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Functional diversity turnover in the western Mediterranean saltmarshes: Effects of edaphic features and biotic processes on the plant functional structure

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1 Title page**2 Title**

3 Functional diversity turnover in the western Mediterranean saltmarshes: effects of edaphic
4 features and biotic processes on the plant functional structure

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14 Abstract

15 Salinity and soil moisture are considered main drivers of the plant zonation in Mediterranean
16 saltmarshes. Therefore, both factors could have a remarkable effect on the plant functional
17 structure of these habitats. The aim of this study was to identify the effects of abiotic and biotic
18 factors on the plant functional structure of western Mediterranean saltmarshes. A total of 20
19 saltmarshes were assessed, and seven plant traits were considered. Community weighted mean
20 and Rao index were used to measure the functional structure of the plant communities.
21 Redundancy analysis was used to estimate the effects of soil variables on the community-
22 weighted mean trait and functional diversity, and standardised effect size was used to assess the
23 effect of biotic interactions. The functional traits showed a clear zonation along the salinity
24 gradient in Mediterranean saltmarshes, mainly related to the electrical conductivity, and mainly
25 gathered in trait syndromes. The succulent nanophanerophytes grew at the highest salinity

zones. Salt excretors, both chamaephytes and mesophanerophytes, appeared in the intermediate and lowest salinity zones, respectively. Finally, geophytes with both selective cation root uptake and rhizome were mostly located in the lowest salinity zones. The abiotic factors strongly modulated the biotic interactions, and some convergence patterns were observed. The highest functional diversity was observed in the lowest salinity zones, a marked turnover. These findings indicate that multiple assembly processes determine the plant structure of Mediterranean saltmarshes, yet abiotic environmental filters strongly shape the local species assemblages and functional diversity turnover. Our results support that the whole salinity gradient should be protected to conserve the widest range of functional traits.

Keywords

biotic interactions; community assembly; conservation; environmental filtering; functional structure; plant traits.

1. Introduction

Saltmarshes are natural environments characterised by highly saline soils, which are distributed worldwide (Chapman, 1974). These habitats are dominated by halophytes, plants able to resist highly saline conditions (at least 200 mM of NaCl) (Flowers and Colmer, 2008). These plant species are distributed in a marked zonation with a well-delimited spatial structure throughout the saltmarsh (Chapman, 1974), and with salinity and soil moisture as the most relevant drivers of the plant zonation in the Mediterranean saltmarshes (Álvarez-Rogel et al., 2000, González-Alcaraz et al., 2014, Moreno et al., 2018). It could be therefore expected that the variation in edaphic conditions have a remarkable effect on the functional structure of these environments.

Functional traits have proved to be a useful tool to perceive ecological processes (Lavorel and Garnier, 2002, Garnier et al., 2004). Species with similar traits would be able to live under the same ecological conditions. Trait convergence and divergence could be observed when co-existing species are, respectively, more or less functionally different than expected by chance (Grime, 2006). Moreover, functional diversity (FD) –defined as the extent of trait differences between species (Pavoine and Bonsall, 2011, Dainese et al., 2015)– would be relevant to predict the response of plant communities to environmental changes. Therefore, the study of FD and its control factors would be essential to understand the structure, composition and dynamics of plant communities (Pavoine and Bonsall, 2011, Dainese et al., 2015). Regarding Mediterranean saltmarshes, certain studies were focused on the effects of some environmental factors (e.g. salinity) about the plant physiology on halophytes (see Flowers and Colmer, 2008, Flowers et al., 2010). Nonetheless, there is a lack of studies, focused on community level in the Mediterranean area.

Diamond (1975) defined the ‘assembly rules’ as generalised restrictions on the species presence or abundance that are based on the presence or abundance of one or several other species (Graves and Gotelli, 1993, Wilson, 1994), specifying the values and the domain of factors that structure or constrain the properties of ecological assemblages (Weiher and Keddy, 1999). Furthermore, ecological filters would be involved in these processes, indicating restrictions in

the community structure and composition (Wilson and Gitay, 1995) and predicting which subset of the total species pool for a given region will co-occur in a specific habitat (Keddy, 1992). These processes would lead the ecological assemblage at different scales, considering abiotic processes (e.g. environmental filtering) and biotic interactions (e.g. competition or facilitation) (Keddy, 1992, Díaz et al., 1999, Kraft et al., 2015). Both processes would shape local community patterns of plant species from regional pool based on their functional traits (Götzenberger et al., 2012, de Bello et al., 2013, Kraft et al., 2015).

Our research assesses the effects of edaphic properties and biotic processes on the plant functional structure of western Mediterranean saltmarshes, representing the first attempt to understand the functional structure of these saline communities based on quantitative data. The main aims of this study were: (1) to assess the effects of edaphic factors on the plant functional structure of Mediterranean saltmarshes; (2) to assess the effect of biotic interactions on the halophytic community structure; and (3) to provide insights on the functional trait assemblage of the saltmarsh plant communities. Furthermore, human activities (e.g. grazing, farming or urban pressure) have notably increased biodiversity loss and habitat fragmentation in these saline environments (Álvarez-Rogel et al., 2007). In this framework, our research aims to provide useful information about the functional ecology of Mediterranean saltmarshes that could be applied to the conservation and management of these vulnerable and fragmented ecosystems.

2. Material and methods

2.1. Study area and sampling

The study area was located in the southeast of the Iberian Peninsula (Spain), including 20 independent and well-separated saltmarshes located within an area of approximately 13000 km² (Fig. 1 and Appendix A in Supplementary material). In each saltmarsh, different plant zones were recognised according to the dominant plant species, and plots of 100 m² were established randomly in each studied area. The number of plots in each saltmarsh ranged from two to five

depending to the presence of dominant vegetation (Appendix A in Supplementary material). For this study, a total of 63 plots were sampled every three months for one year (July 2013–April 2014).

Plant composition and plant cover were recorded in each plot using the Braun-Blanquet scale with seven levels (r, +, 1, 2, 3, 4, 5) (Braun-Blanquet, 1979). Regional keys for plant identification (Castroviejo, 1986–2019, Mateo and Crespo, 2014, Blanca et al., 2011) and specialised research papers (Piirainen et al., 2017, Moreno et al., 2016, 2018) were used to identify plant species. A total of 252 vegetation relevés (63 plots $\times$ 4 times) were obtained, which were averaged for each studied plot due to the scarce vegetation variation between periods (Appendix B in Supplementary material). Besides, subsurface soil samples were collected at 20 cm depth to avoid the superficial salt crust. Three soil subsamples were collected randomly in each plot and were mixed to obtain a representative soil sample. A total of 252 soil samples (63 plots $\times$ 4 times) were obtained and they were averaged for each studied plot (Appendix C in Supplementary material).

Soil moisture was estimated by the water retention method on field-moist samples, over-drying the samples for 12 h at 110 °C (Burt, 2004), and without considering correction for the structural water of gypsum. The remaining sample was air-dried and 2-mm-sieved to remove coarse fragments before laboratory analyses. Saturation extracts were obtained from saturated pastes through vacuum filtering. Electrical conductivity (E.C.) was measured as a salinity estimator using a conductivity meter Crison© CM 35+, and pH was measured using a pH meter Crison© 25. Saturated pastes were dried for 12 h at 110 °C and the saturation percentage was calculated to estimate available water capacity (Burt, 2004), hereafter named Plant Available Water Capacity (PAWC). For the calculation of PAWC no correction for the structural water of gypsum was considered. The specific concentrations of sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}) and sulphur (S) [used as an indicator of sulphate (SO_4^{2-})] in the saturation extracts were measured by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES) (Perkin Elmer 7300 DV). The wavelengths used were 589 nm for Na^+ ,

766 nm for K^+ , 317 nm for Ca^{2+} , 279 nm for Mg^{2+} and 180.7 and 182.0 nm for S. The cation concentrations were then used to calculate the Ca^{2+}/Mg^{2+} , Ca^{2+}/Na^+ , and K^+/Na^+ ratios, and also the Sodium Adsorption Ratio (SAR) (Burt, 2004). SAR corresponds to the measure of the amount of sodium relative to calcium and magnesium in the water extract from saturated soil paste (USDA, 2017), so it was necessary to observe relevant ionic relations in the saline habitats (see Álvarez-Rogel et al., 2000). Chloride (Cl^-) concentration was measured using argentometry with silver nitrate ($AgNO_3$) in the saturation extracts (Harris, 2003). Besides, the percentages of clay and sand were also determined using a Bouyoucos densitometer (Juárez et al., 2004). Therefore, the environmental data for each plot included measurements of the following 16 edaphic variables: soil moisture; E.C.; pH; plant available water capacity (PAWC); Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Cl^- and SO_4^{2-} concentrations; Ca^{2+}/Mg^{2+} , Ca^{2+}/Na^+ and K^+/Na^+ ratios; SAR; and percentages of sand and clay (Appendix C in Supplementary material).

2.2. Functional traits

Considering plant strategies related to establishment, persistence and resistance in saline environments (Pérez-Harguindeguy et al., 2013), seven plant traits were selected to be assessed for the recorded plant species: salt adaptation –succulence, salt excretion, selective root cation uptake and salt location–; life form –therophyte, chamaephyte, hemicryptophyte, nanophanerophyte, mesophanerophyte and geophyte–; life span –perennial and annual plant–; presence of rhizome; reproductive type –seed and clonal reproduction–; presence of basal rosette; and maximum plant height (Appendix D in Supplementary material). Trait data were compiled from the literature (Castroviejo, 1986-2019, Mateo and Crespo, 2014) and also from direct observations of the collected plant material. Following Šmilauer and Lepš (2014), salt adaptation, life form, life span, and presence of rhizome were defined as dummy variables, while reproductive type and presence of basal rosette as fuzzy variables. Maximum height was a quantitative continuous variable, which was log-transformed before calculations (Appendix E in Supplementary material).

2.3. Community structure calculation

Community weighted mean (CWM) was used to measure the functional structure of the halophytic communities (equation 1). CWM represents the average trait value in a plant community and it was weighted by the relative abundance of the species carrying each trait value (Garnier et al., 2004):

$$CWM = \sum_{i=1}^n p_i x_i \quad (\text{equation 1})$$

where x_i is the mean trait value and p_i is the relative abundance of the i -th species. For binary traits x_i can be either zero or one, and the index reflects the relative abundance of each category. CWM was calculated using ‘dbFD’ function implemented in the ‘FD’ package (Laliberté and Legendre, 2010) in R (R Core Team, 2016).

Rao Quadratic Entropy Index of Diversity was used to calculate FD of each considered trait in each studied community (equation 2) (Rao, 1982, Lepš et al., 2006). FD was calculated by weighting the functional distances of each species according to their relative abundance:

$$Rao = \sum_{i=1}^n \sum_{j=1}^n d_{ij} p_i p_j \quad (\text{equation 2})$$

where d_{ij} is the functional distance between species i and j , and p_i and p_j are the relative abundances of the i -th and j -th species. Species’ functional distance was calculated using the Gower distance index, based on both quantitative and categorical traits (Lepš et al., 2006). The Gower distance was calculated with the function ‘gowdis’, and the Rao Quadratic Entropy Index of Diversity was obtained using ‘dbFD’; both functions were implemented in the ‘FD’ package (Laliberté and Legendre, 2010) using R (R Core Team, 2016).

Both Gower distance and Rao Quadratic Entropy Index have been considered as efficient functional indexes by several previous works (e.g. Garnier et al., 2004, Lepš et al., 2006, Ricotta and Moretti, 2011). The measures of CWM and FD were integrated in the response matrices (Appendix F in Supplementary material).

2.4. Statistical analysis

The effect of soil properties on the functional structure of the halophytic plant community were

assessed by Redundancy Analysis (RDA) of CWN and FD values, using CANOCO v.5 (Microcomputer Power, Ithaca, NY, US). The CWM values for each plant trait were used as response variables for the CWM-RDA and the FD values for each trait were used as response variables for the FD-RDA. In both cases, the study edaphic properties were considered as predictor variables. The $\text{Ca}^{2+}/\text{Mg}^{2+}$ and $\text{Ca}^{2+}/\text{Na}^+$ ratios, SAR, pH, PAWC, percentage of sand and Mg^{2+} concentration were log-transformed, whereas Cl^- , K^+ , Na^+ and SO_4^{2-} concentrations, E.C., soil moisture, K^+/Na^+ ratio and percentage of clay were transformed using square root. The CWM variability explained by the RDA was calculated for marginal and conditional effects. Marginal effects indicated the variability explained by the given set of edaphic variables without considering other environmental factors, whereas conditional effects were performed by a stepwise selection and denoted the variability explained by the given environmental set after removing the confounding effect of one or more other environmental variables (covariables) (Šmilauer and Lepš, 2014). Both effects were tested for significance ($P \leq 0.05$), using Monte Carlo permutation tests with 9999 permutations with CANOCO v.5 (Microcomputer Power, Ithaca, NY, US).

The analyses of trait convergence/divergence patterns were performed using the standardised effect size (SES) (equation 3), as defined by Gotelli and McCabe (2002):

$$SES = \text{observed FD} - \text{mean of expected FD} / \text{standard deviation of expected FD} \quad (\text{equation 3})$$

SES was calculated using the 'ses.mpd' function in the 'picante' package (Kembel et al., 2010) in R (R Core Team, 2016). The significance was tested against null models. Species data was kept constant, including the cover plant values, and the identity of individual species was randomised in the trait matrix (999 randomizations). Null models were carried out for each individual trait and for the complete set of individual traits. $SES < -2$ indicates trait convergence, whereas $SES > 2$ shows trait divergence. In this analysis, filters were applied to avoid abiotic processes (de Bello et al., 2012), classifying the samples in three different $\text{Ca}^{2+}/\text{Na}^+$ ratio groups: (i) ≤ 0.14 ; (ii) $0.15-0.25$; and (iii) ≥ 0.26 (according to the obtained FD-RDA results). Analyses of variance (ANOVAs) were performed using the 'lm' and 'anova'

functions to check significant differences ($P \leq 0.05$) among SES values in the different $\text{Ca}^{2+}/\text{Na}^{+}$ ratio ranges, and Tukey tests were performed with the 'glht' function ('multcomp' package) for significant differences (R Core Team, 2016).

3. Results

The CWM-RDA model showed a highly significant effect ($P = 0.001$), with the first two axes explaining 88.65% of fitted variation (41.77% of total variation) (Fig. 2). Regarding salt adaptation, succulence was related to high E.C., whereas salt excretion and selective root cation uptake appeared related to low E.C. (Fig. 2). Similarly, the life form was also notably explained by E.C., since the nanophanerophytes appeared close to high values of E.C. whereas the chamaephytes and geophytes were related to low E.C. values. Seed reproduction was also related to high E.C., whereas clonal reproduction, the presence of rhizome and leaves in basal rosette related to low E.C. (Fig. 2). Therefore, three main functional trait groups were identified based on the obtained data (Fig. 2): (1) succulence, nanophanerophyte and seed reproduction appeared related to high E.C; (2) salt excretion, chamaephyte, presence of basal rosette and clonal reproduction were related to low E.C.; and (3) selective root cation uptake, geophyte and the presence of rhizome were also grouped in the low E.C. Regarding the edaphic variables (Table 1), E.C., Na^{+} , K^{+} , Ca^{2+} , Cl^{-} and SO_4^{2-} concentrations, SAR, $\text{K}^{+}/\text{Na}^{+}$ and $\text{Ca}^{2+}/\text{Na}^{+}$ ratios, pH and soil moisture were significant to explain the variation in the marginal effects analysis ($P \leq 0.05$). The largest part of the variance was explained, in order of relevance, by E.C. (27.7%), Na^{+} and Cl^{-} concentrations (23.5% and 19.0%, respectively) and SAR (15.8%). However, conditional effects indicated that only E.C. was significant ($P \leq 0.05$) (Table 1).

The FD-RDA model also showed a significant effect ($P = 0.001$), with the first two axes explaining 80.53% of fitted variation (26.87% of total) with (Fig. 3). This analysis disclosed that most of the studied traits were notably related to the highest values of the $\text{Ca}^{2+}/\text{Na}^{+}$ ratio (Fig. 3). For the marginal effects analysis (Table 1), several edaphic variables –E.C., Na^{+} and Cl^{-} concentrations, $\text{K}^{+}/\text{Na}^{+}$ and $\text{Ca}^{2+}/\text{Na}^{+}$ ratios, PAWC and soil moisture– were significant to explain the variation in FD ($P \leq 0.05$), being the largest part of the variance explained by

Ca²⁺/Na⁺ ratio (10.0%), E.C. (8.5%) and Cl⁻ concentration (7.0%). Nevertheless, the conditional effects indicated that Ca²⁺/Na⁺ ratio was the only significant explanatory variable ($P \leq 0.05$) (Table 1).

The analysis of trait convergence/divergence patterns (Fig. 4) showed a marked significant convergence for all traits as a whole, salt adaptation and life form in the lowest Ca²⁺/Na⁺ ratio group. The intermediate Ca²⁺/Na⁺ ratio group showed a slight tendency to a convergence pattern for life form and presence of basal rosette. Finally, significant differences between the SES values of the lowest and highest Ca²⁺/Na⁺ ratio groups were found for all traits as a whole, salt adaptation and life form (Fig. 4 and Appendix G in Supplementary material).

4. Discussion

4.1. Abiotic factors

A species trait turnover related to the changes in salinity has been observed in the studied Mediterranean saltmarshes. This turnover is a crucial component to shape local community patterns of plant species and it would reflect the functional characteristics of the local dominant species and their variability, as other authors already stated (Lepš et al., 2011, Dainese et al., 2015). According to the ecological theory, deterministic factors such as the environmental filtering would determine the assemblages of local species by progressively filtering out maladaptive species from the species pool to local communities (Weiher and Keddy, 1999, de Bello et al., 2013). In saline environments, salinity precisely causes stress to plants, enabling only the well-adapted plant species to survive within the most stressful areas. Likewise, the concept of trait-environment linkage refers to sets of plant attributes consistently associated with certain environmental conditions, independent of the species involved; hence, plant traits are the subject of assembly processes (Keddy, 1992, Díaz et al., 1999). Thus, some of the studied functional traits (e.g. salt adaptation or life form) appeared clearly assembled in the different saltmarsh zones, suggesting the existence of an environmental filtering along the salinity gradient, with E.C. as the most responsible edaphic variable for the changes in

functional traits within the Mediterranean saltmarshes. Nonetheless, our data pointed out the $\text{Ca}^{2+}/\text{Na}^+$ ratio as the main edaphic variable to explain the FD differences, with a notable increased of the FD in the low stressful saline zones, which were characterised by a high $\text{Ca}^{2+}/\text{Na}^+$ ratio plus low E.C. values. Although similar edaphic factors could affect differently to the both studied functional indices (CWM and FD), as Dias et al. (2013) and Dainese et al. (2015) previously stated, our data revealed that the two achieved soil variables – $\text{Ca}^{2+}/\text{Na}^+$ ratio and E.C.– were both related to the same salinity gradient. Consequently, the obtained soil gradient entails an environmental filtering and it generally reduces FD as the viable traits under stressful environmental conditions. So, the highest FD has been located in high $\text{Ca}^{2+}/\text{Na}^+$ ratio zones, coinciding with the lowest salinity zones.

Furthermore, the studied functional traits have mostly shown a trait convergence in the highly saline zones, and this pattern appeared attenuated or absent in the intermediate and less saline zones, respectively. This trade-off would be due to the increment of trait variability in the latter zones. Succulent nanophanerophytes successfully colonise high saline zones (convergence pattern), whereas salt excretor chamaephytes with basal rosette, rhizomatous geophytes with selective salt absorption, and even salt excretor mesophanerophytes appear in the remaining zones. This model could be explained by the predominant strategy to tolerate the high salinity. Nevertheless, these findings showed a remarkable effect of the abiotic filters, even after having tried to avoid their influence. Therefore, the observed convergence patterns could be explained more by abiotic factors than by biotic interactions.

4.2. Biotic interactions

The abiotic factors have shown a relevant effect in the plant distribution within the saltmarshes (Álvarez-Rogel et al., 2000, González-Alcaraz et al., 2014, Moreno et al., 2018), concealing possibly the biotic interactions; and hence, the biotic effects might have not been untangled accurately in saline environments. The soil salinity would have a strong ecological effect, so the abiotic processes would hold a noticeable influence over biotic interactions. In this context, the observed trait convergences could be originated by the exclusion of those species with low

competitive abilities in relatively homogenous environmental conditions (Mayfield and Levine, 2010). For instance, succulent species would not coexist with the remaining halophytes, forming their own plant communities over high salinity soils in where other species were not competitive (Moreno et al., 2018). Finally, despite trait divergence has been reported more commonly than trait convergence (Götzenberger et al., 2012), the obtained patterns for Mediterranean saltmarshes have been focused on trait convergence. The most dissimilar traits would be selected from the pool of the functional species, emphasising on those species with traits related to salt adaptation.

4.3. Functional trait assemblage

Our results revealed that salt adaptation and life form showed a marked edaphic zonation, highly related to the salinity gradient, within the Mediterranean saltmarshes. However, these two functional traits appeared gathered in trait syndromes, which link different trait features as an adaptation response. Thus, three main trait syndromes –succulent nanophanerophytes, salt excretor chamaephytes and geophytes with selective salt absorption– were sequentially distributed from the highest (41.94-72.25 mS/cm) to the lowest salinity zones (up to 24.78 mS/cm). Succulence reduces the respiration in the leaves and increases the K^+ storage in the vacuoles (Flowers and Colmer, 2008). The presence of succulent nanophanerophytes in the highest salinity zone would be favoured by their high rates of transport of monovalent cations (Wickens and Cheeseman, 1991). Conversely, the presence of the geophytes with selective salt absorption within the lowest salinity zones would be related to a more regulated transport of Na^+ and K^+ (Inada et al., 2005). The abundance of salt excretor chamaephytes in the intermediate and lowest salinity zones would be directly related to optimal conditions for the efficiency of the salt excretion systems, a combination of low external salt concentration and high atmospheric humidity (Pollak and Waisel, 1979). Batanouny et al. (1992) found that increasing the external concentration of NaCl resulted in a direct increase in the amount of fluid secreted by salt glands, as reported for *Limonium delicatulum* (Girard) Kuntze; but a further increase in the concentration of NaCl caused an obvious decrease in the amount of secreted fluid. This

research exposed that NaCl, till a certain concentration, could enhance the process of salt secretion from the glands (Batanouny et al., 1992). Our results suggest that salt secretion would be heavily dependent on soil salinity under natural field conditions, as Rozema and Riphagen (1977) exposed for eastern European halophytes.

The effect of soil moisture also contributed to the spatial zonation of the functional trait syndromes related to succulent nanophanerophytes, salt excretor chamaephytes and geophytes with selective salt absorption. The succulent nanophanerophytes were notably dominant in the wet zones, which could be explained by the presence of aerenchyma, since it would seem to support the internal aeration (Pellegrini et al., 2017). In the driest zones, the dominant functional trait syndromes were the salt excretor chamaephytes, characterised by the presence of basal rosette, plus the geophytes with selective salt absorption. These halophytes would avoid the flooded zones because these two life forms –chamaephytes and geophytes– could not be adequately adapted to survive during the flooding periods. Another life form linked to salt excretors corresponded to the mesophanerophytes, which usually grow over non-permanently flooded saline soils, although they would tolerate eventual flooding periods (Álvarez-Rogel et al., 2000). The characteristic deepest roots of these salt excretor mesophanerophytes might avoid the negative effects of salinity and increase their colonization ability. However, due to the relative scarcity of this functional group in the studied saltmarshes, our results did not find support for this ecological behaviour of mesophanerophytes.

Sexual reproduction by seeds was the most frequent reproductive trait in the highest salinity zones, together with succulent nanophanerophytes. Succulent shrub communities have shown different germination syndromes, with high rates of germination after salinity exposure (Muñoz-Rodríguez et al., 2017), and they usually conform well-separated vegetation bands (Moreno et al., 2018). Conversely, clonal reproduction and salt excretors were two functional traits notably related to low salinity soils, although their seeds were able to germinate throughout the year (Brock, 1994, Crespo and Lledó, 1998). Salt excretor mesophanerophytes can produce new shoots from their stems and roots and even develop adventitious roots (Brock, 1994), and salt

excretor chamaephytes are able to originate a numerous population from a reduced number of individuals in a short time, combining seed and clonal reproduction (Crespo and Lledó, 1998). Moreover, the presence of rhizome would markedly favour the clonal reproduction, especially in geophytes (Conesa et al., 2007), appearing as one of the dominant traits in the lowest salinity zones.

Although our obtained results are in concordance by the recent ecological studies about plant zonation in Mediterranean saltmarshes (Álvarez-Rogel et al., 2000, González-Alcaraz et al., 2014, Moreno et al., 2018), further studies would be needed to include additional analyses about quantitative physiological features (e.g. accumulated ions and their ratios) and other functional traits (e.g. root and rhizome characters or seed features) to discern their variation under different environmental factors.

4.4. Conservation and management

In the Mediterranean saltmarshes, the habitat fragmentation through the soil gradient has a negative effect on the ecological balance due to the alteration of the plant zonation (González-Alcaraz et al., 2014). According to our results, the implementation of the conservation and management measures should not be only restricted to those saline areas characterised by a high FD, since a drastic loss of biodiversity could be observed within these saltmarshes, and consequently, a loss of functional diversity. Therefore, we suggest the management of each specific halophytic plant community, characterised by a peculiar FD and trait syndromes, along the whole saline ecosystem. Furthermore, the different ecological and edaphic aspects related to the halophytes within the saltmarsh should be considered and, hence, each plant zone should be separately handled. Consequently, the management and conservation of the whole salinity gradient should be considered to avoid the disappearance of some functional traits and, consequently, changes in the functional structure.

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510 Tables

511 Table 1. Marginal and conditional effects for Redundancy Analysis (RDA) on community
 512 weighted mean (CWM) and functional diversity (FD), showing pseudo-F values and the amount
 513 of the variance explained (Explains %) by every edaphic variable, ordered by their marginal
 514 effects. Abbreviations: E.C., electrical conductivity; SAR, sodium absorption ratio; PAWC,
 515 plant available water capacity. Significance legend: ns, non-significant; *, $P \leq 0.05$; **, $P \leq$
 516 0.01.

	CWM				FD			
	Marginal effects		Conditional effects		Marginal effects		Conditional effects	
	Explains %	pseudo-F	Explains %	pseudo-F	Explains %	pseudo-F	Explains %	pseudo-F
E.C.	27.7	23.3**	27.7	23.3**	8.5	5.7**	3.6	2.6 ns
[Na⁺]	23.5	18.7**	1.2	1.0 ns	6.3	4.1*	0.7	0.5 ns
[Cl⁻]	19.0	14.3**	1.4	1.0 ns	7.0	4.6*	0.9	0.6 ns
SAR	15.8	11.4**	1.5	1.3 ns	3.6	2.3 ns	2.5	1.8 ns
[K⁺]	14.2	10.1**	0.7	0.6 ns	4.4	2.8 ns	1.6	1.1 ns
[Ca²⁺]	12.6	8.8**	0.8	0.7 ns	4.5	2.9 ns	1.0	0.8 ns
[Mg²⁺]	7.1	4.6**	0.8	0.7 ns	4.3	2.7 ns	1.0	0.7 ns
Soil moisture	6.4	4.1**	0.8	0.7 ns	5.8	3.7*	1.0	0.7 ns
pH	6.3	4.1*	0.2	0.2 ns	4.0	2.5 ns	0.2	0.1 ns
K⁺/Na⁺	5.9	3.8*	0.8	0.7 ns	6.1	4.0*	1.0	0.7 ns
[SO₄²⁻]	5.7	3.7*	2.5	2.2 ns	4.1	2.6 ns	1.5	1.1 ns
Ca²⁺/Na⁺	4.3	2.7*	1.4	1.3 ns	10.0	6.8*	10.0	6.8*
PAWC	3.5	2.2 ns	2.1	1.8 ns	5.1	3.2*	4.0	2.8 ns
Ca²⁺/Mg²⁺	3.3	2.1 ns	2.3	2.1 ns	1.4	0.9 ns	1.6	1.2 ns
% Clay	1.0	0.6 ns	1.1	1.0 ns	1.3	0.8 ns	1.2	0.9 ns
% Sand	1.0	0.6 ns	2.3	2.0 ns	0.5	0.3 ns	1.5	1.1 ns

Figure captions

Figure 1. Map of the study area, showing the position of the study sites in Mediterranean saltmarshes.

Figure 2. Redundancy Analysis (RDA) on community weighted mean (CWM) for plant traits using edaphic variables as E.C.; pH; PAWC; Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Cl^- and SO_4^{2-} concentrations; $\text{Ca}^{2+}/\text{Mg}^{2+}$, $\text{Ca}^{2+}/\text{Na}^+$ and K^+/Na^+ ratios; SAR; and percentages of sand and clay. Environmental variable abbreviations: E.C., electrical conductivity; PAWC, plant available water capacity; SAR; Sodium Adsorption Ratio.

Figure 3. Redundancy Analysis (RDA) on functional diversity (FD) for plant traits using edaphic variables as E.C.; pH; PAWC; Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Cl^- and SO_4^{2-} concentrations; $\text{Ca}^{2+}/\text{Mg}^{2+}$, $\text{Ca}^{2+}/\text{Na}^+$ and K^+/Na^+ ratios; SAR; and percentages of sand and clay. Environmental variable abbreviations: E.C., electrical conductivity; PAWC, plant available water capacity; SAR; Sodium Adsorption Ratio.

Figure 4. SES values for each trait in every $\text{Ca}^{2+}/\text{Na}^+$ ratio range. Different letters indicate significant differences between $\text{Ca}^{2+}/\text{Na}^+$ ratio ranges.

Supplementary material

Appendix A. Study sites in Mediterranean saltmarshes.

Appendix B. Cover values for 62 species from 63 average relevés taken in the 20 studied Mediterranean saltmarshes during 2013-2014 one-year period. Abundance scale: r, isolated individuals with very low cover; +, < 1% cover; 1, 1-5% cover; 2, 5-25% cover; 3, 25-50% cover; 4, 50-75%; 5, > 75%.

Appendix C. Annual average values per plot for the environmental variables assessed in the studied Mediterranean saltmarshes.

Appendix D. Plant functional traits in saltmarshes.

Appendix E. Trait matrix for 62 species based on 63 average relevés taken in the 20 studied Mediterranean saltmarshes.

Appendix F. Measures of CWM and FD for the studied functional traits.

Appendix G. Analysis of variance (ANOVA) of $\text{Ca}^{2+}/\text{Na}^{+}$ ratio group effect on SES values for each assessed trait. Numbers in bold indicate significant differences ($P \leq 0.05$) between $\text{Ca}^{2+}/\text{Na}^{+}$ ratio groups. Abbreviation: df, degrees of freedom.

RDA axis 2 (10.85% of fitted, 5.12% of total variation)

Highlights

- The highest FD would be observed in the lowest saline zones, showing a marked turnover.
- Multiple assembly processes determine the vegetal structure of the Mediterranean saltmarshes, and that environmental filters would shape the local species assemblages.
- The whole salinity gradient protection should be considered to avoid the disappearance of some functional traits and, consequently, changes in the functional structure.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: