



Environmental control of plant species abundance in a microtidal Mediterranean saltmarsh

Efrem Batriu, Joan Pino, Pere Rovira & Josep M. Ninot

Keywords

halophytes; helophytes; realized niche; soil vegetation relationships; water table

Abbreviations

SAR, Sodium Adsorption Ratio; CCA, Canonical Correspondence Analysis; GLM, Generalized Linear Model

Nomenclature

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Batriu, E. (efrembatriu@hotmail.com) & **Pino, J.** (corresponding author, joan.pino@uab.es):

Centre for Ecological Research and Forestry Applications (CREAF), Autonomous University of Barcelona, E-08193 Bellaterra, Spain

Rovira, P. (pere.rovira@ctfc.es): Centre Tecnològic Forestal de Catalunya (CTFC), Pujada del Seminari s/n, E-25280 Solsona, Spain

Batriu, E. (efrembatriu@hotmail.com) & **Ninot, J.M.** (jninot@ub.edu): Department of Plant Biology, University of Barcelona, Av. Diagonal 645, E-08028 Barcelona, Spain

Abstract

Question: To what extent are environmental factors the main determinants of species abundance in Mediterranean coastal marshlands?

Location: The Llobregat delta, Barcelona, Spain.

Methods: Vegetation relevés were performed and a set of water table and soil variables were periodically monitored in 43 sampling points randomly distributed in four marsh areas (sites) along a coastal–inland gradient. A canonical correspondence analysis (CCA) was performed to identify the primary water and soil correlates of species cover, after considering the effect of site and point spatial location. The realized niches of dominant species were modeled through GLMs performed on the first two axes of CCA. Niche overlapping among these species was compared with their coexistence, assessed through pairwise correlations of relative species cover in each sampling point.

Results: Water and soil variables explained more of the variation in species' abundance than site and spatial position. Mean water table level, maximum water conductivity and sodium adsorption ratio (SAR), summarized in the two first CCA axes, explained 23.8% of the variability in species' cover. *Arthrocnemum fruticosum*, *Phragmites australis* subsp. *australis*, *Juncus acutus*, *Spartina versicolor* and *Juncus maritimus* dominated the vegetation stands. Niches obtained from GLM response curves showed moderate overlapping among all these species except for *A. fruticosum*. However, pairwise correlations were mainly negative or non-significant, indicating low coincidence, and even segregation, between species' cover.

Conclusions: The abundance of dominant plants in Mediterranean marshes is only partly explained by the environmental gradients summarized in niche models. The role of other factors such as facilitation or competition between species and random recruitment should be explored.

Introduction

Vegetation stands in coastal marshes are commonly species-poor and dominated by a single or few species (Day et al. 1988; Adam 1993). Identifying the factors that determine the distribution and abundance of these dominant species might, therefore, improve the management of the diverse marsh vegetation types, and this will ultimately help to preserve marshland biodiversity and ecological services.

Soil properties and gradients of salinity and moisture have been identified as the main environmental factors that constrain plant distribution in all salt marsh environ-

ments (Ranwell 1972; Adam 1993). Experimental studies have also indicated the importance of competitive exclusion processes in the distribution of wetland plants along these gradients in macrotidal salt marshes (Snow & Vince 1984; Bertness 1991; Pennings & Callaway 1992). However, this has not been observed in Mediterranean coastal marshes owing to: (1) an irregular microtidal regime (Costa et al. 2003); (2) micro-scale variations in soil salinity and moisture in both space (Adam 1993; Silvestri et al. 2005) and time (Álvarez Rogel et al. 2001); and (3) a long history of human-driven disturbance (Curcó et al. 2002). All these factors interact and may determine, in turn, a

heterogeneous distribution of plant species in the landscape, which could favor species coexistence.

The mechanisms that enhance or limit this coexistence have been a main focus of interest for ecologists (McCann et al. 1998; Chesson 2000; Bastolla et al. 2005; Wilson 2011). As dictated by Gause's competitive exclusion principle, classical theories assume that it is primarily mediated by a differentiation in ecological niches (Tilman 1988, 2004). However, the coexistence of presumably competing species seems to be more common in real ecosystems than expected under the competitive exclusion principle owing to a number of stabilizing and equalizing mechanisms (Rohde 2005; Wilson 2011).

Modeling the species' responses to environmental gradients is a common approach to study species' niches, either fundamental or realized. Niches are conceived as a set of overlapping response curves (Austin & Smith 1989) such that in a particular portion of space certain species have a relative performance advantage over other species, representing niche segregation.

In this study we analysed the environmental factors determining the distribution of the dominant plants in a Mediterranean coastal marshland. Our hypotheses were that the distribution of dominant plant species results from diverse soil properties and aspects of the hydrologi-

cal regime, and that this results in niche segregation among species. Using both CCA (Canonical Correspondence Analysis) and GLM (Generalized Linear Models), we evaluated the relationship between species composition and site, and soil and water characteristics for a set of marsh vegetation stands in order to: (1) identify the main factors that affect the distribution of species; (2) model the realized niche of the dominant species using these factors; and (3) evaluate niche overlapping versus species' coexistence through their relative abundance.

Methods

Study site

The study was performed in the delta of the Llobregat River, a microtidal wetland area of 7000 ha currently included in the Barcelona conurbation (Catalonia, NE of Iberian Peninsula; Fig. 1). The climate is typically humid Mediterranean with maritime influence, showing an annual rainfall of 640 mm with minimum peaks in summer and winter, and a mean annual temperature of 15.5 °C with hot summers and mild winters (International Airport of Barcelona, period 1971–2000). Natural habitats, dominated by marshlands, account for only 13% of the delta. Salt marshes belong to the dry coastal type

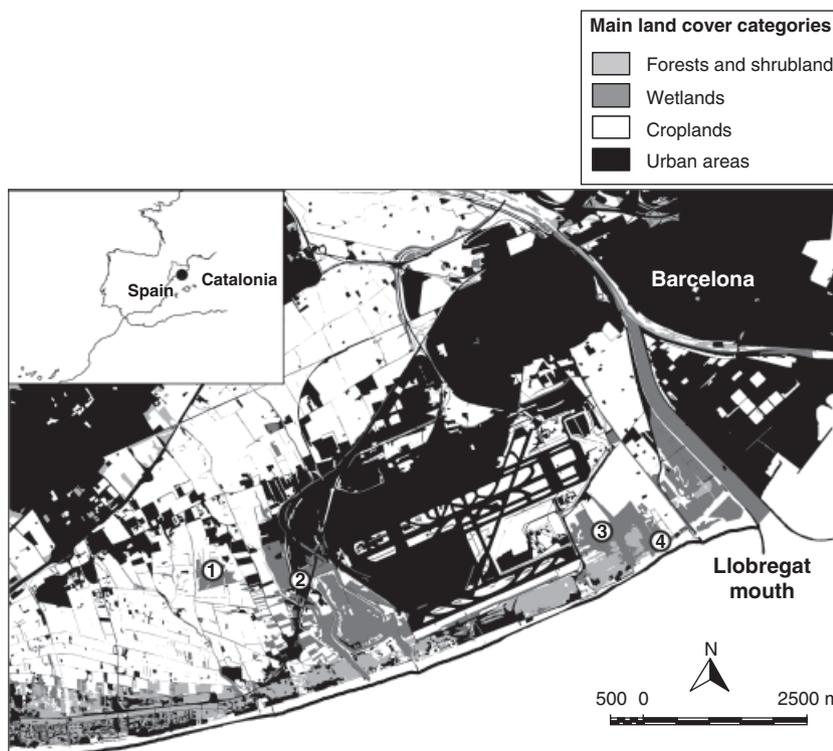


Fig. 1. The study area showing the main land cover categories and the four study sites (circles): (1) Reguerons; (2) Can Sabadell; (3) Ricarda; (4) Magarola.

(Adam 1993), and are dominated by reedbeds (*Phragmites australis*), rushbeds (*Juncus maritimi*), and halophytic scrublands (*Arthrocnemum fruticosum*) of variable conservation status (Pino et al. 2006).

Field sampling

We sampled 43 points within the four most preserved marshland remnants in the delta (sites thereafter) placed along an inland–coastal gradient (Fig. 1). Points were randomly selected on a recent vegetation map and located in the field by GPS (mean error < 5 m). Phytosociological vegetation relevés were performed within a circle of 2 m radius (12.56 m²) in each sampling point. Plant species cover was estimated following the Braun-Blanquet (1979) scale (+, < 5%; 1, < 10%; 2, 10–25%; 3, 25–50%; 4, 50–75%; 5, > 75%).

Bolòs et al. (2005) distinguished two reed subspecies in the study zone: *Phragmites australis* subsp. *australis* (widespread), and *Phragmites australis* subsp. *chrysanthus* (less frequent but sometimes dominating the edge of water bodies). Because of their panicle morphology, both subspecies were easily identified in the field, and they were recorded separately because of their contrasting ecology. However, we considered that in the literature, when no reed subspecies was indicated, reference was being made to the cosmopolitan subspecies *australis* (the subspecies *chrysanthus* is restricted to the Mediterranean coast).

We sunk a PVC pipe, 1.5 m long and 32 mm in diameter, to a soil depth of 1.3 m in the center of each relevé. The pipe walls were drilled (holes of 2 mm in diameter) to allow water inflow, and they were covered with filter gauze to prevent soil infilling. These pipes were used to monitor the water table level and the electrical conductivity of pore water, which are known to be primary correlates of the distribution and abundance of marsh plants (Adam 1993). Measurements were recorded at monthly intervals from Dec 2004 to Dec 2006, using a WTW TetraCon 325 sensor (WTW, Weilheim, DE).

Every 4 months from Jan 2005 to Jan 2006, two soil samples were obtained from the relevé area of each sampling point, using a corer of 2.6 cm diameter and 20 cm length, thus sampling the soil layer where seedling establishment takes place and most fine roots occur. At each sampling date, the two soil samples at each point were mixed, air-dried and passed through a 2-mm mesh sieve.

Soil analyses

Soil properties, both physical (texture, organic matter) and chemical (carbonates, pH, C, N, ionic composition, etc.), have also been proposed as primary correlates for the distribution of plant species in Mediterranean marshes (Álvarez-Rogel et al. 1997; Molina et al. 2003).

Soil samples obtained in the first sampling date (Jan 2005) were used to determine a set of soil properties which were expected to remain relatively constant over the study: (1) particle size distribution, by the pipette method after destruction of organic cement by hydrogen peroxide and dispersion by sodium hexametaphosphate; (2) total carbonate, by the Bernard calcimeter method (Lamas et al. 2005); (3) pH, from a 1:2.5 water dilution; (4) total C and N, using a ThermoQuest analyzer (San José, CA, US); and (v) organic carbon, by removing the carbonate-C from the total C.

Samples collected from Apr 2005 to Jan 2006 were used to periodically evaluate soil conductivity and ionic contents. At each sampling date, we obtained a saturation extract (Bower & Wilcox 1965). The conductivity of the saturation extract was measured using a WTW TetraCon 325 sensor and the ionic concentration in the extracts obtained was determined as follows: Ca²⁺, Mg²⁺, Na⁺ and K⁺ using ICP-OES (optical emission spectroscopy with inductive plasma), Cl⁻ by precipitation with Ag, using an automatic titrimeter, and SO₄²⁻ using high performance liquid chromatography (HPLC). The sodium adsorption ratio (SAR) was calculated (Richards 1974).

Niche segregation versus coexistence of dominant species

To model the species' ecological niches from abundance data one must face the problem of choosing an adequate function to estimate the shape of the response curve with respect to a given factor. Both GLM and CCA, which assume unimodal shapes, are the most widely used approaches. A CCA provides a broad view of ecological gradients and GLM is commonly applied to fit specific species' response curves (Guisan et al. 1999). Thus, we used CCA to identify the study variables that most greatly influenced species' cover.

Braun-Blanquet categories of the relevés were transformed to the mean value of the corresponding cover interval (Leps & Smilauer 2003). All species were included except those occurring in only one relevé. The initial pool of explanative variables ($n > 40$) comprised the soil properties evaluated at the commencement of the study and the minimum, mean and maximum values of each water and soil property evaluated periodically. In order to reduce the number of variables, pairwise $|r| > 0.8$ was used to determine unacceptable colinearity between these variables. Then, from each pair of variables, we eliminated the variable less correlated with the rest or that with less biological sense according to previous literature. The variables finally included in the CCA were: mean level and maximum conductivity of water table, and percentage of clay, total carbonates, pH, organic C/total N

ratio, mean $[K^+]$, mean SAR, mean K^+/Na^+ ratio, mean Ca^{+2}/Na^+ ratio and mean SO_4^{2-}/Cl^- ratio in soil.

First, the effect of water and soil variables, sites and Universal Transverse Mercator coordinate system (UTM) coordinates on species' cover was assessed through partition of variance analyses using CCA (Leps & Smilauer 2003). A new CCA limited to environmental variables was then performed using sites and UTM coordinates as covariables. Monte Carlo permutation tests were used as forward stepwise procedure to select the significant correlates ($P < 0.05$) of species' cover. Permutations followed a split-plot design and were restricted within sites. All CCA were performed using CANOCO (v.4.5; Plant Research International, Wageningen, the Netherlands).

An abundance–dominance curve was plotted to identify dominant species from the mean percentage cover of each species in the relevés. Once identified, we estimated their abundance (i.e. the percentage cover) from the CCA axes using GLMs through R (v. 2.12; R Development Core Team, <http://www.r-project.org/>, January 2011). The two first CCA axes and their quadratic terms without interactions were used as explanatory variables; thus only monotonic and unimodal responses were allowed. The GLMs were fitted using a Poisson errors model (Leps & Smilauer 2003) and were simplified using a stepwise procedure (Crawley 2007). The association between the explanatory variables and dominant species' cover was tested for significance using the Wald test. To assess the degree of fit of the GLMs, we calculated the percentage of

deviance explained by the model using D^2 (Guisan et al. 2002). Finally, coexistence between dominant species was assessed through pairwise Spearman correlations on the relative cover of these species in each sampling point.

Results

Environmental correlates of species cover

Partition of variance showed that environmental (soil and water) variables explained more variation in species cover (37.6% of variance) than site and UTM coordinates (11.6%). However, according to Monte Carlo tests (see the Supporting Information, Appendix S1), species' cover was significantly related to only three environmental variables: mean water table level, maximum conductivity of water table and mean SAR. The first and second axes of CCA limited to environmental variables explained 16.1% and 7.7% of variability in species' cover, respectively. The first axis was mainly associated with salinity (Fig. 2), as it was positively correlated with the maximum conductivity of the water table ($r=0.8$; $P < 0.001$) and mean SAR ($r=0.75$; $P < 0.001$). The second axis was correlated with the mean water table level ($r=0.57$; $P < 0.01$) and, secondarily, with the maximum conductivity of the water table ($r=0.27$; $P < 0.05$).

Niche models of the selected species

The abundance–dominance curve of the 41 plant species recorded in the relevés showed an exponential trend

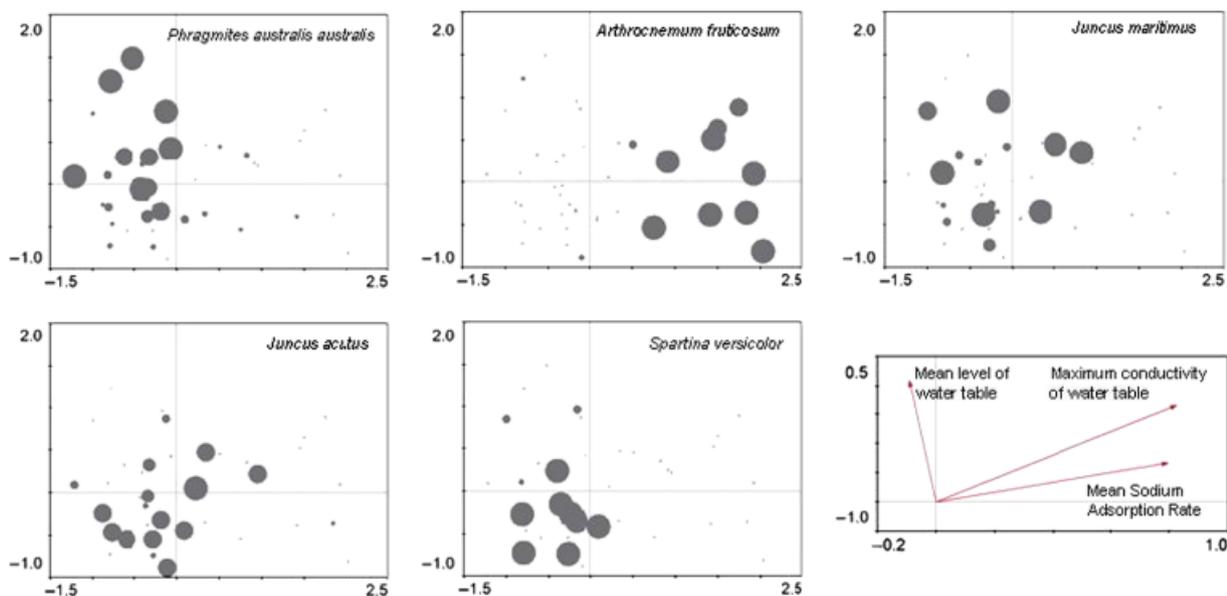


Fig. 2. Distribution and abundance of the dominant species in the environmental gradients studied summarized through canonical correspondence analysis (CCA). Circle centers correspond to the position of each relevé on the first two CCA axes, and size indicate cover of each species in each relevé according to seven categories: 87.5%, 62.5%, 37.5%, 17.5%, 5%, 0.1% and 0%. The bottom right plot summarizes the environmental variables significantly related to species cover according to Monte Carlo tests. Arrow angle stands for dispersion and arrow length for the weight of each variable.

Table 1. Frequency and abundance of plant species in the relevés, and their distribution across the main studied environmental gradients summarized through CCA. The table shows the species found in more than one relevé, their cover (both absolute and relative to total plant cover in the relevé) and the number of relevés where found. The range of CCA values in axes 1 and 2 in which each species occurs also are provided. The associated abundance–dominance curve obtained from total cover shows an exponential trend ($r=0.902$; $F=170.308$; $P<0.0001$), with a gap between the five most abundant species (in bold) and the rest, in terms of cover percentage.

Taxa	Absolute cover (%, mean)	Relative cover (%, mean \pm SD)	Relevés (n)	Range of CCA values (minimum, maximum)	
				Axis 1	Axis 2
<i>Phragmites australis</i> ssp. <i>australis</i>	18.7	21.2 \pm 32.7	27	(– 1.54, 1.53)	(– 1.56, 2.81)
<i>Juncus acutus</i>	16.6	18.8 \pm 27.5	20	(– 1.54, 2.14)	(– 1.45, 1.02)
<i>Arthrocnemum fruticosum</i>	15.9	18.1 \pm 33.8	13	(– 0.95, 2.35)	(– 1.45, 2.52)
<i>Spartina versicolor</i>	15.2	16.7 \pm 31.2	15	(– 1.26, 0.16)	(– 1.56, 1.38)
<i>Juncus maritimus</i>	14.7	4.5 \pm 17.0	6	(– 1.26, 1.12)	(– 1.35, 1.38)
<i>Elymus pungens</i> ssp. <i>campestris</i>	4.0	3.5 \pm 16.2	2	(– 1.54, 0.42)	(– 1.45, 0.47)
<i>Paspalum vaginatum</i>	3.1	2.4 \pm 10.1	5	(– 0.95, – 0.87)	(– 0.73, – 0.23)
<i>Juncus subulatus</i>	2.1	1.2 \pm 5.8	5	(– 0.95, 2.35)	(– 0.04, 2.52)
<i>Suaeda vera</i> ssp. <i>vera</i>	1.1	1.1 \pm 5.8	5	(– 0.8, 2.14)	(– 1.45, 0.77)
<i>Phragmites australis</i> ssp. <i>chrysanthus</i>	1.0	1 \pm 5.8	3	(– 0.81, – 0.38)	(– 0.36, 2.81)
<i>Calystegia sepium</i>	0.9	0.5 \pm 2.8	4	(– 1.54, – 0.47)	(– 0.73, 2.52)
<i>Atriplex prostrata</i>	0.5	0.5 \pm 2.8	3	(– 0.38, 0.57)	(– 0.24, 0.43)
<i>Galium aparine</i> ssp. <i>aparine</i>	0.5	0.5 \pm 2.8	2	(– 0.38, 0.57)	(– 1.22, 0.43)
<i>Brachypodium phoenicoides</i>	0.5	0.4 \pm 2.7	3	(– 1.06, – 0.34)	(– 1.56, – 0.55)
<i>Inula crithmoides</i>	0.3	0.4 \pm 2.7	5	(– 0.95, 1.11)	(– 0.73, 0.77)
<i>Agrostis stolonifera</i>	0.2	0.4 \pm 2.7	3	(– 1.54, – 0.18)	(– 1.22, 2.52)
<i>Aster squamatus</i>	0.2	0.3 \pm 1.3	2	(– 0.87, 0.42)	(– 1.22, – 0.24)
<i>Scirpus maritimus</i>	0.2	0.2 \pm 1.1	2	(– 0.69, 1.9)	(0.95, 2.81)
<i>Atriplex portulacoides</i>	0.2	0.2 \pm 1.1	2	(1.82, 2.35)	(– 0.04, 0.79)
<i>Sonchus maritimus</i> ssp. <i>maritimus</i>	0.2	0.2 \pm 1.1	2	(– 1.06, – 0.34)	(– 1.56, – 0.55)
<i>Dorycnium pentaphyllum</i> ssp. <i>gracile</i>	0.2	0.2 \pm 1.1	2	(– 0.34, – 0.23)	(– 0.55, – 0.06)
<i>Schoenus nigricans</i>	0.2	0.2 \pm 1.1	2	(– 1.06, – 0.34)	(– 1.56, – 0.55)

($r=0.902$; $F=170.308$; $P<0.001$), with a gap between the five most abundant species and the rest. These five species were, in decreasing abundance, *P. australis*, *Juncus acutus*, *A. fruticosum*, *Spartina versicolor* and *J. maritimus* (Table 1).

The distribution of *A. fruticosum* was skewed to the highest values of the first axis (corresponding to the most saline soils) but much broader on the second axis associated to water table (Fig. 2). *Phragmites australis* showed the highest values in CCA axis 2 (i.e. in the most waterlogged soils) and was more restricted to negative values in CCA axis 1 (i.e. in non-saline environments). *Juncus acutus* stands were skewed to negative values of both axes, although the species was also present in some saline points. *Spartina versicolor* was more restricted to dry and non-saline areas than *J. acutus*, and *J. maritimus* was the species most concentrated in the central values of both CCA axes.

The GLMs (Table 2) explained a variable percentage of deviance in species' cover, from 72% in *A. fruticosum* to 18% in *J. maritimus*. *P. australis* subsp. *australis* showed a unimodal response skewed to low values of CCA axis 1, with significant association with linear and quadratic terms of this axis, and a monotonic (linear) and positive association with CCA axis 2. In *J. acutus*, cover monotonically increased with decreasing values of both CCA

axes, and it was significantly associated to CCA axis 2 and only marginally to axis 1 ($P=0.0501$). In *A. fruticosum*, species cover showed a unimodal response significantly associated with CCA axis 1 and its quadratic term. In *S. versicolor*, the model also was unimodal, with a significant association of species cover with both CCA axes and their quadratic terms. For *J. maritimus* we obtained a similar model to that of *S. versicolor*, but maximum species cover was close to the origin of CCA coordinates, and was significantly related only to the CCA axis 2 and the quadratic terms of both axes.

Contrasting with the overlapped distribution of the study species in the first two CCA axes (Fig. 2), pairwise correlations between relative species' cover were mostly negative or non-significant. Thus, *A. fruticosum* showed a marginally significant, negative association with *J. acutus* ($r=-0.26$, $P=0.081$) and negative associations with *J. maritimus* ($r=-0.35$, $P=0.018$), *P. australis* subsp. *australis* ($r=-0.53$, $P<0.001$) and *S. versicolor* ($r=-0.37$; $P=0.014$); *J. acutus* was negatively correlated with *J. maritimus* ($r=-0.44$, $P=0.003$) and not correlated with *P. australis* subsp. *australis* ($r=-0.23$, $P=0.14$) or with *S. versicolor* ($r=-0.24$, $P=0.12$); *P. australis* subsp. *australis* was not significantly associated to *J. maritimus* ($r=0.19$,

Table 2. Response of the dominant species to the studied environmental gradients summarized through canonical correspondence analysis (CCA). The table shows the results from the simplified GLM models for species cover as response to the two first CCA axes and their quadratic terms. (D^2 , percentage of deviance explained by the models; z , statistic of Wald test; significance of the test: ${}^{\text{ns}}P \geq 0.05$, ${}^*P < 0.05$, ${}^{**}P < 0.01$, ${}^{***}P < 0.001$).

Species	D^2	Parameters	Coefficients	z
<i>Phragmites australis</i> subsp. <i>australis</i>	0.4416	Intercept	0.858	5.695 ^{***}
		Axis 1	-0.717	-3.618 ^{***}
		(Axis 1) ²	-0.500	-2.608 ^{**}
		Axis 2	0.284	3.167 ^{**}
<i>Juncus acutus</i>	0.2576	Intercept	1.0729	6.474 ^{***}
		(Axis 1) ²	-0.352	-2.671 ^{**}
		Axis 2	-0.495	-2.537 [*]
		(Axis 2) ²	-0.469	-2.358 [*]
<i>Arthrocnemum fruticosum</i>	0.7258	Intercept	-0.913	-2.673 ^{**}
		Axis 1	2.540	4.737 ^{***}
		(Axis 1) ²	-0.598	-2.845 ^{**}
<i>Spartina versicolor</i>	0.3137	Intercept	0.132	0.553 ^{ns}
		Axis 1	-1.904	-2.922 ^{***}
		(Axis 1) ²	-1.34	-2.351 [*]
		Axis 2	-0.387	-2.505 [*]
<i>Juncus maritimus</i>	0.1825	Intercept	0.950	5.621 ^{***}
		(Axis 1) ²	0.518	-3.205 ^{**}
		Axis 2	0.643	3.298 ^{***}
		(Axis 2) ²	-0.321	-2.603 ^{**}

$P = 0.21$) or with *S. versicolor* ($r = 0.09$, $P = 0.55$); *J. maritimus* and *S. versicolor* were the only species that were positively associated ($r = 0.34$, $P = 0.027$).

Discussion

The conservation of marsh vegetation, which is commonly dominated by a reduced set of species, clearly benefited from identifying the factors that determine the distribution and abundance of these dominant plants. Our study contributes in two ways to this goal in Mediterranean salt marshes: (1) by improving the knowledge about the realized ecological niches of the species studied, based on soil and hydrological parameters, and (2) by showing that the observed niche differences between species do not justify their segregation in space.

Main gradients and niche models

The best of our knowledge, this is the first study that has successfully modeled the abundance of dominant plant species in Mediterranean marshlands. We used small-scale predictors associated with soil and water table properties, in contrast to other work that used proxies of large-scale gradients (e.g. tidal regime; Silvestri et al. 2005). Our results are consistent with the general rule that flooding and salinity are the main physical factors

affecting the distribution of marshland species (Ranwell 1972; Adam 1993). In accord with other works (Álvarez-Rogel et al. 1997; Molina et al. 2003), we also highlight that some ions such as Ca^{2+} and Mg^{2+} (summarized in SAR) play a significant role in the distribution of species in Mediterranean marshes.

Arthrocnemum fruticosum is considered a true halophyte, thus dominating saline or hypersaline marshes (Ranwell 1972), as corroborated by the biased response towards saline environments observed in our study (Fig. 2, Table 1). Seeds can remain dormant and germinate after long-term exposure to salinity (Pujol et al. 2000; Redondo et al. 2004). The enforced dormancy of seeds under hypersaline exposure distinguishes halophytes such as *A. fruticosum* from glycophytes, and is a key factor allowing halophytes to occupy the most saline environments (Ungar 2001). In contrast, there is a lack of literature quantifying the response of *A. fruticosum* to waterflooding *per se*. Nevertheless, a decreasing response of *A. fruticosum* cover might be expected as the mean water table increases, because soil ions are frequently washed in waterlogged soils.

The remaining species occupy less skewed positions in the flooding and salinity gradients. Our results confirm the broad ecological niche of *P. australis* subsp. *australis* in water table and salinity reported by other authors (Romero et al. 1999). Indeed, tolerance of *P. australis* to soil salinity varies greatly (from 5 to 60‰) at local and regional scales throughout the world, thus suggesting local adaptations of reed clones (Lissner & Schierup 1997). However, high water table salinity generally inhibits seed germination (Mauchamp & Mesleard 2001; Greenwood & MacFarlane 2006), seedling survival (Hootsmans & Wiegman 1998), and tiller growth, and this may explain the absence of *P. australis* subsp. *australis* from clearly saline environments in the Llobregat Delta. Water level is another primary driver of *P. australis* distribution. Helophytes such as the common reed are particularly abundant in water-saturated soils, but an excessively high water level inhibits seed germination, seedling survival and growth (Armstrong et al. 1999), and clonal growth (Bodensteiner & Gabriel 2003; Dienst et al. 2004). Our model showed a decline in reed cover as the soil became drier, but we failed to detect the upper water table threshold which inhibits the species growth, probably because of a lack of sampling points in the highest part of the water table gradient.

Few studies have addressed the response of *J. acutus* to environmental variables, despite the broad distribution of the species over diverse salt marshes (Greenwood & MacFarlane 2006). According to Yoav (1972), this rush can thrive in highly saline areas, whereas Greenwood & MacFarlane (2009) found a negative relationship between soil salinity and the species biomass, and Martínez-Sánchez et al. (2006) observed low tolerance to salinity in its seeds. Our results agree with the relatively

low tolerance to salinity and also show that species cover responded negatively to increasing water table level.

Juncus maritimus occupies similar environments to those of *P. australis* (Sánchez et al. 1998). However, we have found that *J. maritimus* is more tolerant to salinity than *P. australis* but less tolerant to waterlogging. Despite some related adaptive traits (e.g. accumulation of polyol compounds and improvement of germination after seed exposure to salinity), tolerance of *J. maritimus* to salinity is limited (Adam 1993). Our results, like those of Álvarez-Rogel et al. (2006), showed that *J. maritimus* mainly occurs in a combination of moderate waterlogging and saline stress.

No previous ecological information was available for *S. versicolor*. Our results show that this species is very restricted to soils with low salinity. Dense belts of *Spartina* spp. are typical of marshland areas where macrotidal or mesotidal regimes reduce the salinity of the low marsh zone (Adam 1993; Curcó et al. 2002). The position of *S. versicolor* on axis 2 of the CCA and the model indicates that, unlike its congeners, it does not tolerate waterlogged conditions.

Niche overlapping and species distribution of dominant marsh plants

It can be concluded that there is some niche segregation of the study species along the main environmental gradients in Mediterranean marshlands, as they can be split into two groups: *A. fruticosum* and the remaining species. *Arthrocnemum fruticosum* shows one of the broadest niches of the study species (Fig. 2) yet it is clearly skewed towards saline environments. For the remaining species, niche differentiation along the main environmental gradients is not total but moderate. Nevertheless, pairwise correlations on the relative species' covers indicate that the distribution of these species along the environmental gradients is highly segregated. This means that the mono-specific stands frequently observed in Mediterranean salt marshes cannot be solely explained by environmental niche segregation.

Although the aim of our study does not include determining these alternative mechanisms affecting species' abundance, we can contribute in some points. Saline tolerance does not exclude *per se* *A. fruticosum* occurring in non-saline sites, but the constitutive physiological costs inherent to halophyte specialization might lead to a low competitive capacity against glycophytes when coinciding in non-saline soils (Adam 1993). For the other dominant species, selective herbivory (the marshes studied were regularly grazed by sheep until recent times) and the founder effect could be responsible for their distribution patterns. While no specific data are available, both factors might be implicated by the noticeable amount of variation

in species distribution explained by site and UTM coordinates. The overlapping ecological niches match with founder effects playing a primary role in plant species distribution in several irregularly flooded marshes (Costa et al. 2003). Disentangling the role of founder effects and biotic interactions on species distribution in Mediterranean coastal marshlands is an avenue for future research that must be addressed by performing specific field experiments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Pearson's correlations of the study variables with the two first canonical correspondence analysis (CCA) axes, and results of Monte Carlo tests assessing the association of these variables with species cover. Variables: maximum conductivity of water table (MCWT), mean sodium adsorption ratio in soil (SAR), mean level of the water table (MLWT), soil pH (SpH), mean K^+/Na^+ ratio in soil (K^+/Na^+), mean K^+ concentration in soil ($[K^+]$), mean soil conductivity (SCond),

percentage of CO_3^{2-} in soil ($S_CO_3^{2-}$), ratio between organic C and total N in soil (C_{org}/N_t), mean Ca^{2+}/Na^+ ratio in soil (Ca^{2+}/Na^+), mean SO_4^{2-}/Cl^- in soil (SO_4^{2-}/Cl^-), and percentage of clay in soil (SClay). Significance of the correlations: ^{ns} $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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