Journal of Vegetation Science ■■ (2014)

Filtering of plant functional traits is determined by environmental gradients and by past land use in a Mediterranean coastal marsh

Efrem Batriu, Josep Maria Ninot & Joan Pino

Keywords
coastal marshes; past land use; plant functional traits; RLQ; salinity; waterlogging

Nomenclature
Bolòs et al. (2005)

Received 13 January 2014
Accepted 6 October 2014
Co-ordinating Editor: Leandro Duarte

Batriu, E. (corresponding author, efrembatriu@hotmail.com)[1],
Ninot, J.M. (jninot@ub.edu)[1],
Pino, J. (joan.pino@uab.cat)[2]
[1]Department of Plant Biology, University of Barcelona, Av. Diagonal 645, E-08028 Barcelona, Spain;
[2]Centre for Ecological Research and Forestry Applications (CREAF), Department of Animal and Plant Biology and Ecology, Autonomous University of Barcelona, E-08193 Bellaterra, Spain

Abstract

Question: What is the effect of past land use and environmental gradients on plant functional traits within coastal marsh plant communities?

Location: Mediterranean microtidal marshes in the Llobregat Delta, NE Spain.

Methods: We used a data set collected previously comprising 45 vegetation plots with associated soil parameters, water table conditions and past land use. For each species we obtained the values or states for a set of plant functional traits: plant height, leaf dry matter content, specific leaf area, seed production, seed weight, life form and lateral expansion. To account for the effect of phylogeny, we evaluated trait diversity skewness by means of an ultrametric phylogenetic tree specifically constructed for the species studied. The association between both environmental gradients and past disturbance, and plant functional traits was tested by means of RLQ analysis.

Results: Of all the traits, only seed weight showed a phylogenetic signal; consequently, phylogeny was not included in the RLQ analysis. Conductivity was negatively correlated with seed weight, whereas water table conditions and soil ionic balance were negatively correlated with specific leaf area. Past disturbance was negatively correlated with leaf dry matter content and with lateral expansion.

Conclusions: Plant traits of Llobregat Delta coastal marsh communities are conditioned by environmental gradients and by past land use. Soil ionic balance and water table conditions determine key plant functional traits such as specific leaf area. This finding also corroborates the importance of soil ionic balance as a plant life driver in microtidal Mediterranean marshes. The effect of past land use on species traits might, however, be partially indirect and mediated by associated environmental changes.

Introduction

The vegetation in a particular area reflects the selection, through environmental and biotic filters, from the flora available of those species capable of co-existing under the prevailing conditions (Keddy 1992). Plant species thus selected might exhibit some common traits that, in turn, determine ecosystem functions such as biogeochemical cycling or response to disturbance (Lavorel & Garnier 2002). Consequently, exploring the relationship between environment and species traits might help us to understand the response of organisms and ecosystems to environmental constraints at different levels (Lavorel & Garnier 2002; Wesuls et al. 2012).

In coastal marshes, salinity and moisture gradients have been identified as the main natural factors that constrain plant distribution (Chapman 1974). Only a few lineages of vascular plants have developed plant traits such as succulence, a photosynthetic pathway, or aerenchymatous roots that allow them to inhabit coastal marshes (Adam 1993). Except in the upper marsh zone, most plant communities in coastal marshes are species-poor and dominated by a few phylogenetically closely related species that share many of their physiological traits (e.g. Bertness et al. 1992; Costa et al. 2003; Pennings et al. 2003). Since one

Doi: 10.1111/jvs.12251

mechanism that permits plant co-existence is trait differentiation, coastal marshes offer an interesting context in which to study the complex associations between environmental gradients, plant community composition and plant traits. However, few studies have addressed this issue (Minden & Kleyer 2011; Minden et al. 2012), especially in terms of accounting for phylogenetic signal (Pavoine et al. 2011). According to the research that has been published, key environmental factors such as waterlogging and salinity might promote changes in plant species traits in coastal marshes, despite evidence still being limited and inconclusive. For example, waterlogging and salinity might increase (Minden & Kleyer 2011) or decrease (Minden et al. 2012) the frequency and abundance of plants with a low specific leaf area (SLA) in these habitats.

Although costal marshes have traditionally been drained for sanitary reasons and reclaimed for agricultural use, their conservation and restoration have become common in Europe over the last few decades, following increasing concern for the conservation of their natural values. It is known that disturbance affects plant traits in certain ways, as widely reported for arable fields and pastures, after cropping and grazing cessation (Kleyer 1999; Kahmen & Poschlod 2004; Pakeman 2004; Louault et al. 2005; Purschke et al. 2012), as well as for other types of vegetation (McIntyre et al. 1999; Cornelissen et al. 2003). Those studies report that disturbance commonly favour species with high SLA, low leaf dry matter content (LDMC), high seed production and low seed weight. These effects could be interpreted in a successional context yet modulated by intrinsic and climate factors (Pakeman 2004; De Bello et al. 2005; Díaz et al. 2007). To our knowledge, the relationship between level of disturbance and plant traits in coastal marshes has only been studied for a small number of traits (Dupré & Diekmann 2001; Pino et al. 2009; Benot et al. 2011). Those studies suggest that disturbance reduces plant height and the abundance of both geophytes and plants with high lateral expansion (Dupré & Diekmann 2001). In contrast, the effect of past disturbance (i.e. associated with contrasting changing histories of land use) on plant species traits has not been taken into account, despite land use legacy affecting current species distribution in these marshes (Domènech et al. 2005; Pino et al. 2009). There is increasing evidence that past land use leaves a historical signal on current plant species distribution (e.g. Cristofoli et al. 2010; Jackson & Sax 2010) and also on species traits (Lindborg 2007; Bagaria et al. 2012; Purschke et al. 2012).

Here we study the relationship between both environmental gradients and past land use, and the distribution of plant functional traits in an area of Mediterranean coastal marshes. The research focuses on a coastal marsh with a complex history of changing land use (Batriu et al. 2011), where we have recorded species abundances at 45 sampling points. We hypothesize the existence of combined effects of environmental factors and past land use on the distribution of plant functional traits. Despite the effects of environmental factors scarcely being known, we expect that salinity and flooding affect traits related to species growth and reproduction. We also expect that disturbance associated with past land use promotes attributes of pioneer species (high SLA and seed production) but penalizes those more frequent in late-successional species (i.e. large plant size, high levels of expansion, persistence and clonality and increased LDMC and seed weight). We have built a database of relevant biological and ecological plant traits, with regard to species persistence and reproduction (Weiher et al. 1999), and we use a single, three-table ordination analysis (RLQ) to explore the roles of species abundances, and environmental and past land use variables on the distribution of species traits, after testing for the phylogenetic signal on these traits (Pavoine et al. 2011).

Methods

Study area

The study was conducted in the southern hemi-delta of the River Llobregat (Llobregat Delta hereafter), south of the city of Barcelona (41°N, 2°E; Catalonia, NE Spain). The Llobregat Delta is a microtidal wetland area currently included in the Barcelona conurbation. Climate data obtained from Barcelona International Airport (located in the middle of the delta) record an average annual precipitation of 640 mm for the period 1971–2000, with minimum rainfall in July (20 mm) and maximum in October (91 mm). The mean annual temperature is 15.5 °C, with the highest mean maximum in August (28 °C) and the lowest mean minimum in January (4.4 °C). The area is thus under a Mediterranean pluviseasonal–oceanic bioclimate. Coastal marshes in the Llobregat Delta are dominated by reedbeds (*Phragmition australis*), rushbeds (*Juncion maritimi*) and halophytic scrubland (*Arthrocnemion fruticosi*).

Environmental gradients and species

We randomly selected 45 sampling points distributed among the four best-preserved marshland remnants in the delta (sites hereafter) situated along an inland–coastal gradient and with different past and present land uses. These sites are: Magarola Ricarda, Can Sabadell and Reguerons (for details of their locations see Batriu et al. 2011). All the sites occupy at least 18 ha and have diverse vegetation types such as grasslands, coastal marsh communities, coastal pine forest and dune vegetation. At each site we set up six to 19 sampling points, depending on marsh vegetation cover, randomly distributed among the three main coastal marsh vegetation types (reedbeds, rushbeds and halophytic shrubs). The distance between the points was at least 20 m and the distance between the points and roads was at least 50 m. Ricarda and Magarola are located close to the shoreline; although the former has substantial freshwater input, whereas the latter is more heavily influenced by seawater. Can Sabadell and Reguerons are located 2 km from the shoreline; the former includes some patches of saline soil, whereas the latter may be considered mesohaline. Thus, mesohaline and saline habitats are present in both inland and shoreline localities. According to Pino et al. (2006), Magarola and Ricarda are stable sites (long-standing natural areas) while Can Sabadell and Reguerons are semi-stable sites (abandoned and spontaneously restored since 1956). The four sites represent two different past land use situations that were codified by a two-value variable hereafter called past disturbance (0 = stable sites since at least 1956; 1 = disturbed sites in 1956).

At each sampling point we recorded the species composition and abundance in a circular area of 2 m radius (12.56 m^2) using the Braun-Blanquet method (Braun-Blanquet 1979). Species were identified according to Bolòs et al. (2005) and taxonomy was later corrected to fit current phylogenetic criteria (see below). The Braun-Blanquet cover–abundance scale was transformed following the Dagnelie (1960) transformation, that is: + (<5%, few individuals), 0.2; 1 (<5%, abundant), 1; 2 (5–25%), 2; 3 (25–50%), 3; 4 (50–75%), 4 and 5 (>75%), 5.

Each sampling point was marked with a vertically sunk PVC pipe, 1.5 m in length (reaching 1.3 m in depth) and 32 mm in diameter. The water level (in cm) and conductivity (in $\mu S \cdot cm^{-1}$) were measured monthly at each pipe from December 2004 to December 2006 using a WTW TetraCond 325 sensor (WTW, Weilheim, DE). From April 2005 to January 2006, two soil samples were taken from the top 20 cm at each sampling point every 3 mo. From these samples we obtained a saturation extract following Bower & Wilcox (1965). The concentrations of Ca^{2+}, Mg^{2+}, Na^+ and K^+ of this saturation were determined using ICP-OES (optic emission spectroscopy with inductive plasma). The balance between the concentrations of Na^+, Mg^{2+} and Ca^{2+} ions, called the SAR (sodium adsorption ratio), was calculated following Richards (1974).

Traits

We obtained the values of seven plant traits for each of 40 species occurring in the relevés, namely: plant height, LDMC, SLA, seed production, seed weight, capacity for lateral expansion and life form. These traits indicate the responses of plants to their environmental challenges (Weiher et al. 1999). SLA, LDMC and plant height were measured according to the recommended sample sizes given in Cornelissen et al. (2003): ten individuals for plant height and five leaves from two different individuals for SLA and LDMC. However, the collected leaves were pooled to form a single sample to obtain a single measure. Moreover, for six species, the SLA and LDMC data were obtained from the LEDA traitbase (Kleyer et al. 2008). Seed production was specifically measured according to Sera & Sery (2004); with the exception of one species (*Galium aparine*), for which the value was obtained directly from Sera & Sery (2004). Seed weight was obtained from the Seed Information Database (v 7.1, http://data.kew.org/sid/), except for eight species not in that database which were sampled according to Cornelissen et al. (2003): using a minimum of five seeds from three different individuals. In our case, however, the seeds were air-dried instead of oven-dried, based on the protocol used by the Seed Information Database (v 7.1, http://data.kew.org/sid/). We assigned the Raunkiaer life forms according to Bolòs et al. (2005), except that chamaephytes and phanerophytes were merged into a single category. To assess capacity for lateral expansion, we considered the four categories described in the LEDA standards (Kleyer et al. 2008): no lateral spread (mainly therophytes), low lateral spread (<0.001 $m \cdot yr^{-1}$), moderate lateral spread (0.01–0.25 $m \cdot yr^{-1}$; mainly plants that adopt a phalanx strategy *sensu* Grime 1979), and high lateral spread (>0.25 $m \cdot yr^{-1}$, mainly plants that adopt a guerrilla strategy, cf. Grime 1979). The species were classified into one of these four categories according to personal observations and descriptions in standard floras (mainly Bolòs et al. 2005). Life form and lateral expansion were transformed into dummy nominal variables. All the trait variables showed pair-wise Spearman correlation, $|r| < 0.75$, for all the study species.

Phylogeny

Phylogenetically closely related species may share more plant traits than expected by chance (Cahill et al. 2008). That being so, any study dealing with the relation between plant traits and gradients should first test this effect, i.e. check for phylogenetic signal. If there is such a signal, the results cannot be completely attributed to environmental filtering, but must also be partially attributed to phylogenetic relations. To check for a phylogenetic signal, we constructed a tree topology using the topology of the APG III (2009) classification as the basic structure. For families with more than one species, we completed this basic tree using specific studies. We then used the TimeTree database (Hedges et al. 2006; www.timetree.org) to obtain the molecular age of 20 nodes dated in recently published studies. For more details of the tree topology resolution and node dating see App. S1.

To test for the presence of phylogenetic signal, we used the skewness test devised by Pavoine et al. (2010). The method involves decomposing trait diversity among the nodes of a phylogenetic classification tree. The value attributed to a node is a function of the trait diversity among the clades descending from it. Species traits show a phylogenetic signal if the trait diversity is biased to the root or to the tip of the phylogenetic tree. The skewness test was performed using R (R Foundation for Statistical Computing, Vienna, AT) and the R scripts provided by Pavoine et al. (2010). For more details of this test see App. S1.

Overall, neither trait diversity nor any trait (except for seed weight) showed significant skewness towards the root or the tips of the phylogenetic tree ($P > 0.05$). Based on this, we did not incorporate phylogeny into the RLQ analysis.

Statistical analysis

For the study we considered past land use and three selected variables that are representative of the main environmental gradients in coastal marshlands: maximum water table conductivity (hereafter conductivity), mean water table level (hereafter water table) and mean soil SAR. These variables were identified as the most important factors that constrain species distribution in coastal marsh plant communities in the Llobregat Delta through a CCA analysis and showed a pair-wise Spearman correlation, $|r| < 0.75$ (Batriu et al. 2011).

Quantitative traits (plant height, LDMC, SLA, seed production, seed weight) and environmental variables were tested for normality using the Shapiro-Wilk normality test, and all variables with $P < 0.1$ were log transformed. All variables except seed production fulfilled the normality condition. Then, all trait and environmental quantitative variables were standardized (mean = 0, SD = 1).

We assessed the association between environmental variables and plant traits by means of an RLQ analysis (Dolédec et al. 1996). According Kleyer et al. (2012), this method provides an excellent overview of the trait–environment relationships at the species level. RLQ is an extension of co-inertia analysis that searches for a combination of traits and environmental variables of maximal covariance, which is weighted by the abundances of the species in the plots. To perform the RLQ analysis, we first performed a correspondence analysis (CA) on the species relevé matrix (L matrix), then we performed principal components analysis (PCA) on the species traits (Q matrix) and also on the environmental factors (R matrix) using the species weights from the CA previously performed on the L matrix as row weights. Finally, the RLQ analysis was performed using the CA and both PCAs. The overall significance of the RLQ analysis was tested using a Monte-Carlo permutation test with 999 repetitions.

The significance of the correlation between each environmental variable and each trait was tested using two models of permutations detailed in Dray & Legendre (2008). In the first model, we used a permutation of the site vectors in the L table that tests whether species assemblages are dependent on environmental gradients, permutation 2 in Dray & Legendre (2008). In the second model, we used a permutation of the species vectors of the L table that tests whether the distribution of species depends on the traits of these species, permutation model 4 in Dray & Legendre (2008). In accordance with Dray & Legendre (2008), we combined the two models in order to attain the correct Type I error level. The permutations were performed using a Monte Carlo permutation test with 999 repetitions.

All the analysis were performed using the package ade4 (Dray & Dufour 2007) from R (v 2.15, www.r-project.org) and the R scripts provided by Kleyer et al. (2012).

Results

The RLQ test was significant ($P = 0.02$) and its first two axes explained almost all the total co-inertia (97.4%). The first axis explained 88.5% of the co-inertia, and it was positively correlated with past disturbance and negatively correlated with water table, conductivity and SAR (Fig. 1). As for traits, the first axis was negatively correlated with LDMC, high lateral expansion capacity (guerrilla strategy) and chamaephyte life form; and positively correlated with seed weight, therophyte life form and no lateral expansion capacity. Based on the hypotheses we outlined in the introduction, this axis split the plots in two groups: plots under low natural stress (i.e. the magnitude of stress caused by salinity and flooding was low) and located on past disturbed sites; and communities under high natural stress and located on past disturbed sites. Species with a low LDMC, no lateral expansion capacity, therophyte life form and high seed weight were common in this ecological situation. The second axis explained only 8.9% of the total co-inertia. It was mainly negatively correlated with water table, and to a minor degree positively correlated with conductivity and negatively correlated with SAR. It should be noted that in high positions on axis 2, the plots have a low water table that has high conductivity, and in this situation roots do not tend to be exposed to salinity stress. In terms of traits, the second axis was positively correlated with seed production, high lateral expansion capacity (guerrilla strategy) and SLA; and negatively correlated with seed weight, no lateral expansion capacity, therophyte life form and plant height. This second axis should be understood as an

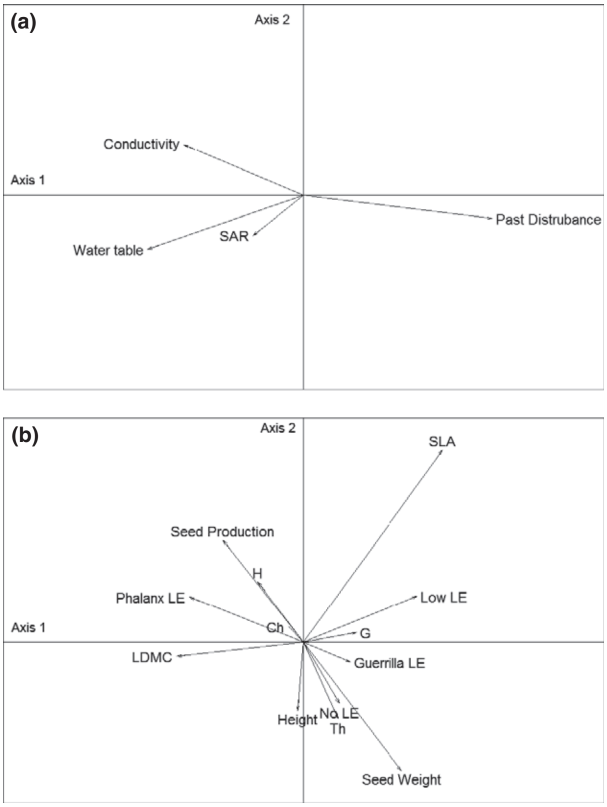

Fig. 1. Position of the environmental variables (**a**) and traits (**b**) in the space defined by the first two RLQ axes. Variable codes: Sar, sodium adsorption rate; SLA, specific leaf area; LDMC, leaf dry mass content. Trait codes: Ch, chamaephyte life form; H, hemicryptophyte life form; G, geophyte life form; Th; therophyte life form; LE; lateral expansion capacity.

Table 1. Pearson correlations between traits and environmental variables obtained through permutation models 2 and 4 detailed in Dray & Legendre (2008).

	Past Disturbance	Max. Conduct.	Water Table	SAR
Plant Height	0.004	−0.036	0.06	0.021
LDMC	−0.265*	0.162	0.233	0.075
SLA	0.238	−0.087	−0.358*	−0.181*
Seed Production	−0.176	0.18	0.109	−0.04
Seed Weight	0.204	−0.254*	−0.09	−0.04
Life Form				
Ch	−0.055	0.017	−0.003	0.025
H	−0.127	0.075	0.05	−0.035
G	0.133	−0.036	−0.103	−0.004
Th	0.113	−0.07	−0.001	−0.015
Lateral Expansion				
No	0.11	−0.066	−0.01	−0.008
Low	0.211	−0.14	−0.243	−0.071
Phalanx	0.149	−0.04	−0.03	−0.049
Guerrilla	−0.28*	0.156	−0.158	−0.048

*$P < 0.05$.

Variable and trait codes: Sar, sodium adsorption rate; SLA, specific leaf area; LDMC, leaf dry mass content; Ch, chamaephyte life form; H, hemicryptophyte life form; G, geophyte life form; Th, therophyte life form.

axis that reflects both waterlogging and high soil SAR gradients (Fig. 1). In plots where waterlogging or soil SAR is high, most plants showed high seed production, high lateral expansion capacity, high SLA, low seed weight and low height.

The RLQ permutations revealed five significant ($P < 0.05$) negative correlations between environmental variables and plant traits. These are the relations between past disturbance and high lateral expansion capacity (guerrilla strategy), past disturbance and LDMC, conductivity and seed weight, water table and SLA, and SAR and SLA (Table 1).

Discussion

Environmental gradients

We found a significant relationship between environmental gradients and plant traits in Mediterranean coastal marshlands. First, we found significant effects of water table and salinity on SLA. According to previous studies, the effects of the salinity–flooding gradient on SLA might be negative (Minden & Kleyer 2011) or positive (Minden et al. 2012). This apparent contradiction may be caused by succulent species, which sometimes are abundant in highly saline conditions. The particular leaf anatomy of succulent plants gives high SLA values, which conflicts with the expected trend of lower SLA values in species growing in stressful environments (Vendramini et al. 2002). Environmental gradients in our case study were not as mixed as those reported by Minden & Kleyer (2011) and Minden et al. (2012) in macrotidal salt marshes, due to the absence of a tidal regime; thus better disentangling the effects of salinity and flooding. Mediterranean coastal marshes are characterized by dominant succulent Chenopodiaceae in highly saline habitats (Adam 1993). However, other plant types can also overcome osmotic water stress thanks to noticeable lignification of the leaves or photosynthetic stems, as seen in rushes (*Juncus acutus* and *Juncus maritimus*). The presence of species using this strategy explains the negative association between salinity and SLA observed in our study. The salinity effect is due to the balance between Na^+, Mg^{2+} and Ca^{2+} (SAR) in soil. This is consistent with the identification of soil SAR as an important environmental driver in vegetation composition in microtidal Mediterranean coastal marshes (Álvarez Rogel et al. 2001; Molina et al. 2003; Batriu et al. 2011). According to Mommer et al. (2006), flooding promotes plants with high SLA values. Under the water, gases enter the leaf through the cuticle and epidermal cells; therefore thin leaves can improve gas exchange in these circumstances.

Doi: 10.1111/jvs.12251 © 2014 International Association for Vegetation Science

However, in most of the species thriving in high water table conditions in our study, only the root system was under water and most of the leaves were out of the water. In these circumstances, plants may suffer drought stress as anoxic soil conditions reduce root water uptake, while the evaporative demand of leaves remains constant (Poorter et al. 2009). This effect explains the negative relation observed between water table and SLA.

Shumway & Bertness (1992) identified two types of plant functional groups in temperate coastal marshes: the perennial turfs (persisting through dense clonal growth) and the fugitive herbs (without clonal growth capacity). Perennial turfs dominate in late successional stages, where the slow dynamics is dependent on clonal growth and persistence, and sexual recruitment plays only a minor role (Shumway & Bertness 1992). Strong saline-tolerant plants can be associated with fugitive behaviour, since constitutive physiological costs inherent to halophyte specialization lead to a low competitive capacity against less tolerant species when growing in less saline soils (Adam 1993). Thus, as Erfanzadeh et al. (2010) showed, saline-tolerant species are forced to be good seed producers and dispersers in order to colonize new available high saline gaps within the less saline matrix. This would explain the negative relation between conductivity and seed weight.

Coastal marshes are one of the Central European vegetation types that exhibit a high proportion of clonal species (Sosnová et al. 2010). However, in the case of Mediterranean dry salt marshes, halophytic shrubs with a low capacity for lateral expansion play an important role in highly saline conditions (Adam 1993). For instance, the dominating species in the most saline conditions of the Llobregat Delta marshes is *Arthrocnemum fruticosum*, a sub-shrub with no capacity for lateral spread. Therefore, a clear negative correlation between conductivity or SAR and lateral expansion might be expected along a pronounced salinity gradient, ranging from highly saline to very low saline conditions. However, semi-stable sites found mainly on non-saline soils promoted annual species without the capacity for lateral spread, which buffered the expected trend.

Past land use

Our study also detected a significant negative effect of historical disturbance associated with past agricultural use on two species traits: lateral expansion capacity and LDMC. Previous studies also detected a significant association between past land use and species traits, suggesting that these traits might mediate plant response to land-use change (Verheyen et al. 2003; Kolb & Diekmann 2005; Adriaens et al. 2006; Lindborg 2007; Bagaria et al. 2012). In our case, the effect on traits might also be partially masked by changes in environmental conditions determined by the previous land use. Indeed, post-agricultural soils tend to have high resource availability (Knops & Tilman 2000), and past agricultural use might have determined an increase in the soil fertility of semi-stable marshlands compared with stable ones, as suggested by their mean values of organic C:N ratio (Table 2). Hence, species growing in semi-stable marshlands might show higher SLA and lower LDMC than those in stable marshlands, as these traits are known to be related to high resource availability (Lavorel & Garnier 2002; Cornelissen et al. 2003). However, we only found this association in the case of LDMC; a trait related to the average density of leaf tissue and relatively opposed to SLA (Cornelissen et al. 2003). The strong dependence of SLA on leaf thickness (Wilson et al. 1999) seems to make LDMC a better proxy for nutrient availability than SLA in the case of marshland plants, as suggested by our results.

The negative association between past disturbance and capacity for lateral expansion detected in our study has also been observed in grazed pastures (Wesuls et al. 2012), agrarian landscapes (Kleyer 1999) and managed meadows (Klimešová et al. 2008). Again, however, the potential effect of past land use on current environmental conditions should be taken into account. Indeed, soil moisture gradient is a key factor determining the abundance of plants with lateral expansion (Klimešová et al. 2008), and this factor might have been affected by historical agricultural use (e.g. through field drainage), as suggested by the low

Table 2. Water table, soil and land-use characteristics of the study sites. Water table and soil variables are characterized by mean ± SD values.

Site	Stable Sites		Semi-Stable Sites	
	Ma	Ri	Sa	Re
Water Table (cm)	−14.66 ± 10.93	−14.42 ± 14.4	−38.86 ± 10.02	−49.04 ± 9.07
Max. Conduct. (μS·cm^{-1})	57 425 ± 35 633	33 108 ± 12 939	37 269 ± 21 242	28 215 ± 11 777
Sodium Adsortion Rate	36.07 ± 2.52	33.76 ± 3.12	40.26 ± 0.95	21.88 ± 0.84
Org C/N	13.24 ± 15.11	13.56 ± 10.85	8.82 ± 27.03	9.36 ± 7.84
Land Use in 1956	Marshland	Marshland	Cropland/pasture	Cropland/pasture
Land Use in 2012	Marshland	Marshland	Marshland	Marshland

Site codes: Ma, Magarola; Ri, Ricarda; Sa, Sabadell; Re, Reguerons.

water table of semi-stable sites compared with that of stable ones (Table 2).

The remaining plant attributes studied did not show any association with past land use, contrary of our expectations. Indeed, Raunkiaer life forms were conceived to reflect the persistence of plant species in relation to climate, but they also partially reflect the capacity to respond to disturbance (Cornelissen et al. 2003). Plant height is expected to increase with decreasing disturbance intensity (Kleyer 1999; Lavorel & Garnier 2002). Seed mass and seed production commonly show significant but opposite trends with disturbance (Lavorel & Garnier 2002; Cornelissen et al. 2003). Seedlings from larger seeds better survive in stable, competitive habitats than those from smaller seeds (Leishman 2001). Hence, late successional species tend to have large seeds but low seed production due to the known trade-off between these components (Leishman 2001). In contrast, pioneer species dominating in disturbed habitats show high colonization capacity due to high seed production, but seeds are commonly small and seedlings cannot establish themselves in crowded conditions (Burke & Grime 1996; Leishman 2001). The lack of association of any of these traits with past land use indicates that the species reaction to land-use change has probably been rapid enough to ensure that no historical signal persists in present marshland communities. Moreover, the flora and vegetation dynamics of costal marshlands has some intrinsic characteristics that may make it difficult to detect some typical relations between disturbance and traits. That is, halophyte plants thriving on undisturbed marshlands have high seed production and low seed mass; or stable marshland communities are usually dominated by geophytes. The historical landscape has also been identified as determinant of plant species traits in present-day grasslands (Purschke et al. 2012) due to its effects on species colonization. More information on the landscape history of the study area, especially on grazing pressure, and more quantitative information on key reproductive traits such as autogamy, seed production and seed bank fertility, would help to better assess the role of plant land use in species trait distribution in the Mediterranean marshlands studied, as in other changing habitats (Lindborg 2007; Bagaria et al. 2012).

Concluding remarks

In the strongly human-altered microtidal Mediterranean coastal marshes, environmental gradients and past land use affect species composition through functional plant traits and independently of species phylogeny. Regarding environmental gradients, conductivity affects seed production, seed weight and SAR, whereas water table determines SLA. These results diverge from those observed in macrotidal coastal marshes in that soil ion balance (SAR) and water table determine key plant functional traits such as SLA, due to the weak tidal regime and the existence of a dry summer season. In contrast, past disturbance only affects LDMC and capacity for lateral expansion. The effect of land use on species traits might be partially mediated by the strong environmental gradients and by the effect of past (agricultural) land use on these environmental conditions that, in turn, affect species traits.

From a conservation point of view, our results may help in predicting vegetation changes in these marshes, driven by shifts in plant functional traits directly or indirectly caused by habitat alterations. As Mediterranean coastal marshes have a long history of human transformation, which continues today (Curcó et al. 2002), changes in the disturbance regime but also in some environmental factors (e.g. through human-induced alterations of marshland hydrological regimes) are expected. This might affect key plant functional traits which, in turn, affect ecosystem processes (Lavorel & Garnier 2002), such as changes in the dead biomass accumulation observed in Central European salt marshes due to changes in the SLA of dominating species (Minden & Kleyer 2011).

References

Adam, P. 1993. *Saltmarsh ecology*. Cambridge University Press, Cambridge, UK.

Adriaens, D., Honnay, O. & Hermy, M. 2006. No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biological Conservation* 133: 212–224.

Álvarez Rogel, J., Ortiz Silla, R. & Alcaraz Ariza, F. 2001. Edaphic characterization and soil ionic composition influencing plant zonation in a semiarid Mediterranean salt marsh. *Geoderma* 99: 81–98.

APG 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105–121.

Bagaria, G., Pino, J., Rodà, F. & Guardiola, M. 2012. Species traits weakly involved in plant responses to landscape properties in Mediterranean grasslands. *Journal of Vegetation Science* 23: 432–442.

Batriu, E., Pino, J., Rovira, P. & Ninot, J.M. 2011. Environmental control of plant species abundance in a microtidal Mediterranean saltmarsh. *Applied Vegetation Science* 14: 358–366.

Benot, M.-L., Mony, C., Merlin, A., Marion, B., Bouzillé, J.-B. & Bonis, A. 2011. Clonal growth strategies along flooding and grazing gradients in Atlantic coastal meadows. *Folia Geobotanica* 46: 219–235.

Bertness, M.D., Gough, L. & Shumway, S.W. 1992. Salt tolerances and the distribution of fugitive salt-marsh plants. *Ecology* 73: 1842–1851.

Bolòs, O.d., Vigo, J., Masalles, R.M. & Ninot, J.M. 2005. *Flora Manual dels Països Catalans*. Editorial Pòrtic, Barcelona, ES.

Bower, C.A. & Wilcox, L.V. 1965. Soluble salts. In: Black, C.A. (ed.) *Methods of soil analysis part. 2*, pp. 933–940. American Society of Agronomy, Madison, WI, US.

Braun-Blanquet, J. 1979. *Fitosociología. Bases para el estudio de las comunidades vegetales*. J.H. Blume, Madrid, ES.

Burke, M.J.W. & Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776–790.

Cahill, J.F. Jr, Kembel, S.W., Lamb, E.G. & Keddy, P.A. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics* 10: 41–50.

Chapman, V.J. 1974. *Salt marshes and salt deserts of the world.* J. Cramer, Leher, DE.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.t., Morgan, H.D., (...) & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Costa, C.S.B., Marangoni, J.C. & Azevedo, A.M.G. 2003. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology* 91: 951–965.

Cristofoli, S., Monty, A. & Mahy, G. 2010. Historical landscape structure affects plant species richness in wet heathlands with complex landscape dynamics. *Landscape and Urban Planning* 98: 92–98.

Curcó, A., Ibáñez, C., Day, J.W. & Prat, N. 2002. Net primary production and decomposition of salt marshes of the Ebre delta (Catalonia, Spain). *Estuaries* 25: 309–324.

Dagnelie, P. 1960. Contribution à l'étude des communautés végétales par l'analyse factorielle. *Bulletin du Service de la Carte Phytogeographique* 7–71: 93–195.

De Bello, F., Lepš, J. & Sebastià, M.-T. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology* 42: 824–833.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D., Skarpe, C., Rusch, G., Sternberg, M., (...) & Campbell, B. 2007. Plant trait responses to grazing – a global synthesis. *Global Change Biology*. 13: 313–341.

Dolédec, S., Chessel, D., Ter Braak, C. & Champely, S. 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics* 3: 143–166.

Domènech, R., Vilà, M., Pino, J. & Gesti, J. 2005. Historical land-use legacy and *Cortaderia selloana* invasion in the Mediterranean region. *Global Change Biology* 11: 1054–1064.

Dray, S. & Dufour, A.B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22: 1–20.

Dray, S. & Legendre, P. 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89: 3400–3412.

Dupré, C. & Diekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. *Ecography* 24: 275–286.

Erfanzadeh, R., Garbutt, A., Pétillon, J., Maelfait, J.-P. & Hoffmann, M. 2010. Factors affecting the success of early salt-marsh colonizers: seed availability rather than site suitability and dispersal traits. *Plant Ecology* 206: 335–347.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Chichester, UK.

Hedges, S.B., Dudley, J. & Kumar, S. 2006. TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* 22: 2971–2972.

Jackson, S.T. & Sax, D.F. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution* 25: 153–160.

Kahmen, S. & Poschlod, P. 2004. Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science* 15: 21–32.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Kleyer, M. 1999. Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation Science* 10: 697–708.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., (...) & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* 23: 805–821.

Klimešová, J., Latzel, V., Bello, F.d. & Groenendael, J.M.v. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. *Preslia* 80: 245–253.

Knops, J.M.H. & Tilman, D. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81: 88–98.

Kolb, A. & Diekmann, M. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* 19: 929–938.

Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

Leishman, M.R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294–302.

Lindborg, R. 2007. Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *Journal of Ecology* 95: 555–564.

Louault, F., Pillar, V.D., Aufrère, J., Garnier, E. & Soussana, J.-F. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* 16: 151–160.

McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. 1999. Disturbance response in vegetation – towards a global perspective on functional traits. *Journal of Vegetation Science* 10: 621–630.

Minden, V. & Kleyer, M. 2011. Testing the effect–response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science* 22: 387–401.

Minden, V., Andratschke, S., Spalke, J., Timmermann, H. & Kleyer, M. 2012. Plant traits environment relationships in salt marshes: deviations from predictions by ecological concepts. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 183–192.

Molina, J.A., Casermeiro, M.A. & Moreno, P.S. 2003. Vegetation composition and soil salinity in a Spanish Mediterranean coastal ecosystem. *Phytocoenologia* 33: 475–494.

Mommer, L., Lenssen, J.P.M., Huber, H., Visser, E.J.W. & De Kroon, H. 2006. Ecophysiological determinants of plant performance under flooding: a comparative study of seven plant families. *Journal of Ecology* 94: 1117–1129.

Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology* 92: 893–905.

Pavoine, S., Baguette, M. & Bonsall, M.B. 2010. Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs* 80: 485–507.

Pavoine, S., Vela, E., Gachet, S., de Béair, G. & Bonsall, M.B. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology* 99: 165–175.

Pennings, S.C., Selig, E.R., Houser, L.T. & Bertness, M.D. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84: 1527–1538.

Pino, J., Seguí, J.M. & Álvarez, N. 2006. Invasibility of four plant communities in the Llobregat delta (Catalonia, NE of Spain) in relation to their historical stability. *Hydrobiologia* 570: 257–263.

Pino, J., Vila, M., Álvarez, N., Seguí, J.M. & Guerrero, C. 2009. Niche breadth rather than reproductive traits explains the response of wetland monocotyledons to land-cover change. *Applied Vegetation Science* 12: 119–130.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.

Purschke, O., Sykes, M., Reitalu, T., Poschlod, P. & Prentice, H. 2012. Linking landscape history and dispersal traits in grassland plant communities. *Oecologia* 168: 773–783.

Richards, L.A. 1974. *Diagnóstico y rehabilitación de suelos salinos y sódicos*. Ed. Limusa, México D.F.

Sera, B. & Sery, M. 2004. Number and weight of seeds and reproductive strategies of herbaceous plants. *Folia Geobotanica* 39: 27–40.

Shumway, S.W. & Bertness, M.D. 1992. Salt stress limitation of seedling recruitment in a salt-marsh plant community. *Oecologia* 92: 490–497.

Sosnová, M., van Diggelen, R. & Klimesová, J. 2010. Distribution of clonal growth forms in wetlands. *Aquatic Botany* 92: 33–39.

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D.R. 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91: 563–577.

Vendramini, F., Díaz, S., Gurvich, D.E., Wilson, P.J., Thompson, K. & Hodgson, J.G. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* 154: 147–157.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.

Wesuls, D., Oldeland, J. & Dray, S. 2012. Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. *Journal of Vegetation Science* 23: 98–113.

Wilson, P.J., Thompson, K. & Hodgson, J.G. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* 143: 155–162.

Supporting Information

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

Appendix S1. Supplementary information on the phylogeny construction.

Appendix S2. Species traits and sources.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.

We investigate the relationship between environment and species traits in a microtidal Mediterranean coastal marsh. We use a dataset of 45 sampling points on marsh communities that encompass species cover, environmental variables, past land use information and plant traits. Using a RLQ analysis we conclude that both conditions past land use and environmental gradients conditions present plant traits.

Appendix S1. Supplementary information on the phylogeny construction.

Tree topology was constructed using the topology of Angiosperm Phylogeny Group classification (Group 2009) as the basic structure. For families with more than one species we completed this basic tree using the following studies: for Amaranthaceae we used Kadereit et al. (2003, 2010, 2006) and Kapralov et al. (2006); resolution of Apiaceae followed Downie et al. (2000); the general phylogenetic tree of Asteraceae followed Torices (2010); Sonchus genus followed Kim et al. (2007); Aster genus followed Li et al. (2012); Juncaceae followed Drábková & Vlcek (2009) and Roalson (2005); Poaceae followed Bouchenak-Khelladi et al. (2010); for the Bromus phylogeny we used Saarela et al. (2007); and Cyperaceae were assessed according to Musaya et al. (2009).

We used the timetree database (Hedges et al. 2006) (www.timetree.org) to obtain the molecular age of 20 nodes dated in recently published studies. Most of ages came from the study of Arakaki et al (2011), for more details see Table 1-1 and in Figure 2-1, where nodes, theit age and references are shown. We used the bladj algorithm to estimate the tree branch lengths of non-dated tree fragments. Tree construction and dating were performed using the program Phylocom v. 4.2 (Webb et al. 2008).

To test for the presence of phylogenic bias we used the test developed by Pavoine et al. (2010). To do so we built a matrix of pairwise phylogenetic distances among species using the square root of the sum of branch lengths along the shortest path that connects species, which provides Euclidean distances (Pavoine et al. 2010). We also constructed matrices of pairwise trait distances among species, trait by trait, and also pooled together. Euclidean distances were applied on both dummy-transformed nominal and quantitative traits. We then applied the skewness with 999 Monte Carlo simulations for each matrix. This test was done using R (R Development Core Team, 2012) and the R scripts provided by Pavoine et al.(2010).

This methodology decomposes trait diversity among the nodes of a classification. The value attributed to a node is a function of the trait diversity among the clades descending from it. The objective is to highlight main among-clade differences in the trait states of the species that contribute significantly to the total trait diversity of the species considered. Species traits show a phylogenetic bias if trait diversity is biased to the root or to the tip of the phylogenetic tree.

Only seed weight showed clear skewness ($p < 0.05$) towards the root of the phylogenetic tree, meaning that the maximum diversity of this trait is found in the first tree dichotomies. None of the remaining traits or all traits tested together showed any significant skewness towards the root or the tips of the phylogenetic tree ($p > 0.05$) (Table S1-2).

Table S1-1. Estimated age and source for the 20 dated nodes.

Node	**Estimated age (Mya)**	**Reference**
1	134.1	(Arakaki et al. 2011)
2	119.7	(Arakaki et al. 2011)
3	112.5	(Arakaki et al. 2011)
4	110.6	(Arakaki et al. 2011)
5	86.5	(Arakaki et al. 2011)
6	77.2	(Arakaki et al. 2011)
7	32	(Arakaki et al. 2011)
8	27.5	(Kim et al. 2005)
9	24.4	(Liu et al. 2002)
10	75.4	(Arakaki et al. 2011)
11	71	(Arakaki et al. 2011)
12	70	(Arakaki et al. 2011)
13	78	(Kadereit et al. 2003)
14	65	(Bremer et al. 2004)
15	102.7	(Arakaki et al. 2011)
16	113	(Janssen et al. 2004)
17	88	(Janssen et al. 2004)
18	31.6	(Arakaki et al. 2011)
19	17.9	(Inda et al. 2008)
20	15.4	(Inda et al. 2008)

Figure S1-1. Phylogenetic tree of the plant species. Dated nodes are numbered in the tree and their estimated ages are given in Table S1-1.

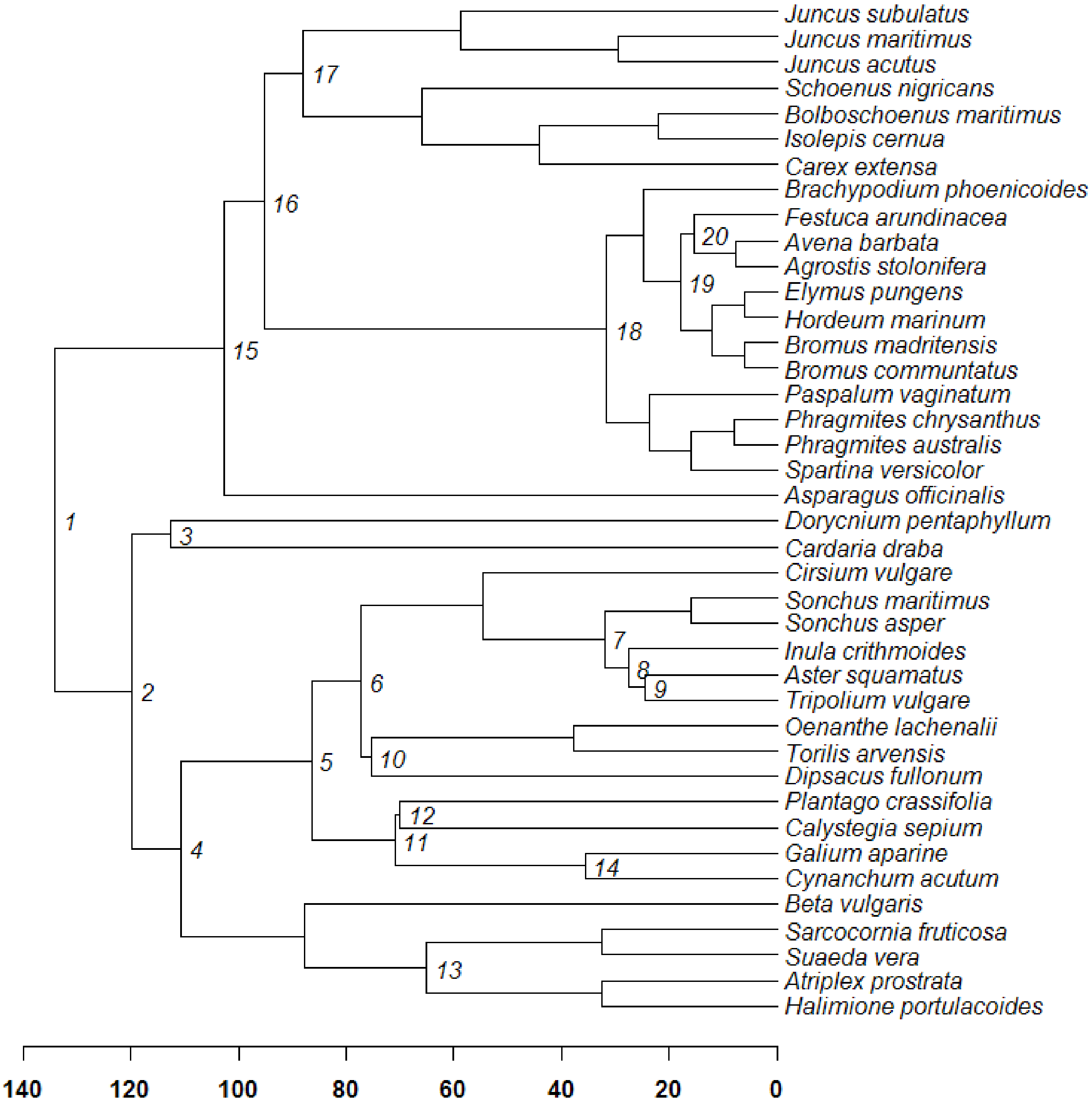

Table S1-2. Results of Skewness test of trait diversity towards the root or the tips of the phylogenetic tree constructed with all species found in relevés. Test was performed using a MonteCarlo permutation procedure (* p<0.05).

	Skewed towards	
	Root	Tips
All traits	0.366	0.621
Plant height	0.521	0.506
LDMC	0.483	0.536
SLA	0.759	0.268
Seed production	0.073	0.906
Seed weight	0.048*	0.957
Life form	0.571	0.41
Lateral expansion	0.881	0.21

References:

Arakaki, M., Christin, P.A., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M., Spriggs, E., Moore, M.J. & Edwards, E.J. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences* 108: 8379-8384.

Bouchenak-Khelladi, Y., Verboom, G.A., Savolainen, V. & Hodkinson, T.R. 2010. Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society* 162: 543-557.

Bremer, K., Friis, E. & Bremer, B. 2004. Molecular phylogenetic dating of asterid flowering plants shows early Cretaceous diversification. *Systematic Biology* 53: 496-505.

Downie, S.R., Katz-Downie, D.S. & Watson, M.F. 2000 A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA rpl16 and rpoC1 intron sequences: towards a suprageneric classification of subfamily Apioideae *American Journal of Botany* 87 273-292

Drábková, L. & Vlcek, C. 2009. DNA variation within Juncaceae: comparison of impact of organelle regions on phylogeny. *Plant Systematics and Evolution* 278: 169-186.

Group, A.P. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.

Hedges, S.B., Dudley, J. & Kumar, S. 2006. TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* 22: 2971-2972.

Inda, L.A., Segarra-Moragues, J.G., MÃ¼ller, J., Peterson, P.M. & CatalÃ¡n, P. 2008. Dated historical biogeography of the temperate Loliinae (Poaceae, Pooideae) grasses in the northern and southern hemispheres. *Molecular Phylogenetics and Evolution* 46: 932-957.

Janssen, T. & Bremer, K. 2004. The age of major monocot groups inferred from 800+ rbcL sequences. *Botanical Journal of the Linnean Society* 146: 385-398.

Kadereit, G., Borsch, T., Weising, K. & Freitag, H. 2003. Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C4 photosynthesis. *International journal of plant sciences* 164: 959-986.

Kadereit, G., Mavrodiev, E.V., Zacharias, E.H. & Sukhorukov, A.P. 2010. Molecular phylogeny of Atripliceae (Chenopodioideae, Chenopodiaceae): Implications for systematics, biogeography, flower and fruit evolution, and the origin of C4 photosynthesis. *American Journal of Botany* 97: 1664-1687.

Kadereit, G., Mucina, L. & Freitag, H. 2006. Phylogeny of Salicornioideae (Chenopodiaceae): diversification, biogeography, and evolutionary trends in leaf and flower morphology. *Taxon* 55: 617-642.

Kapralov, M., Akhani, H., Voznesenskaya, E., Edwards, G., Franceschi, V. & Roalson, E. 2006. Phylogenetic Relationships in the Salicornioideae / Suaedoideae / Salsoloideae s.l. (Chenopodiaceae) Clade and a Clarification of the Phylogenetic Position of Bienertia and Alexandra Using Multiple DNA Sequence Datasets. *Systematic botany* 31: 571-585.

Kim, K.-J., Choi, K.-S. & Jansen, R.K. 2005. Two Chloroplast DNA Inversions Originated Simultaneously During the Early Evolution of the Sunflower Family (Asteraceae). *Molecular Biology and Evolution* 22: 1783-1792.

Kim, S.-C., Chunghee, L. & Mejías, J.A. 2007. Phylogenetic analysis of chloroplast DNA matK gene and ITS of nrDNA sequences reveals polyphyly of the genus Sonchus and new relationships among the subtribe Sonchinae (Asteraceae: Cichorieae). *Molecular Phylogenetics and Evolution* 44: 578-597.

Li, W.-P., Yang, F.-S., Jivkova, T. & Yin, G.-S. 2012. Phylogenetic relationships and generic delimitation of Eurasian Aster (Asteraceae: Astereae) inferred from ITS, ETS and trnL-F sequence data. *Annals of Botany* 284: 153-169.

Liu, J.-Q., Gao, T.-G., Chen, Z.-D. & Lu, A.-M. 2002. Molecular phylogeny and biogeography of the Qinghai-Tibet Plateau endemic Nannoglottis (Asteraceae). *Molecular Phylogenetics and Evolution* 23: 307-325.

Muasya, A., Simpson, D., Verboom, G., Goetghebeur, P., Naczi, R., Chase, M. & Smets, E. 2009. Phylogeny of Cyperaceae Based on DNA Sequence Data: Current Progress and Future Prospects. *The Botanical Review* 75: 2-21.

Pavoine, S., Baguette, M. & Bonsall, M.B. 2010. Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs* 80: 485-507.

Roalson, E. 2005. Phylogenetic relationships in the Juncaceae inferred from nuclear ribosomal DNA internal transcribed spacer sequence data. *International journal of plant sciences* 166: 397-413.

Saarela, J.M., Peterson, P.M., Keane, R.M., Cayouette, J. & Graham, S.W. 2007. Molecular phylogenetics of Bromus (Poaceae: Pooideae) based on chloroplast and nuclear DNA sequence data. 23: 450-467.

Team, R.D.C. 2012. R: A language and environment for statistical computing, reference index version 2.15. In: R Foundation for Statistical Computing, Vienna.

Torices, R. 2010. Adding time-calibrated branch lengths to the Asteraceae supertree. *Journal of Systematics and Evolution* 48: 271-278.

Webb, C.O., Ackerly, D.D. & Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098-2100.

Appendix 2. Plant traits

Table 2-1. Compilation of values or states of plant traits for all species treated. Taxonomy follows Bolòs et al. (2005) with a few exceptions. For quantitative traits all values come from our own measurements, except those marked with: * (Kleyer et al. 2008); @ (Sera et al. 2004); + (Kew 2008)). Life form and lateral expansion come from Bolòs et al. (2005) with some modifications (e.g. Phanerophytes were merged together with Chamaephytes) and our own observations. Units used are: Plant height in cm; Leaf Dry Mass Content (LDMC) in mg/g; Specific Leaf Area (SLA) in mm^2/mg of dry weight; Seed production in seeds/m^2; Seed weight in g per 1,000 seeds.

Taxon	Plant height	LDMC	SLA	Seed production	Seed weight	Life form	Lateral expansion
Agrostis stolonifera	44.3	359.68	22.78	577,688	0.06+	H	Phalanx
Asparagus officinalis	142.5	280.26*	10.95*	1,166	26.12+	G	Low
Aster squamatus	99.1	172.23	21.49	285,757	0.1+	Ch	No
Atriplex portulacoides	43.5	176.46	13.49	155,533	1.31+	Th	No
Avena barbata	80	237.66*	24.96*	9,917	9.27+	Th	No
Beta vulgaris	86.3	88.97	17.04	218,080	15.4+	H	Low
Bolboschoenus maritimus	87.2	275.10	12.46	9,898	2.3+	G	Phalanx
Brachypodium phoenicoides	51.2	405.63	12.87	3,820	3.2+	H	Guerrilla
Bromus commutatus	70	235*	25.48*	63,150	4.64+	Th	No
Bromus madritensis	28	173.94*	35.64*	87,891	3.3+	Th	No
Calystegia sepium	281	150.84	33.84	158	25.58+	G	Low
Cardaria draba	37.6	161.67*	20.5*	209,851	2.04+	H	Low
Carex extensa	59.8	257.96	12.35	45,878	1.15+	H	Guerrilla
Cirsium vulgare	116.8	120.67*	17.16*	5,704	2.91+	H	Low
Cynanchum acutum	281	177.19	23.76	567	10.41+	G	Low
Dipsacus fullonum	158.8	167*	22.3*	291,897	2.26+	H	No
Dorycnium pentaphyllum	73.7	247.86	14.79	28,143	2.8+	Ch	No
Elymus pungens	80.6	437.03	8.51	26,057	4.84+	H	Phalanx
Festuca arundinacea	42.4	254.56	18.55	36,869	2.4+	H	Guerrilla
Galium aparine	95.7	140*	34.68*	25,180@	8.9+	Th	No
Halimione portulacoides	28.9	117.32	9.89	16,646	3.03+	Ch	Guerrilla

Hordeum marinum	11.6	324.68	31.6	67,800	2.16	Th	No
Inula crithmoides	74.7	136.73	26.74	250,929	0.37^{+}	Ch	No
Isolepis cernua	6	143.86	20.41	600,000	0.13^{+}	Th	No
Juncus acutus	162.7	381.41	2.63	630,601	0.08^{+}	H	Guerrilla
Juncus maritimus	115.5	408.51	3.88	663,627	0.03^{+}	H	Guerrilla
Juncus subulatus	97.2	286.70	10.34	8,060,467	0.02^{+}	G	Guerrilla
Oenanthe lachenalii	106	206.11	8.18	108,699	0.9^{+}	H	Low
Paspalum vaginatum	24.4	248.07	23.59	142,626	0.16	Ch	Phalanx
Phragmites australis subsp. *australis*	223	446.66	13.12	47,707	0.11	G	Phalanx
Phragmites australis subsp. *chrysanthus*	281	413.35	10.95	42,643	0.04	G	Phalanx
Platago crassifolia	9.2	152.34	6.51	16,371	0.26	H	Low
Sarcocornia fruticosa	90	131.21	12.10	532,374	0.14	Ch	No
Schoenus nigricans	82.5	431.54	5.25	2,396	0.6^{+}	H	Guerrilla
Sonchus asper	70.5	123.67*	24.97*	221,593	0.28^{+}	Th	No
Sonchus maritimus	91.6	103.82	21.65	17,369	0.33	H	Low
Spartina versicolor	116.4	329.87	8.54	1.4	0.5	Ch	Phalanx
Suaeda vera	92.4	149.50	8.53	120,703	0.33	Ch	No
Torilis arvensis	35.5	267.44	20.29	53,507	2.1^{+}	Th	No
Tripolium vulgare	93.5	124.34	10.39	90,569	0.43^{+}	Th	No