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**TITLE**

# Abandonment of traditional saltworks facilitates degradation of halophytic plant communities and *Carpobrotus edulis* invasion.

**SHORT TITLE**

**Degradation of halophytic communities**

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## ABSTRACT

**Aims**: In Mediterranean countries, traditional salt exploitation has been practiced over centuries. However, there is a progressive reduction of active saltworks, causing changes in the adjacent halophytic communities and, ultimately, the invasion by opportunistic plant species. Assessing the impact of land-use change is key to understand and protect these fragile wetland ecosystems. Here, we explore how the abandonment of saltworks is impacting plant communities. We assess if the reduction in saltworks activity alters the composition of protected halophytic communities and favours the invasion by *Carpobrotus edulis*, an invasive species in many coastal regions throughout the world.

**Location**: the Natural Park of Ria Formosa (Algarve, Portugal).

**Methods**: We studied variations in the structure of halophytic communities affected to different degrees by *Carpobrotus edulis* over three saltworks land-use regimes in the Ria Formosa. Plant cover and soil salinity were estimated in a total of 60 transects pertaining to two saltworks complexes harbouring different land-use and hydrologic regimes. We performed a non-metric multidimensional scaling ordination of saltworks based on plant cover and identified the indicator species of each saltworks class.

**Results**: We found that plant communities significantly varied among types of saltworks according to a pattern of soil salinity and hydrologic regime. We identified *C. edulis* as the main indicator species of the abandoned saltworks' communities, characterized by less saline soils and being desiccated in summer.

**Conclusions**: Land-use change caused by the abandonment of *salinas* facilitated the transition of halophytic into psammophytic communities and the invasiveness of *C. edulis*. The

maintenance of traditional saltworks activities is vital for the preservation of this fragile wetland ecosystem.

**KEYWORDS**

Halophytic plant communities, GIS, invasive species, land-use change, saltworks, soil moisture, soil salinity, wetlands

## 1. INTRODUCTION

Habitat change is a key driver of biodiversity loss and degradation of coastal wetland ecosystems (Millennium Ecosystem Assessment, 2005). Half of the world's wetlands have been lost over human history due to land conversion, infrastructure development, pollution, water withdrawals, overharvesting, and the introduction of invasive alien species; besides, their degradation is faster than that for other ecosystems (Millennium Ecosystem Assessment, 2005; Mitsch & Gosselink, 2007). Wetlands provide important ecosystem services, and human-made wetlands such as traditional saltworks (*salinas*) have also been designated as requiring protection both for ecological and socio-economic reasons (Ramsar Convention, www.ramsar.org/).

Saltworks comprise a series of interconnected ponds in which solar energy produce seawater evaporation and precipitation of salts. Traditional salt exploitation has been practiced in the Mediterranean basin over centuries, mainly in its northern coast (Spain, Greece, Italy, France and Portugal). Abandonment of saltworks began in the twentieth century and reached a peak during its second half (Crisman, 1999). Along the Portuguese coast, *salinas* are recently threatened by destruction, transformation or abandonment, and the number of active saltworks dropped from 1170 in 1960 to 87 in 2000 (Neves 2005, Rodrigues, Bio, Amat, & Vieira, 2011). Land-use transformation may result in changes in ecosystem properties and increase opportunities for non-indigenous species (NIS) (Hobbs & Huenneke, 1992; Vitousek, D'Antonio, Loope, & Westbrooks, 1996; Hobbs, 2000; Byers, 2002; Dethier & Hacker, 2005). The establishment and early survival of NIS can also be favoured by the stressful nature of saline systems, which provides windows of opportunity for invasion (Dethier &

Hacker, 2005). Thus, the change in land-use caused by the abandonment is susceptible to promote the invasion of *salinas* by non-indigenous plants.

This study analyses the expansion of *Carpobrotus edulis* (L.) N.E.Br. during the last decade in the halophytic plant communities on the edges of active and abandoned *salinas* in Southern Portugal. *C. edulis* is original from South Africa but it is known to compete aggressively with endangered autochthonous species throughout the world (D'Antonio, 1993; Draper, Rosselló-Graell, Garcia, Gomes, & Sérgio, 2003; Stevens & Lanfranco, 2006; Troìa & Pasta, 2006). Although the effects of the invasiveness of *C. edulis* on the coastal dune plant communities of the Iberian Peninsula have been explored (e.g. Ley et al., 2007; Maltez-Mouro et al., 2010; Novoa & Gonzalez, 2014), little is known on the mechanisms behind its invasion of coastal saline systems. Our study focuses on saltworks complexes belonging to the Ramsar Site and Natural Park of Ria Formosa (Algarve, Portugal) where the abandonment and conversion of *salinas* to other uses are considered a threat to waterbird and plant communities (Plano Setorial da Rede Natura 2000; www.icnf.pt). There is evidence of Ria Formosa's saltworks at least since 1812 (Archivo Popular, 1837). Until the end of the 1960s the extraction activity alternated periods of stagnation with periods of increase. Afterwards, the number of active saltworks in the Algarve dropped from 136 in 1960 to 15 in 2000 (Neves, 2005). In Ria Formosa, the salt is harvested during the dry season from the crystallizer ponds. In active *salinas*, water is pumped and circulated through the different basins to regulate its salinity and depth. Thus, natural brackish habitats -adapted to come into contact with saline water that irrigates twice a day Ria Formosa's marshland along the tidal cycle- are transformed into regulated saline habitats. However, once the water regulation ceases to exist in the abandoned *salinas*, the basins' water level depends on seasonal variations of the groundwater table depth. In spring, the groundwater table begins to descend in the Ria Formosa, reaching its maximum depth in summer (Costa, Lousã, & Espírito-Santo, 1996). Therefore, it is frequent to find abandoned *salinas* desiccated during summer.

According to the definitions provided by McDonald, Gann, Jonson, & Dixon (2016), the *salinas* could be considered as cultural ecosystems because they are composed of local native species but have a human-imposed structure. Human-induced water regulation in *salinas* has led to an altered composition of the original flora and fauna communities (Walmsley, 1999; Bouzillé, Kernéis, Bonis, & Touzard, 2001). The natural halophytic communities of the Iberian Peninsula are dominated by perennial succulent chenopodiaceous shrubs both in salt-marshes and saltworks (Rivas-Martínez et al., 2002), so the *salinas* are suitable habitats for particular halophytic communities constituting high nature value systems (Costa et al., 1996; de Melo Soares, de Assunção, de Oliveira Fernandes, & Marinho-Soriano, 2018). The *salinas* harbour halophytic protected habitats listed in Annex I of the Habitats Directive: “Mediterranean and thermo-Atlantic salt marshes and salt meadows” (habitats 1410, 1420, 1430), and “Salt and gypsum inland steppes” (habitat 1510). These halophytic communities are home of several rare, endangered and endemic species (for details see Costa, Monteiro-Henriques, Neto, Arsénio, & Aguiar, 2007; European Commission, 2007). In particular, Ria Formosa’s saltworks harbour and contribute to the density of key wetland-dependent species of waterbirds such as the black-tailed godwit (*Limosa limosa*), the Kentish plover (*Charadrius alexandrinus*) and the pied avocet (*Recurvirostra avosetta*) (Rufino, Araujo, Pina, & Miranda, 1984; Catry et al., 2011). However, the communities found in halophytic protected habitats are highly threatened, showing unfavourable conservation status in most member states of the European Union, largely due to NIS and human-induced changes in hydrology (ETC/BD, 2014).

Here, we seek to investigate whether the abandonment of traditional saltworks may have led to an expansion of *Carpobrotus edulis* and to a degradation of protected halophytic communities in the space of a decade. To do that, we combine field data collection with the use of geographical information systems (GIS) and statistical analyses. The specific objectives of this research are: i) to estimate the spatial spread of *Carpobrotus edulis* from 2004 to 2015 throughout the saltworks of Ria Formosa, ii) to analyse the plant community structure of saltworks according to their degree of abandonment, hydrologic regime and soil salinity, and iii) to assess the relationship between the different types of saltworks and the abundance of *C. edulis*.

## 2. METHODS

### *2.1. Study area and survey of* Carpobrotus edulis

The Ria Formosa Natural Park (7º 49' W, 37º 1' N) is included in the Natura 2000 Network and in the Ramsar List. It extends along a coastal lagoon system in Algarve (Southern Portugal) (Fig. 1). The park covers an area of 179000000 $m^2$ (17900 ha) with high ecological importance due to its variety of habitats and biodiversity.

To estimate the expansion of *Carpobrotus edulis* throughout the saltworks of Ria Formosa Natural Park, we compared its cover in 2004 with that in 2015 by means of field surveys and GIS. To estimate *C. edulis* distribution in 2015, we visited all the saltworks of Ria Formosa a total of five times (once per season) from the spring of 2014 to the spring of 2015. We digitized the patches covered by the NIS using ArcGIS Desktop 10 software from ESRI. For the year 2004, digital information on the distribution of *C. edulis* was retrieved from the "Plano de Ordenamento do Parque Natural da Ria Formosa" (www.icnf.pt) in which plant species information is presented as polygon layers. We calculated the total area occupied by

*C. edulis* at each moment (2004 and 2015) using ArcGIS. During the one-year survey we also detected the type of activity of the *salinas* (active *vs.* abandoned), and assessed their hydrologic regimes across the four seasons to identify the abandoned desiccated *salinas* during summer. We used this information to select the most invaded saline complexes to be used as study sites in the subsequent community analyses.

### *2.2. Sampling strategy and soil salinity and moisture measurement*

During the initial survey, we found two salt extraction complexes were by far the most affected by the invasion of *C. edulis*: site A (“Faro Airport”: 37º 00’ N, 7º 58’ W) and site B (“Bias do Sul”: 37º 02’ N, 7º 45’ W) (Fig. 1). We carried out the study of plant communities in active and abandoned saltworks located in these two sites. We classified the saltworks into three types according to their observed land-use and hydrologic regime in 2015: i) saltworks where salt extraction activity is carried out (“active saltworks”), ii) “abandoned saltworks”, and iii) abandoned saltworks desiccated during summer (“desiccated abandoned saltworks”) (Fig. 1 and Fig. 2). At site A, we found no record of change of activity since 2004, with the exception of a small area of ponds which went from being active in 2004 to abandoned in 2015 (see Fig. 1). Some of the abandoned ponds at site A have restarted their activity after our survey. At site B, all saltworks were abandoned in 2004, including those that were active in 2015.

A total of 60 linear transects were systematically distributed over the two sites and saltworks types (10 transects x 3 saltworks types x 2 study sites). Plant sampling was performed during spring 2016 using the point intercept method at each 25-m transect (51 points spaced every 50 cm; see Nunes et al. (2014) for details). Transects were conducted on the dykes of the salt pans (Fig. 2). At each point, a 5 mm diameter rod was stuck in the ground making a 90° angle. All plant species touching the rod were recorded and cover estimates for individual species were calculated as the proportion of points intercepted per transect. Botanical nomenclature follows the "Checklist da Flora de Portugal" (Sequeira et al., 2011), and species were determined using "Flora Ibérica" (Talavera & Castroviejo, 2000) and "Nova Flora de Portugal" (Franco, 1984; Franco & Afonso, 2003).

Soil pore water conductivity (ECp) and moisture were simultaneously measured *in situ* using a WET-2 Sensor and a HH2 Moisture Meter (Delta-T Devices, Cambridge, England). Measurements were made at the starting, middle and ending intersect points of each linear transect (points 1, 26 and 51, respectively), next to the roots, at the maximum depth allowed by the moisture sensors. ECp and soil moisture of each transect were estimated as the average of the three recorded conductivity values. Then, ECp was converted to salinity using the Practical Salinity Scale 1978 (Fofonoff & Millard Jr, 1983) and its extension (Hill, Dauphinee, & Woods, 1986) by means of the "ec2pss" function of the "wq" R package.

### *2.3. Analysis of the plant communities*

We performed a non-metric multidimensional scaling (NMDS) ordination on the matrix of species cover to explore the relationship among the plant communities of each saltworks type, soil salinity and moisture, and the cover of *C. edulis*. Estimated plant cover values were square-rooted to reduce the influence of large values. In addition, uncommon species occurring on less than 5% of transects were excluded to avoid an excessive influence of rare taxa. In this way, 38 species (out of 67) were retained for analysis (Table S1, Appendix S1). Data were submitted to a Wisconsin double standardization (species were first divided by the maxima, and then locations standardized for total), and the Bray-Curtis dissimilarity index was used to compute the distance matrix. We used permutation tests (n = 999) to determine vector fits and assess the correlation coefficient and the significance to the NMDS axes of soil salinity, soil moisture, and species cover. A smooth surface fitting of soil salinity and moisture within the NMDS was estimated by a generalized additive model. Finally, to test if there was a significant difference among the communities found in the three types of saltworks, we used an analysis of similarities (ANOSIM; Clarke, 1993). ANOSIM was performed using the Bray-Curtis dissimilarity index and 999 permutation tests. ANOSIM's index (R value) ranges from -1 to 1, a positive value indicating higher dissimilarities between groups than within groups. NMDS and ANOSIM analyses were performed using metaMDS, envfit, ordisurf and anosim functions of the R Package "vegan" (Oksanen et al., 2017).

To find indicator species for the communities of each type of saltworks, we used the Dufrene-Legendre analysis (Dufrene & Legendre, 1997) computed with the "labdsv" R package (Roberts, 2016). The indicator value (IndVal) quantifies the fidelity and relative abundance of species in each type of saltworks. The index ranges from 0 to 1, and it shows the maximum value when all the individuals of a single species are observed at all sites belonging to a single cluster.

## 3. RESULTS

### *3.1. Spatial spread of* Carpobrotus edulis *in the* salinas *of Ria Formosa*

We found that *Carpobrotus edulis* had increased 330 per cent its distribution from 2004 to 2015. In 2004, the NIS had occupied 8 patches in the Ria Formosa: one patch inside the saltworks (site A) with a surface of 23400 $m^2$, and 7 patches located in sandy soils outside the *salinas* which were not considered in the study (Table S2, Appendix S1). In 2015, *C. edulis* expanded to invade a total of 100467 $m^2$ across the *salinas* of Ria Formosa, where we found 136 patches (Fig. 1 and Table S3, Appendix S1). The expansion of *C. edulis* occurred predominantly throughout the abandoned *salinas* (98131 $m^2$), while the invaded area in the active *salinas* was much smaller (2336 $m^2$). Interestingly, we found 78.8 % of the invaded area in the abandoned *salinas* was located in saltworks desiccated during the summer. The totality of the currently invaded areas in the *salinas* corresponded to halophytic communities in 2004. The most invaded *salinas* were those situated near the Airport of Faro (site A) and close to Bias do Sul (site B) (Fig. 1). Thus, we selected these saltworks as study sites for all subsequent analyses.

Soil salinity and moisture were lower in the “desiccated abandoned saltworks” (mean = 3.9 and 17.48, respectively), than in the “abandoned” (mean = 4.27 and 19.19) and the “active” (mean = 4.86 and 23.83) (Table S4 and Fig. S1, Appendix S1). However, there was no significant difference between the means of the “desiccated abandoned” and the other two groups in any case (paired t-tests: $p > 0.05$).

*3.2. Plant communities in each type of saltworks*

A three-dimensional NMDS provided a representation of plant cover across the three types of saltworks (stress value = 0.16; Fig. 3). The ordination discriminated among the plant communities found in the 60 transects and showed a gradient along the NMDS1 axis from the “active” to the “desiccated abandoned saltworks”. The “desiccated abandoned saltworks” showed lower soil salinity and moisture, and more *Carpobrotus edulis* cover than the other two types of saltworks (Fig. 3, Table S4, and Figs. S1 and S2, Appendix S1). *C. edulis* cover decreased from the “desiccated abandoned saltworks” to the “abandoned saltworks”, being practically inexistent in the “active saltworks”.

ANOSIM found statistically significant compositional dissimilarities among the three types of saltworks (R = 0.42; $p < 0.001$), the plant communities were significantly more dissimilar among the types of saltworks than within each type (Fig. 4). Dissimilarities found between sampling sites (A and B) were lower (R = 0.126; $p < 0.002$).

There was a high coincidence between NMDS and IndVal analyses. Most of the characteristic species identified by IndVal showed also significant correlations with the NMDS ordination axes (Table 1, Fig. 3C, and Table S5, Appendix S1). Considering only those species with highly significant indicator values (IndVal > 0.5; $p < 0.001$), we found that: i) *Mesembryanthemum nodiflorum* was the main species representing plant communities of active saltworks, ii) *Arthrocnemum macrostachyum* was indicator of abandoned saltworks, and iii) *Carpobrotus edulis* and *Vulpia alopecuros* were indicator species of desiccated abandoned saltworks (Table 1).

## 4. DISCUSSION

The abandonment of saltworks promoted the expansion of *Carpobrotus edulis* and facilitated the transition from halophytic to psammophytic (i.e. growing in sandy soil) communities in the *salinas* of Southern Portugal. Land-use change caused by the cessation of traditional salt extraction has led to more than a four-fold increase of the cover of *C. edulis* throughout the abandoned *salinas* over a decade, while the presence of the NIS is practically inexistent in the active saltworks. The three types of saltworks studied showed a significant difference in plant community composition. Plant composition and *C. edulis* cover varied along a gradient of soil salinity and moisture, and *C. edulis* cover was inversely related to soil salinity. Thus, well-developed halophytic communities dominated by *Mesembryanthemum nodiflorum* and with scarce *C. edulis* cover were found in the active saltworks. Whereas the exotic *C. edulis* arose as one of the indicator species in the abandoned saltworks desiccated during summer, which are characterized by less soil salinity and moisture.

The Ria Formosa vegetation has essentially been described as halophytic in salt marshes and *salinas*, and psammophytic in the dunes and pine forests (Costa et al., 1996). Therefore, our results could be reflecting a natural turnover between autochthonous communities. The four most significant indicator species (*Mesembryanthemum nodiflorum, Arthrocnemum macrostachyum, Carpobrotus edulis* and *Vulpia alopecuros*) are coastal species which share similar thermal conditions in mainland Portugal (SPBotânica, 2014). Despite these bioclimatological similarities, these species differ in their edaphic requirements related to salinity and moisture. *M. nodiflorum,* an indicator of active saltworks, is typical of saltpans dykes and inhabits temporarily inundated soils (SPBotânica, 2014). This succulent plant has been described as the dominant species of the *Spergulario bocconei-Mesembryanthemetum nodiflori* community growing in the dykes of the salinas of Ria Formosa (Costa et al., 1996). The main indicator species of the abandoned saltworks (*A. macrostachyum*) is still associated with halophilic environments, occurring in the highest elevations of salt-marshes and saltpans on exceptionally inundated soils (Costa et al., 1996; Rivas Martinez et al. 2001). Whereas *C. edulis* and *V. alopecuros*, the indicators of desiccated abandoned saltworks, are associated with non-saline sandy soils (Costa et al., 1996; Talavera & Castroviejo, 2000; SPBotânica, 2014). Thus, colonization by non-halophytic species increases with decreasing salinity. In the abandoned desiccated saltworks, there is a lack of halophytes among the indicator species. In addition, the dominance of good colonizers of sandy littoral disturbed lands (i.e. *V. alopecuros* and *C. edulis*) together with other psammophilous species (e.g. *Briza maxima* and *Trifolium angustifolium*) may evidence the degree of perturbation that affects these saltworks when abandoned and the subsequent transition from halophytic to psammophytic communities.

Ria Formosa shows a remarkable variability in both temperature and salinity over the year and along the lagoon (Newton & Mudge, 2003). Despite these variations, we found greater dissimilarities across saltworks types than between sampling sites (A and B). The invasion by *C. edulis* in the *salinas* of Ria Formosa was mostly associated with abandoned saltworks desiccated during summer, characterized by less soil salinity than the other saltworks types. In fact, variations in the depth of groundwater table and in salinity are known factors affecting the distribution of halophytic communities in the Ria Formosa (Costa et al., 1996). Moreover, hydrologic alterations can change the distribution of wetland species (Cronk & Fennessy, 2001). Although *C. edulis* also expands through clonal growth, our results are consistent with the fact that its seed germination is inhibited by salt (Weber & D'Antonio, 1999). Besides, this NIS has a preference for well-drained soils (DAISIE European Invasive Alien Species Gateway, 2006), circumstance that especially affects "desiccated abandoned" saltworks.

The abandonment of *salinas* seems to alter the abiotic conditions of certain saltworks in Ria Formosa. In particular, the long-established human-controlled hydrologic regime disappears, so the saltworks' water level oscillates according to the groundwater table and precipitation. Abandoned solar saltworks are inclined to degrade by desiccation (González-Alcaraz, Aránega, Tercero, Conesa & Álvarez-Rogel, 2014). We found that soil moisture was lower in the "desiccated abandoned saltworks" despite the fact that the measures were taken during spring, when the salt ponds are not yet desiccated. In addition, we found lower soil salinity in saltworks desiccated during summer than in the other types. A possible explanation may be that seawater flow is lower in these ponds, especially in summer when the groundwater table is deeper, so salt content in the dykes mainly results from the previous salt extraction.

We identified a shift in plant community composition in response to abandonment. Land-use change constitutes a perturbation for the halophytic communities adapted to the *salinas*, which are shifting toward psammophytic assemblages where ultimately *Carpobrotus edulis* becomes dominant. Disturbance has been previously found to contribute to the invasibility of communities (Hobbs & Huenneke, 1992; Vitousek et al., 1996; Hobbs, 2000; Byers, 2002; Dethier & Hacker, 2005). Anthropogenic disturbance is thought to alter habitats and favour invasions by: i) creating new microhabitats, ii) decreasing native populations, iii) introducing non-indigenous species propagules, and iv) placing native species at a competitive disadvantage with non-native species (see Byers, 2002). Non-indigenous species pose a major threat to wetlands biodiversity, especially in communities undergoing habitat modifications (Cronk & Fennessy, 2001). In saline systems, the lack of biotic resistance seems important in the plant invasion process (Dethier & Hacker, 2005). Although the *salinas* are not strictly natural systems, their traditional activity has collaborated to the preservation of relevant halophytic communities. Thus, the cessation of saltworks activity represents a perturbation for these communities maintained by management. Disturbance on the vegetation of coastal communities can facilitate *C. edulis* propagation by clonal growth (D’Antonio, 1993), and once established, *C. edulis* can be competitively superior because it forms thick mats and it can also interfere with the belowground root distribution of resident species (D’Antonio, 1993; D’Antonio & Mahall, 1991). Moreover, *C. edulis* seedlings have been found to negatively affect the recruitment of native coastal dune species (Novoa & Gonzalez, 2014). Consistent with the literature, our results show halophytic species impoverishment in saltworks invaded by *C. edulis*.

The presence of *C. edulis* has been identified as a major threat for endangered coastal species and its eradication has been suggested (e.g. Stevens & Lanfranco, 2006; Troìa & Pasta, 2006). But *C. edulis* removal is time and money-consuming and it requires long-term control of germination and resprout (Chenot et al., 2017) since the species forms a soil seed bank viable for at least two years (DAISIE European Invasive Alien Species Gateway, 2006). Unfortunately, a recent meta-analysis found that recovery of biological structure and biogeochemical functioning of restored wetland ecosystems were lower than in reference sites (Moreno-Mateos, Power, Comín, & Yockteng, 2012). The existing fauna and flora composition adapted to hypersaline habitats could be irremediably damaged if salt extraction activity continues to disappear. The saltworks abandonment and their reconversion to aqualculture ponds, as well as NIS invasions, are among the main concerns for the conservation of the Ria Formosa Natural Park (Plano Setorial da Rede Natura 2000; www.icnf.pt). Despite its artificial origin, saltworks have a great value as conservation areas and their extended abandonment makes necessary a rethink of how to rehabilitate these wetland ecosystems (Crisman 1999; Neves, 2005; Crisman, Takavakoglou, Alexandridis, Antonopoulos, & Zalidis, 2009). The case reported by González-Alcaraz et al. (2014) showed that the irrigation with seawater can prevent changes in the vegetation of abandoned saltworks. In Brazil, abandoned saltworks areas were restored to their original mangrove ecosystems (Dos Reis-Neto & Meireles, 2013). Petanidou & Dalaka (2009) proposed a different approach focused on rehabilitation of abandoned saltworks as tourism places, such as information centers and salt museums. During the time-span between our survey and the publication of the present study, some abandoned saltworks restored their activity. This is a good sign, and further investigation would allow us to test if the preexistent halophytic communities could be recovered. Given the high potential for invasiveness of *C. edulis* in coastal areas, the maintenance of traditional saltworks activities seems vital for the preservation of this fragile wetland ecosystem.

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## AUTHOR CONTRIBUTIONS

R.M.C. conceived the idea, R.M.C. and S.C. designed and conducted fieldwork, S.C. identified the species, R.M.C. and S.C. analysed the data, R.M.C. produced the figures, R.M.C. led the writing and S.C. made substantial contributions to the writing. All authors discussed the results and commented on the manuscript.

## DATA ACCESSIBILITY

Primary data is presented as Supporting information.

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**Appendix S1.** Tables and additional figures.

**TABLES**

**Table 1** Indicator species of the plant communities found in each type of saltpans analysed. Only significant indicator values (IndVal; $p < 0.05$) are shown. Correlations with NMDS axes for those species are also shown.

| | | **IndVal** | | **NMDS** | |
|---|---|---|---|---|---|
| **Type of saltworks / Species** | **Code** | **Value** | ***p*** | ***r2*** | ***p*** |
| **Active** | | | | | |
| *Mesembryanthemum nodiflorum L.* | Mno | 0.6 | 0 | 0.34 | 0 |
| *Suaeda vera* Forssk. ex J.F.Gmel | Sver | 0.25 | 0.04 | 0.41 | 0 |
| **Abandoned** | | | | | |
| *Arthrocnemum macrostachyum* (Moric.) Moris | Ama | 0.6 | 0 | 0.39 | 0 |
| *Sonchus tenerrimus* L. | Ste | 0.38 | 0.04 | 0.22 | 0 |
| *Polypogon maritimus* Willd. | Pma | 0.28 | 0.01 | 0.02 | 0.65 |
| **Desiccated abandoned** | | | | | |
| *Carpobrotus edulis* (L.) N.E.Br. | Ced | 0.63 | 0 | 0.47 | 0 |
| *Vulpia alopecuros* (Schousb.) Dumort. | Val | 0.52 | 0 | 0.36 | 0 |
| *Salsola vermiculata* L. | Sve | 0.36 | 0.03 | 0.03 | 0.37 |
| *Juncus maritimus* Lam. | Jma | 0.33 | 0.01 | 0.2 | 0 |
| *Trifolium angustifolium* L. | Tan | 0.26 | 0.02 | 0.07 | 0.11 |
| *Briza maxima* L. | Bma | 0.24 | 0.03 | 0.12 | 0.02 |

## FIGURES

**Figure 1**

Location of Ria Formosa Natural Park and saltworks complexes where plant composition and soil salinity and moisture were sampled: Site A (“Faro Airport”) and site B (“Bias do Sul”). The distribution of *Carpobrotus edulis* in 2015 and the types of saltworks in each site are shown. At Site A, the most recently abandoned saltworks from 2004 to 2015 are bordered in black.

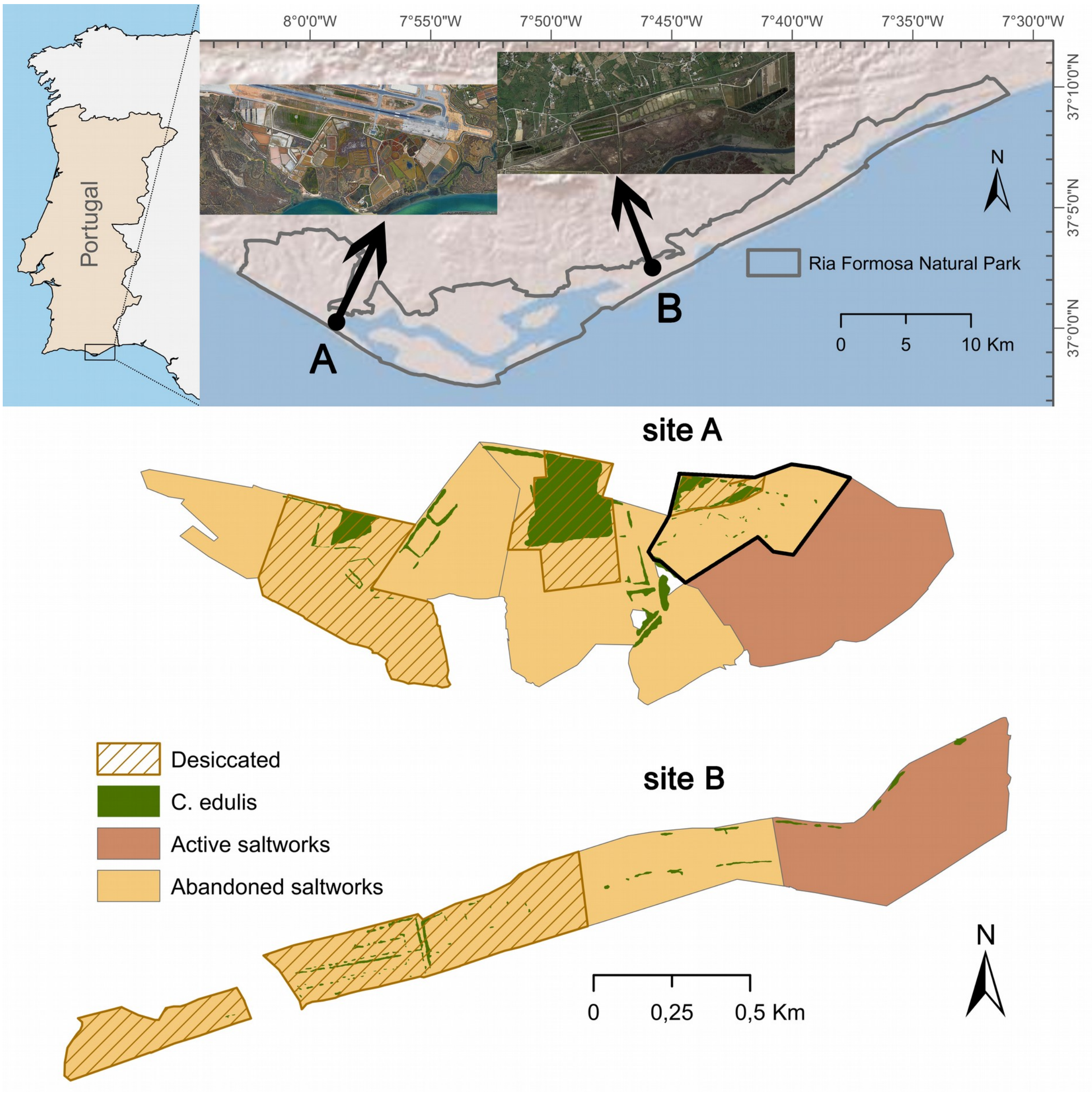

**Figure 2**

Types of saltworks used in the study: “active saltworks” (upper panel), “abandoned saltworks” (middle panel), and abandoned saltworks desiccated during summer (lower panel). Vegetation was sampled on the dykes of the saltworks. The two types of abandoned saltworks (lower pictures) show the presence of *Carpobrotus edulis*. The inset in the upper right corner shows how soil salinity and moisture were measured.

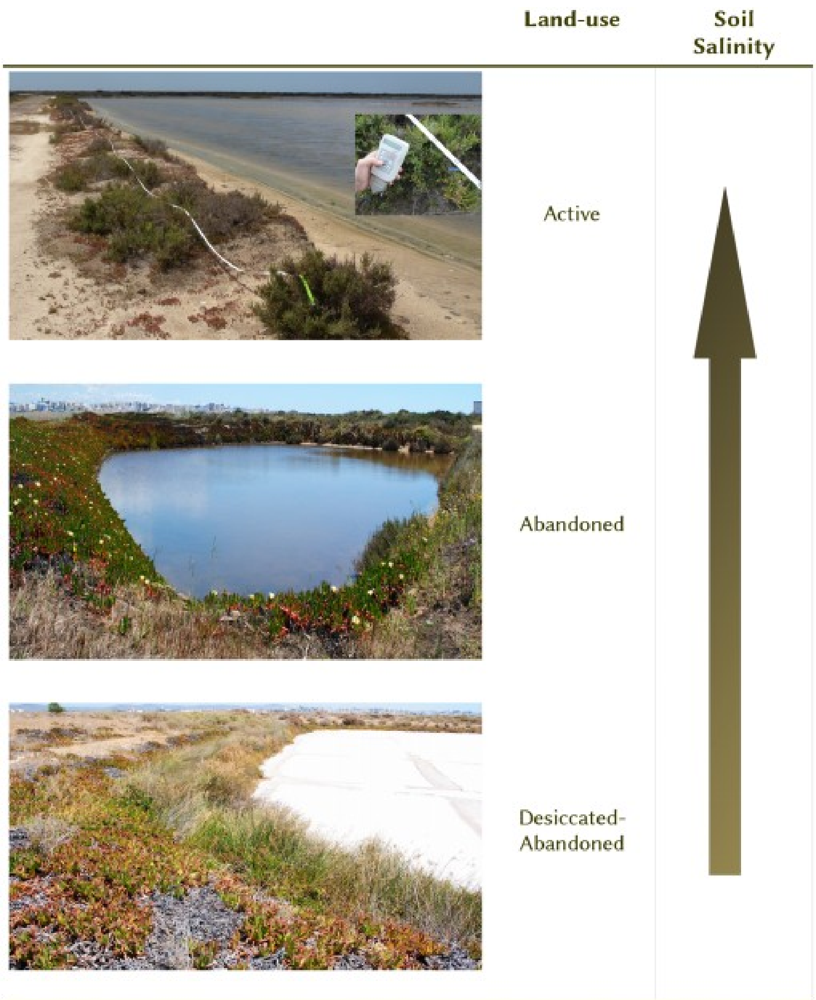

**Figure 3**

Axes 1 and 2 of the three-dimensional non-metric multidimensional scaling (NMDS) ordination of plant community composition across the three types of saltworks sampled: “active saltworks”, “abandoned saltworks” and “desiccated abandoned saltworks”. (**a** and **b**) Dissimilar plant cover was found across the three types of saltworks. The codes for the species are described in Table S1. (**c**) Vectors represent correlations between species contributing significantly to the NMDS axes, plotted in red ($p < 0.001$) and black ($p < 0.05$). *Carpobrotus edulis* (Ced) showed a relevant contribution to both axes and its cover was higher in desiccated abandoned saltworks. (**d**) Smooth surface of soil salinity fitted by means of a generalized additive model. Soil salinity is measured in psu (practical salinity unit). An inverse relationship between soil salinity and *C. edulis* was found.

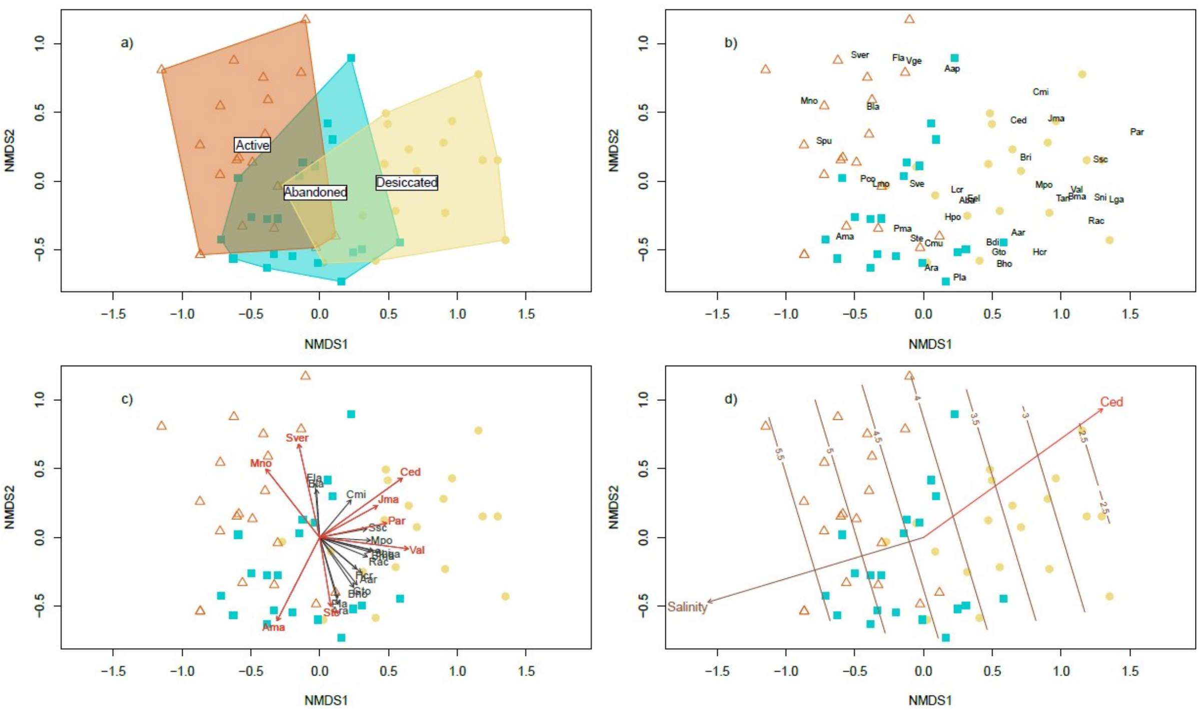

**Figure 4**

Analysis of similarity (ANOSIM) among the three types of saltworks sampled in the study. Plant compositional dissimilarities between types were significantly higher than within types. Notches at medians are drawn in each side of the boxes.