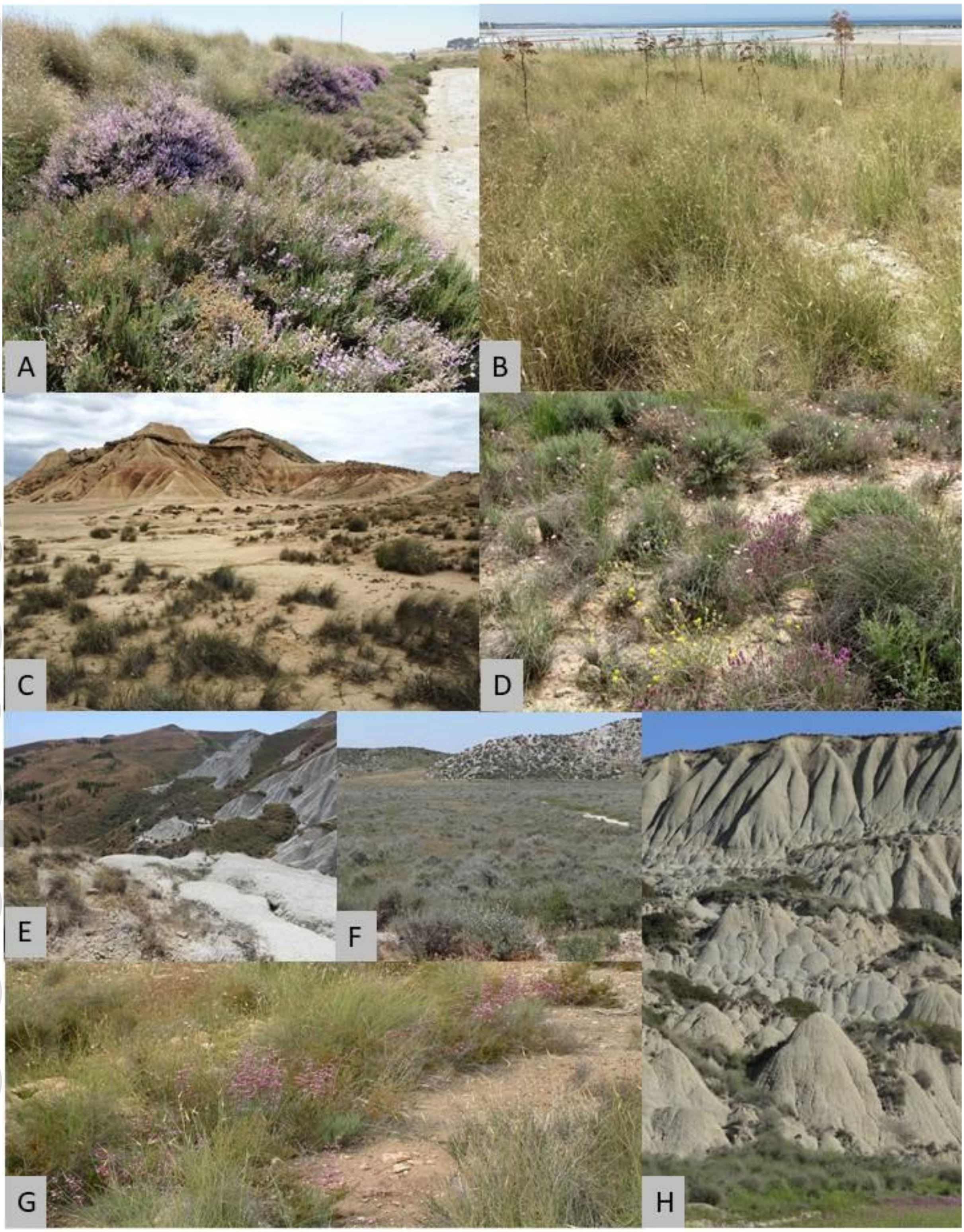

Fig. 5. db-RDA ordination of the alliances classified in the class *Lygeo-Stipetea*. DQ: driest quarter of the year; WQ: warmest quarter of the year.

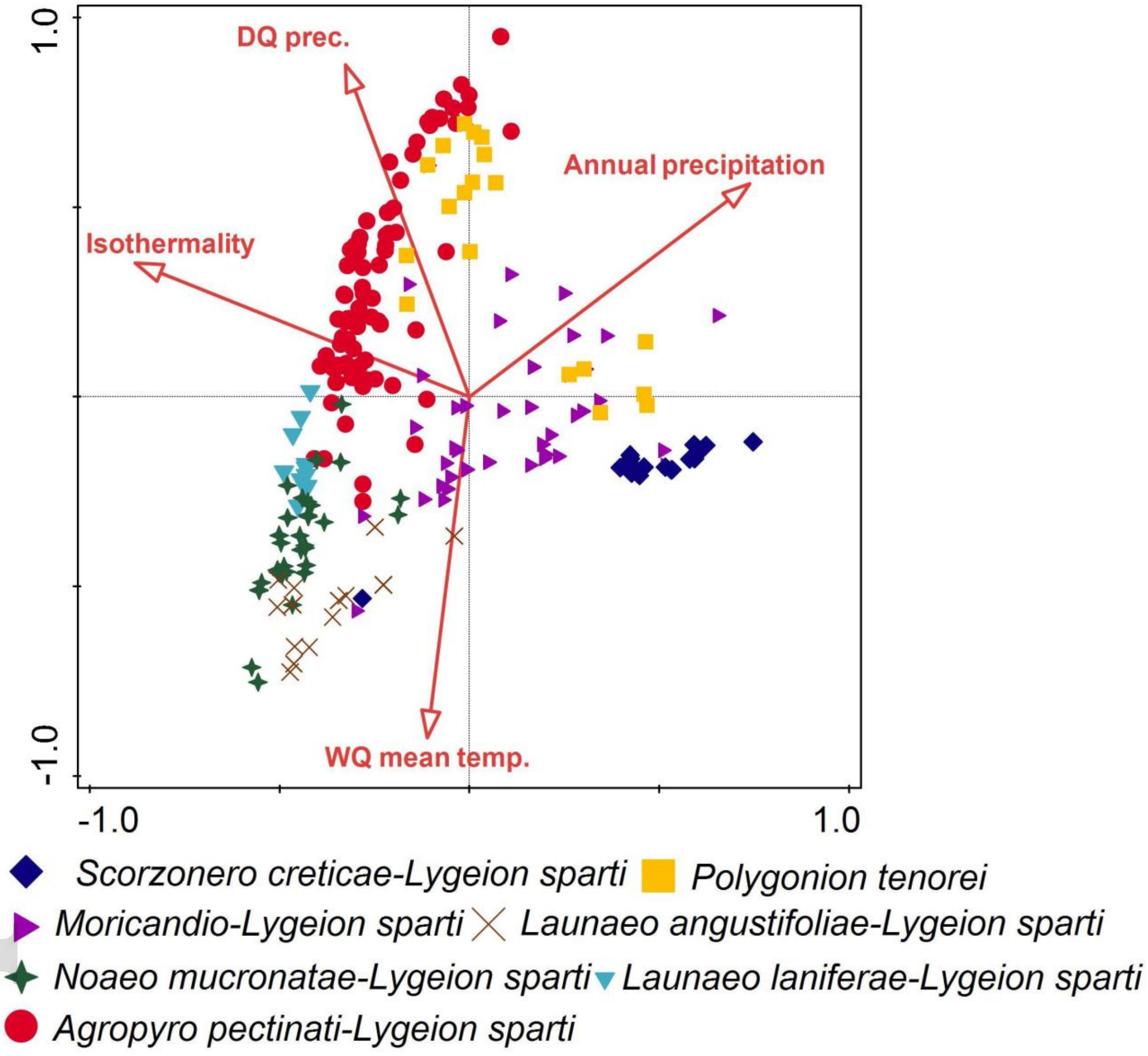

Fig. 6 db-RDA ordination of the alliances classified in the class *Salicornietea fruticosae*. DQ: driest quarter of the year; WQ: warmest quarter of the year.