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Mediterranean landscapes and plant communities relationship

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Abstract. On the basis of an earlier landscape classification of Huelva (Andalusia, Spain) using the Twinspan multivariate classification method, which resulted in eight landscape types, the study sought to test the hypothesis that a relationship may exist between landscape types and plant communities. Samples of serial scrub communities were examined by stratified sampling between landscape types. Samples were classified using phytosociological and Twinspan methods. After merging landscape types and Twinspan-classified community types, the possible association between the two was analysed by means of a two-way contingency table between five landscape units and five plant communities. Findings enabled the null hypothesis, i.e. that both descriptors were independent, to be rejected. Given the high degree of overall agreement between phytosociological and multivariate plant community classifications, inter-community variation was studied via ecological characterization of the syntaxa identified. The results indicated that parent material played a more important role than climate-related variables in accounting for this variation. This conclusion supports the role assigned to each of the two factors in the biogeographical domain, according to the scale of the study.

Keywords: Landscape characterization; Mediterranean scrub; Twinspan, phytosociology; Huelva (Andalusia).

[es] Paisajes mediterráneos y su relación con las comunidades vegetales

Resumen. A partir de la realización previa de una clasificación del paisaje de Huelva (Andalucía, España) mediante el uso del método multivariante de clasificación Twinspan, con la diferenciación de ocho tipos de paisaje, se ha planteado la hipótesis de la posible existencia de una relación tipos de paisajes-comunidades vegetales. El estudio se ha realizado a partir de comunidades de matorrales bajos, muestreados de forma estratificada entre los tipos de paisajes. Las muestras fueron clasificadas según la metodología fitosociológica y según el Twinspan. Después de un proceso de fusión entre tipos de paisajes, por una parte, y tipos de comunidades (según clasificación Twinspan) por otra, se ha procedido a un análisis de la posible asociación entre paisajes y comunidades. Este análisis, realizado mediante tabla de contingencia de doble vía entre cinco unidades de síntesis de paisajes y cinco de comunidades vegetales, ha permitido rechazar la hipótesis nula de que ambos descriptores fueran independientes. A partir de la buena correspondencia global entre la clasificación fitosociológica y la multivariante de las comunidades, se ha realizado un análisis de la variación entre comunidades en base a la caracterización ecológica de los sintaxones identificados. Del mismo se ha concluido el papel más determinante del material parental frente a variables climáticas, para explicar esta variación. Lo que concuerda con el papel atribuido a unas y otras en el ámbito biogeográfico, según la escala de estudio.

Palabras clave: Caracterización del paisaje; matorrales mediterráneos; Twinspan; fitosociología; Huelva (Andalucía).

Introduction

According to the European Landscape Convention (Anon., 2000), landscape is the framework within which policies regarding the socio-economic development and conservation of Europe's natural and cultural resources must converge. The objectives of this Convention are the protection, management, and planning of the landscape. Outstanding fea-

tures of this approach include: (a) taking into account all landscapes, and therefore all territories; (b) studying all the elements involved in each landscape – cultural, environmental, social, and economic; and (c) the advisability of integrating the landscape in the territorial and sectorial policies of different levels of government (Anon., 2008). This scenario has formed the backdrop for a range of initiatives, including landscape studies in the UK (Swan-

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wick, 2002), the *Atlas de los Paisajes de España* (Sáenz Herráiz *et al.*, 2003), the European Landscape Map (LANMAP; Múcher *et al.*, 2003; Wascher, 2005), and the *Bases para la realización del Sistema Compartido de Información sobre el Paisaje de Andalucía* (SCIPA; Moreira & Zoido, 2014).

Identification of the landscapes in a territory is inseparable from their classification, and is indispensable for any action guided by the principles set out above (Wascher, 2005; Anon., 2008). In turn, landscape classification is associated with the identification of landscape-type indicators. With respect to these indicators, a review of 49 national and regional landscape maps of various European countries (Wascher, 2005) showed a clear predominance of biophysical factors (geology, relief, climate, etc.) over cultural factors (land uses, settlement patterns, etc.). Predominant among the biophysical factors are those relating to relatively independent abiotic phenomena rather than relatively dependent biotic variables (Múcher *et al.*, 2003). The three variables whose attributes were used to map the landscapes of Europe were topography, parent material, and land uses (Múcher *et al.*, 2003). One of the biotic variables systematically taken into account in the classification of landscapes is vegetation (Forman & Godron, 1986; Zonneveld, 1995; Múcher *et al.*, 2003; Farina, 2006).

Vegetation may be regarded as the most conspicuous feature of most landscapes (Box & Fujiwara, 2013). Its importance for the recognition of biomes accounts for its worldwide use in the classification of large regional ecosystems (Kent & Coker, 2003; Leuschner, 2013), since it distinguishes vegetation types based on their physiognomy (formations) (Mueller-Dombois & Ellenberg, 2002; Box & Fujiwara, 2013). The vegetation's physiognomy depends on the dominant plants and their form or structure (form of growth and life-forms). Given the interdependence of form and function, structural morphological characteristics depend on basic physiological processes, particularly those related to "water and energy budgets" (Box, 1981: 2). The physiological processes are in turn climatically controlled (Woodward, 1996). Hence the emergence, through processes of convergent evolution, of similar physiognomic responses in taxa lacking a close phylogenetic relationship, but which grow under similar climate conditions, regardless of the geographical distance between them (Box & Fujiwara, 2013).

The main alternative to the physiognomic-structural classification of vegetation is the floristic classification based on the presence or absence of species in plant communities. Of the various systems of floristic classification currently in use, one of the most widespread is the Braun-Blanquet system (1964), usually termed "phytosociology". The definition of plant community by Westhoff & van der Maarel (1978) explicitly highlights the crucial role that species play in this classification system (a system whose fundamental typological unit is the association). Equally determinant in phytosociology are the environmental conditions with which a given plant community is associated: "The only way variations in vegetation and plant species distributions can be properly understood and explained is within an ecological framework" (Kent & Coker, 2003: 1). While physiognomic-ecological systems allow global comparisons of vegetation, floristic systems are meaningful at smaller geographical scales (Mueller-Dombois & Ellenberg, 2002).

An earlier landscape classification study of the province of Huelva (Spain) using multivariate methods distinguished eight types of landscape. Given the differences between these landscape types in terms of their predominant physical factors, the present study sought to test the hypothesis that such differences are reflected in the natural vegetation.

Material and Methods

Study area

The study was carried out in the province of Huelva (Andalusia, Spain), which has an area of 10128 km² (Figure 1). Due to its proximity to the Atlantic, it has an oceanic Mediterranean climate (Pita, 2003), reflected in a smaller interval between the average temperatures of the warmest and coolest months. The rise in altitude from south to north also influences temperatures, which decrease northwards. Winters are mild, with monthly averages above 10°C and summer averages of around 25°C. The maximum temperature rarely exceeds 40°C. Annual rainfall ranges from 500 to 600 mm (in the hilly area of the interior, it can reach 1000 mm). Maximum rainfall is recorded in late autumn-winter, and rainfall is sparse in summer. The thermo-Mediterranean and meso-Mediterranean belts are present, as well as dry, subhumid and humid ombrotypes (Valle, 2004).



Figure 1. Map of the study area, Huelva province (Andalusia, Spain).

Huelva has two large geostructural units. The northernmost almost two thirds form part of the Hesperian Massif (of Hercynian orogen), with a predominance of Precambrian and Palaeozoic materials – shales, quartzite, and volcano-sedimentary and plutonic rocks. These mainly acidic rocks generally produce poor soils with underdeveloped profiles. The rest of the territory forms part of the Baetic (Guadalquivir) Depression. It acts as a receiving basin for eroded sediment from the Hesperian Massif and, above all, from the Baetic Ranges. The materials filling the basin during the most recent (Quaternary) period are lacustrine, fluvial (terraces and alluvial deposits), colluvial, eolian (coastal dunes, mantles), and from marshes formed by the closure of different river estuaries (Moreira, 2003).

Landscape types

The landscape classification used in the present study is that reported by Alcántara-Manzanares & Muñoz-Álvarez (2015a). The study area was sectorized into a 1 km × 1 km georeferenced grid. To each of the resulting 10464 grid cells, information was associated on land

use and vegetation coverage, lithology and relief. By means of a TWINSPLAN divisive multivariate hierarchical analysis, eight types of landscapes were distinguished. On the basis of this initial, a merged set of five landscape types was used for the present study (Figure 2).

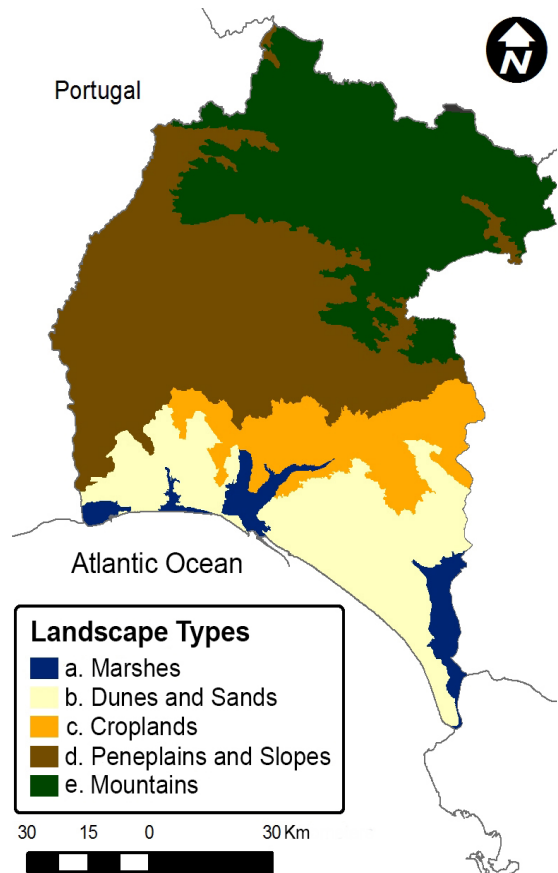


Figure 2. Map of Huelva province with the distribution of landscape types studied.

The diagnostic characteristics of these landscapes are:

Marshes: flat areas (without orientation); slope < 3%; silt; land use – marshes with and without vegetation.

Dunes and Sands: slope 3-7%; average altitude 18-44 m asl; sand; land use – scattered scrubland with conifers.

Croplands: slope 7-15% and 15-30%; average altitude 44-178 m asl; marl land use – rain fed herbaceous crops.

Peneplains and Slopes: altitude ranges 100-200 m asl and 200-300 m asl.

Mountains: slope 30-45% and > 45%; altitude ranges 400-500 m asl and 500-600 m asl; land use – dense oak woodland.

These last two landscapes share shales and quartzite as the predominant lithology, which differentiates them from the first three (indicator value: 0.73).

Twinspan works by dividing a set of samples (in this case, the grid cells) into two groups, one characterized by a first set of indicator variables and the other by a second set of indicator variables. A good indicator variable is one which is present in most samples in one group and in only a small number of samples in the other. A variable—for example, a type of land use—may thus be a diagnostic characteristic of a certain landscape type, without the need for another type of land use to appear as a diagnostic characteristic of the other landscape type. The initial subdivision of relief variables, such as altitude or slope ranges, and the area of the landscapes, accounts for the presence of different relief variable ranges in some landscape types.

Vegetation

The analysis of plant communities focused on samples of low serial scrub, with the exception of marshland communities, which consist of stable non-serial scrub. Samples were collected using the Digital Mapping of Land Use and Vegetation Cover in Andalusia (scale 1:25000; available from the Andalusia Environmental Information Network), taking polygons typified as dense scrubland whose dominant species is of a serial type. Of these, 20 were selected at random for each of the eight originally-differentiated landscape types. Accordingly, the following major vegetation series domains were sampled: *Pyro bourgeanae-Quercus rotundifoliae* S., *Myrto communis-Quercus rotundifoliae* S., *Oleo-Quercus suberis* S., *Sanguisorbo-Quercus suberis* S., *Myrto communis-Quercus suberis* S. and *Smilaco mauritanicae-Quercus rotundifoliae* S. (Valle, 2003).

Samples were inventoried phytosociologically (Braun-Blanquet, 1964). The sampling area was 100 m². The final number of samples used was 140 (Marshes: 15; Dunes and Sands: 40; Croplands 12; Peneplains and Slopes: 36; Mountains 37). The nomenclature followed is that of Flora Iberica (Castroviejo, 1986-2015 and Flora Vasculare de Andalucía Occidental (Valdés *et al.*, 1987).

Samples were classified by phytosociological and multivariate methods. The phytosociological framing mainly followed Ri-

vas-Martínez *et al.* (2001). To reflect floristic differences between syntaxa, a synthesis table was prepared. For multivariate analysis, samples and species were subjected to an outlier analysis using Chi-squared as a measure of distance (McCune & Mefford, 1999). This procedure yielded a matrix of 140 samples and 53 species, which was subjected to a TWINSpan classification analysis (Kent & Coker, 2003) using the PC-ORD 4.0 software package (McCune & Mefford, 1999).

Comparison of landscape and plant community classifications

Landscape and plant community classifications were compared using a two-way contingency table (Legendre & Legendre, 1998). The vegetation samples were the objects assigned to table cells as a function of landscape type (where sampling was performed) and community type. The plant community types used were those resulting from the TWINSpan classification. Although the initial contingency tables were generated using the eight landscape types distinguished by Alcántara-Manzanares & Muñoz-Álvarez (2015a) and the seven plant community types yielded by TWINSpan analysis, the large number of cells with expected values of below 5 prompted the need to cluster both landscape types and communities; ultimately, since expected frequencies continued to be too low, Fisher's exact test was performed (Quinn & Keough, 2002) by means of a Monte Carlo simulation (Manly, 1997) using the Exact Test 1.0.0.1 software package for Windows.

Results

Comparative analysis of vegetation type classifications

Nine associations were identified phytosociologically, one of which had two sub-associations (Table 1). Table 2 shows the distribution of species among different syntaxa. Figure 3 shows the TWINSpan classification of relevés, and Table 3 the correspondence between the two classifications. It can be deduced from the comparison in this table that there is an acceptable correspondence between six of the syntaxa and six of the clusters: 1-I, 2-II, 3-III, 5-V, 7-VI, and 8-VII. Each of the other four syntaxa (4, 6, 9, 10), all

of which comprised just a few samples and were floristically related to other, better-represented syntaxa (Table 2), is included in one of the six clusters mentioned above.

One striking feature of Table 3 is the splitting of the 15 *Ulici eriocladi-Cistetum ladaniferi* samples into two TWINSPAN clusters V and VI. Analysis of Figure 3 and Table 3 shows that this separation occurs in TWINSPAN Division 5. This disjunction can be traced to the essentially-simultaneous presence/absence of differential species for Division 5 (Figure 3). The presence of *Cistus monspeliensis* and *Genista hirsuta* together with the absence of *Erica australis*, *E. umbellata*, *Pterospartum tridentatum*, *Halimium ocymoides*, and *Cistus populifolius* is crucial for the establishment of the cluster of 57 relevés, and vice versa for that of the cluster of 37 relevés. The presence of *Ulex eriocladus* in all samples, decisive for phytosociological identification, is

of secondary importance in the multivariate classification.

Also worthy of note is the appearance of a type of community –IV– not differentiated phytosociologically. It is a split-off cluster of samples of *Genisto-Cistetum ladaniferi cistosum ladaniferi* (most of which - 32 - make up cluster V; Table 3). Given the indicator species of this cluster IV (Figure 3), we can deduce that its appearance is determined by *Cistus monspeliensis* ($I=0.70$), accompanied by certain other species, each of which is individually infrequent, such as *Retama sphaerocarpa*, *Asparagus aphyllus*, *Ulex argenteus* subsp. *subsericeus*, *Olea europea* var. *sylvestris*, *Chamaerops humilis*, and *Phlomis purpurea*, these being mostly species that are either missing or are only present in up to 2 of the 46 samples of cluster V. A further factor is the absence of *Cistus ladanifer*, characteristic of cluster V with important cover values.

Table 1. Syntaxonomical and ecological framework of the associations and sub-associations identified according to Rivas-Martínez et al., 2001. The number of relevés (N. rel.) is also indicated.

Association/subassociation	N. rel.	Syntaxonomy	Ecological categories
<i>Spartinetum densiflorae</i> Rivas-Martínez, Costa, Castroviejo & E. Valdés 1980	4	<i>SPARTINETEA MARITIMAE</i> <i>Spartinetalia glabrae</i> <i>Spartinion glabrae</i>	III. Coastal and continental halophilous and sand dune vegetation
<i>Halimiono portulacoidis-Sarcocornietum alpini</i> Rivas-Martínez & Costa 1984	11	<i>SALICORNIETEA FRUTICOSAE</i> <i>Salicornietalia fruticosae</i> <i>Arthrocnemion glauci</i>	IIIb. Coastal and continental halophilous vegetation
<i>Erico australis-Cistetum populifolii</i> Rivas Goday 1964	5	<i>CALLUNO-ULICETEA</i> <i>Ulicetalia minoris</i> <i>Ericion umbellatae</i>	
<i>Erico scopariae-Ulicetum australis</i> Rivas-Martínez, Costa, Castroviejo & E. Valdés 1980	1		
<i>Halimio ocymoidis-Ericetum umbellatae</i> Rivas Goday 1964	1		
<i>Genisto hirsutae-Cistetum ladaniferi cistosum ladaniferi</i> Rivas Goday 1956	46	<i>CISTO-LAVANDULETEA</i> <i>Lavanduletalia stoechadis</i> <i>Ulici argentei-Cistion ladaniferi</i>	VIII. Heathland, dwarf scrub and scrub vegetation
<i>Genisto hirsutae-Cistetum ladaniferi ericetosum australis</i> Rivas Goday 1956	26		
<i>Ulici eriocladi-Cistetum ladaniferi</i> Rivas-Martínez 1979	15		
<i>Scillo maritimae-Lavanduletum pedunculatae</i> Ladero 1970	3		
<i>Halimio halimifolii-Stauracanthetum genistoidis</i> Rivas-Martínez, Costa, Castroviejo & E. Valdés 1980	28	<i>Stauracantho genistoidis-Halimietalia calycini</i> <i>Coremation albi</i>	VIIIa. Heathland, and dwarf scrub vegetation

Analysis of the relationship between plant community types and landscape types

The results of the contingency table (Table 4) enable rejection of the null hypothesis, i.e. that the two descriptors –types of landscapes and types of plant communities– are independent.

This relationship can be analysed on the basis of plant communities and the differential characteristics of landscape types (see Material and Methods).

Syntaxonomic findings (Table 1) show that, ecologically, three fundamental axes fit the basic pattern of variation in vegetation: one

corresponding to a salinity gradient, another to a gradient associated with the fine sandy texture of the soils, and a third to an ombic gradient reflecting the distribution of higher or lower rainfall over the territory. In relation to the first of these ecological gradients, association of the classes *Spartinetea maritimae* and *Sarcocornietea fruticosae* (Table 1) –C1 (Figure 3)– is differentiated from the rest. These are typical marsh communities (Figure 2, Table 4, Photo 1). For the second of the gradients, the most striking association is that of the order *Stauracantho genistoidis-Halimietalia calycini* (C2, Figure 3), an order which includes sandy fine-textured soil communities (sands and palæodunes) (Rivas-Martínez *et al.*, 2011), characteristic of Dunes and Sand landscapes (Figure 2, Table 4, Photo 2).

With the exception of *Erico scopariae-Ulicetum australis*, in the remaining subset of associations and sub-associations, it is the ombic gradient which underlies their classification into two sub-clusters, one encompassing typical dry ombroclimate syntaxa –C3 and C4 (Figure 3)– of *Ulici-Cistion ladaniferi* (Table 1, Photo 3), and the other encompassing more humid ombroclimate syntaxa –C5 (Figure 3, Photo 4). These C5 communities are mostly linked to the Mountain landscape type (Figure 2, Table 4) in which a large part of the territory corresponds to the *Sanguisorbo hybridae-Quercus suberis* sigmetum cork oak forest vegetation serie (Rivas-Martínez, 1987; Valle, 2003), whose characteristic serial stage consists of heaths and rockrose-heaths of C5.

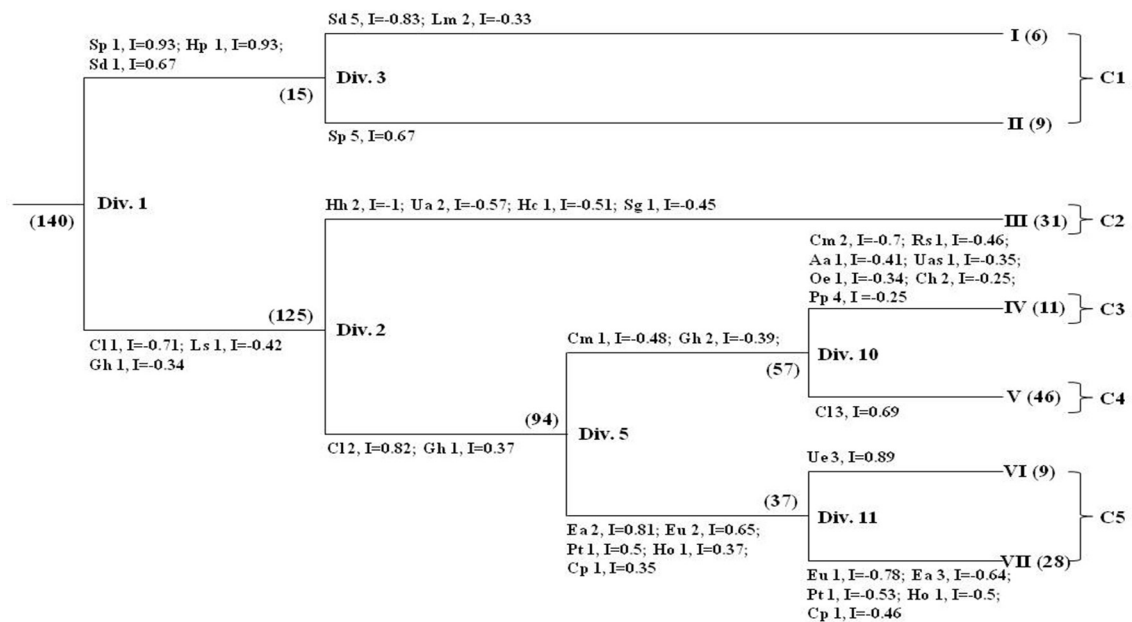


Figure 3. Dendrogram with the Twinspan classification of the relevés: the original (clusters I-VII) and that of synthesis (clusters C1-C5). The successive Twinspan divisions are identified (Div. 1, 2, 3, 5, 10 and 11), as well as the indicator species and their indicator value (I). Aa, *Asparagus aphyllus*; Ch, *Chamaerops humilis*; Cl, *Cistus ladanifer*; Cm, *Cistus monspeliensis*; Cp, *Cistus populifolius*; Ea, *Erica australis*; Eu, *Erica umbellata*; Gh, *Genista hirsuta*; Hc, *Halimium calycinum*; Hh, *Halimium halimifolium*; Ho, *Halimium ocymoides*; Hp, *Halimione portulacoides*; Ls, *Lavandula stoechas*; Lm, *Limoniastrum monopetalum*; Pt, *Pterospartum tridentatum*; Sd, *Spartina densiflora*; Sg, *Stauracanthus genistoides*; Sp, *Sarcocornia perennis* subsp. *alpini*; Ua, *Ulex australis*; Uas, *Ulex argenteus* subsp. *subsericeus*; Ue, *Ulex eriocladus*. Shown for each species is the level of relative abundance on an ordinal scale (1: 0–2%; 2: 2–5%; 3: 5–10%; 4: 10–20%; 5: 20–100%). In parentheses is the number of samples of each cluster.

Table 2. Synthetic table of the identified syntaxa. 1. *Spartinetum densiflorae*; 2. *Halimiono portulacoidis-Sarcocornietum alpini*; 3. *Halimio halimifolii-Stauracanthetum genistoidis*; 4. *Erico scopariae-Ulicetum australis*; 5. *Scillo maritimae-Lavanduletum sampaianae*; 6. *Genisto hirsutae-Cistetum ladaniferi cistosum ladaniferi*; 7. *Ulici eriocladi-Cistetum ladaniferi*; 8. *Genisto hirsutae-Cistetum ladaniferi ericetosum australis*; 9. *Erico australis-Cistetum populifolii*; 10. *Halimio ocymoidis-Ericetum umbellatae*. Taxa presence is indicated by roman or arabic numerals, depending on the number of samples, ≥ 6 or < 6 , respectively (Géhu & Rivas-Martínez, 1981). The second number or symbol indicates the value or range of the most frequent Braun-Blanquet cover-abundance index.

N. relevés	4	11	28	1	3	46	15	26	5	1
Relevé N.	1	2	3	4	5	6	7	8	9	10
<i>Spartina densiflora</i> Brongn.	4, 5	III, +
<i>Halimione portulacoides</i> (L.) Aellen	4, 1-2	V, +-1
<i>Limoniastrum monopetalum</i> (L.) Boiss.	1, 2	II, +
<i>Sarcocornia perennis</i> subsp. <i>alpini</i> (Lag.) Castrov.	3, 2	V, 4-5
<i>Arthrocnemum macrostachyum</i> (Moric.) Moris	.	I, 1-2
<i>Stauracanthus genistoides</i> (Brot.) Samp.	.	.	III, 2
<i>Helichrysum picardii</i> Boiss. & Reut.	.	.	II, +2
<i>Halimium halimifolium</i> subsp. <i>halimifolium</i> (L.) Willk. in Willk. & Lange	.	.	V, 3-4	1, 3	.	+, +	.	r, +	.	.
<i>Halimium calycinum</i> (L.) K. Koch	.	.	I I I , 1-2	.	.	r, 1-2
<i>Cytisus grandiflorus</i> (Brot.) DC.	.	.	II, 1-2	.	.	r, +
<i>Armeria velutina</i> Welw. ex Boiss & Reut.	.	.	I, +	1, +
<i>Erica scoparia</i> L.	.	.	r, 1	1, 2	.	.	.	r, +	.	.
<i>Ulex australis</i> subsp. <i>australis</i> Clemente	.	.	III, 2	1, 2	.	r, +-1	.	r, 1	.	.
<i>Lavandula pedunculata</i> (Mill.) Cav.	.	.	II, 2	.	3, 4	.	+, 2	.	.	.
<i>Urginea maritima</i> (L.) Baker	2, +	r, +	+, +	r, r	.	.
<i>Genista hirsuta</i> Vahl	.	.	+, r-1	.	2, 1-2	III, 2	II, 1	II, 2	3, +	.
<i>Cistus ladanifer</i> L.	.	.	+, r-+	.	2, +	V, 4-5	V, 4-5	V, 5	5, 2	1, 1
<i>Cistus monspeliensis</i> L.	.	.	I, +	.	1, 2	III, 4	II, 2	I, 1	.	.
<i>Phlomis purpurea</i> L.	+, 2
<i>Ulex eriocladius</i> C. Vicioso	V, 2	.	.	.
<i>Erica australis</i> L.	r, r-+	I, 1	V, 3-4	5, 4	1, 1
<i>Erica umbellata</i> Loeffl. ex L.	.	.	+, +-1	.	.	r, +-1	+, r	IV, 2	5, 2	1, 4
<i>Halimium ocymoides</i> (Lam.) Willk.	r, +	.	II, +-1	2, 1	1, 3
<i>Genista triacanthos</i> Brot.	.	.	+, 1	.	.	r, r-1	.	I, +-1	1, +	.
<i>Cistus populifolius</i> L.	r, 3	.	II, +	5, 1-3	.
<i>Pterospartum tridentatum</i> subsp. <i>lasianthum</i> (Spach.) Talavera & P.E. Gibbs	IV, 1-2	3, 2	1, 2
<i>Phillyrea angustifolia</i> L.	.	.	r, r	.	.	.	+, r	I, r-1	2, 1	.
<i>Chamaerops humilis</i> L.	.	.	+, r-2	.	.	I, + 1-2
<i>Cistus salvifolius</i> L.	.	.	I I I , 1-2	.	1, 1	+, +	I, 1-3	II, +	1, +	.
<i>Asparagus aphyllus</i> L.	.	.	I, r	.	.	I, +
<i>Calluna vulgaris</i> (L.) Hull	.	.	II, r-1	1, 2	.	.	.	I, + 1-2	.	.
<i>Rosmarinus officinalis</i> L.	.	.	II, 1-2	1, +	.	I, 2	.	I, 2	1, 1	.
<i>Helichrysum stoechas</i> (L.) Moench	.	.	I, r-1	1, +	.	I, +	.	r, +	1, +	.
<i>Lavandula stoechas</i> subsp. <i>stoechas</i> L.	.	.	I, 1	.	.	II, 1	III, 1	III, 1	.	.

<i>Thymus mastichina</i> (L.) L.	.	.	II, 1	.	.	+, +
<i>Cistus crispus</i> L.	.	.	+, r-2	.	1, 2	r, 1	I, +	-	.	.
<i>Carlina corymbosa</i> subsp. <i>hispanica</i> (Lam.) O. Bolós & Vigo	.	.	+, +	.	1, 1	I, +	I, +-1	+, +	.	.
<i>Olea europea</i> var. <i>sylvestris</i> (Mill.) Lehr	+, r+	+, 1	.	.	.
<i>Quercus rotundifolia</i> Lam.	I, r+	II, 2	+, +	1, +	.
<i>Arbutus unedo</i> L.	II, +	2, +	.
<i>Phagnalon saxatile</i> (L.) Cass.	I, +	+, 2	.	.	.
<i>Pistacia lentiscus</i> L.	+, r-1	+, +	.	1, +	.
<i>Lavandula stoechas</i> subsp. <i>luisieri</i> (Rozeira) Rozeira	I, 1	II, 1-2	II, +	2, +	1, +
<i>Lavandula viridis</i> L'Hér.	.	.	+, 2	1, 2	.	r, r+	.	+, 1	2, 1-2	.
<i>Asparagus acutifolius</i> L.	r, +	+, +	.	.	.
<i>Retama sphaerocarpa</i> (L.) Boiss.	+, 2	+, +	r, +	.	.
<i>Quercus coccifera</i> L.	r, +-2	.	+, r-1	.	.
<i>Myrtus communis</i> L.	.	.	+, r-1	.	.	r, +-1	.	II, 1	.	.
<i>Quercus suber</i> L.	+, r-1	2, r+	.
<i>Cistus libanotis</i> L.	.	.	+, 1	.	.	r, +
<i>Ulex argenteus</i> subsp. <i>subsericeus</i> (Cout.) Rothm.	.	.	+, 2	.	.	I, 2	.	r, 3	.	.
<i>Elaeoselinum foetidum</i> (L.) Boiss.	+, +
<i>Dactylis glomerata</i> L.	2, +-1	r, +
<i>Thapsia villosa</i> L.	.	.	II, +	.	.	r, +	+, +	.	.	.

The C4 communities correspond basically to rockroses with *Genisto-Cistetum cistetosum ladaniferi* gorses (Figure 3, Table 3). These grow on siliceous oligotrophic soils that are shallow and decapitated (Rivas-Martínez, 1979). Such soils are predominant in the Peneplain and Slope and Mountain landscapes, characterized by shale and quartzite lithology. Hence, the C4 communities are associated with Peneplain and Slope landscapes, in which the ombroclimatic and edaphic characteristics indicated above converge.

The ecological determinants of the C3 community can be explained by the indicator species (Figure 3) and the distribution of the relevés among landscape types (Table 4). Seven of the eleven samples were taken in Cropland landscape, characterized by marl lithology, the predominance of average altitudes of 44-178 m asl, and the use of the territory for farming (rainfed crops). These characteristics imply the existence of soils with a developed profile, suitable for the growth of *Cistus monspeliensis* (present in all C4 samples). The presence of *Ch. humilis*, *A. aphyllus*, and, to a lesser extent, *Ph. purpurea* –indicator species of the thermo-Mediterranean belt (at those indicated

altitudes)– adds to the edaphic variable a thermal-type climate variable, thus more clearly profiling the ecological conditions of the Cropland landscape. Finally, the location of olive groves and pastureland in some areas of this more anthropized landscape (Alcántara-Manzanares & Muñoz-Álvarez, 2015b) would account for the appearance of *R. sphaerocarpa* and *O. europea* var. *sylvestris*.

The statistically significant relationship between landscapes and communities implies that certain landscapes are more or less strongly associated with certain community types. The degree of intensity of this association is reflected in the Chi-squared terms which show the contribution of each contingency table cell to this value (313.83; Table 5). There is a gradient of these values. At one extreme is the coastal communities/Marshes pair, with the greatest contribution (111.61), and therefore the greatest relationship of dependency. At the opposite extreme (16.98) it is the rockroses association of *Genisto-Cistetum cistetosum ladaniferi* (C4)/Peneplains and Slopes. In second place (50.47), the association *Halimio-Stauracanthetum genistoides*/Dunes and Sands is particularly noteworthy. The varying degree of intensity

of these relationships goes together with the degree to which the samples of a community are restricted to a particular type of landscape, and, vice versa, to the degree to which in one type of landscape a single type of community is present. Hence the maximum value found for coastal communities/Marshes: the 15 samples of these communities are confined to the Marshes landscape type, and, conversely, within this type of landscape there is no other type of community. At the opposite extreme, the 46 samples of the C4 community typical of the Peneplains and Slopes landscape are distributed among all types of landscape except Marshes (Table 4).

The different values of Chi-squared terms indirectly reflect the ecological valence of plant communities, progressively higher from halophilic coastal communities –the most stenoic– to the Peneplains and Slopes rockrose communities. The Marshes conditions are particularly extreme and limiting: communities above or under water depending on tidal flows, and with variable concentrations of salts (Lendínez *et al.*, 2014). This is the reason for the clear hiatus in the floristic composition of these two associations and the other syntaxa (Table 2), as well as for their early separation in Division 1 of TWINSPAN (Figure 3).

Tabla 3. Correspondence between syntaxa and Twinspan clusters at the original (I-VII) and synthesis classification levels (C1-C5). In bold the best correspondences.

Phytosociological classification		TWINSPAN classification							Total			
		C1		C2		C3		C4		C5		
		I	II	III	IV	V	VI	VII				
1	<i>Spartinetum densiflorae</i>	4	4	
2	<i>Halimiono portulacoidi-Sarcocornietum alpinii</i>	2	9	11	
3	<i>Halimio halimifolii-Stauracanthetum genistoidis</i>	.	.	28	28	
4	<i>Erico scopariae-Ulicetum australis</i>	.	.	1	1	
5	<i>Genisto hirsutae-Cistetum ladaniferi cistetosum ladaniferi</i>	.	.	2	10	32	1	1			46	
6	<i>Scillo maritimae-Lavanduletum sampaianae</i>	3	3	
7	<i>Ulici eriocladi-Cistetum ladaniferi</i>	8	7	.	.	.	15	
8	<i>Genisto hirsutae-Cistetum ladaniferi ericetosum australis</i>	.	.	.	1	3	1	21	26			
9	<i>Erico australis-Cistetum populifolii</i>	5			5	
10	<i>Halimio ocymoidis-Ericetum umbellatae</i>	1			1	
Total		6	9	31	11	46	9	28	140			

Discussion

Role of climate and soil in the plant distribution

The above analysis of the ecological factors governing variations in vegetation in the study area is consistent with the generally accepted view that the relative influence of climate and soils on plant distribution differs at different scales. Since the work of Alexander von Humboldt in the first half of the nineteenth century (Kruckeberg, 2004), it has been clear that the environment’s physical variables are crucial in shaping the areas of distribution of living beings in general (Lomolino *et al.*, 2006), and

plants in particular (Schimper, 1903; Cain, 1944; Kruckeberg, 2004). Among these variables the primary role is played by climate; soil play a secondary role. Thus, at a large scale, of the principles related to plant geography formulated by Cain (1944: 10), Principle 1 is that “Climatic control is primary” and Principle 4 that “Edaphic control is secondary”. This justifies the emphasis placed on climate when considering plant distributions worldwide (Box, 1981; Woodward, 1996). At a smaller scale, as stated by Schimper (1903: 160): “This fine differentiation of the vegetation and flora within a climatic district is chiefly determined by the soil”.

Table 4. Contingency table comparing relevé classifications to synthetic landscape and vegetation types (observed values). Landscape types: a, Marshes; b, Dunes and Sands; c, Croplands; d, Penneplains and Slopes; e, Mountains. Types of vegetation synthesis: C1-C5 (see Table 3). Expected values in brackets. Pearson's chi-sq (X^2) = 313.83 ($v = 16$, $p < 0,001$).

Vegetation types	Landscape types					Total
	a	b	c	d	e	
C1	15 (1.6)	0 (4.3)	0 (1.3)	0 (3.9)	0 (4.0)	15
C2	0 (3.3)	30 (8.9)	1 (2.7)	0 (8.0)	0 (8.2)	31
C3	0 (1.2)	3 (3.1)	7 (0.9)	0 (2.8)	1 (2.9)	11
C4	0 (4.9)	7 (13.1)	4 (3.9)	26 (11.8)	9 (12.2)	46
C5	0 (4.0)	0 (10.6)	0 (3.2)	10 (9.5)	27 (9.8)	37
Total	15	40	12	36	37	140

The consistency indicated earlier is apparent in the predominant role played by edaphic factors with respect to climate-related factors in explaining the distribution of the study communities. Of the five clusters (C1-C5, Figure 3), in three of them (C1-C3) edaphic factors (saline, sandy, and marly soils, respectively) were decisive in differentiating their distribution. In the other two (C4, C5), the factor determining differentiation was climate-related (rainfall). The differentiation of these two from the first three clusters (C1-C3) was again determined by an edaphic factor – their association with a shale and quartzite lithology.

Nevertheless, it should be borne in mind that the relative role of climate and soils in plant distributions derives from research at worldwide scale. Consequently, the secondary nature of soils is also at worldwide scale. Since the province of Huelva is just part of a Mediterranean climate zone, one might expect edaphic factors to play a relatively more crucial role than climate-related factors in the distribution of the study communities, as indeed was found to be the case.

There is partial agreement, too, with the findings reported by Siefert *et al.* (2012), who studied the influence of spatial scale on the relative importance of climate or soils in determining the floristic composition of plant communities. From 89 analyses derived from 63 different studies, they concluded that there is a transition from a primarily edaphic influence to a primarily climate-related influence as the spatial scale increases. All those stud-

ies involved zones corresponding to specific biomes or climate regions (for example, their median area was just 158 km²). So variations in the climate variables they analysed would have been analogous to the variations in rainfall obtained here between C3 and C4 on one hand and C5 on the other. Overall, they found that the edaphic variable accounted for 49% of the variance in community composition, and the climate variable 27%.

Value of the results for landscape classification

If the process of characterizing a landscape involves "... identifying areas of similar character, classifying and mapping them and describing their character" (Swanwick, 2002: 8) then the main value of the present results would be related to "describing their character".

However, this value is relative: although the communities studied form part of specific ecosystems about which they provide information, structural heterogeneity – i.e. the coexistence of different ecosystems – is a common feature of all the landscapes in the study area. The information obtained constitutes just a small part of a broader reality: moreover, such heterogeneity is particularly marked in the Mediterranean region (Di Castri, 1981). Nevertheless low Mediterranean scrublands are among the most frequent natural or semi-natural phytocœnoses: "It is clear that scrubland landscapes ... play an important role in this region [the Mediterranean]" (Quézel, 1981: 107).

Table 5. Pearson's chi-squared terms of the contingency table (Table 4) according to Fisher's exact test, comparing the classifications of the relevés according to the syntheses of landscape types and of vegetation types. Landscape types: a, Marshes; b, Dunes and Sands; c, Campiñas; d, Peneplains and Slopes; e, Sierras. For synthesis of vegetation types C1-C5, see Table 3.

Synthesis Vegetation types	Landscape types of synthesis				
	a	b	c	d	e
C1	111.61	4.29	1.29	3.86	3.96
C2	3.32	50.47	1.03	7.97	8.19
C3	1.18	0.01	38.91	2.83	1.25
C4	4.93	2.87	0.00	16.98	0.82
C5	3.96	10.57	3.17	0.02	30.33

This is explained by the many centuries of strong anthropic pressure in the Mediterranean basin (felling, fire, grazing, terracing, crops, abandoned land, etc.; Pausas, 1999), and by the fact that these communities constitute the first stage in the process of succession that follows these environmental alterations. A second point to be made is that the degree to which each of the clusters of communities studied (C1-C5) is representative of the landscape varies depending on the intensity of the relationship, as evidenced by the values of the Chi-squared terms.

The interest of the results for the description of each landscape's character is in part based on the complexity of those landscapes. The character of a landscape, what makes it different, depends as much on the "particular combinations of geology, landforms, soils, vegetation, land use, field patterns and human settlement" as on "the interaction between all these factors ..." (Swanwick, 2002: 9). This multiplicity of relationships within ecosystems and landscapes led Bastian & Steinhardt (2002: 154) to warn that: "Insights into complex systems can only be gained for selected components." This in turn leads to the recognition of the role played in landscape analyses by indicators –

in this case, the plant communities that were identified.

Conclusions

In landscape classification studies carried out at a regional or national scale (1:250000), it is to be expected that differences will be found between the plant communities associated with the different landscapes. Edaphic factors, rather than climate-related factors, are among the physical factors most determining landscapes at this scale. They are the main factors responsible for differences in the distribution of plants, and therefore of plant communities, between landscapes. From the plant communities identified, one can draw information of interest for the identification of the character of the landscape (*sensu* Swanwick, 2002 and Wascher, 2005).

The combined use of a phytosociological method and TWINSpan to classify the vegetation samples also proved fruitful, in that the multivariate method enabled recognition of a community not detected phytosociologically, while the phytosociological method enabled analysis of the communities in ecological terms that would not otherwise have been possible.



Photo 1. Halophilous coastal communities (*Halimiono portulacoidis-Sarcocornietum alpinii*) proper to the Marshes landscapes, in December.



Photo 3. Rockroses with gorses of *Genisto-Cistetum cistetosum ladaniferi*, associated to Peneplains and Slopes landscapes. In the foreground, white flowers, *Cistus ladanifer*.



Photo 2. Xerophytic matorral or “monte blanco” characteristic of the Dunes and Sands landscapes, under canopy of *Pinus pinea*. In the foreground, on the left, with yellow flowers, *Stauracanthus genistoides*; behind it shrub layer with predominance of *Halimium halimifolium*.



Photo 4. Rockrose-heaths of *Ericoaustralis-Cistetum populifolii*, association included in C5, cluster linked to Sierras landscapes. Pink flowers: *Erica australis*; white flowers: *Cistus populifolius*.

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