

## Geographic variation among Iberian communities of the exotic halophyte *Cotula coronopifolia*

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**Abstract** The exotic annual forb *Cotula coronopifolia* has locally invaded salt marsh communities naturally dominated by *Spergularia marina* along large parts of the Iberian coastline. While the floristic composition of *C. coronopifolia* dominated communities on the Atlantic coast of northern Portugal has already been described, this information was missing for the southern part of the country. We carried out a phytosociological study at 21 sites along the south-western and southern coast of mainland Portugal to determine the ecology and syntaxonomical status of these communities, and to compare them to the Atlantic ones. Plant communities co-dominated by *C. coronopifolia* and *S. marina* were generally found in the

sub-halophilous inner part of salt marshes. They occupied gaps within taller perennial vegetation (*Juncus maritimus* formations), such as small pools temporarily inundated with brackish waters. Southern communities differed from the northern ones by the high abundance of *Triglochin barrelieri* and the absence of salt-intolerant species that are present in the Atlantic communities. This difference may result from the drier summer climate in southern regions, leading to intense water evaporation and thus, more saline conditions. We propose to classify the Mediterranean communities in a new association, the *Cotulo coronopifoliae–Triglochinetum barrelieri*. High abundance of *Limonium diffusum* further allowed the distinction of a new subassociation *limonietosum diffusi* for the southernmost part of Portugal. Results show that invasive exotic plants can form new phytosociological associations with a characteristic species composition, but that these community types, despite being dominated by the same invader, still show ecological and geographical differentiation.

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### Introduction

*Cotula coronopifolia* (Compositae) is a yellow-flowered forb with succulent leaves, occupying the edges of salt marshes on damp, muddy and salty soils. It is native to South Africa (Franco 1984) but has spread through the coasts of Europe, South and North America, New Zealand, Australia and Tasmania (Coutinho 1939; Hultén 1968; Ramírez et al. 1989; Bueno 1997). In temperate Europe, *C. coronopifolia* is an annual plant (Partridge and Wilson 1987; Bueno 1997), whereas in its original territory, South

Africa, it is sometimes perennial, with longer stems trailing and rooting (Manning and Golblatt 1996). In Portugal, the species is predominantly annual north of Tagus River and perennial southwards, where the Mediterranean climate is more similar to that of South Africa.

The spread of *C. coronopifolia* is promoted by its ability to colonize a wide range of extreme habitats, including beaches, estuaries, intertidal flats, disturbed salt marshes and human-disturbed inland sites (Van der Toorn 1980). An effective aquatic dispersion of seeds (up to 450 m/year; van der Toorn 1980) enables the species to rapidly colonize disturbed places, where it can form almost pure stands thanks to its fast seed germination (Partridge and Wilson 1987; Van der Toorn 1980; Van der Toorn and ten Hove 1982). As a consequence, Campos et al. (2004) considered *C. coronopifolia* an accidentally introduced, invasive plant for Spain. In France, *C. coronopifolia* is regarded as a 'restricted' invasive species in aquatic plant communities of the Mediterranean region and as 'potentially invasive' in the Atlantic region, although it is not included in the group of the most dangerous invasive plants (Thiébaud 2007).

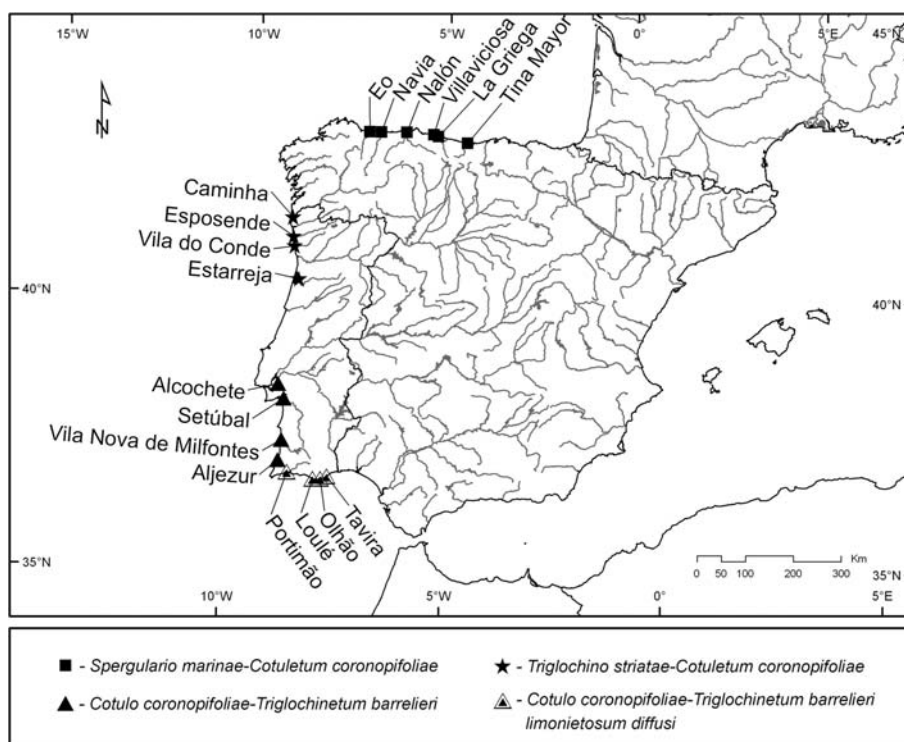
Plant invasions raise new questions for phytosociology. Traditionally, phytosociology assumes that plant communities consist of characteristic species assemblages reflecting abiotic conditions as well as biotic interactions. Invasive exotic plants can alter both abiotic conditions and biotic interactions in multiple ways. This may cause exotic plant invaders to assemble new types of plant communities around them. Alternatively, invaded plant communities

may retain their characteristic native species composition despite the presence of a competitive invader. So far, it is not possible to predict for a particular exotic species what the effect of its invasion on native communities will be. It also appears that the species composition of invaded communities is sometimes determined by habitat conditions similarly to native communities, whereas in other cases the influence of the dominant exotic invader overrides habitat factors, leading to a homogenization of the vegetation.

Two phytosociological associations dominated by *C. coronopifolia* have been described from the north-western part of the Iberian Peninsula: the *Spergulario marinae-Cotuletum coronopifoliae* on Asturian estuaries (Bueno 1997) and the *Triglochino striatae-Cotuletum coronopifoliae* on Galician-Portuguese estuaries (Alves 2004). Both communities occur in sub-halophilous openings within *J. maritimus* communities; these are small ponds with barely saline water due to the humid climate of north-western Iberia (Díaz González and Fernández Prieto 2005). Similar sites also occur along the Mediterranean coast in southern Iberia, and some of them are also colonized by *C. coronopifolia*. However, their syntaxonomy and ecology has not yet been studied in detail.

The aims of this study were (1) to describe the species composition and ecology of communities invaded by *C. coronopifolia* in southern Iberia, (2) to determine whether and how they differ from those in northern Iberia, and (3) to examine their relationship with uninvaded communities

**Fig. 1** Geographic location of the analyzed salt marsh communities



**Table 1** Synthetic table of *Cotula coronopifolia* communities of the Iberian Peninsula

Community type	1	2	3	4	5
Number of relevés	58	10	8	7	10
Characteristics and differentials of associations					
<i>Cotula coronopifolia</i>	V	V	V	V	.
<i>Spergularia marina</i>	V	IV	V	V	V
<i>Triglochin maritima</i>	III	.	.	.	.
<i>Puccinellia fasciculata</i>	III	.	.	.	.
<i>Parapholis strigosa</i>	II	.	.	.	.
<i>Puccinellia maritima</i>	II	.	.	.	.
<i>Polypogon monspeliensis</i>	II	.	.	.	.
<i>Juncus ambiguus</i>	II	.	.	.	.
<i>Juncus gerardii</i>	II	.	.	.	.
<i>Paspalum vaginatum</i>	I	III	.	.	.
<i>Agrostis pseudopungens</i>	II	II	.	.	.
<i>Triglochin striata</i>	.	V	.	.	.
<i>Triglochin barrelieri</i>	.	.	V	V	V
<i>Limonium ferulaceum</i>	.	.	IV	V	V
<i>Polygonum equisetiforme</i>	.	.	IV	IV	IV
<i>Centaurium tenuiflorum</i>	.	.	I	I	I
<i>Limonium diffusum</i>	.	.	.	V	V
<i>Limonium algarvense</i>	.	.	.	V	V
<i>Frankenia boissieri</i>	.	.	.	III	III
Characteristics of <i>Molinio-Arrhenatheretea</i>					
<i>Cynodon dactylon</i>	+	.	I	I	I
<i>Lolium perenne</i>	r	I	.	.	I
<i>Trifolium repens</i>	r	.	.	.	I
<i>Bellis perennis</i>	+	.	.	.	I
<i>Polypogon viridis</i>	+	.	.	.	I
<i>Bromus hordeaceus</i>	r	.	.	.	r
<i>Holcus lanatus</i>	r	.	.	.	r
<i>Lythrum junceum</i>	r	.	.	.	r
<i>Plantago major</i>	r	.	.	.	r
<i>Juncus inflexus</i>	r	.	.	.	.
<i>Lolium multiflorum</i>	r	.	.	.	.
<i>Paspalum distichum</i>	r	.	.	.	.
<i>Carex divisa</i>	r	.	.	.	.
<i>Potentilla repens</i>	r	.	.	.	.
<i>Taraxacum officinale</i>	r	.	.	.	.
Characteristics of <i>Juncetea maritimi</i>					
<i>Juncus maritimus</i>	III	III	IV	V	IV
<i>Aster tripolium</i> s.l.	I	II	I	II	I
<i>Frankenia laevis</i>	r	.	IV	II	I
<i>Carex extensa</i>	I	.	.	.	.
<i>Apium graveolens</i>	+	.	.	.	.
<i>Glaux maritima</i>	r	.	.	.	.
<i>Plantago maritima</i>	r	.	.	.	.
<i>Armeria depilata</i>	r	.	.	.	.
<i>Festuca rubra</i>	r	.	.	.	.
<i>Spartina patens</i>	.	I	.	.	.

**Table 1** continued

Community type	1	2	3	4	5
Number of relevés	58	10	8	7	10
<i>Spergularia media</i>	.	.	IV	IV	IV
<i>Blackstonia imperfoliata</i>	.	.	.	I	I
Characteristics of <i>Sarcocornietea fruticosae</i>					
<i>Sarcocornia perennis</i>	+	.	.	.	.
<i>Halimione portulacoides</i>	r	.	II	I	II
<i>Inula crithmoides</i>	.	.	II	III	III
<i>Limonium lanceolatum</i>	.	.	II	.	II
Characteristics of <i>Saginetea maritimae</i>					
<i>Parapholis incurva</i>	I	.	II	II	II
<i>Polypogon maritimus</i>	.	III	IV	V	IV
<i>Parapholis filiformis</i>	.	.	IV	V	IV
<i>Centaurium spicatum</i>	.	.	.	III	III
<i>Hordeum marinum</i>	.	.	II	III	II
Characteristics of <i>Isoeto-Nanojuncetea</i>					
<i>Isolepis cernua</i>	II	.	.	.	.
<i>Isolepis setacea</i>	r	.	.	.	.
<i>Lythrum hyssopifolia</i>	r	.	.	.	.
<i>Juncus bufonius</i>	r	.	II	II	II
<i>Juncus hybridus</i>	.	.	V	III	III
Companions					
<i>Plantago coronopus</i>	I	I	IV	III	III
<i>Aster squamatus</i>	+	I	.	III	II
<i>Atriplex prostrata</i>	II	.	.	III	II
<i>Scirpus compactus</i>	I	II	.	.	.
<i>Samolus valerandi</i>	+	I	.	.	.
<i>Leontodon taraxacoides</i>	r	I	.	.	.
<i>Salicornia</i> sp.	I	.	.	.	.
<i>Lotus tenuis</i>	I	.	.	.	.
<i>Elymus pycnanthus</i>	+	.	.	.	.
<i>Polygonum aviculare</i>	r	.	.	.	.
<i>Ranunculus sardous</i>	r	.	.	.	.
<i>Trifolium squamosum</i>	r	.	.	.	.
<i>Sonchus oleraceus</i>	r	.	.	.	.
<i>Hordeum secalinum</i>	r	.	.	.	.
<i>Carex cuprina</i>	r	.	.	.	.
<i>Pulicaria dysenterica</i>	r	.	.	.	.
<i>Sagina apetala</i>	r	.	.	.	.
<i>Apium nodiflorum</i>	r	.	.	.	.
<i>Centaurium acutiflorum</i>	r	.	.	.	.
<i>Matricaria maritima</i>	r	.	.	.	.
<i>Anagallis tenella</i>	r	.	.	.	.
<i>Medicago lupulina</i>	r	.	.	.	.
<i>Vicia nigra</i>	r	.	.	.	.
<i>Phragmites australis</i>	.	II	.	.	.
<i>Aetheorhiza bulbosa</i>	.	.	I	.	I
<i>Melilotus messanensis</i>	.	.	.	II	II
<i>Spergularia heldreichii</i>	.	.	.	I	I

**Table 1** continued

Community type	1	2	3	4	5
Number of relevés	58	10	8	7	10
<i>Dittrichia revoluta</i>	.	.	.	I	I

Frequency of plant species across relevés from each association or sub-association: 1 *Spergulario marinae*–*Cotuletum coronopifoliae* (BUE-NO 1997, table 23); 2 *Triglochino striatae*–*Cotuletum coronopifoliae* (ALVES 2004, table 1); 3 *Cotulo coronopifoliae*–*Triglochinetum barrelieri typicum*; 4 *Cotulo coronopifoliae*–*Triglochinetum barrelieri limonietosum diffusae*; 5 Clearings in rush-community without *C. coronopifolia*. Frequency classes are: V: 80–100% of the relevés, IV: 60–80%, III: 40–60%, II: 20–40%, I: 10–20%, +: 5–10%, r: 1–5%

occurring under the same abiotic conditions (Bueno 1997; Alves 2004).

## Materials and methods

Vegetation relevés were made between 2006 and 2008 at the sites found during the last 20 years in the southwest part of the Iberian Peninsula (Fig. 1) that were taken as a representative sample of *C. coronopifolia* communities, namely those with presence of *C. coronopifolia* with cover >20% in small ponds within clearings of undisturbed *J. maritimus* communities. A total of 15 relevés were made, the area of which ranged from 1 to 6 m<sup>2</sup> based on an estimate of the minimum sampling area. Relevés were also made in clearings corresponding to analogous habitat conditions to those occupied by *C. coronopifolia*, as perceived by the researchers. The later relevés—those not having *C. coronopifolia*—are used informally as a ‘post hoc null hypothesis’ concerning similar habitat conditions for comparison sake in the final synthetic table.

For the comparison with northern Iberian communities, original relevés dominated by *C. coronopifolia* were obtained from the authors (relevés 16–25 from Alves 2004, and relevés 26–83 from Bueno 1997). Relevés were submitted to principal coordinate analysis (PCoA), based on log-transformed percentage cover and with the similarity ratio as resemblance measure using SYNTAX 2000 software (Gower 1966; Podani 2001). Principal coordinate analysis (PCoA) is a multidimensional scaling method that can be based on any similarity or dissimilarity index, making possible the use of ecologically meaningful indices (Chae and Warde 2006).

The biogeographical and bioclimatological typologies used in the description of syntaxa follow Costa et al. (1999), Rivas-Martínez et al. (2001, 2002) and Rivas-Martínez (2007), while syntaxa nomenclature follows the International Code of Phytosociological Nomenclature (Weber et al. 2000). Botanical nomenclature follows

Castroviejo et al. (1986–2006), Franco (1971, 1984), Franco and Rocha Afonso (1994, 1998, 2003).

## Results and discussion

### Distribution and species composition of *Cotula coronopifolia* communities in Iberia

Within Iberian Peninsula, *C. coronopifolia* is frequently associated to the sub-halophilous inner part of salt marshes. These sites are characterized by a strong fluctuation of soil salinity between wintertime, with the incoming of fresh water due to rainfall, and summertime, dry and hot, with the increase of soil salt concentration owing to the capillary rising of water from the saline phreatic sheet. In the Iberian Peninsula, these communities of small plants are always linked to sites where the higher hemicriptophytic vegetation has been destroyed, which also the high constancy of *Spergularia marina* in all Iberian *C. coronopifolia* communities (Table 1). *S. marina* is a species which makes extensive seed banks (Ungar 1998) and whose germination is light requiring (Thompson and Grime 1979; Carter and Ungar 2004), so that its occurrence depends on frequent disturbances. This explains the presence of *S. marina* with *C. coronopifolia* in gaps among *J. maritimus* communities’ openings of the inner part of salt marshes, where human influence is most significant.

In the dry-thermomediterranean bioclimate of southern Iberia (Coastal Lusitan-Andalusian province), communities of *C. coronopifolia* develop during late spring and early summer. They are co-dominated by *C. coronopifolia* and *Triglochin bulbosa* ssp. *barrelieri*, accompanied by characteristic species of the *Juncetea maritimi* class as well as the *Sarcocornietea fruticosa*, *Saginetea maritima*, *Isoetoneanojuncetea*, and nitrophilous species, as shown in Table 2.

Compared to the other Iberian communities dominated by *C. coronopifolia* and *S. marina*, the southern Iberian communities present an original floristic composition. In particular, they differ from the Atlantic communities on the Galician-Portuguese and Cantabrian shores by the presence of Mediterranean species, such as *Triglochin bulbosa* ssp. *barrelieri*, *Limonium ferulaceum*, *Parapholis filiformis*, and by the absence of Eurosiberian species, such as *Puccinellia fasciculata*, *P. maritima*, *Paspalum vaginatum*, *Triglochin striata*, *T. maritima*, *Agrostis stolonifera* var. *pseudopungens*, *Parapholis strigosa*, etc. (Table 1). These differences justify a new phytosociological designation.

We propose the name *Cotulo coronopifoliae*–*Triglochinetum barrelieri* ass. nova hoc loc (Table 2, *typus* relevé no. 2) for this new association. The optimal conditions for its development are depressions on sandy–silty or silty–clayish

**Table 2** Vegetation relevés in *Cotula coronopifoliae*–*Triglochinetum barrelieri* communities

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Area of the relevé (m <sup>2</sup> )	2	1	1	1	4	4	2	4	4	6	4	4	4	4	2
Number of species	7	9	12	8	17	14	12	16	18	22	15	17	13	15	12
Characteristics of the association															
<i>Cotula coronopifolia</i>	3	2	3	3	3	3	1	3	3	3	2	3	2	3	2
<i>Triglochin bulbosa</i> ssp. <i>barrelieri</i>	3	3	2	1	3	1	3	2	2	3	3	1	3	2	3
<i>Limonium ferulaceum</i>	.	2	1	.	2	2	1	1	1	+	1	+	1	.	1
<i>Juncus maritimus</i>	1	2	.	1	1	+	1	1	1	1	1	.	1	1	1
<i>Spergularia media</i>	+	.	+	.	.	+	+	1	1	1	+	.	.	+	+
<i>Polygonum equisetiforme</i>	.	.	.	+	1	+	+	1	+	1	.	1	1	.	+
<i>Inula crithmoides</i>	.	.	+	.	+	.	.	.	.	+	.	.	1	+	+
<i>Frankenia laevis</i>	.	.	.	1	2	1	2	1	.	.	.	+	.	+	.
<i>Halimione portulacoides</i>	.	.	1	.	1	+	.	.	.	.	.	.	.	1	.
<i>Aster tripolium</i> ssp. <i>pannonicus</i>	.	.	.	.	+	.	.	.	.	+	.	.	.	1	.
<i>Limonium lanceolatum</i>	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.
<i>Centaurium tenuiflorum</i>	.	.	.	.	.	.	.	+	.	1	.	.	.	.	.
Differentials of <i>limonietosum diffusum</i> subassociation															
<i>Limonium diffusum</i>	.	.	.	.	.	.	.	.	1	+	1	+	1	+	2
<i>Limonium algarvense</i>	.	.	.	.	.	.	.	.	1	+	+	+	.	+	+
<i>Frankenia boissieri</i>	.	.	.	.	.	.	.	.	.	+	1	2	.	.	.
Characteristics of <i>Isoeto-Nanojuncetea</i>															
<i>Juncus hybridus</i>	2	2	3	3	1	1	+	2	1	.	1	2	+	.	.
<i>Juncus bufonius</i>	.	.	1	.	+	.	.	.	.	.	.	1	1	.	.
Characteristics of <i>Saginetea maritimae</i>															
<i>Spergularia marina</i>	2	1	1	1	1	1	2	2	2	2	1	1	.	1	+
<i>Polypogon maritimus</i>	+	+	+	.	1	.	.	+	1	1	2	1	2	.	1
<i>Parapholis filiformis</i>	.	1	.	.	1	2	2	2	2	1	+	1	1	1	.
<i>Hordeum marinum</i>	.	.	1	.	.	.	.	+	1	.	+	+	.	.	.
<i>Parapholis incurva</i>	.	.	.	2	+	.	.	.	+	.	.	+	.	.	.
<i>Centaurium spicatum</i>	.	.	.	.	.	.	.	.	.	1	.	.	1	+	.
Companions															
<i>Plantago coronopus</i>	.	1	+	.	1	1	.	1	1	+	2	.	.	.	.
<i>Atriplex prostrata</i>	.	.	.	.	+	.	.	+	.	+	.	+	.	1	+
<i>Aster squamatus</i>	.	.	.	.	.	+	.	.	+	+	+	.	.	.	.
<i>Melilotus messanensis</i>	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.
<i>Cynodon dactylon</i>	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.

Also: 2 *Aetheorhiza bulbosa*, 1 *Lotus hispidus* in 6; 1 *Centaurium maritimum*, + *Blackstonia imperfoliata* in 11; + *Spergularia heldreichii* in 13, + *Dittrichia viscosa* ssp. *revoluta* in 14

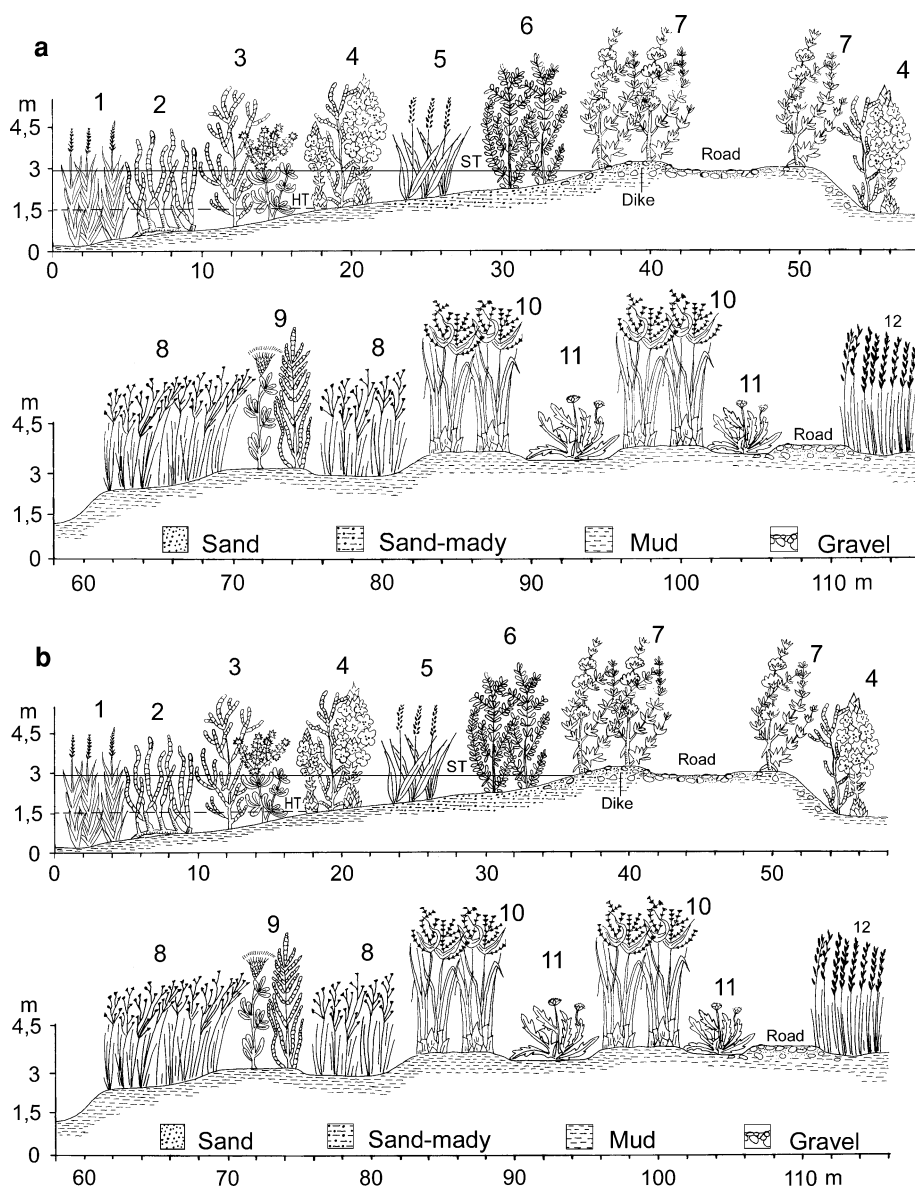
Location of relevés: 1, 2, 3, 4 Hortas (Alcochete, Tagus river), 5 Praias do Sado (Setúbal, Sado River), 6 Vila Nova de Milfontes (Mira river), 7, 8 Amoreira (Aljezur); 9 Ria de Alvor (Portimão, Ria Formosa), 10 Quinta do Ludo (Loulé, Ria Formosa), 11, 12 Quinta de Marim (Olhão, Ria Formosa), 13 Ilha de Tavira (Ria Formosa), 14 Fuzeta (Olhão, Ria Formosa), 15 Bias do Sul (Olhão, Ria Formosa)

compact soils, temporarily inundated with brackish waters during winter and early spring (rainfall accumulates on small brackish ponds with salt content) and dried out in late spring or in the beginning of summer. The association can also be found along footpaths, which explains the abundant presence of ruderal and nitrophilous species. From a catenal point of view, *C. coronopifoliae*–*T. barrelieri* occurs in the high sub-halophilous salt marsh, occupying gaps within the *Polygonum equisetiformis*–*Juncetum maritimi* (Fig. 2).

Due to differences in species composition between communities from the western and southern coast of the Coastal Lusitan-Andalusian province (Fig. 1), and taking into account that the definition of subassociations can be based on floristic differences related to biogeographic limits (Géhu and Rivas-Martínez 1981), we further propose the distinction of two subassociations: The typical subassociation, which dwells along the western coast (Ribatagan-Sadensean sector and Coastal Vincentine district), and the

**Fig. 2** Community types found in different microhabitats of the salt marsh of the Tagus Estuary (Central Portugal):

1 *Spartinetum maritimae*;  
 2 *Puccinellio ibericae*–*Sarcocornietum perennis*;  
 3 *Halimiono portulacoidis*–*Sarcocornietum alpini*;  
 4 *Cistancho phelypaeae*–*Sarcocornietum fruticosae*;  
 5 *Elytrigietum athericae*;  
 6 *Cistancho phelypaeae*–*Suaedetum verae*; 7 *Frankenio laevis*–*Salsolietum vermiculatae*;  
 8 *Limonio vulgare*–*Juncetum subulati*; 9 *Inulo crithmoidis*–*Arthrocnemetum macrostachyi*;  
 10 *P. equisetiformis*–*J. maritimi*; 11 *Cotulo coronopifoliae*–*Triglochinetum barrelieri*; 12 *Spartina versicolor* community. HT high tide, ST spring tide



subassociation *limonietosum diffusi* along the southern coast (Algarvian district). Differential species of the subassociation *limonietosum diffusi* subass. nova hoc loc (relevés no. 9 to 15, Table 2, *typus* relevé no. 11) are *Limonium diffusum*, *L. algarvense* and *Frankenia boissieri*.

### Syntaxonomic classification

Iberian *C. coronopifolia* communities recognized up to now have been positioned into the class *Molinio-Arrhenatheretea* (Rivas-Martínez et al. 2001, 2002; Table 3) because of the occasional presence of many characteristic species of this class (Table 1). This syntaxonomic classification does not seem appropriate for the southern communities for three main reasons:

1. With the exception of *Cynodon dactylon*, no *Molinio-Arrhenatheretea* taxa have been observed;
2. The co-dominant species *Triglochin bulbosa* ssp. *barrelieri* is a characteristic species of the *Sarcocornietea fruticosae*;
3. Characteristic species of the *Sarcocornietea fruticosae* and *Juncetea maritimi* are generally frequent.

We therefore propose to position the southern Iberian communities in the class *Juncetea maritimi* (Table 3).

The statistical analysis confirms that the relevés of the Mediterranean association are very different from the Cantabrian-Atlantic ones. Indeed, the ordination plots obtained with PCoA (Fig. 3) shows a group of relevés clearly separated from the remaining ones, which coincides with *C. coronopifoliae*–*T. barrelieri* (Group 1: relevés 1–15).

**Table 3** Syntaxonomical scheme proposed for coastal communities of *Cotula coronopifolia* (a) in southern Iberia (this study) and (b) in northern Iberia (Rivas-Martínez et al. 2001, 2002)

(a)
<b>JUNCETEA MARITIMI</b> Br.-Bl. in Br.-Bl., Roussine & Nègre 1952
<b>Juncetalia maritimi</b> Br.-Bl. ex Horvatic 1934
<i>Juncion maritimi</i> Br.-Bl. ex Horvatic 1934
<b>Juncenion maritimi</b>
<i>Cotulo coronopifoliae–Triglochinatum barrelieri</i> ass. nova hoc loc
<i>Limonietosum diffusi</i> subass. nova hoc loc
(b)
<b>MOLINIO-ARRHENATHEREATA</b> Tüxen 1937
<b>Crypsio-Paspaletalia distichi</b> Br.-Bl. in Br.-Bl., Roussine & Nègre 1952
<i>Paspalo-Polypogonion viridis</i> Br.-Bl. in Br.-Bl., Roussine & Nègre 1952
<b>Spergulario-Paspalenion vaginati</b> Bueno & F. Prieto in Bueno (1997)
<i>Spergulario marinae–Cotuletum coronopifoliae</i> Bueno & F. Prieto in Bueno (1997)
<i>Triglochino striatae–Cotuletum coronopifoliae</i> Alves 2004

There is also a segregation between the *Triglochino striatae–Cotuletum coronopifoliae* (Group 2: 16–25) and *Spergulario marinae–Cotuletum coronopifoliae* (Group 3: 26–83), but they are closer to each other. The clear separation between the Mediterranean and the Cantabrian-Atlantic communities along the first axis justifies their inclusion in two different phytosociological classes (Table 3).

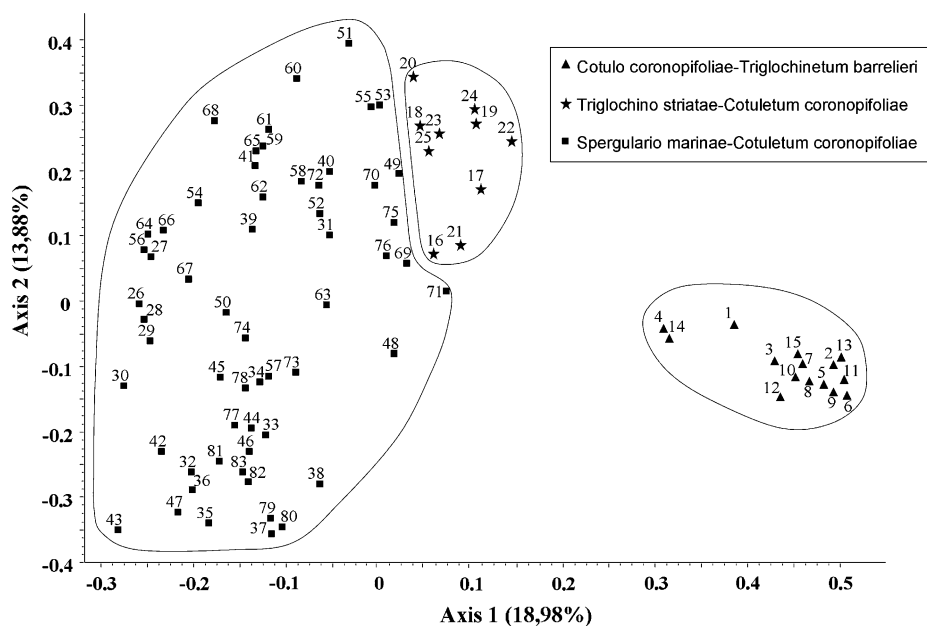
Plant communities occurring in similar habitats as the *C. coronopifoliae–Triglochinatum barrelieri*, but from which *C. coronopifolia* is absent, have the same native species composition, except for the occasional occurrence

of characteristic species of the *Molinio-Arrhenatheretea* (Table 1). The combination of several high-rank characteristic species of *Juncetalia maritimi* or *Molinio-Arrhenatheretea* (Table 1) is a peculiarity of these communities, which does not contravene considering them as an association of its own. However, the presence of *C. coronopifolia* itself appears not to be necessary to the development of the association. Since *C. coronopifolia* is a potentially invasive alien species, this fact suggests that where the species occurs, it occupies clearings in the rush-community created by a disturbance without preventing the subsequent establishment of a distinct native community that is specific to these habitats.

Ecological and biogeographic differentiation

The differentiation between the various associations of *C. coronopifolia* here can be explained with both ecological and biogeographic factors. All associations occur at sites with similar edaphic condition, but with different bioclimate. Climatically, the two associations existing in the north of the Iberian Peninsula belong to the Eurosiberian bioclimatic region. The *Spergulario marinae–Cotuletum coronopifoliae* occurs on the northern coast (Fig. 1), with humid to subhumid-thermotemperate bioclimate, whereas the *Triglochino striatae–Cotuletum coronopifoliae* occurs on the north-western coast, with humid to subhumid-mesomediterranean bioclimate (Alves 2004). This community differs from the former one by the presence of *Triglochin striata* and *Polypogon maritimus* and by the absence of *Puccinellia fasciculata*, *Parapholis strigosa*, *Juncus ambiguus* and *J. gerardi*, reflecting the hotter summer and therefore slightly more saline conditions.

**Fig. 3** Principal coordinates analysis (PCoA) of vegetation relevés in Iberian *Cotula coronopifolia* communities, with different symbols for the three associations (Table 1)



Communities from southern Iberia are characterized by the absence of *Triglochin maritima* and *T. striata* and the presence of *T. bulbosa* ssp. *barrelieri*. These congeners are vicarious species. The first one is an Atlantic species, while the third is a Mediterranean species and can be found only south of the Tagus Estuary (Costa et al. 2009). *Triglochin striata* is a neophyte from the Austral-Asian, South African and American territories, whose occurrence in Iberia is restricted to the north-western coast (Izco et al. 1992; Franco and Rocha Afonso 1994).

Besides this biogeographic distinction, northern and southern communities also differ ecologically due to the different climate. In northern Iberia (Cantabrian-Atlantic Province) the salt rising is low, owing to the humid climate (Díaz González and Fernández Prieto 2005) while in southern Iberia the upper salt marsh becomes saltier as a consequence of dryer and warmer summers, thus fresh water species are lacking (Costa et al. 1997). Therefore the communities where *C. coronopifolia* is present in north and southwest of the Iberian Peninsula are in different phytosociological classes, and only the southern ones belong to the typical halophytic communities. A similar distinction between more or less halophytic communities dominated by *C. coronopifolia* but associated with different species has been described for Chile (Ramírez et al. 1987; San Martín et al. 2006).

## Conclusions

Invasion by *C. coronopifolia* has apparently not led to the significant disappearance of characteristic native species since most of these can still be found in the *C. coronopifolia* relevés. We also found no evidence of a homogenization of the invaded vegetation. Rather, communities dominated by this exotic plant invader are still diverse and reflect variation in ecological conditions as well as biogeographic limits similarly to native plant communities. Nevertheless, we cannot exclude the possibility that native communities could in the future suffer from a reduced area of potential habitat due to *C. coronopifolia* expansion.

## Sommario

Studiando la composizione floristica, l'ecologia e la corologia delle comunità dominate da *C. coronopifolia* e *Spergularia marina*, si è scoperto che frequentemente occupano aperture nella vegetazione perenne più alta, nella zona interna sub-alofila delle praterie e fruticeti alofil. Negli ultimi venti anni sono stati condotti numerosi rilevamenti nel sud del Portogallo continentale che hanno

messo in evidenza differenze di composizione floristica rispetto a comunità simili della Penisola Iberica. Si propone di conseguenza una nuova associazione: *C. coronopifoliae*-*Triglochinsetum barrelieri*. Questa comunità si incontra in aperture di formazioni di *Juncus maritimus*, solitamente in piccole pozze temporaneamente inondate con acqua salmastra durante l'inverno ma secche in estate. È presente predominantemente negli estuari termomediterranei Ribatagano-Sadensi e Costiero Vicentini, ma per il distretto Algarviano è stata identificata una nuova sub-associazione, *limonietosum diffusi*.

L'analisi statistica (Analisi delle coordinate principali—PCoA) eseguita con tutti i rilevamenti pubblicati della penisola Iberica evidenzia una netta distinzione tra tre differenti comunità dominate da *C. coronopifolia*, sottolineando la peculiarità floristica della nuova associazione nei confronti di quelle Cantabro-Atlantiche.

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