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Dynamics of perennial halophytic communities in the Salicornioideae subfamily: a case study from the Tinto river and Western Iberian Peninsula

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Abstract. This study investigates perennial halophyte vegetation communities within the Salicornioideae subfamily (Amaranthaceae-Chenopodiaceae) in the marshlands of the southwestern Iberian Peninsula, with a particular emphasis on the Tinto River salt marshes. We focus on communities dominated by three *Sarcocornia* species (*S. perennis*, *S. pruinosa*, and *S. alpini*) and *Arthrocnemum macrostachyum*. Utilizing geobotanical analysis, we reaffirm existing classifications, delineating one association for *A. macrostachyum* (*Inulo crithmoidis-Arthrocnemetum macrostachyi*) and three for *Sarcocornia* (*Puccinellio ibericae-Sarcocornietum perennis*, *Cistancho phelypaeae-Sarcocornietum pruinosae*, and *Halimiono portulacoidis-Sarcocornietum alpini*). Our research comprises 70 relevés, which reveal distinct zonation patterns among these species in relation to their proximity to water and tidal influences. This investigation contributes to a deeper understanding of halophyte biodiversity and provides comprehensive floristic inventories, thereby facilitating future ecological assessments and restoration initiatives in fragile saline ecosystems.
Keywords: Halophytes, Salicornioideae, salt marshes, vegetation communities, ecological adaptations, Phytosociology.

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Introduction

The challenging conditions of saline environments require remarkable adaptations in halophytic flora. Saline marsh vegetation faces several ecological constraints, including high concentrations of salts in both water and soil, daily and seasonal fluctuations caused by tidal influences in coastal areas, the extent of flooding in inland salt marshes, and the compactness of clayey soil, which restricts aeration and transforms it into an anaerobic and persistently waterlogged medium (Llobera & Valladares, 1989; Álvarez, 1997; Gil *et al*., 2014). In inland salt marshes and coastal estuaries, the distance from the sea often results in efflorescence or salt crusts in the soil during periods of elevated evaporation. These characteristics significantly contribute to the development of distinct vegetation zones characterized by their physiognomy and floristic composition.

The species belonging to the Amaranthaceae-Chenopodiaceae family (subfamily Salicornioideae) are the most specialized in these extreme environments and represent the primary lineage with the highest proportion of dominant genera in salt marsh vegetation communities. Spain and Portugal, with approximately 10,000 km of coastline and a significant number of inland saline lakes and wetlands, harbor six out of the twelve Salicornioideae genera found worldwide: *Arthrocnemum* Moq., *Halocnemum* M.Bieb., *Halopeplis* Bunge ex Ung.-Sternb., *Microcnemum* Ung.-Sternb., *Salicornia* L., and *Sarcocornia* A.J.Scott.

Among them, the genera of significant importance in annual vegetation communities are found within the phytosociological class *Thero-Salicornietea*, which includes *Halopeplis*, *Microcnemum*, and *Salicornia*. Additionally, the class *Salicornietea fruticosae* encompasses perennial succulent chamaephytes and nanophanerophytes such as *Arthrocnemum*, *Halocnemum*, and *Sarcocornia* (Biondi *et al*., 2013; de la Fuente *et al*., 2013a,b, 2016; Del Arco Aguilar *et al*., 2017; Flowers

et al., 2010; Mucina *et al*., 2016; Piirainen *et al*., 2017; Ramírez *et al*., 2019; Rivas-Martínez, 1984; Rivas-Martínez *et al*., 2001, 2002; Rivas-Martínez *et al*., 2011; Rivas-Martínez & *et al*., 2007; Rodwell, 2000).

The study of vegetation in the Salicornioideae subfamily has seen significant advancements between 2016 and 2021. Rufo *et al*. (2016) provided a comprehensive description and summary of the associations, alliances, and orders of halophytic vegetation predominantly composed of perennial species belonging to the genus *Sarcocornia*. These authors profoundly described the *Sarcocornia* plant associations and made various nomenclatural proposals, including, two new orders (*Sarcocornio pruinosae-Halimionetalia portulacoidis* and *Arthrocnemo macrostachyi-Suaedetalia braun-blanquetii*).

In a recent synthesis by Salazar-Mendías & Lendínez (2021) it was revealed that the class *Salicornietea fruticosae* comprises a total of 45 associations distributed across the Mediterranean biogeographic region of Spain and Portugal. This study includes a valuable review of the taxonomical framework proposed by Rufo *et al*. (2016), shedding light on the intricate classification of plant communities within this specific ecological context.

Our recent study evaluated the halophilic vegetation dominated by *Arthrocnemum macrostachyum* in Spain and Portugal (Ramírez *et al*., 2021). We found that there are five associations dominated by *A. macrostachyum* in these territories, as opposed to the previously described seven associations. Following geobotanical analysis and interpretation by our team, relevés traditionally assigned to the *Frankenio corymbosae-Arthrocnemetum macrostachyi* association in inland saline habitats of the Central Iberian Mediterranean biogeographical province (Murcia and Almería biogeographical province and the Bética province, were reassigned to two communities dominated by the nanophanerophyte *Sarcocornia hispanica* (*Arthrocnemo macrostachyi-Sarcocornietum hispanicae* and *Limonio majoris-Sarcocornietum hispanicae*).

Additionally, in this same research, a proposal was made to assimilate the *Puccinellio fasciculatae-Arthrocnemetum macrostachyi* association (Castroviejo & Cirujano, 1980) into the *Suaedo braun-blanquetii-Arthrocnemetum macrostachyi* association, given its priority based on antiquity. Numerical analysis supported the finding that *A. macrostachyum* and *S. carinata* do not coexist in the same territory, and *P. fasciculata* is not present in the inland saline association of the Central Iberian Peninsula. These two species were used by their authors to distinguish the two communities of the central Iberian Peninsula and the Ebro Depression, which are now integrated into a single association. Nevertheless, the remaining communities dominated by *A. macrostachyum* remained stable, with *Inulo crithmoidis-Arthrocnemetum macrostachyi* being the characteristic association of the southwestern Iberian Peninsula.

This research aims to explore the vegetation communities predominantly consisting of perennial species within the subfamily Salicornioideae in the marshlands of the provinces of Cádiz and Huelva, focusing on the saltmarshes of the Tinto River in Spain and diverse regions of Portugal. This study encompasses a diverse array of saline environments in the southwestern Iberian Peninsula, building upon the framework presented in the *Salicornietea fruticosae* class. Consequently, this study focuses on the four dominant shrubby Salicornioideae species in the marsh landscape of southwestern Iberia, aiming to analyze and describe the vegetation communities dominated by this halophyte complex and to delineate the ecological characteristics of each taxon within its habitat.

Material and Methods

Main Study Area: The Marshes of the Tinto River (Huelva)

In the province of Huelva, the primary focus of study lies within the geographical region encompassing the ultimate section of the Tinto River. This area is defined by marshes that develop at the river's mouth, where it converges with the vast expanse of the Atlantic Ocean. The Tinto River basin estuary displays a mesotidal range with an average amplitude of 2.1 meters and daily pH fluctuations ranging from 2.1 to 6.9 (Abramov *et al*., 2020). The soils in this estuarine environment exhibit an average electrical conductivity of 6.22 dS/cm, indicating slight salinity.

It is noteworthy that the high concentrations of ferric iron and sulfates resulting from pyrite bio-oxidation, are the primary mineral component of the system. Additionally, significant levels of Na, Mg, P, Cu, Zn, Pb, and As have been documented in the estuary soils (Amils *et al*., 2007; Rufo *et al*., 2010).

The study area in the province of Huelva (Figure 1) falls within the Western Mediterranean Iberian and Lusitano-Andalusian coastal biogeographic provinces (Rivas-Martínez *et al*., 2017). The marshes of the Tinto River exhibit a Mediterranean macrobioclimate, experiencing an oceanic pluviseasonal Mediterranean bioclimatic regime with a predominance of the thermomediterranean thermotype. Frost is absent in this region, and the ombrotype in the lower course stations is classified as dry, while the upper course, away from the marsh areas, ranges from subhumid to humid. Precipitation patterns indicate that Huelva and Moguer stations receive minimal rainfall ($P < 500$ mm), with the rainy season peaking in winter and summer being the driest period (Rufo, 2009). This rainfall distribution contrasts with Mediterranean regions in the eastern part of the Peninsula, where the highest rainfall occurs in autumn or spring (Rivas-Martínez & *et al*., 2007).

Figure 1 displays a map illustrating the key sampling locations we have frequented during our expeditions across the Tinto River-influenced marshes. These marshes span from the uppermost region near the municipality of San Juan del Puerto to its estuarine mouth where it converges with the Atlantic Ocean, influenced by the Odiel River. Within this area, a diverse array of plant communities exists within proximity, arranged along a gradient of flooding. These communities predominantly consist of perennial grass species (*Spartina densiflora* and *S. maritima*) and succulent shrubs from the Amaranthaceae-Chenopodiaceae family.

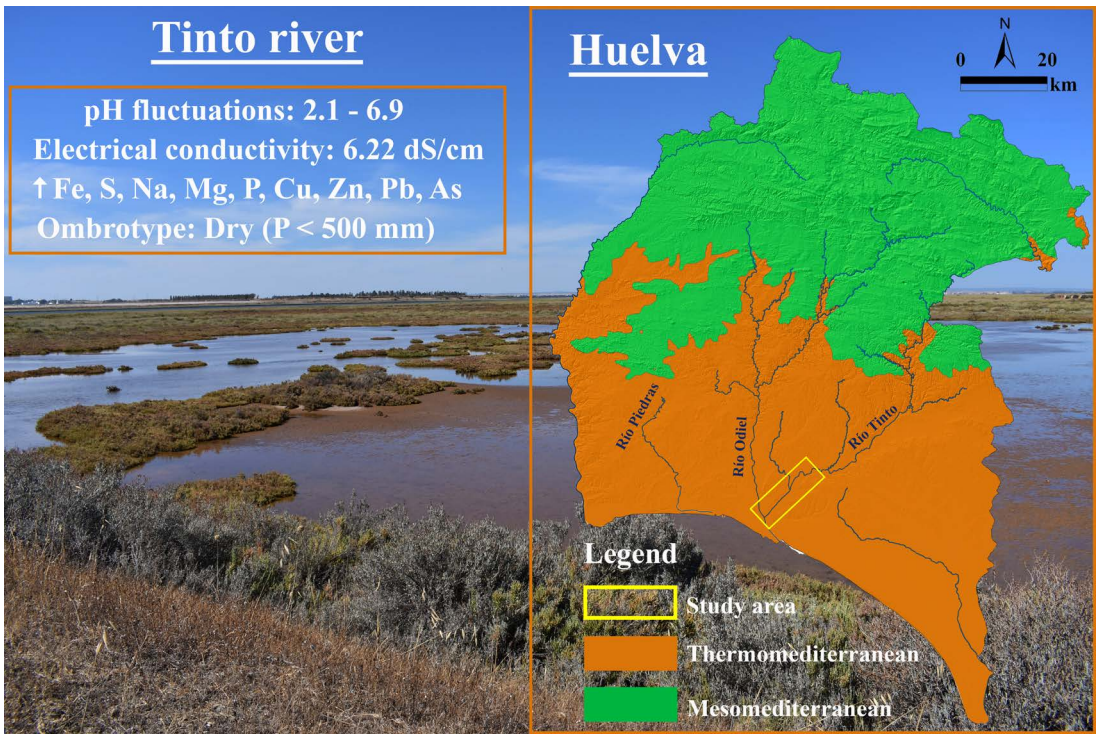

Figure 1. Salt marshes of the Tinto River ("La Santa marshes"), created with ArcGIS 10.7.1. Left, key physical and bioclimatic features in Huelva, Spain, and the main study area; Right, map of the Tinto River salt marshes and their confluence with the marshes of the Odiel River in Huelva Province, Spain. The bioclimatic belts are also indicated for this area.

Shrubby species of the Salicornioideae subfamily in southwestern Iberia

The examination of plant communities in the Tinto River marshes focuses on four dominant species of succulent perennial Chenopodiaceae that significantly shape the marsh landscapes and define the region. These species consist of the halophytic shrub *Arthrocnemum macrostachyum*, alongside three species from the genus *Sarcocornia*: *S. perennis*, *S. pruinosa*, and *S. alpini* (Figure 2).

In the Iberian Peninsula, *A. macrostachyum* is a prevalent species that dominates vegetation communities across various salt marshes, particularly within the distinctive ecological context of the Tinto River marshes in Huelva. *Arthrocnemum macrostachyum* (Moric.) K. Koch is one of three species classified within the genus *Arthrocnemum*, alongside *A. franzii* Sukhor. and *A. meridionale* (Ramírez *et al*., 2021; Fuente *et al*., 2013b). Those species share key characteristics, including a perennial life cycle and fused leaves that form an opposite decussate arrangement on their fleshy stems. The inflorescences are composed of two triflorous cymes, each featuring three prominent flowers that are not embedded within the succulent segments, unlike the arrangements seen in *Sarcocornia* and *Salicornia*. Each flower consists of four tepals that are fused at the apex, creating an opening formed by two lateral membranous, orbicular lobes and two more frontally positioned, scarious lobes. The seeds are glossy black (occasionally brown and smaller in size), with or without papillae, and possess a substantial perisperm. *A. macrostachyum* is distributed across the northern Mediterranean basin of Europe, extending to the Atlantic coastline in coastal Portugal and reaching as far as the Canary Islands (Fuerteventura and Lanzarote). This species tetraploid species (2n = 36) was first described from the Laguna di Venezia in Malamocco (holotype: G-G00177362).

Flora Iberica recognizes three taxa within the genus *Sarcocornia*: *S. fruticosa*, *S. perennis* subsp. *perennis*, and *S. perennis* subsp. *alpini* (Castroviejo, 1990). However, 35 years after the publication of the Chenopodiaceae, recent morphological and phylogenetic studies have reclassified *Sarcocornia* into six taxa in the region: *S. perennis*, *S. alpini*, *S. pruinosa*, *S. carinata*, *S. hispanica*, and *S. lagascae*. Notably, recent analyses exclude *S. fruticosa* from the Iberian Peninsula, as no sequences match its nomenclatural type (established in the French Mediterranean marshes at Montpellier) that correspond to the Iberian *Sarcocornia*. The distribution of *S. fruticosa* extends into Eastern Europe and across Africa (de la Fuente *et al*., 2020, 2013a; Hayder *et al*., 2022; Piirainen *et al*., 2017; Sciandrello, 2020). This interpretation aligns with a rigorous evolutionary framework, promoting a classification that increasingly reflects natural relationships.

Sarcocornia perennis (Miller) A.J. Scott is a key species in salt marsh communities, characterized by its direct exposure to tidal fluctuations and experiencing complete flooding twice daily. These low-growing halophytes typically reach 20–30 cm heights and exhibit a prostrate growth habit, forming narrow bands along the coastal regions of the Atlantic-European landscape, particularly in the UK, France, Portugal, and Spain. This species is closely related to *S. pruinosa*, and the two can be differentiated based on specific morphological traits. *S. perennis* can be identified as a subshrub with decumbent to prostrate stems, featuring three

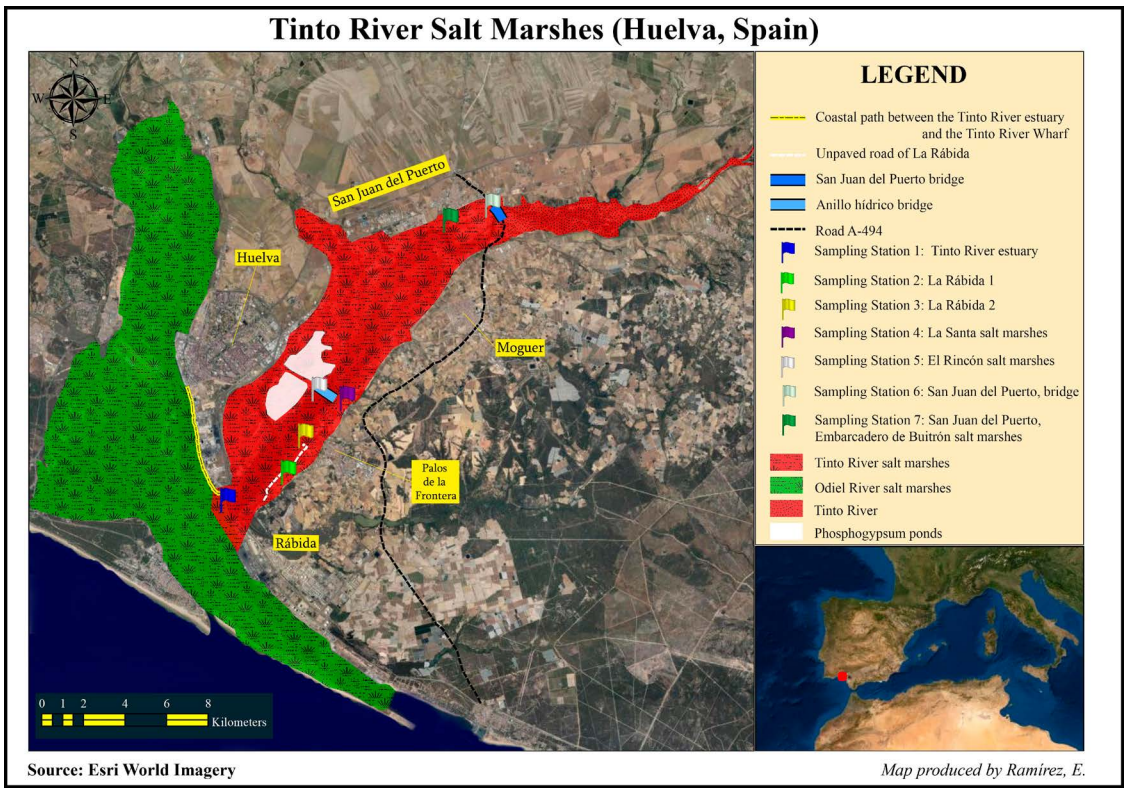

Figure 2. Tinto river (red) and Odiel river (green) salt marshes. The flags indicate the different sampled stations in Tinto river.

to five flowers by segment near the upper part of the plant. The succulent segments display a rich green coloration. At the same time, the seeds are adorned with prominent, erect, and elongated trichomes, which may sometimes appear slightly appressed or even hooked, dispersing to cover the entire seed surface. Chromosome number (2n = 18).

Sarcocornia pruinosa de la Fuente, Rufo & Sánchez-Mata inhabits low to mid-intertidal zones subjected to regular, partial inundation from daily tides. Its distribution spans the Atlantic-European provinces and the Lusitano-Andalusian coastline, with recent populations identified in Western Sahara (Lemmel *et al*., 2023), extending its geographical range from northwest Morocco to coastal areas of Brittany, France. This species can be characterized as an erect subshrub, reaching heights of up to 50 cm, with three main flowers positioned distally from the upper segments. The stems display a glaucous coloration, contrasting with the rich green of *S. perennis*. The seeds are covered with short, erect trichomes that provide a distinctive micrornamentation. *S. pruinosa* is polyploid (2n = 72) and occupies slightly elevated zones within salt marsh habitats compared to *S. perennis*. This ecological niche differentiation underscores the adaptive strategies of these closely related halophytes in response to their intertidal environments.

Sarcocornia alpini (Lag.) Rivas Mart. is primarily found in mid- and high-intertidal zones, thriving in river-adjacent habitats and elevated depressions that experience infrequent flooding. Its distribution encompasses Mediterranean regions across Europe and Africa, including Portugal, Spain, Sicily, Greece, Morocco, Algeria, and Tunisia. This species is characterized as a subshrub, ranging from erect to prostrate forms, with heights of up to 30-40 cm. It features scale-like leaves with acute to subacute apices, a distinctly keeled structure, and three flowers close to the upper segments. The flowers tend to be more compressed and tightly clustered, often displaying vibrant reddish hues that distinguish them from *S. perennis*. The seeds of *S. alpini* are notable for their long, appressed trichomes, which are generally flat and may occasionally be bifurcated, covering the entire seed surface. While some researchers continue to classify *S. alpini* as a subspecies of *S. perennis*, emerging evidence indicates that *S. perennis* has a closer evolutionary relationship with *S. pruinosa* than with *S. alpini*. This suggests that *S. alpini* should be regarded as a separate species rather than a subspecies of the Atlantic taxon *S. perennis*. Morphological, ecological, and phylogenetic distinctions further substantiate the unique identity of *S. alpini*. It is a diploid species (2n = 18), with its closest relatives including *S. carinata* and *S. lagascae*.

Phytosociological methodology and vegetation communities

The syntaxonomic classification of the class *Salicornietea fruticosae* follows the proposals of Ramírez *et al*. (2021), Rufo *et al*. (2016), and Salazar-Mendías & Lendínez (2021) (Appendix S1). The primary biogeographical units are based on Rivas-Martínez *et al*. (2017). Taxonomic nomenclature is aligned with the Plants of the World Online (POWO, 2023), with the exceptions of the genera *Arthrocnemum* (Ramírez *et al*., 2022), *Sarcocornia* (de la Fuente *et al*. 2020), *Salicornia* (Rivas-Martínez & Herrera 1996) and *Spartina* (Bortolus *et al*. 2019) (Appendix S2). Despite phylogenetic evidence (Piirainen *et al*., 2017) suggesting *Sarcocornia*'s paraphyly within *Salicornia*, we maintain

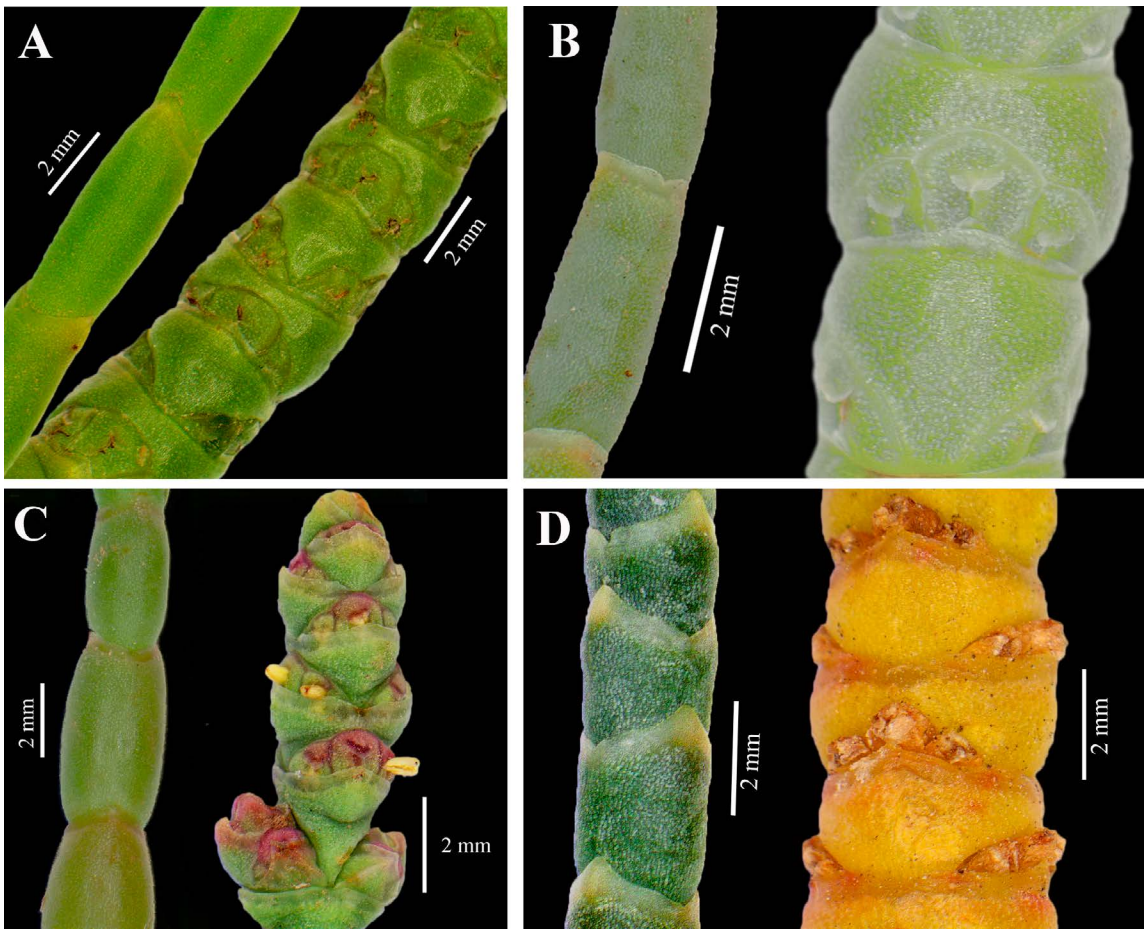

Figure 3. Succulent vegetative stems and inflorescences of the four shrubby species from the Salicornioideae subfamily found along the Tinto River. A, *Sarcocornia perennis*, B, *S. pruinosa*; C, *S. alpini*; D, *Arthrocnemum macrostachyum*.

Sarcocornia as a distinct genus in this study. This delineation emphasizes the perennial species, as opposed to annual species, in Europe, Africa (except South Africa), Asia, and the American continents, differentiated by unique ecological zonation along salinity gradients and key morphological traits.

Our study of the vegetation in the marshes of the Tinto River employs the traditional phytosociological method established by Braun-Blanquet (1979). We performed a total of 42 phytosociological relevés specifically targeting vegetation communities dominated by Salicornioideae species during field campaigns conducted between 2018 and 2021. Additionally, we incorporated and adapted 28 phytosociological relevés collected by our research group prior to 2009, ensuring comprehensive representation for each association (Rufo, 2009). These adaptations followed the latest taxonomic and syntaxonomic criteria for the genus *Sarcocornia* (de la Fuente *et al*., 2013a,b, 2016; Rufo *et al*., 2016, Hayder *et al*., 2022). The relevés include data from the Tinto River marshes, as well as adjacent areas in the provinces of Cádiz and Huelva (Spain), and various coastal regions of Portugal.

Results

This study compiles 70 relevés from four distinct vegetation communities, derived from field campaigns conducted by our research group in the Tinto River (Huelva) and parts of the southwestern Iberian Peninsula, supplemented with adapted data from Rufo (2009). Specifically, these include 17 relevés for the *Puccinellio ibericae-Sarcocornietum perennis*, 14 relevés for the *Cistancho phelypaeae-Sarcocornietum pruinosae*, 8 relevés for the *Halimiono portulacoidis-Sarcocornietum alpini*, and 31 relevés for the *Inulo crithmoidis-Arthrocnemetum macrostachyi*.

The zonation of these taxa within their natural habitat allows for a clear differentiation among the various species. *Sarcocornia perennis* communities are located closest to the water and are subjected to two daily flooding events. The next slightly drier zone is characterized by communities of *S. pruinosa*, which are partially inundated by daily tides and experience complete inundation during spring tides. Communities of *Sarcocornia alpini* can be found either fully or partially submerged during daily tidal events and are also commonly present in channels and depressions within high intertidal zones, where they are occasionally flooded but are situated further away from marine waters. This species often dominates clay-rich soils. Finally, *Arthrocnemum macrostachyum* forms vegetation communities in marshes that occupy the driest areas, which are the least influenced by tidal actions. Figure 4 delineates the zonation gradient across these four marsh communities, ranging from the most saturated areas to the driest zones.

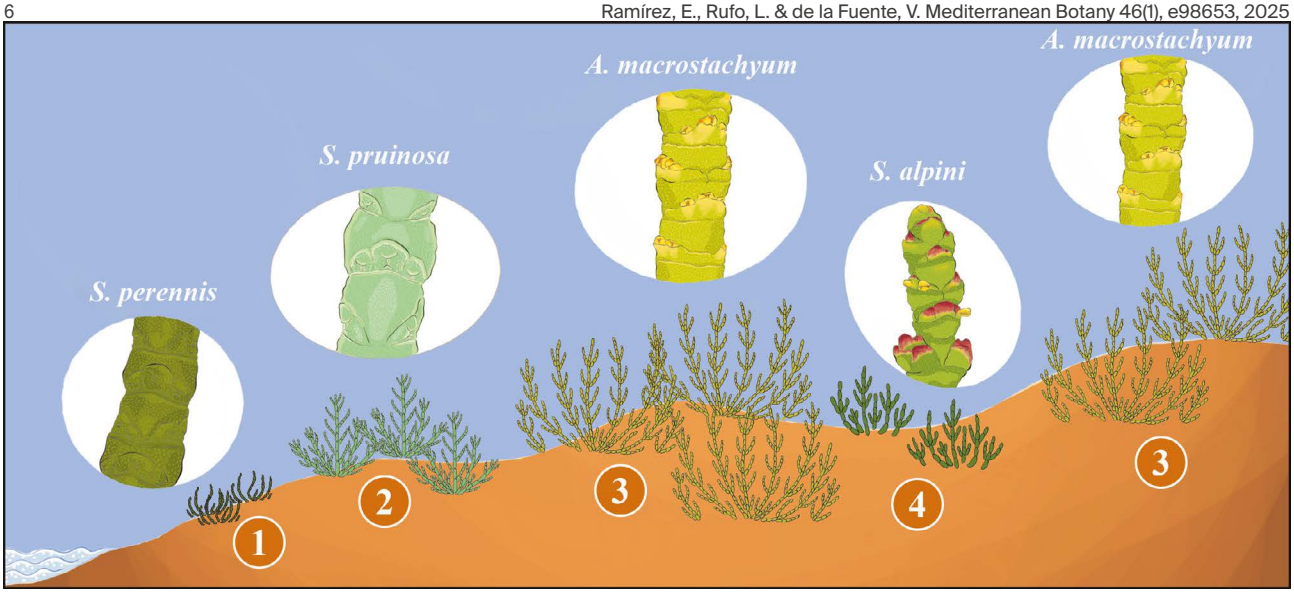

Figure 4. Vegetation gradient of the Tinto River marshes, transitioning from the most humid, marine-influenced, and tide-affected zones to the driest sections, with a focus on the Salicornioideae subfamly shrublands.: 1. *Puccinellio ibericae-Sarcocornietum perennis*; 2. *Cistancho phelypaeae-Sarcocornietum pruinosae*; 3. *Inulo crithmoidis-Arthrocnemetum macrostachyi*; 4. *Halimiono portulacoidis-Sarcocornietum alpini*. Illustration by Celia Arias Vaquerizo.

This association is dominated by the prostrate hemicryptophyte *Sarcocornia perennis*, occupying the lowest vegetation belt closest to the sea, where it is subject to daily tidal flows, resulting in complete submersion. The most common plants within this zone include *Spartina maritima*, *Atriplex portulacoides* (a taxonomic synonym of *Halimione portulacoides*), and *Salicornia patula*. Moving from the areas with the highest tidal influence on those with reduced influence, *Sarcocornia pruinosa* may appear in slightly elevated zones further from the sea, coexisting with *S. perennis*.

Table 1. *Puccinellio ibericae-Sarcocornietum perennis* (*Halimionion portulacoidis*, *Sarcocornio pruinosae-Halimionetalia portulacoidis*, *Salicornietea fruticosae*)

Area (m^2)	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Number of species	2	2	3	3	4	4	4	4	5	5	5	5	5	5	5	6	7
Order number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Characteristics																	
Sarcocornia perennis	4	4	5	5	3	4	5	4	4	5	3	5	4	4	5	3	5
Atriplex portulacoides	.	.	.	.	1	2	1	1	2	1	1	1	.	.	+	2	1
Sarcocornia pruinosa	.	.	+	+	1	3	.	.	.	.	1	2	1	+	+	+	1
Arthrocnemum macrostachyum	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.
Other species																	
Spartina maritima	1	1	.	1	.	.	1	1	.	2	.	.	.	+	+	1	+
Salicornia patula	.	.	+	.	.	.	2	+	.	+	1	.	+	.	.	+	2
Puccinellia iberica	.	.	.	.	.	1	.	.	1	.	2	.	1	+	.	.	.
Spartina densiflora	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	+	+
Suaeda maritima	.	.	.	.	.	.	.	.	+	2	.	.	.	+	.	.	1

Localities: 1,7: Huelva, San Miguel marshes, before 2009, 29SPB6321; 2: Huelva, La Rábida, before 2009, 29SPB8320; 3: Huelva, El Terrón, 18-07-2018, 29SPB6119; 4: Portugal, Isla de Tavira, Pedras d´el Rei, 18-07-2018, 29SPB1705; 5,6,14: Portugal, Sta Luzia-Tavira, harbor, 18-07-2018, 29SPB1806; 8: Huelva, Catalán marshes, El Terrón, before 2009, 29SPB6121; 9,11: Huelva, El Rompido, before 2009, 29SPB6019; 10,12: Huelva, Punta del Moral, 18-07-2018, 29SPB4717; 13: Huelva, Odiel marshes, Cabeza Alta, before 2009, 29SPB8022; 15: Huelva, Isla Cristina, La Gola, 24-11-2021, 29SPB4817; 16: Huelva, seafront near the mouth of the Tinto River, 06-08-2019, 29SPB8123; 17: Huelva, Tinto River mouth, 17-07-2018, 29SPB8220.

Cistancho phelypaeae-Sarcocornietum pruinosae Géhu ex Géhu & Géhu Franck 1977 corr. & nom. mut. propos. Rufo, Fuente & Sánchez Mata 2016 (Table 2, Figure 6)

This association is characterized by the nanophanerophyte *Sarcocornia pruinosa*, which follows the zone gradient with the highest tidal influence dominated by *Sarcocornia perennis*. *Atriplex portulacoides* and *Arthrocnemum macrostachyum* are frequently encountered in the relevés of this community. Other notable species include *Spartina densiflora* and *Limonium narbonense*.

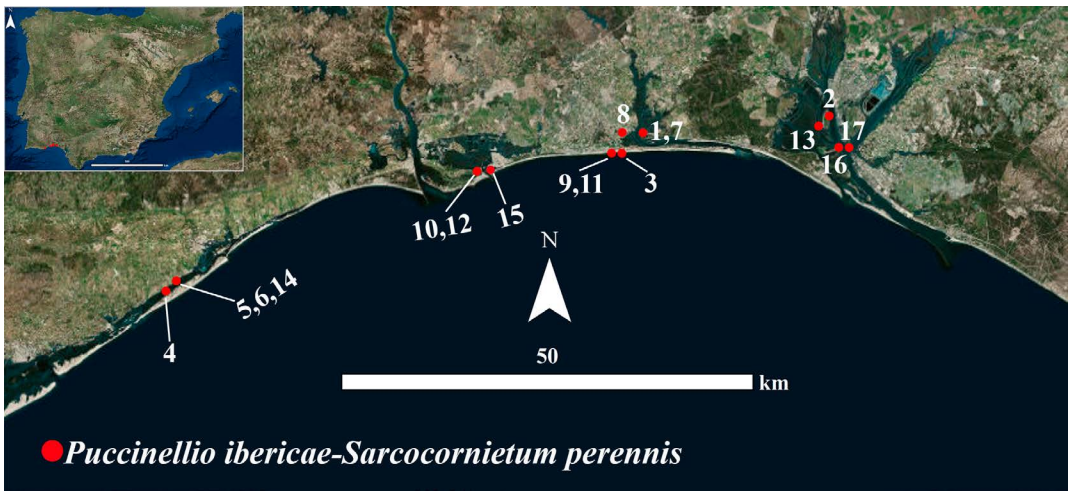

Figure 5. Locations of the 17 relevés from Table 1 for the *Puccinellio ibericae-Sarcocornietum perennis* association in the southwestern Iberian Peninsula.

Table 2. *Cistancho phelypaeae-Sarcocornietum pruinosae* (*Halimionion portulacoidis*, *Sarcocornio pruinosae-Halimionetalia portulacoidis*, *Salicornietea fruticosae*)

Area (m^2)	5	20	10	20	10	5	10	10	10	10	10	20	5	20
Number of species	4	4	4	4	5	5	5	6	5	7	7	7	9	12
Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Characteristics														
Sarcocornia pruinosa	4	4	4	5	5	5	3	5	4	5	4	3	4	4
Atriplex portulacoides	2	1	2	3	2	3	2	3	+	3	1	1	2	3
Arthrocnemum macrostachyum	.	1	+	.	.	.	1	1	.	+	2	1	1	+
Sarcocornia perennis	.	.	.	.	2	.	.	.	1	+	.	1	+	.
Other species														
Limonium narbonense	.	.	.	2	+	1	+	1	.	.	1	.	+	1
Sparitna densiflora	1	.	+	.	.	.	.	+	+	+	1	1	+	+
Suaeda maritima	.	.	.	.	.	+	1	.	1	1	.	1	+	.
Salicornia patula	2	1	.	.	.	.	.	.	.	2	.	+	.	.
Spartina maritima	.	.	.	1	1	.	.	.	.	.	.	.	.	1
Limoniastrum monopetalum	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Suaeda vera	.	.	.	.	.	.	.	.	.	.	+	.	.	1
Puccinellia iberica	.	.	.	.	.	.	.	+	.	.	.	.	+	.

Other species: *Cistanche phelypaea* + in 6; *Atriplex halimus* + in 11; *Limbarda crithmoides* 2, *Limonium algarvense* and *Myriolimon ferulaceum* 1, and *Frankenia laevis* + in 14.
Localities: 1: Huelva, La Rábida, 17-07-2018, 29SPB8320; 2: Huelva, El Rompido, before 2009, 29SPB6019; 3, 4: Huelva, Punta del Moral, 18-07-2018, 29SPB4717; 5, 6: Portugal, Isla de Tavira, Pedras d´el Rei, 18-07-2018, 29SPB1705; 7: Huelva, Caño de la Cruz, estero del tamujar chico, 24-11-2021, 29SPB4720; 8: Huelva, Ayamonte, 18-07-2018, 29SPB4218; 9: Huelva, Isla Cristina, La Gola, 24-11-2021, 29SPB4817; 10, 11: Huelva, Tinto River mouth, 17-07-2018, 29SPB8220; 12: Huelva, Odiel marshes, Visitor Center, before 2009, 29SPB8218; 13: Huelva, El Terrón, 18-07-2018, 29SPB6119; 14: Huelva, San Miguel marshes, before 2009, 29SPB6321.

Halimiono portulacoidis-Sarcocornietum alpini Rivas-Martínez & Costa 1984 (Table 3, Figure 7)

This community, characterized by a low species diversity, occupies a zone in the upper marshes that is furthest from sea level, in contrast to the two associations dominated by species of the genus *Sarcocornia* (*S. perennis* and *S. pruinosa*). The prostrate hemicryptophyte-nanophanerophyte *Sarcocornia alpini* dominates this Mediterranean association. The community exhibits a slightly lower number of species; with the succulent nanophanerophyte *Arthrocnemum macrostachyum* being the most common and having the highest biomass after *S. alpini*. This association typically thrives in areas with minimal or no tidal influence and wet, silty-clay soils.

Inulo crithmoidis-Arthrocnemetum macrostachyi Fontes ex Géhu & Géhu Franck 1977 (Table 4, Figure 8)

This community is structured and dominated in the southwestern Iberian Peninsula by the succulent nanophanerophyte *Arthrocnemum macrostachyum*. Among the four communities presided over by different shrubby Salicornioideae species along the Tinto River and adjacent territories, this association occupies the highest and driest band of the marshes and salt flats, where tidal influence is minimal or absent. It endures significant fluctuations in salinity and tolerates the intense desiccation of soils during the summer months. The association shows a preference for saline, silty-clay soils. The most common species found in the surveyed area,

alongside *A. macrostachyum*, include *Atriplex portulacoides*, *Sarcocornia pruinosa*, *Limoniastrum monopetalum*, *Spartina densiflora*, and *Suaeda vera*.

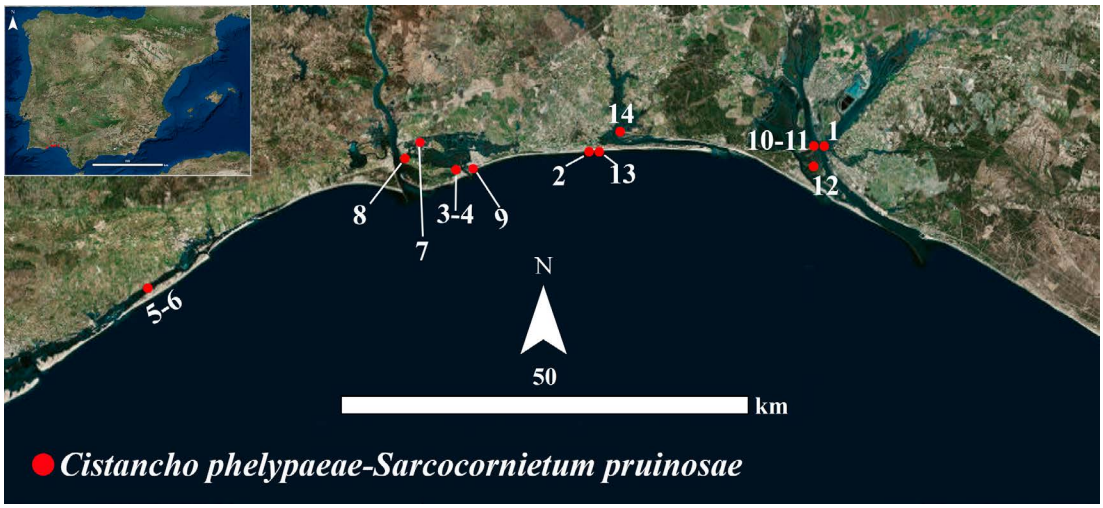

Figure 6. Locations of the 14 relevés from Table 2 for the *Cistancho phelypaeae-Sarcocornietum pruinosae* in the southwestern Iberian Peninsula.

Table 3. *Halimiono portulacoidis-Sarcocornietum alpini* (*Sarcocornion alpini*, *Sarcocornio pruinosae-Halimionetalia portulacoidis*, *Salicornietea fruticosae*)

Area (m^2)	5	10	10	10	10	10	10	10
Number of taxa	2	3	3	3	3	3	4	7
Order number	1	2	3	4	5	6	7	8
Association characteristics and higher units								
Sarcocornia alpini	4	4	5	4	4	4	3	3
Arthrocnemum macrostachyum	.	2	+	+	+	.	1	+
Atriplex portulacoides	.	.	+	1	2	.	.	.
Sarcocornia pruinosa	.	.	.	.	.	1	.	.
Companion species								
Plantago coronopus	.	.	.	.	.	.	1	1
Salicornia patula	.	+	.	.	.	+	.	.
Spergularia marina	.	.	.	.	.	.	+	+

Other species: *Juncus subulatus* + in 1; *Mesembryanthemum nodiflorum* 1, *Frankenia laevis* and *Sphenopus divaricarus* + in 8.
Localities: 1: Portugal, esteiro de Carrasqueira, 18-07-2018, 29SPB3918; 2: Huelva, La Rábida, 17-07-2018, 29SPB8320; 3, 4: Huelva, San Juan del Puerto, Embarcadero de Buitrón, 07-08-2019, 29SPB9031; 5: Huelva, San Juan del Puerto, before 2009, 29SPB9130; 6: Huelva, Caño de la Cruz, estero del tamujar chico, 24-11-2021, 29SPB4720; 7: Huelva, San Juan del Puerto, caño San Juan, 07-08-2019, 29SPB9131; 8: Huelva, La Santa marshes, 06-08-2019, 29SPB8724.

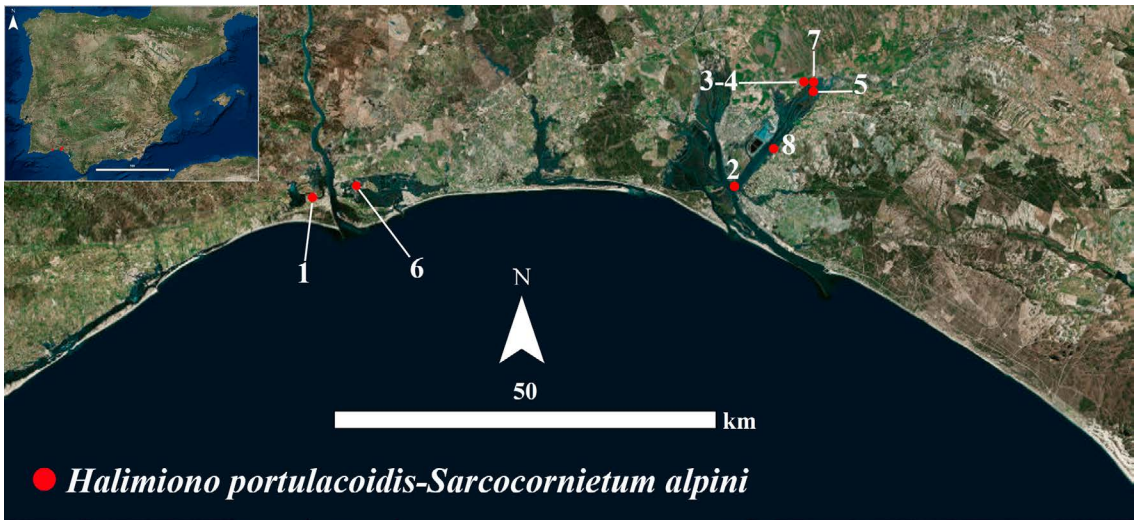

Figure 7. Locations of the 8 relevés from Table 3 of *Halimiono portulacoidis-Sarcocornietum alpini* in the southwestern Iberian Peninsula.

Table 4. *Inulo crithmoides-Arthrocnemetum macrostachyi* (*Arthrocnemion macrostachyi*, *Arthrocnemo macrostachyi-Suaedetalia braun-blanquetii*, *Salicornietea fruticosae*)

Area (1=10m²)	1	1	1	5	5	5	1	1	1	.5	.5	1	5	1	1	1	1	5	1	1	1	.5	1	1	1	.5	1	1	1	1	1
N. of species	2	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	6	6	6	6	7	7	7	7	8	8	9	9	10
N. of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Characteristics:																															
Arthrocnemum macrostachyum	5	4	3	3	4	4	3	3	3	4	3	3	4	5	4	3	3	4	4	5	3	4	5	3	3	3	5	4	4	4	2
Atriplex portulacoides	.	.	1	.	2	.	+	2	.	.	.	1	1	.	1	.	2	1	.	+	1	.	+	+	3	+	.	+	2	1	.
Sarcocornia pruinosa	.	.	.	3	1	1	1	.	.	3	1	.	1	.	2	.	.	1	.	.	1	.	.	.	.	+	.	+	+	+	1
Sarcocornia alpini	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	1	+	.	.	+	1	.	.	.	.	.	.	.
Other species:																															
Limoniastrum monopetalum	.	.	1	1	.	.	.	.	2	+	3	+	.	.	+	+	+	.	1	.	.	.	2	2	1	2	.	2	1	3	1
Spartina densiflora	.	.	+	.	1	.	.	2	2	.	1	2	1	.	2	+	.	2	1	.	1	.	.	3	.	.	.	1	+	.	.
Suaeda vera	+	+	.	1	.	.	.	+	2	.	.	.	.	.	.	+	+	.	+	1	2	+	1	2	+	.	1	1	.	1	+
Limonium algarvense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	.	1	.	.	2
Juncus subulatus	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	.	.	.	.	1	.	.	.	.	+	.	.	.	.
Atriplex halimus	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+	+	+	+	.
Cistanche phelypaea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	+	.	.	.	+	.
Spergularia marina	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	+	.	.
Frankenia laevis	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	2
Hordeum marinum	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Soda inermis	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	2

Other species: *Myriolimon ferulaceum* 2 in 25, + in 31; *Suaeda maritima* and *Limbarda crithmoides* + in 30, 1 in 31; *Cotula coronopifolia* 1 in 14, + in 22; *Juncus acutus* + in 10; *Polygonum equisetiforme* 1 in 11; *Parapholis filiformis* + in 14; *Plantago maritima* + in 20; *Juncus bufonius* and *Polypogon maritimus* + in 22; *Caroxylon vermiculatum* 1, *Retama monosperma* + in 26; *Spartina maritima* + in 27; *Thinopyrum elongatum* + in 29.

Localities: 1,23: Huelva, La Santa marshes, 06-08-2019, 29SPB8724; 2,17,20: Huelva, San Juan del Puerto, caño San Juan, 07-08-2019, 29SPB9131; 3: Huelva, San Juan del Puerto, Embarcadero de Buitrón, 07-08-2019, 29SPB9031; 4,5,6,18: Huelva, Odiel marshes, before 2009, 29SPB8022; 7,8: Huelva, río Aljaraque/Estero Morfé, 07-08-2019, 29SPB7926; 9. Huelva, Estero Morfé, 07-08-2019, 29SPB7826; 10, 25, 31: Huelva, San Miguel marshes, before 2009, 29SPB6321; 11, 27: Cádiz, Sanlúcar de Barrameda, before 2009, 29SQA3883; 12-14, 29: Huelva, La Rábida, before 2009, 29SPB8320; 15: Huelva, anillo hídrico bridge, 06-08-2019, 29SPB8624; 16: Huelva, El Almendral, before 2009, 29SPB8020; 19,24: Huelva, San Juan del Puerto, before 2009, 29SPB9130; 21: Huelva, El Rompido, before 2009, 29SPB6019; 22: Portugal, esteiro de Carrasqueira, 18-07-2018, 29SPB3918; 26: Huelva, Punta del Moral, 18-07-2018, 29SPB4717; 28: Huelva, Tinto River mouth, 17-07-2018, 29SPB8220; 30: Portugal, Isla de Tavira, Pedras d´el Rei, 18-07-2018, 29SPB1705.

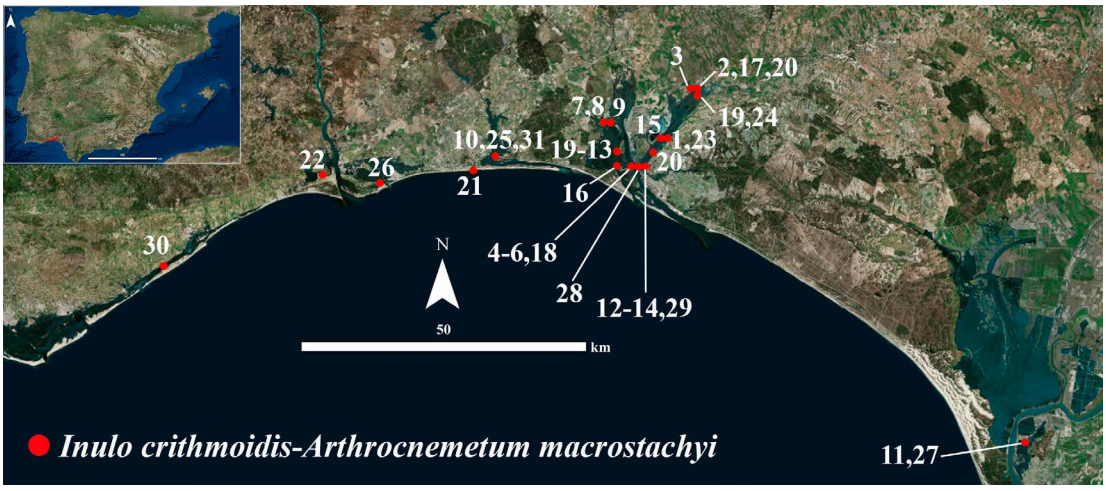

Figure 8. Locations of the 31 relevés from Table 4 of *Inulo crithmoidis-Arthrocnemetum macrostachyi* in the southwestern Iberian Peninsula.

Discussion

The 70 phytosociological relevés presented in this study for the salt marshes of the Tinto River and adjacent areas in southwestern Iberia are consistent with those previously conducted by various authors in Spain and Portugal (Costa *et al*., 1996; Costa & Lousã, 1989; Lendínez, 2010; Neto *et al*., 2009; Rivas-Martínez *et al*., 1980, 1990; Tamajón & Muñoz, 2001). This study diverges from prior research on halophytic plant communities primarily due to updated syntaxonomic nomenclature, reflecting recent taxonomic advancements within the genus *Sarcocornia* (de la Fuente *et al*., 2016; Rufo *et al*., 2016). Moreover, these revisions, together with the new phytosociological relevés presented in this study, provide a precise and up-to-date framework for evaluating biodiversity in

marshland ecosystems in the southwestern Iberian Peninsula.

The Mediterranean coastline, characterized by elevated water temperatures, reduced hydrodynamic energy, and negligible tidal fluctuations, contrasts sharply with the Atlantic coast. Consequently, the spatial delineation of biological communities is more sharply defined along the Iberian Atlantic margin compared to the Mediterranean regions of Spain (Salazar-Mendías & Lendínez, 2021). In contrast to these Mediterranean characteristics, the estuarine system in the province of Huelva exhibits a semi-diurnal mesotidal regime, with an average tidal range of 2.69 m, reaching up to 3.06 m during spring tides and a minimum of 1.7 m during neap tides (Morales *et al*., 2005; Rufo, 2009).

In the initial band of low-lying formations within the phytosociological class *Spartinetea maritimae*, *Spartina maritima* is the dominant species, consistently inhabiting low marshes characterized by periodically inundated silty substrates (de la Fuente *et al*. 2008; Sánchez-Gullón, 2001). Adjacent to these *S. maritima* communities is the association *Puccinellio ibericae-Sarcocornietum perennis*. Within the class *Salicornietea fruticosae*, *S. perennis* communities are situated closest to the water and are subject to complete flooding bi-daily. These communities extend along coastal regions in a relatively narrow band and are characterized by their low height, typically not exceeding 0.5 meters in height, and their high canopy cover. Their predominant growth form is prostrate and rooting, which enhances their adaptability to dynamic tidal conditions (Rufo *et al*., 2016).

The next most prevalent association within the ecological continuum of the southwestern Iberian Peninsula is *Cistancho phelypaeae-Sarcocornietum pruinosae*. Both associations are characterized by succulent chamaephytes and nanophanerophytes, specifically *Sarcocornia perennis* and *S. pruinosa*, and are consistently subjected, either directly or indirectly, to tidal fluxes. They thrive in thermomesotemperate, subhumid to humid coastal zones, as well as in arid to humid thermomesomediterranean environments (Figure 9). Their distribution across the Iberian Peninsula extends along the Atlantic coast (Rufo *et al*., 2016).

Sarcocornia pruinosa communities experience partial flooding from tides twice daily and are fully submerged during spring tides. These communities exhibit dense and substantial canopy coverage, slightly taller than the preceding community, reaching up to 50 cm in height. The boundary between these two communities is visually discernible due to the distinct coloration of the vegetation: a bright green for the initial band of *S. perennis* and a lighter green with bluish or grayish hues for the formation dominated by *S. pruinosa*, which flourishes in a slightly elevated microtopographic position.

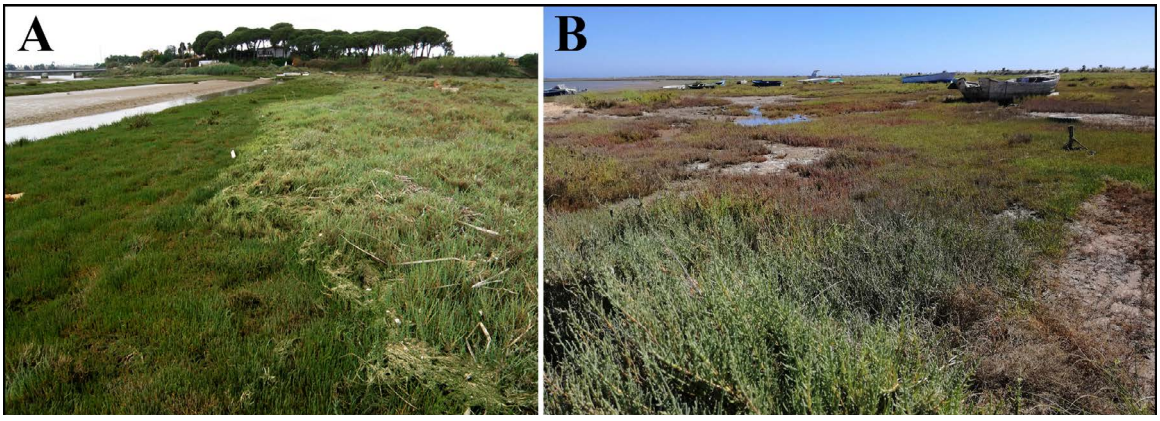

Figure 9. *Puccinellio ibericae-Sarcocornietum perennis*, characterized by a prostrate growth form with a more intense green coloration, is situated closer to the marine environment. In contrast, *Cistancho phelypaeae-Sarcocornietum pruinosae* represents a shrub-chamaephyte vegetation band displaying a blue-green hue and located further from the sea. A, Piedras River, Huelva, Spain; B, Tavira, Portugal.

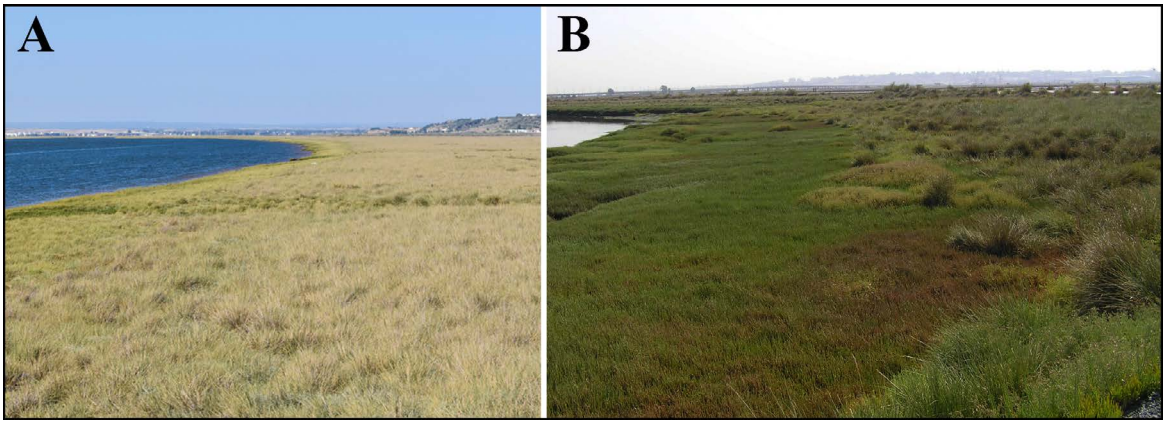

Figure 10. Monospecific stands of *Spartina densiflora* displacing Salicornioideae communities. A, Tinto River, Huelva, Spain; B, Odiel marshes, Huelva, Spain.

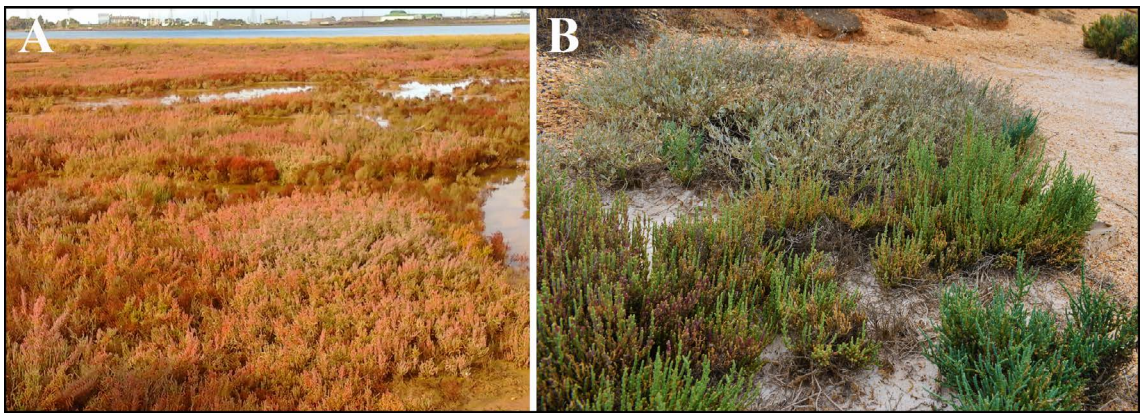

Figure 11. *Halimiono portulacoidis-Sarcocornietum alpini*. A, Tinto River (Huelva); B, San Juan del Puerto (Huelva).

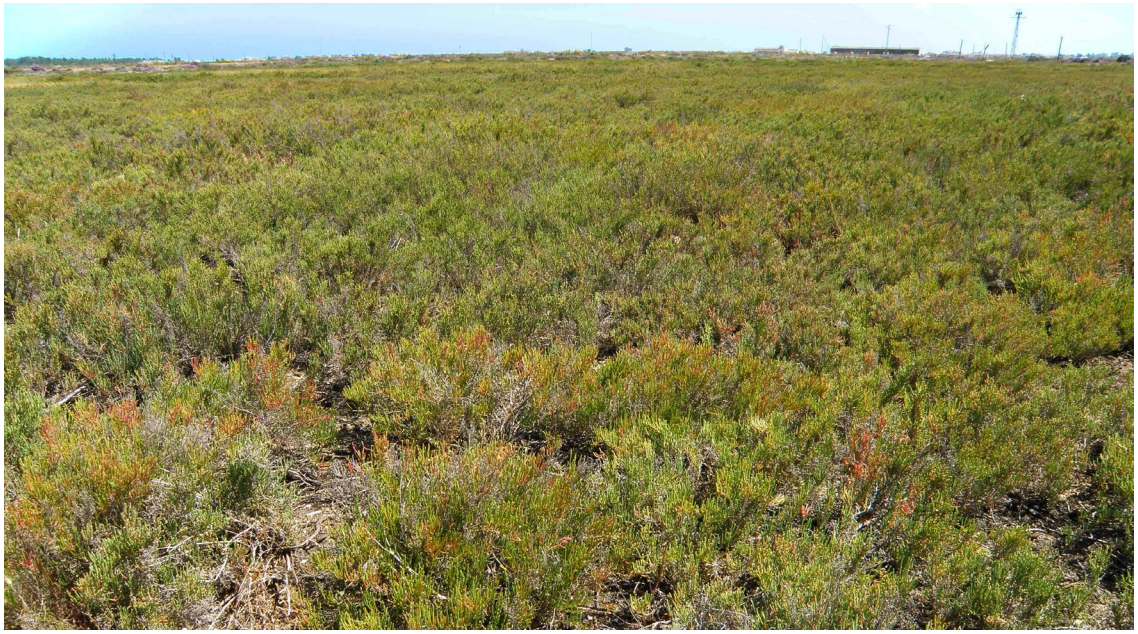

Figure 12. *Inulo crithmoidis-Arthrocnemetum macrostachyi*. Odiel marshes (Huelva).

The invasive species *Spartina densiflora*, native to America, dominate certain communities in the marshes and estuaries of the western Iberian Peninsula, occasionally displacing native Salicornioideae communities (Rufo, 2009; Salazar-Mendías & Lendínez, 2021). This American neophyte colonizes high, continental marshes characterized by sandy-loam soils, which are occasionally inundated by equinoctial spring tides (Sánchez-Gullón, 2001). Consequently, communities primarily dominated by *Sarcocornia pruinosa* (specifically *Cistancho phelypaeae-Sarcocornietum pruinosae*) and, to a lesser extent, *Arthrocnemum macrostachyum* (within *Inulo crithmoidis-Arthrocnemetum macrostachyi*), may be displaced by extensive monospecific stands of *S. densiflora* (Figure 10).

Halimiono portulacoidis-Sarcocornietum alpini is represented by halophytic shrubland communities composed of succulent chamaephytes, either decumbent or erect, that thrive in the extensive estuaries of the Atlantic and Mediterranean regions of southwestern Europe. These communities are adapted to coastal areas characterized by arid to subhumid ombrotypes within thermomesotemperate bioclimatic zones. In the Iberian Peninsula, their distribution spans the Atlantic coastline from the mouth of the Tagus River (Lisbon) to Cape Tarifa (Cádiz) (Rufo *et al*., 2016).

Sarcocornia alpini communities are found in the coastal regions of the Lusitano-Andalusian biogeographic province. They occupy mid-intertidal zones adjacent to river waters and can experience total or partial inundation from daily tides. Additionally, these communities are also present in channels and depressions within high intertidal zones that are subject to occasional flooding yet remain distant from direct marine influence (Figure 11). The physiognomy of these communities varies according to the ecological conditions: those subjected to daily inundation resemble *S. perennis* communities, featuring multiple woody, rooting branches extending toward the water, alongside numerous erect secondary branches. When situated away from water and experiencing only occasional inundation, *S. alpini* assumes a more erect shrub form.

The Mediterranean association *Inulo crithmoidis-Arthrocnemetum macrostachyi* (Figure 12) is delineated by its northern boundary at the mouth of the Tagus River, where it was initially described by Fontes in 1945 (Rivas-Martínez *et al*., 1980). Costa *et al*. (2009) indicate that this

association's distribution limit coincides with the Tagus River estuary, primarily due to the moderating influence of cold Atlantic waters on the estuarine and marsh vegetation. Notably, in monitoring studies conducted on the flora and vegetation of the Ria de Aveiro, the *Inulo crithmoidis-Arthrocnemetum macrostachyi* association was not observed (Almagro *et al*., 2006). Our findings corroborate those of Almagro *et al*., suggesting that *Arthrocnemum macrostachyum* is predominantly confined to temperate climate regions within the Ria de Aveiro, as well as in the marshes at the mouth of the Mondego River in Figueira da Foz, marking its northernmost distribution limit.

Inulo crithmoidis-Arthrocnemetum macrostachyi association frequently interfaces with the *Cistancho phelypaeae-Sarcocornietum pruinosae* in wetter substrates. Conversely, in elevated and drier positions, the transition occurs with formations dominated by the succulent halophyte *Limoniastrum monopetalum* (known as *Polygono equisetiformis-Limoniastretum monopetali*). In these saline soils, when subjected to significant disturbance (such as soil removal, nitrification, or sandy substrates enriched with organic matter), the community transitions to the *Cistancho phelypaeae-Suadetum verae* association, which is characterized by the halonitrophilic shrub *Suaeda vera*.

Within the clearings created by suffruticose and succulent shrubs of the subfamily Salicornioideae, therophytic communities thrive, exhibiting varying degrees of inundation and tidal influence. These include communities classified under *Thero-Salicornietea* that are characterized by high inundation levels, as well as spring ephemeral communities belonging to the *Saginetea maritimae*, which experience a lower degree of inundation (Rufo, 2009; Salazar-Mendías & Lendínez, 2021).

Understanding plant communities and their hierarchical classification is essential for the effective management and conservation of biodiversity. This knowledge is crucial for interpreting landscapes and implementing successful reforestation and restoration programs. Halophytic shrubby communities (*Salicornietea fruticosae*), which are included in Annex I of Directive 92/43/EEC, are recognized as Habitats of Community Interest (HIC), emphasizing their significance for European conservation efforts (Rufo *et al*., 2016). Despite their importance, these ecosystems face significant threats, including aquatic pollution from agricultural runoff, urbanization, wetland drainage, and invasive species. Overgrazing, particularly during summer, further exacerbates the degradation of halophytic vegetation. The Atlantic coastal marshes, in particular, are classified as Vulnerable Habitats (Salazar-Mendías & Lendínez, 2021), underscoring the urgent need for targeted conservation strategies to preserve these critical ecosystems.

Conclusion

In this study, we analyzed vegetation communities dominated by four species of shrubby halophytes in the Tinto River marshes and adjacent regions of southwestern Iberia. This research provides current data on the structure and ecology of these plants within their habitat while synthesizing the species typically found in each association along a clear zonation gradient. It highlights the differentiation of these four closely related species, which often exhibit taxonomic and morphological complexities in the studied area. Additionally, we provide floristic relevés with precise localities for future assessments of community composition and structure. This work contributes to the protection of biodiversity in marshland areas and informs future restoration programs for fragile ecosystems that host high faunal diversity alongside specialized flora, which is of significant interest in biotechnology, pharmacology, and food science.

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Author contributions

E.R., L.R. and V.d.l.: Conceptualization and methodology; V.d.l.F. and L.R.: software; E.R.: validation; E.R., L.R and V.d.l.F.: resources; V.d.l.F.: data curation; E.R and L.R.: writing, original draft preparation; E.R., L.R. and V.d.l.F.: review and editing; V.d.l.F.: project administration. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

None.

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Supplementary material

Appendix S1. Syntaxonomic scheme.
Appendix S2. Floristic appendix.