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Ecological Ordination and Distribution of Hygrophilous Species Growing on a Mediterranean Riverbank (SW Spain)

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Abstract

The Guadiamar riverbanks are home to riparian plant communities, such as alder, poplar and ash forests, *tamujares*, salt marshes, reed beds, etc. characteristic of Mediterranean rivers. A data set of these communities, including floristic relevés and environmental variables (physical and chemical soil properties, bioclimate) was analysed to correlate their floristic composition/species distribution with environmental variables. By means of an RDA (redundancy analysis) and a complementary cluster analysis four groups of species were discriminated according to their ecological requirements. The RDA displayed three major, parallel-running gradients (i.e., textural, bioclimatic and chemical) in environmental variables. Other less conspicuous, crossed gradients revealed the impact of man-made alterations, particularly in the middle reaches of the river. The results can be helpful in the planning of future ecologically oriented restoration programmes of wetlands.

Keywords: autoecology, green corridor, river Guadiamar, soil-plant relationships

Introduction

In the last decades wetlands have been widely recognized as ecologically valuable assets for a sustainable development strategy. Not only have they been extensively studied, but policies intended for their protection, preservation and efficient management have also been implemented (Montes del Olmo *et al.,* 2007). However, only a few restoration or regeneration initiatives for these wetlands were successful (Mitsch and Gosselink, 2000). Most of the errors were the result of a lack of knowledge about the specific environmental conditions required by the organisms inhabiting these wetlands (Lee *et al.,* 2005). There is no doubt that the success of these restoration projects is dependent on the available information about the ecological interactions responsible for the succession of riparian vegetation (Glenz *et al.,* 2006; Lu *et al.,* 2006).

Therefore, it is necessary to assess the impact of environmental variables on these hygrophilous plant communities, detect which variables play a decisive role in the maintenance of the different communities and establish proper bioindicator species for each of them.

These ecological data will eventually be used to plan the most suitable management strategies for the restoration of these threatened ecosystems.

The number of studies on the autoecology of forest species increases daily and this research line has more and more supporters (Castillo *et al.,* 2000; Konisky and Burdick, 2004; Navarro *et al.,* 2006; Rubio *et al.,* 1997, 2003; Thuiller *et al.,* 2003). However, the available knowledge of many of the most frequent species of our plant heritage is still far from sufficient.

For correct planning of restoration plans it is interesting to use plant bioindicators, which will enable us to know the ecological conditions of the environment and choose in a proper way the species to be introduced. Studies on bioindicators are widely used in relation to different factors, such as pollutants (Klumpp and Klumpp, 1994; Zuccarini and Kampuš, 2011), water quality (Ceschin *et al.,* 2010; Robach *et al.,* 1996) soil quality (Böer, 1996; Galuszka, 2000; Migaszewski *et al.,* 2001).

Given the shortage of studies on the response of riparian species to the different environmental variables, it is important to carry out a study to estimate as accurately as possible the tolerance shown by species to the different environmental factors that influence their biological dynamics and shape their distribution. For this purpose we first defined plant groups according to homogeneous response patterns to find out any possible relation with the ecological factors involved. Our final objective is to provide reliable information that could eventually lead to the use of these species as bioindicators in suitable, ecologically oriented restoration programmes.

This research is one of the studies carried out to restore the Corridor Verde del Guadiamar (Seville), in the area affected by the accidental breach of the slag pond of the pyrite mine in Aznalcóllar in 1998 (Gómez Mercado *et al.,* 2007, 2009, 2010, 2012).

Material and methods

Study area

The field work was carried out in the area of the "Corridor Verde del Guadiamar", a narrow strip of land 600 to 800 m wide and over 100 km long, encompassing 7900 ha. The strip is a long corridor connecting two large territories under protection, namely, the Parque Natural/Parque Nacional de Doñana and the Natural Parks of Aracena and Picos de Aroche and the Sierra Norte of Seville, in Andalusia, Spain (Fig. 1).

The territory presents a rich diversity of habitats. The upper third of the reaches of the river flows through the typical oak-studded pastureland ("dehesa") of Sierra Morena, often through deep rock-carved gullies, and substrates are usually metamorphic materials. The middle reaches of the river have long been traditional farming land, with terrains made up of gravels and sands of alluvial origin. The final stretch of the river enters a flood plain, territory where the dominant substrates are sands, silts and clays.

Data collection

Twenty-eight sites representing all types of vegetation found in the study area were selected. For each of these sites an identification sheet with the most relevant macromorphological information was completed with the corresponding data from a relevé of vascular plant species.

10 × 10 m square grids were chosen as sample plots. For each of them floristic relevés were carried out, and their species abundance-dominance was estimated by means of Braun-Blanquet's scale (1964), subsequently modified, for statistical purposes, by van der Maarel (1979).

A soil sample was taken from each site, with a final equivalent volume of 3 dm^3, made up of five evenly distributed subsamples taken in the inventoried zone. Soil samples were taken at a depth of 30 cm, regardless of the horizon sequence on the spot (Díaz-Maroto and Vila-Lameiro, 2008; Hagen-Thorn *et al.,* 2004).

The soil samples were sieved through a 2 mm screen after removing any plant materials and roots. Particle size distribution was determined applying Robinson's pipette method (Soil Conservation Service 1972). Available water capacity was calculated by AWC=W_{33}-W_{1500} (Klute, 1986). W_{33} and W_{1500} refer to the gravimetric water content of a disturbed soil sample placed on a porous plate and equilibrated with an applied pressure of 33 kPa and 1500 kPa, respectively (Richards, 1954). Exchangeable bases and cation exchange capacity (CEC) were determined by the ammonium acetate (pH=7) method. pH was measured electrometrically in a 1:2.5 soil:water suspension and 1:2.5 soil:KCl solution (pH_KCl). Total $CaCO_3$ was determined by the manometric method. Total organic carbon was determined by wet oxidation with potassium dichromate. Total nitrogen was determined by the Kjeldahl method (Bremmer, 1996). Bioavailable phosphorus was measured by the Olsen method (Olsen *et al.,* 1954). Electrical conductivity and dissolved solids were measured on extracts of saturated soil-paste (Bartels, 1996).

The bioclimatic indexes (Io, Itc) were reckoned using the formula suggested by Rivas Martínez and Loidi (1999) and using the data from 36 meteorological stations located in the Guadiamar river basin and other neighbouring areas (data from the State Meteorological Agency, AEMET). From these data and by means of a regression analysis, estimated values for every site in the study area were obtained.

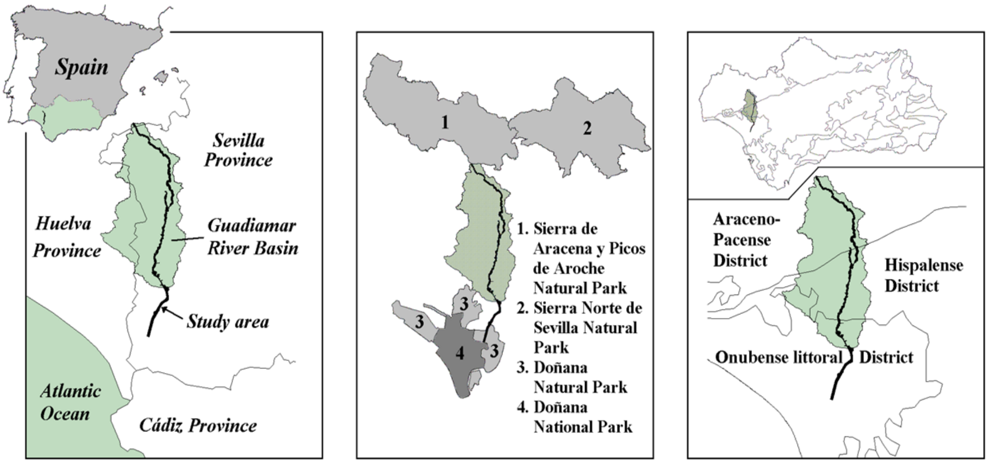

Fig. 1. Left: location of the area of study and the Guadiamar River Basin with regard to Spain, Andalusia and the provinces of Huelva, Seville and Cadiz. In the centre, a position between the protected spaces of Doñana and natural parks of Aracena and Picos de Aroche and Sierra Norte de Sevilla. On the right, situation on the biogeographical outline of Andalusia (Rivas Martinez *et al.,* 1997)

Tab. 1. Estimated environmental variables for each sample

Label	Environmental variable	Unit	F	P	A/B	A/C	A/D	B/C	B/D	C/D
OC	Total Organic Carbon	% w/w	2.149	0.097						+
CEC	Cation Exchange Capacity	$cmol_c·kg^{-1}$	122.080	0.000	+	+	+	+	+	+
Ca	Exchangeable Calcium	$cmol_c·kg^{-1}$	118.312	0.000	+	+	+	+	+	
Mg	Exchangeable Magnesium	$cmol_c·kg^{-1}$	317.657	0.000		+	+	+	+	
Na	Exchangeable Sodium	$cmol_c·kg^{-1}$	35.103	0.000		+	+	+	+	+
K	Exchangeable Potassium	$cmol_c·kg^{-1}$	400.297	0.000		+	+	+	+	+
V	Base Saturation	%	139.630	0.000	+	+	+	+	+	
CO_3	Total Carbonate	% w/w	119.674	0.000	+	+	+	+	+	+
N	Total Nitrogen	% w/w	8.400	0.000	+	+	+		+	
CN	C/N (Total Organic Carbon/Total Nitrogen)		14.951	0.000		+	+	+	+	
P	Bioavailable phosphorus	$mg·kg^{-1}$	7.032	0.000			+		+	+
Caex	Ca in saturation extract	$mmol_c·L^{-1}$	23.307	0.000		+	+	+	+	+
Mgex	Mg in saturation extract	$mmol_c·L^{-1}$	23.751	0.000		+	+	+	+	+
Naex	Na in saturation extract	$mmol_c·L^{-1}$	29.215	0.000		+	+	+	+	+
Kex	K in saturation extract	$mmol_c·L^{-1}$	43.443	0.000		+	+	+	+	+
CO_3ex	CO_3 in saturation extract	$mmol_c·L^{-1}$	22.173	0.000		+	+	+	+	+
HCO_3ex	HCO_3 in saturation extract	$mmol_c·L^{-1}$	17.694	0.000			+		+	+
H33	Moisture content at 33 kPa	% w/w	230.643	0.000	+	+	+	+	+	+
H1500	Moisture content al 1500 kPa	% w/w	210.396	0.000	+	+	+	+	+	
Hsat	Moisture content at saturation	% w/w	59.100	0.000		+	+	+	+	+
AWC	Available Water Capacity: $AWC=W_{33}-W_{1500}$	% w/w	30.932	0.000	+	+	+	+	+	
Sand	Sand	% w/w	389.549	0.000	+	+	+	+	+	
CS	Coarse Silt	% w/w	38.830	0.000	+		+	+	+	
FS	Fine Silt	% w/w	247.344	0.000	+	+	+	+	+	+
Clay	Clay	% w/w	647.962	0.000	+	+	+	+	+	
pH	pH		62.325	0.000	+	+	+	+	+	
pH_KCl	KCl pH		115.709	0.000	+	+	+	+	+	
EC	Electrical Conductivity	$dS·m^{-1}$	31.572	0.000		+	+	+	+	+
Alt	Altitude	m	75.508	0.000	+	+	+	+	+	
Slope	Slope	%	32.538	0.000	+	+	+	+	+	
Io	Ombrothermic index		75.508	0.000	+	+	+	+	+	
It	Thermicity index		75.509	0.000	+	+	+	+	+	

Label used in graphical representations, measurement unit and ANOVA of 32 environmental variables for four groups and results for multiple comparisons for all pairs with LSD (least significant difference) procedure. With "+" pairs of groups different for a 95% confidence

Our survey included 32 environmental variables (Tab. 1 shows the label and the measurement units for each variable), which were incorporated as thematic layers into a geographical information system (ArcGis 9.3).

Data analysis methods

With the data collected from 28 plots, we analysed the relationships between environmental variables and plant species abundance by means of two different matrices. The Kolmogorov-Smirnov test revealed that the ecological response of plant species is not unimodal. Therefore we opted for a redundancy analysis (RDA), which is a direct gradient analysis that assumes a linear response of species. The numerical analysis was performed in Canoco v.4.02 (ter Braak and Smilauer, 1998).

A total of 51 vascular plant species were recorded. The full names and labels of these species are listed in Tab. 2. In the RDA analysis the original species abundance data were logarithmically transformed as follows: $x' = \log(x+1)$.

The Monte Carlo test was used to select the ten most significant environmental variables. By this procedure, redundant variables could be individuated. In addition, a cluster analysis was implemented to group the species according to their scores on the four axes of the RDA. Through this combinatorial technique, we could integrate the information from the RDA four-dimensional space into the graphic representation of the two first axes.

This cluster analysis was made by means of the squared Euclidean distance and the Ward method as grouping techniques. Finally, an ANOVA analysis of 32 environmental variables for all groups of species and post hoc multiple comparisons for all pairs (LSD method) were made.

Results and discussion

Plant ordination

The RDA and complementary cluster analysis produced four ecologically distinct groups of species (A, B, C and D). These groups present significant differences ($p<0.05$) for all the environmental variables involved, except for OC. Most of these variables can be used to discriminate between any possible pair of groups. At all events, OC is significant enough to discriminate between the pair C/D (Tab. 1).

The relation species/environmental variables accounts for 73.3% of the variance conveyed by the four ordination axes (Fig. 2). The eigenvalues of the first two axes of the RDA accounts for 50.0% of that relation. As for the variance percentage accounted for by the environmental variables, the ten most significant ones in decreasing order are: Clay (19%), Sand (7%), K (6%), OC (5%), Slope (5%), Io (5%), N (4%), CEC (4%), CO3 (3%) and Hsat (3%).

Axis 1, which accounts for 34.6% of the total variance observed, attests to an intense environmental gradient in the direction of the river flow. The most noticeable sign of this gradient is the different soil textures observed: in the positive part of the axis the high percentages of Sand heavily contrast with the high contents of Clay in the negative part. Likewise, in the positive part of axis 1 we find high Io and Slope values with low CEC, CO_3 and K values. This fact clearly reveals that, as the river flows downstream, the size of the particles which are deposited and the ombrothermic index decrease as the slope decreases, and the CEC, K and CO_3 values increase dramatically.

Axis 2, which accounts for 15.4% of the variance, is related to Hsat, Io and Slope. It provides better discrimination between the pair A/C according to the Sand content and Io, and between the pair B/D according to Hsat.

One group of species appears in each of the four quadrants of the ordination diagram (Fig. 2). The species groups are positioned along the strong gradient revealed by the whole set of variables under study along the whole course of the river. Groups A and D appear at the ends of this gradient, while B and C appear as transitional groups. Although there is some distributional overlapping between some species belonging to groups A and B, on the one hand, and species belonging to groups C and D, on the

Tab. 2. Species present in the samples with full names and labels for the graphical representation

Label	Name	Label	Name
AEL_LIT	*Aeluropus littoralis* (Gouan) Parl.	POL_AVI	*Polygonum aviculare* L.
ALN_GLU	*Alnus glutinosa* (L.) Gaertner	POL_EQU	*Polygonum equisetiforme* Sm.
ART_MAC	*Arthrocnemum macrostachyum* (Moric.) Moris in Moris & Delponte	POL_MAR	*Polypogon maritimus* Willd. subsp. *maritimus*
ARU_DON	*Arundo donax* L.	POP_ALB	*Populus alba* L.
CAR_ACU	*Carex acuta* L.	POP_NIG	*Populus nigra* L.
CRE_CRE	*Cressa cretica* L.	RAN_TRI	*Ranunculus trilobus* Desf.
CRY_ACU	*Crypsis aculeata* (L.) Aiton	RUB_ULM	*Rubus ulmifolius* Schott
CYP_LON	*Cyperus longus* L.	SAL_ALB	*Salix alba* L.
DAM_BOU	*Damasonium alisma* subsp. *bourgaei* (Cosson) Maire	SAL_NEO	*Salix neotricha* Goerz
EQU_TEL	*Equisetum telmateia* Ehrh.	SAL_PED	*Salix pedicellata* Desf.
FRA_LAE	*Frankenia laevis* L.	SAL_SAL	*Salix salviifolia* Brot.
FRA_ANG	*Fraxinus angustifolia* Vahl subsp. *angustifolia*	SAR_PER	*Sarcocornia perennis* subsp. *alpini* (Lag.) Castrov.
HAL_POR	*Halimione portulacoides* (L.) Aellen	SCH_NIG	*Schoenus nigricans* L.
INU_CRI	*Inula crithmoides* L.	SCI_HOL	*Scirpus holoschoenus* L.
JUN_ACU	*Juncus acutus* L.	SCI_LIT	*Scirpus litoralis* Schradeder
JUN_SUB	*Juncus subulatus* Forsskål	SCI_COM	*Scirpus maritimus* subsp. *compactus* Hoffm.
LYT_SAL	*Lythrum salicaria* L.	SEC_TIN	*Securinega tinctoria* (L.) Rothm.
LYT_TRI	*Lythrum tribracteatum* Spreng.	SPA_DEN	*Spartina densiflora* Brongn.
MEN_SUA	*Mentha suaveolens* Ehrh.	SUA_SPL	*Suaeda splendens* (Pourr.) Gren. & Godr.
MYR_COM	*Myrtus communis* L.	SUA_VER	*Suaeda vera* Forssk. ex J.F. Gmel.
NER_OLE	*Nerium oleander* L.	TAM_AFR	*Tamarix africana* Poir.
OEN_CRO	*Oenanthe crocata* L.	TAM_MAS	*Tamarix mascatensis* Bunge
PAR_INC	*Parapholis incurva* (L.) C.E.Hubb.	TRI_RES	*Trifolium resupinatum* L.
PAR_PYC	*Parapholis pycnantha* (Hack.) C.E.Hubb.	TYP_DOM	*Typha dominguensis* (Pers.) Steudel
PAS_VAG	*Paspalum vaginatum* Swartz	ULM_MIN	*Ulmus minor* Mill.
PHR_AUS	*Phragmites australis* (Cav.) Trin. ex Steud.		

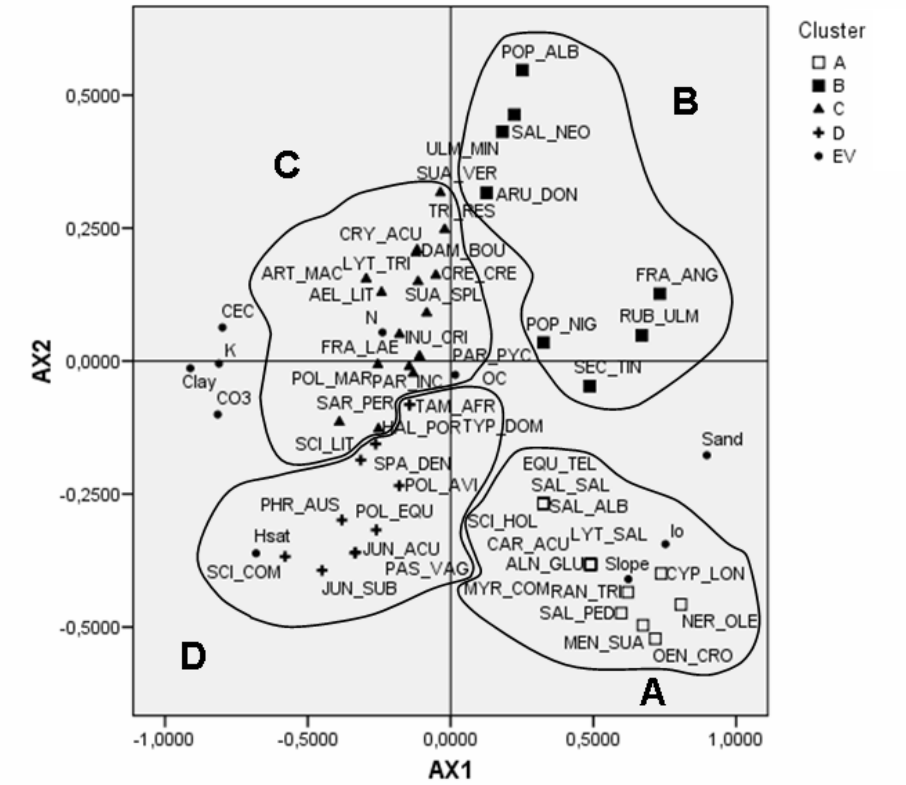

Fig. 2. Ordination of plant species in the space of the first two RDA axes. Species have been ascribed to one of four groups, according to cluster analysis output. (□, ■, ▲, + species group; ● environmental variables). Species abbreviations as in Tab. 2

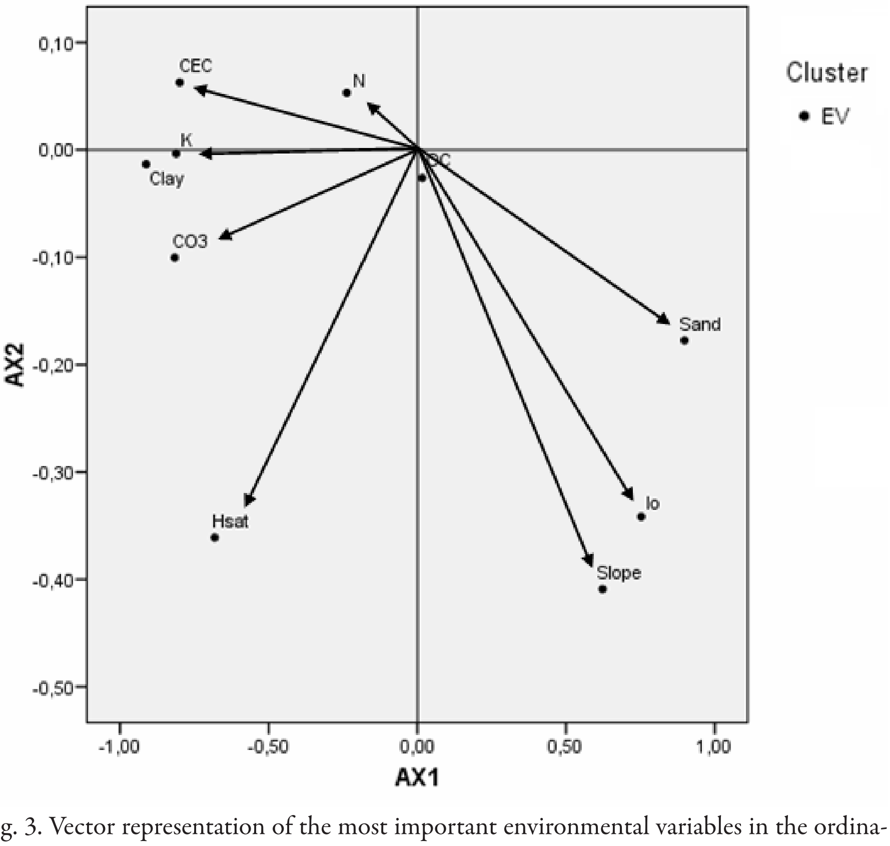

Fig. 3. Vector representation of the most important environmental variables in the ordination space of the first two RDA axes

other, no overlapping whatsoever has been found between blocks A/B and C/D (Fig. 4).

Groups A and B are more closely interrelated with each other than they are with groups C and D. The species of group A align themselves with higher Sand and Io values (Fig. 2 and 3). None of the ten variables selected by the RDA are located in the quadrant of group C. This is due to the transitional character of this zone. Group C is related to high Clay, CEC and K values. Group D is clearly aligned with high Hsat values.

Gradient analysis

The first two RDA axes (Fig. 2 and 3) reveal the change in level of the physical, chemical and bioclimatic parameters along the Guadiamar River watercourse.

The size of the sediment particles decreases in the lower reaches of the river in relation to the geomorphological profile of the river course (Beauchamp *et al.,* 2007; Beauchamp and Stromberg, 2008; Diju and Thamban, 2006).

A bioclimatic gradient with the highest ombrothermic index values (aligned with Alt and Sand) in contrast to those of the thermicity index can also be found. This means that thermicity increases and the ratio precipitation/temperature decreases as the river flows downstream.

It was also found a strong chemical gradient with high values of CEC, Ca, Mg, Na, K, V, Caex, Mgex, Naex, Kex, pH, pH_KCl and EC in the negative quadrant of axis 1 and the positive quadrant of axis 2. In this respect, only CN values are higher in the opposite quadrant.

Heavily aligned with axis 1, these three instances of overlapping are the cause of the highly contrasting zonation of vegetation types along the course of the river (Fig. 4).

As crossed gradients we found high values of P and CS in the positive quadrant of both axes, which indicates a greater man-induced impact (agriculture, waste spills, etc.) on the middle reaches of the river, where soil texture is also transitionally medium-size. By contrast, in the negative quadrant of both axes we found high values of Hsat (in relation to a high percentage of Silt), CO_3ex and HCO_3ex. These two variables reveal that the stagnant water of the marshland areas which are flooded for longer periods of time (where species of group D occur) is of continental origin, whereas the salts concentrated on the seasonal marshland soils have a strong salt water component. This still remaining impact of the sea on the soils is undoubtedly a vestige of a time when the river dynamics were more natural and dependent on sea tides. In more recent times the construction of roads and farming practices put an end to those dynamics.

Analysis of species groups

Plant species are arranged into four groups, according to the correlation coefficients with regard to each canonical axis. Consequently, each group of species corresponds to one of four clear-cut habitats that can be found along the course of the river: enclosed, deep-carved gullies (group A), open river valley with low slopes (group B), high or seasonal marshland (group C) and low or permanent marshland (group D) (Fig. 4).

Group A occurs only in the upper reaches of the river, where the river flows through deep gullies and the superficial water stream never runs dry. This mountainous stretch presents terrains with steep slopes, with soils rich in sand and an ombrothermic index (Io) at the highest levels.

The group grows on dystric soils, poor in exchange cations and with an average pH record under 7. All this is not only due to a remarkably high sand content and a precipitation rate that encourages soil denudation, but also to the short supply of bases in the materials on which the soils develop. The extremely low equivalent calcium carbonate content depends heavily on these materials.

The alder tree (*Alnus glutinosa)* is a salient species of this reach of the river and an effective bioindicator of this group. It is ideally adapted to this kind of environment (Díaz *et al.,* 1987; Naqinezhad, 2008). In these alder tree woods pH is 6.91 (measurements in water) and CN is 19.5. These values correspond to the eutrophic type, as suggested by Prieditis (1997).

The species of group B can be found both in the upper and middle reaches, always in combination with open river course environments, gentle slopes and areas where the superficial water stream may dry up during prolonged, very dry summers. These species present medium values for all the variables involved, except for Hsat, which shows low values here as a result of the still high sand concentration in the soil. The records of Slope, Io, Sand, Clay, CEC and Hsat for this group describe a flat habitat, with average precipitation rates, a dominance of sand over clay, poor salinity and low water saturation in soil. The recorded plant dispersion among the species of the group reveals a certain

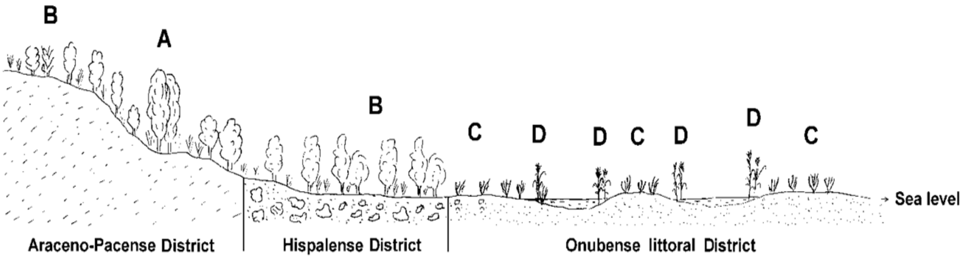

Fig. 4. Distribution scheme of the groups of species along the Guadiamar River

degree of ecological flexibility, in line with transitional environments.

The species of group B prefer eutric soil, richer in bases, higher pH records and higher contents of equivalent calcium carbonate than group A species. The tolerance ranges of B species are, in general, wider than those of group A, whose species assume an extreme position. It is worth noting the preference of these plants for soils with a more balanced texture and better water retentive capacities.

The most significant bioindicators in this group are *Populus alba, P. nigra* and *Ulmus minor.* The assemblages of *Rubus ulmifolius* and *Arundo donax* are frequent in this reach of the river as usually happens in riparian areas where human intervention has taken place (Beerling, 1991; Corbacho *et al.,* 2003; Nilsson *et al.,* 1989). *Ulmus minor* is an element of wet flood plains and grows best on fertile alluvial soils in marshy places (Browicz, 1982).

Groups C and D are found in the lowest reach of the river, always in flat, floodable zones, in marshland-like environments that share identical climatic conditions. The soils occupied by species in these two groups are highly basic, salty and, in general, heavy, which usually impedes water drainage and the washing out of salts. Plants alternate according to microtopography. Thus, the species of group C tend to occur in higher zones subject to severe summer droughts and locally known as "vetas", while the species in group D tend to grow in microdepressions, waterlogged for long periods of time, locally known as "lucios". A zonation of species distribution with respect to elevation is one of the characteristic features of tidal salt marshes (Adam, 1990; Davy and Costa, 1992) and has been interpreted as an expression of past or present succession processes associated with sedimentary accretion (Davy, 2000).

The results obtained for group C confirm that the soils are very clayey (Clay 60.44%, Sand 2.4%), with a correspondingly high Hsat (80.09%), and a high water storage capacity, both values in field capacity (H33), particularly, at wilting point (H1500). Not surprisingly, the amount of water available for plants is not excessively high.

Among the bioindicators of group C, *Arthrocnemum macrostachyum* stands out as a species well adapted to the most extreme habitats. It endures the highest levels of soil salinity (5.21 to 55.5 dS·m^{-1}) and the most severe seasonal fluctuations (Gómez Mercado *et al*., 2012). As for *Sarcocornia perennis* subsp. *alpini*, it can tolerate similar salt concentrations (9.73 to 55.5 dS·m^{-1}), but its optimum occurs on soils subject to less dramatic seasonal changes. Álvarez Rogel *et al.* (2001) already recorded this behaviour in *A. macrostachyum* and *S. fruticosa*.

Group D is found in low or permanent marshland with prolonged flooding and where seasonal drought is short or non-existent. Hsat values are the highest here. The species of this group grow on soils of a clayey texture, where the content of exchangeable ions is very high. EC presents an average value of 12.51 dS·m^{-1}, i.e., much lower than that of group C. However, this group of species can still be considered as definitely halophilous plants.

As happens in other saltmarshes in the SE of the Iberian Peninsula (Álvarez Rogel *et al.,* 2001), in this environment the species of rushes (*Juncus acutus*) are dominant. The EC values of the samples where this species occurs ranged from 9.73 to 11.07 dS·m^{-1}.The best bioindicators in this group are *Phragmites australis*, *Scirpus maritimus* subsp. *compactus*, *Scirpus litoralis* and *Typha dominguensis.*

The reed (*Phragmites australis*) is a moderately halophilous species recorded by Cizkova *et al.* (2001) with electrical conductivity values ranging from 2.52 to 5.03 dS·m^{-1}. We ourselves found the species in sites where the salinity records are higher, ranging from 6.51 to 37.9 dS·m^{-1}.

Watt *et al.* (2007) reported that *Scirpus maritimus* (varietal type unknown) showed wide ecological amplitude and that its distribution was not limited by soil salinity over the range found (0.57-4.1 dS·m^{-1}). Its natural habitat is on the edge of brackish or saline pools with large variations in water chemistry, particularly conductivity (Kadlec and Smith, 1989; Lieffers and Shaym, 1982). In our samples, *Scirpus maritumus* var. *compactus* shows an EC range between 13.79 and 55.5 dS·m^{-1}, whereas *Scipus littoralis* varies between 6.33 and 7.06 dS·m^{-1}.

Spartina densiflora is considered an allochthonous species and an aggressive invader, capable of acting as salt marsh pioneers and persisting in more mature communities (Costa *et al.,* 2003). In our zone, the plant presents an EC tolerance range varying from 19.49 to 37.9 dS·m^{-1}.

Besides the clear difference in the total Na content, the contents of exchangeable ions of the adsorption complex of the soil also show clear differences between groups C and D.

The clear-cut spatial separation between groups A/B, on the one hand, and groups C/D, on the other, testify to a discriminative complex of ecological factors for the distribution of these plant species. There is no doubt that the main ecological factor associated with such a sharp differentiation is salinity. The threshold is about 2.28 dS·m^{-1} EC, which is the distributional limit of wide-ranging, non-halophilous species, such as *Fraxinus angustifolia, Populus alba* and *Ulmus minor.*

As commented by Sieben and Reineke (2008) and Álvarez Rogel *et al.* (2001), further general research on species and plant communities from different backgrounds is required to support efficient future restoration programmes on the basis of general rather than local patterns. This strategy will also allow efficient use of plant species as bioindicators and could save an enormous amount of effort and costs when designing suitable restoration plans for wetlands.

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