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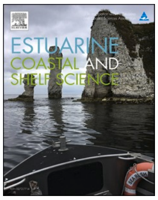

Recruitment niche segregation of halophytes along the tidal gradient

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ABSTRACT

Recruitment is a critical component of the plant life cycle, but little is known about its contribution to community assembly in comparison to later plant stages. We aimed to analyze the relevance of recruitment niche segregation in community assembly using tidal salt marshes in a Mediterranean climate. With this objective, we recorded the spatio-temporal distribution of seedling emergence and its relationships with propagule density and environmental conditions at the community level along the tidal gradient. Results indicate that seedling recruitment was strongly influenced by differential establishment abilities and the effects of sedimentary and meteorological factors that vary seasonally and along the tidal gradient. Taxa colonizing the same habitats showed some similarities in their recruitment patterns, but they also presented enough differences to configure almost a unique recruitment pattern for each taxa. Sediment characteristics segregated recruitment niches at both extremes of the tidal gradient, and the few species colonizing habitats between these two extremes also showed contrasted spatial recruitment patterns. In addition, sequential differences in seedling emergence segregated within high marsh taxa. Most of the taxa exhibited a continuous germination strategy associated to prolonged flowering periods and the ability to germinate along broad salinity ranges. Our results shed light on the importance of recruitment niche segregation to the assembly of plant communities, which is key for understanding their functioning and guiding their management.

1. Introduction

A key aspect of ecology is to clarify the roles of spatio-temporal niche segregation in community assembly. The segregation hypothesis predicts that intraspecific aggregation should increase the weight of intraspecific competition relative to interspecific competition (Raventos et al., 2010). Close evolutionary relatives can coexist depending on evolutionary divergence in niches, which facilitates coexistence relative to divergence in competitive abilities that oppose it (Eckhart et al., 2017). Consequently, strong niche differences and weak fitness differences combine to stabilize local coexistence and biodiversity. Spatio-temporal segregation may be a direct product of interspecific competition, which determines narrower realized niches in relation to fundamental niches (Shiponeni et al., 2014; Simon et al., 2019). Additionally, niche segregation may be driven by contrasted interspecific tolerance to stressors that act as environmental filters limiting the set of potentially coexisting species (Sakai et al., 2014).

In plant communities, processes operating at early life stages, such as dispersal, germination, and seedling emergence and establishment, may account for a large proportion of niche segregation (Sánchez-Gómez et al., 2006; Chu and Adler, 2015). The importance of the recruitment niche in structuring plant communities contrasts with explanations of species segregation invoking physiological tolerance and competition at later life-history stages (Myerscough et al., 1996). Environmental filtering during recruitment stages affects plant distribution and diversity by forming the spatial template on which all following processes operate at later life-history stages (Oki et al., 2013; Fraaije et al., 2015). The influence of the recruitment niche on plant community structure is also modulated by the prevalence of annual species and sexual reproduction (propagule availability) within the community (Moore and Elmendorf, 2006). Even shifts in the regeneration niche after disturbances may promote speciation and taxa coexistence (Navarro-Cano et al., 2017). In this context, characterizing the recruitment niche is useful for better predicting the effect of environmental changes (Mašková and Poschlod, 2022). This is particularly important given the ongoing climate crisis, which is causing rising temperatures and

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disrupting precipitation and evapotranspiration patterns (IPCC, 2023). Although recruitment processes are critical components of the plant life cycle, relatively little is known about their contribution to community assembly in comparison to later stages. The segregation hypothesis remains largely untested by empirical observations at early plant life stages in many ecosystems.

We analyzed the relevance of recruitment niche segregation in community assembly in salt marshes. To our knowledge, this is the first study to analyze spatio-temporal patterns of seedling emergence at community level in salt marshes. Our study system was a salt marsh characterized by a extensive tidal gradient within a Mediterranean climate zone since they are colonized by a relatively low number of plant taxa exposed to high stress levels and seasonality along marked inundation and salinity gradients (Álvarez-Rogel et al., 2000, 2001). These environmental conditions facilitate the analysis of spatio-temporal niche segregation during seedling emergence. Tidal salt marshes are flooded periodically by tides that establish three main zones along the tidal gradient: low, medium and high marshes (Long and Mason, 1983). The tidal elevation gradient determines marked differences in abiotic conditions such as inundation and salinity (Callaway et al., 1990; Davis et al., 1996) and configures clear vegetation zonation patterns (Adam, 1990; Apaydin et al., 2009). These zonation patterns are modeled by the tolerance of species to environmental conditions that mainly determine the lower limits of species distribution and the outcome of interspecific interactions that are most important in determining the upper limits of distribution (Pennings and Callaway, 1992). Stressful environmental conditions associated with long flooding periods, such as low-oxygen (hypoxic) sediments and short photoperiods, use to define the lower limit of halophyte distribution along the tidal gradient (Castillo et al., 2000). Additionally, salinity levels differentiate between halophytes colonizing tidal freshwater and those in salt marshes, whereas salt marsh species are displaced by freshwater species from less stressful environments (Engels and Jensen, 2010). In this context, recruitment processes may settle on adult plant zonation along the tidal gradient (Engels et al., 2011). Firstly, seedling density depends on seed density in the marsh, where soil seed banks show a zonal distribution (Rand, 2000; NOE and Zedler, 2001a). Secondly, seedling emergence is influenced by the colonizer's life-history traits, especially those associated with its germination ecology (Kaminsky et al., 2015), biotic interactions (Bertness and Yeh, 1994), disturbances resulting in bare patches (Tessier et al., 2000), and windows of opportunity related to sedimentary, hydrological and meteorological conditions (Schwarz et al., 2011; van Regteren et al., 2020). Among meteorological conditions, rainfall is considered a major limiting factor for recruitment in seasonally dry climates (Cochrane et al., 2015). Sediment salinity and flooding are often regarded as the most restrictive environmental factors affecting germination and seedling growth (Ungar, 1998; NOE and Zedler, 2001a; Engels et al., 2011). Variation in germination traits among pairs of sympatric species in response to salinity underlies their niche segregation and phenotypic divergence in salt marshes (Castillo et al., 2021a). From the biotic point of view, seedling recruitment is often limited by competition from neighboring adult plants (Rand, 2000) that may vary according to life-history stage and along the tidal gradient (Cui et al., 2011; Keammerer and Hacker, 2013). Adult plants can also facilitate recruitment, buffering the effects of potentially limiting stresses (Bertness and Callaway, 1994; Figueroa et al., 2003; Castillo et al., 2022). Given the global decline in tidal marshes and the many valuable ecological services that they offer (Barbier et al., 2011), we need to understand the mechanisms governing their establishment and maintenance to preserve and restore them in the present scenario of climate change and related sea level rise. Climate change and concomitant sea level rise are altering inundation and salinity patterns in salt marshes (Morris et al., 2002). These changes may disrupt halophyte recruitment, potentially threatening the survival of existing salt marsh communities (Tabot and Adams, 2013). Furthermore, climate-driven environmental changes may also impact the success of salt marsh restoration projects that rely on halophyte recruitment during ecological succession (Ivajnsic et al., 2016). Salt marshes have been extensively investigated but the mechanisms that enable halophyte seedling emergence still require more research.

In the present study we analyzed the spatio-temporal distribution of seedling emergence and its relationships with propagule density and environmental conditions at community level along the tidal gradient in Ria Formosa (Southwest Iberian Peninsula) for one year. We hypothesized that seedling densities would be positively related to seed densities and adult plant covers as most halophytes have transient seed banks (Polo-Ávila et al., 2019). We further hypothesized that harsh environmental conditions would limit seedling emergence according to plant taxa's functional traits, particularly those related to flowering, fruiting, dispersal and germination ecology. Finally, we theorized that the interplay of changing environmental conditions across space and time, along with varying seed densities among taxa and their responses to the surrounding environment would lead to a distinct spatio-temporal segregation in seedling emergence for different halophytes along the tidal gradient.

2. Materials and methods

2.1. Study area

The present study was carried out in tidal salt marshes on the Tavira Island located in the Ria Formosa Natural Park (37° 05′ N 7° 40′ O; Southwest Iberian Peninsula; Fig. 1). This protected area is included in the Ramsar List of Wetlands of International Importance and in the Natura 2000 Network. Ria Formosa is a mesotidal open estuary that occupies an area of ca. 100 km^2, of which 48 km^2 are tidal marshes separated from the Atlantic Ocean by a sand spit that extends for 55 km along the coast (Teixeira and Alvim, 1978). The tidal amplitude of semidiurnal tides in Ria Formosa varies from 0.5 m (neap tide) to 3.5 m (spring tide) (Águas, 1986). The area is under Mediterranean climate with Atlantic influence with mild and wet winters, and hot and dry summers (Fig. 1). The study area was selected for presenting a gentle slope along a wide tidal gradient so that small changes in marsh elevation corresponded to large areas, showing a clear plant zonation pattern. We sampled nine multispecific habitats along the tidal gradient: H1: bare mudflats; H2: *Spartina maritima* (Curtis) Fernald marshes; H3: low marshes dominated by *Sarcocornia perennis* (Mill.) A.J. Scott; H4: middle marshes of *Halimione portulacoides* (L.) Aellen. and *Sarcocornia fruticosa* (L.) A.J. Scott; H5: *Inula crithmoides* L. marshes; H6: high marshes of *Arthrocnemum macrostachyum* (Moric.) C. Koch; H7: high marshes of *Limoniastrum monopetalum* (L.) Boiss.; H8: sandy sediments colonized by *Salsola vermiculata* L.; and H9: the ecotone between H8 and adjacent coastal dunes. Along this tidal gradient, we have previously found strong relationships between plant species abundance and sediment characteristics (Contreras-Cruzado et al., 2017), and the soil seed bank displayed a clear zonation, mirroring the distribution of adult source plants (Polo-Ávila et al., 2019).

2.2. Seedling sampling

The nine tidal habitats (H1 to H9) were sampled upward during low tides in March, May, July, October and December 2012 together with sediment, propagules and vegetation characteristics (Contreras-Cruzado et al., 2017; Polo-Ávila et al., 2019). In each habitat, we sampled seedling density in 30 randomly distributed square plots (20 × 20 cm), except at H1 in which we sampled at 40 plots due to its low vegetation cover, resulting in a total of 1400 samples. We did not sample the exact same point in the marsh twice. Our sampling strategy targeted intact marsh areas exclusively, guaranteeing spatial and temporal representation across the marsh. Every green seedling was collected from each plot and stored in paper envelopes. Once in the laboratory, seedlings were counted and identified to genus or species level using our seedling collection obtained from previous germination studies

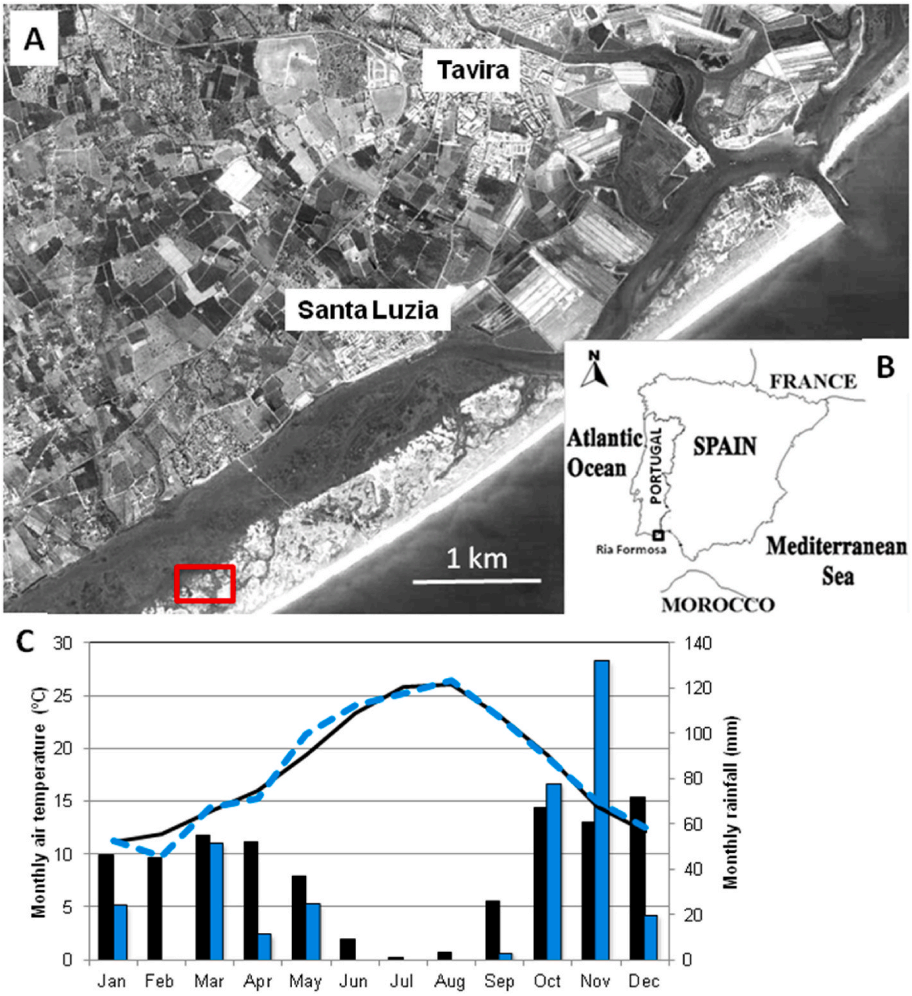

Fig. 1. A) Aerial photography showing the sampling area (red rectangle). B) Location of the Ria Formosa on the southwest coast of the Iberian Peninsula. C) Monthly average air temperature (°C) and rainfall (mm) between 1940 and 1995 (solid line and back bars, respectively) and for 2012 (discontinued blue line and blue bars, respectively) in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Muñoz-Rodríguez et al., 2012, 2017) and by observing the development of similar seedlings in the field. No sign of herbivory or erosion affecting seedlings was recorded.

2.3. Environmental conditions

Environmental data were recorded in each habitat on the same days and in the same plots where seedling samples were collected. To record sediment characteristics and propagule densities, sediment samples were collected using stainless steel cores (50 mm diameter, 50 mm height; n = 9 samples per habitat and date; n = 12 for propagules at H1 due to its low vegetation cover). Samples were placed in bags that were hermetically sealed and stored at −20 °C. Sediment water content (WC; %) was gravimetrically determined using samples of 50 g of sediment. Sediment organic matter content (OM; %) was quantified using the loss-on-ignition method. Five-gram samples of dried sediment were combusted in a muffle furnace at 500 °C for 5 h before cooling in a desiccator. Organic matter content was calculated as the proportion of weight that was lost compared to the weight of the dry sample before incineration. Sediment pH and electrical conductivity (EC; mS cm^{-1}), a measure of salinity, were recorded, as reported by Contreras-Cruzado et al. (2017), in the unfiltered supernatant of a mix of 5 ml of wet sediments and the same volume of distilled water (1:1, v:v) using a pHmeter (Crison pH meter 25, Hach Lange Spain, Barcelona, Spain) and a conductivity meter (Crison Instruments 50 64, Hach Lange Spain, Barcelona, Spain), respectively. To record the density of sexual propagules (seeds and fruits), sediment samples were weighed (107 ± 1 g), and 6 subsamples of 5.0 g were randomly chosen from each soil core. Fine soil particles were eliminated in a solution of sodium polyphosphate (50 g L^{-1}) and sodium bicarbonate (25 g L^{-1}) and by sieving with 0.4 mm mesh spacing. The material that remained in the filter was placed on a white plastic surface and the propagules were counted and identified under a magnifying glass. The density of the propagules (propagules m^{-2}) for each sample point and date was calculated as the mean of the subsamples, and the density of propagules for each habitat and date was calculated as the mean of the 9–12 sample points per habitat (Polo-Ávila et al., 2019). Absolute cover (%) for each plant taxa was visually quantified in randomly placed 10 × 10 m plots (n = 3 per habitat) on the same dates as seedling, propagule, and sediment sample collection. These samples were collected within the vegetation assessment plots. Mean annual plant cover for each plot was obtained using the mean of the cover for each perennial species and the maximum cover for annual species (Contreras-Cruzado et al., 2017). Mean monthly air temperature and total rainfall for sampling months were obtained from Francisco Montenegro meteorological station (code ESAND2100000021003 B, 37.1600 N −6.5700 W) and historical climatic data series from Tavira meteorological station (code PO000008282, 37.1167 N −7.6500 W).

2.4. Statistical analysis

Deviation of the arithmetic mean was calculated as standard error (SE). A significance level (α) ≤ 0.05 was applied for every analysis. Normality of the data series was tested using the Shapiro-Wilk test, and homogeneity of variance using Levene's test. No data series fit a normal distribution even after transformation using the functions $1/x$, $\sqrt{x}$ and $\log(x)$. Seedling density (dependent variable) was compared between habitats and sampling dates (grouping factors) using the Kruskall-Wallis test. Mann-Whitney *U* test was used as *post hoc* test applying the Bonferroni correction. Pairwise Spearman correlations (ρ), applying the Bonferroni correction, were used to explore the relationships between seedling density, plant cover and propagule density for each halophyte taxa. Pairwise Spearman correlations (ρ) with the Bonferroni correction

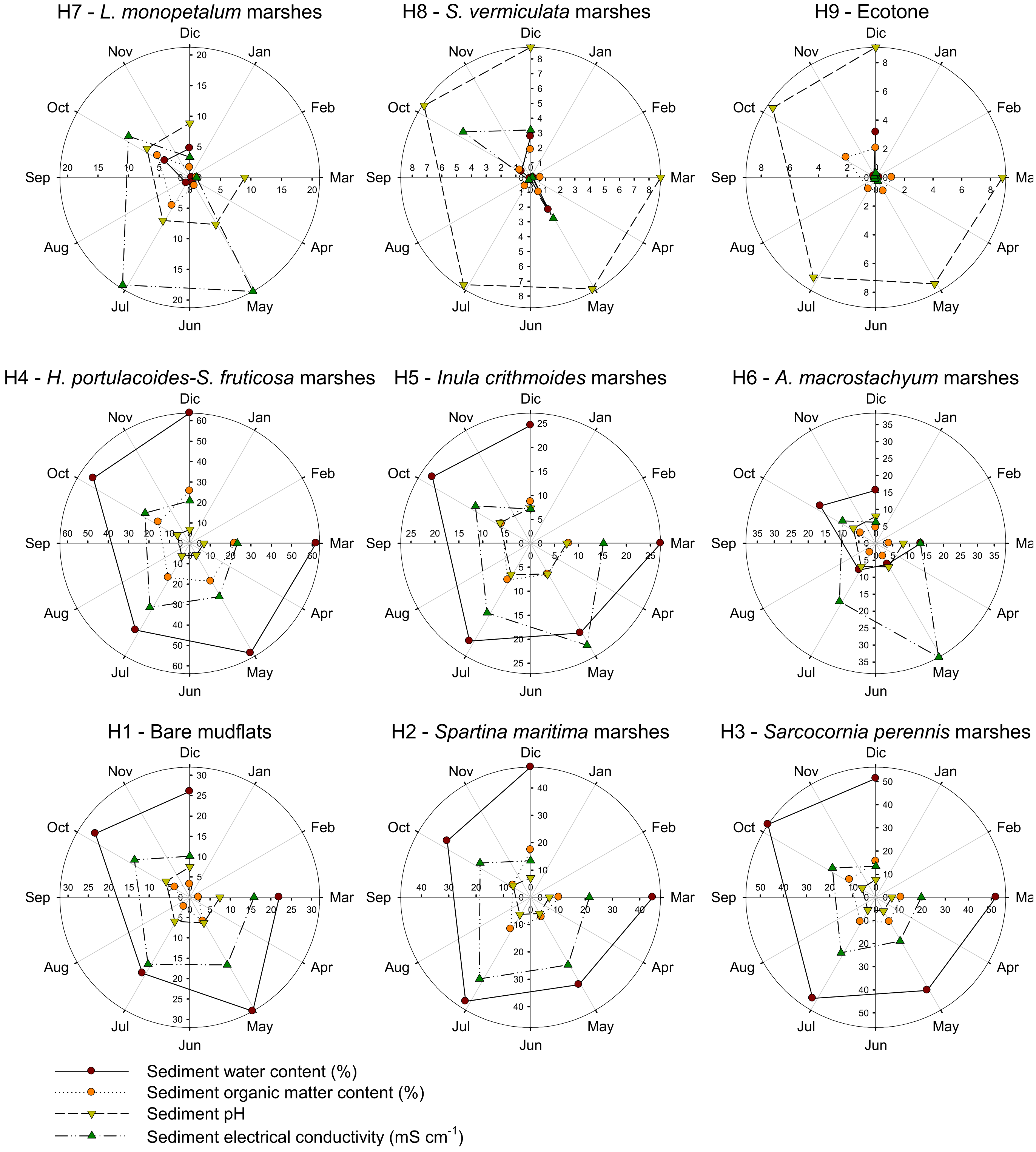

Fig. 2. Sediment factors for nine habitats along the tidal gradient in Ria Formosa (Southwest Iberian Peninsula). Values are arithmetic means (n = 30–40).

were also applied to assess interspecific coexistence, analyzing the relationships between seedling densities of different taxa in each sampling plot. These statistical analyses were carried out using SPSS v.12.0.

We performed Canonical Correspondence Analyses (CCA) to provide a broad view of ecological gradients and to identify the environmental variables that most greatly influenced taxa seedling density, since our data series presented unimodal shapes along the tidal gradient (Guisan et al., 1999). CCA were conducted using a full model to test the significance of the relationships between the environmental variables (using their arithmetic mean for each habitat and date) and the seedling densities of each halophyte taxa. Monte-Carlo permutation tests (999 permutations) were performed for assessing the significance of the canonical correlation coefficients. Total plant cover and total propagule density, including all halophyte taxa, were used in the CCA. Seedling densities of *Sarcocornia* sp. were separated into *S. perennis* for H1-3 and *S. fruticosa* for H4-9 in the CCA. These analyses were carried out using R software (R-core R Core Team, 2022).

3. Results

3.1. Environmental conditions

Mean monthly air temperature varied between +10 °C in February and +26 °C in August 2012. Monthly rainfall was zero in February, June, July and August, and the highest (132 mm) in November 2012 (Fig. 1). Sediment WC decreased in habitats located at higher elevations, with the minimum recorded during summer and the maximum in December. Sediment OM was highest (c. 20%) in H4 and lowest (1–2%) in H8-9. Sediment pH was close to neutrality in all habitats throughout the year, except in H9-10 that presented alkaline sediments (c. 8). Sediment EC was lowest (<5 mS cm^{-1}) in H9-10 and tended to vary seasonally in every habitat with the highest values during July and the lowest values in December (Fig. 2). Total absolute plant cover increased from H1 (0.0%) to H5 (152%) and then decreased until H8-9 (c. 40%) (Fig. 3A). Total propagule density increased from H1 (c. 2400 propagules m^{-2}) to H6 (c. 10000 propagules m^{-2}), then decreased until H8 (c. 1500 propagules m^{-2}) and showed its highest values in H9 (c. 55500 propagules m^{-2}) (Fig. 3B).

3.2. Spatial distribution of seedlings

A total of 2646 seedlings were recorded, from which 2640 seedlings (99.8 %) could be identified to species or genus level. Psammophyte seedlings were 65% of total seedlings and were concentrated in H8-9. Psammophyte seedlings were assigned to 17 taxa with *Polycarpon alsinifolium* as the most abundant taxon (76%). Halophyte seedlings corresponded to 35% of total seedlings and were assigned to 16 taxa with *Sarcocornia* sp. and *Spergularia* sp. as the most abundant taxa (24–25%). *Spergularia* sp., *Limonium ferulaceum-L. diffusum*, *Sarcocornia* sp. and *Suaeda albescens* were the only taxa showing seedling densities higher than 1000 seedlings m^{-2}, always being lower than 2100 seedlings m^{-2} (Table 1). Total seedling density was lowest in H1, H2 and H3, and highest in H9. The density of psammophile seedlings was maximum in H8-9, and the density of halophyte seedlings was highest in H6 (Suplementary Material Fig. S1, Table 2). A maximum of three halophyte taxa established seedlings together in the same plot. The maximum seedling density combining more than one taxa in the same plot was recorded for *Sarcocornia* sp. together with *Limoniastrum monopetalum* in H4 (1026 seedlings m^{-2}). There was a positive correlation between the density of seedlings from a particular halophyte taxa and the density of seedlings from an average of 1.6 ± 0.3 other halophyte taxa, representing approximately 10 ± 2% of the total halophyte taxa studied. The seedling density of *Arthrocnemum macrostachyum* increased together with that of five other taxa (*Halimione portulacoides*, *Limonium algarvense*, *Limonium ferulacuem-L. diffusum*, *Sarcocornia* sp. and *Suaeda vera*), whereas the seedling density of *Limonium narbonense*, *Puccinellia convoluta* and *Spergularia* sp. did not correlate to any taxa (Suplementary Material Table S1).

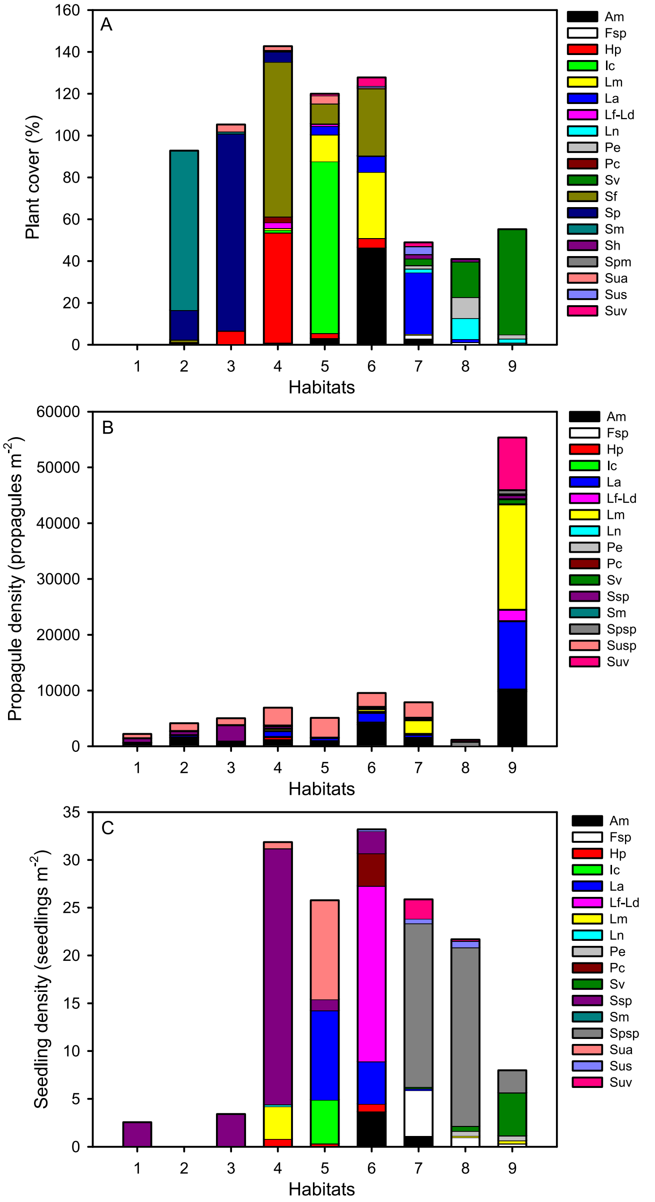

Fig. 3. Absolute plant cover (%), propagule density (propagules m^{-2}) and seedling density (seedling m^{-2}) in nine salt marsh habitats along the tidal gradient in Ria Formosa (Southwest Iberian Peninsula). Habitats: H1: bare mudflats; H2: *Spartina maritima* marshes; H3: *Sarcocornia perennis* marshes; H4: marshes of *Halimione portulacoides* and *Sarcocornia fruticosa*; H5: *Inula crithmoides* marshes; H6: high marshes of *Arthrocnemum macrostachyum*; H7: high marshes of *Limoniastrum monopetalum*; H8: sandy sediments colonized by *Salsola vermiculata*; H9: ecotone between H8 and adjacent coastal dunes. Plant taxa: Am, *Arthrocnemum macrostachyum*; Fsp, *Frankenia* sp.; Hp, *Halimione portulacoides*; Ic, *Inula crithmoides*; Lm, *Limoniastrum monopetalum*; La, *Limonium algarvense*; Lf-Ld, *Limonium ferulaceum - L. diffusum*; Ln, *Limonium narbonense*; Pe, *Polygonum equisetiforme*; Pc, *Puccinellia convoluta*; Sv, *Salsola vermiculata*; Ssp, *Sarcocornia* sp.; Sf, *Sarcocornia fruticosa*; Sp, *Sarcocornia perennis*; Sm, *Spartina maritima*; Spsp, *Spergularia* sp.; Spm, *Spergularia maritima*; Susp, *Suaeda* sp.; Sua, *Suaeda albescens*; Sus, *Suaeda spicata*; Suv, *Suaeda vera*.

The seedling density of every halophyte taxa changed significantly between marsh habitats, except for *Frankenia* sp., *Halimione portulacoides*, *Inula crithmoides*, *Limonium narbonense*, *Polygonum equisetiforme*, *Puccinellia convoluta*, *Limoniastrum monopetalum* and *Suaeda spicata*

Table 1
Seedling types for psammophytes and halophytes, their representation in each group (%) and maximum seedling density (seedlings m^{-2}) along an intertidal gradient in Ria Formosa (Southwest Iberian Peninsula).

Psammophytes	Halophytes
Polycarpon alsinifolium (76.3%; 6159)	*Spergularia heldreichii* (24.9%; 2053)
Plantago coronopus (8.5%; 513)	*Sarcocornia* sp. (24.2%; 1027)
Sagina maritima (6.0%; 513)	*Limonium ferulaceum-L. diffusum* (12.0%; 1540)
Hainardia cylindrica (3.5%; 200)	*Limonium algarvense* (9.1%; 513)
Medicago littoralis (1.2%; 100)	*Suaeda albescens* (7.2%; 1027)
Helichrysum picardii (1.2%; 25)	*Frankenia laevis* (4.0%; 513)
Anthemis maritima (0.9%; 175)	*Salsola vermiculata* (3.4%; 125)
Lotus creticus (0.6%; 50)	*Arthrocnemum macrostachyum* (3.2%; 50)
Carpobrotus edulis (0.3%; 25)	*Inula crithmoides* (3.0%; 513)
Centhranthus ruber (0.3%; 75)	*Limoniastrum monopetalum* (2.6%; 513)
Linaria pedunculata (0.3%; 50)	*Puccinellia convoluta* (2.2%; 513)
Paronychia argentea (0.3%; 75)	*Suaeda vera* (1.4%; 50)
Senecio vulgaris (0.3%; 50)	*Halimione portulacoides* (1.3%; 50)
Malcolmia littorea (0.1%; 25)	*Suaeda spicata* (0.9%; 50)
Pseudorlaya minuscula-P. pumila (0.1%; 25)	*Polygonum equisetifolium* (0.7%; 50)
Corynephorus canescens (0.1%; 25)	*Limonium narbonense* (0.1%; 25)
Elymus farctus (0.1%; 25)	

Table 2
Results of Kruskal-Wallis test for seedling density of halophyte taxa comparing between habitats (degree of freedom = 8, N = 150–200), sampling dates (degree of freedom = 4; N = 280). Significant differences are marked in bold.

Taxon	Habitat	Date
Total seedling density	**χ^2 = 385.030, P < 0.0001**	**χ^2 = 31.067, P < 0.0001**
Arthrocnemum macrostachyum	**χ^2 = 125.351, P < 0.0001**	**χ^2 = 14.228, P = 0.007**
Frankenia laevis	**χ^2 = 27.414, P = 0.001**	χ^2 = 2.190, P = 0.701
Halimione portulacoides	**χ^2 = 25.610, P < 0.001**	χ^2 = 5.047, P = 0.283
Inula crithmoides	**χ^2 = 41.786, P < 0.0001**	χ^2 = 6.014, P = 0.198
Limoniastrum monopetalum	χ^2 = 10.015, P = 0.264	χ^2 = 8.508, P = 0.075
Limonium algarvense	**χ^2 = 77.553, P < 0.0001**	χ^2 = 9.320, P = 0.054
Limonium ferulaceum - L. diffusum	**χ^2 = 151.838, P < 0.0001**	χ^2 = 5.945, P = 0.203
Limonium narbonense	χ^2 = 8.333, P = 0.402	χ^2 = 4.000, P = 0.406
Polygonum equisetiforme	**χ^2 = 19.314, P = 0.013**	**χ^2 = 12.039, P = 0.017**
Puccinellia convoluta	χ^2 = 8.333, P = 0.402	χ^2 = 4.000, P = 0.406
Sarcocornia sp.	**χ^2 = 123.879, P < 0.0001**	χ^2 = 8.303, P = 0.081
Spergularia sp.	**χ^2 = 102.733, P < 0.0001**	**χ^2 = 12.228, P = 0.016**
Suaeda albescens	**χ^2 = 93.568, P < 0.0001**	**χ^2 = 16.846, P = 0.002**
Suaeda spicata	**χ^2 = 15.825, P < 0.0001**	**χ^2 = 10.714, P = 0.003**
Suaeda vera	**χ^2 = 75.256, P < 0.0001**	**χ^2 = 9.521, P = 0.049**
Salsola vermiculata	**χ^2 = 90.077, P < 0.0001**	**χ^2 = 19.551, P = 0.001**

(Table 2). *Sarcocornia perennis* sp., *Limonium narbonense* and *Limoniastrum monopetalum* (with only 3 plots with seedlings) reached their highest seedling densities in H4. *Puccinellia convoluta*, *Limonium algarvense* and *Suaeda albescens* presented their highest seedling densities in H5, *Arthrocnemum macrostachyum* and *Limonium ferulaceum-L. diffusum* in H6, *S. vera* in H7, *Spergularia* sp. in H7-8, and *Salsola vermiculata* in H9 (Fig. 3C, Suplementary Material Table S2).

3.3. Temporal distribution of seedlings

The highest total seedling densities were recorded in March and the lowest in October (Suplementary Material Fig. S1, Table S3). The seedling density of half of the taxa changed between sampling dates (Table 2). *Suaeda albescens* and *Spergularia* sp. reached their maximum seedling densities in March, *Arthrocnemum macrostachyum* in July, and *Salsola vermiculata* in December (Fig. 4, Suplementary Material Table S3). Most of the halophyte taxa were able to set seedlings during more than one sampling date and at different habitats (Suplementary Material Table S4).

3.4. Relationships between environmental conditions and seedling densities

Seedling densities and associated environmental conditions clearly distinguished halophyte taxa according to their position along the tidal gradient and their responses to meteorological conditions (CCA ordination, Fig. 5, Suplementary Material Table S5). The first five axes of the CCA explained 92.5% of the total variance in the relationships between seedling densities and the range of associated environmental variables. Axis 1 (explaining 25.9% of the variance) positively correlated to sediment pH and mostly to the seedling density of taxa such as *Spergularia* sp., *Frankenia* sp. and *Salsola vermiculata*, and negatively to plant cover and sediment conductivity and water and organic matter contents. All the monitoring plots in H1-6 were negatively related and almost all plots in H7-9 were positively related to Axis 1. Thus, low and middle marshes, and those dominated by *Arthrocnemum macrostachyum*, displayed a positive association with less basic, saltier, and more humid sediments rich in organic matter, which supported dense halophyte colonization. In contrast, high marsh habitats exhibited the opposite trends. Axis 2 explained 23.5% of the variance, and positively correlated to total propagule density, mean air daily temperature and the seedling density of *Puccinellia* sp. and *Limonium ferulaceum-L. diffusum*, and negatively to rainfall and the seedling density of *Sarcocornia perennis* and *Limoniastrum monopetalum*. Axis 3 (explaining 19.9% of the variance) positively correlated mostly to the seedling density of *Sarcocornia perennis*, and negatively to sediment organic matter content and the seedling density of *Limoniastrum monopetalum* and *Sarcocornia fruticosa*. Axis 4 explained 15.3% of the variance, and positively correlated to total propagule density and the seedling density of *Puccinellia* sp., *Limoniastrum monopetalum* and *Salsola vermiculata*, and negatively to the seedling density of *Inula crithmoides*, *Halimione portulacoides* and *Limonium algarvense*. Axis 5 (explaining 7.9% of the variance) positively correlated mostly to the seedling density of *Arthrocnemum macrostachyum* and *Suaeda vera*, and slightly positively to sediment conductivity and mean daily air temperature, and negatively to the seedling density of *Salsola vermiculata* (Fig. 5, Suplementary Material Table S5). Seedling density increased together with plant cover of potential source plants for 12 out of 16 halophyte taxa, and with propagule density for *Suaeda albescens* and *Spergularia* sp. (Suplementary Material Table S6).

4. - Discussion

Our results show that halophyte taxa growing along the tidal gradient presented contrasted spatio-temporal patterns of seedling emergence. The complex pattern of seedling emergence across diverse habitats with varying seasonal patterns amplified the differences determined by a highly heterogeneous seed bank composition (Polo-Ávila et al., 2019).

In general, total seedling densities increased as flooding frequency was reduced, as recorded previously in freshwater tidal wetlands (Parker and Leck, 1985; Hopfensperger and Engelhardt, 2008). The abundance of psammophyte seedlings in sandy sediments colonized by *Salsola vermiculata* and the ecotone with adjacent coastal dunes reflected the accumulation of sand in high marshes transported by coastal winds from neighboring dunes and the low sediment salinity recorded in these high marshes (Contreras-Cruzado et al., 2017). Only the seedling densities of *Suaeda albescens* and *Spergularia* sp. were related to their own propagule densities, since most taxa concentrate much of their

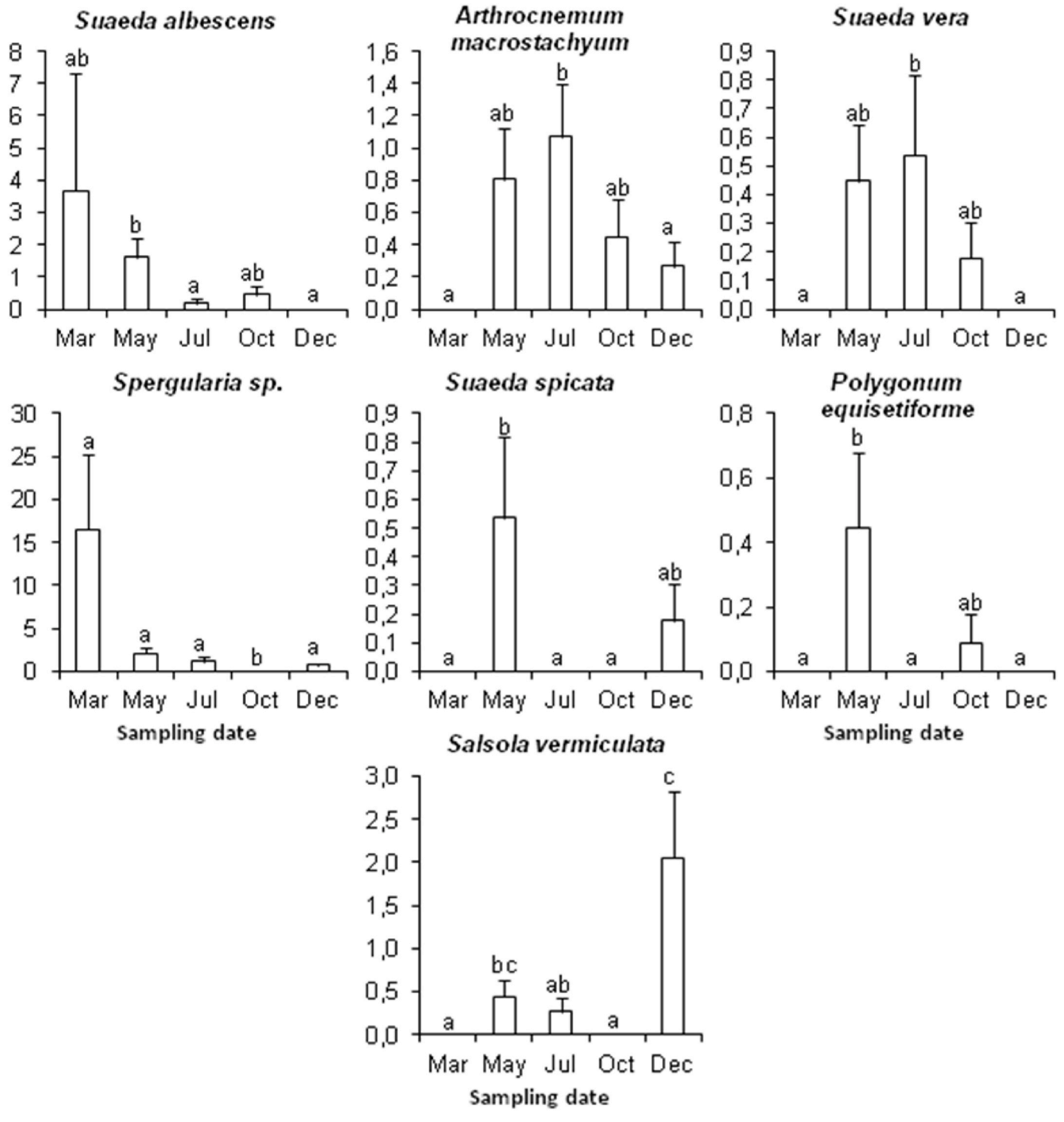

Fig. 4. Seedling densities (seedling m^{-2}) on different sampling dates for halophyte taxa colonizing the intertidal gradient in Ria Formosa (Southwest Iberian Peninsula). Values are arithmetic mean ± SE (n = 280). Different letters indicate significant differences between means (Mann-Whitney *U* test, $p < 0.05$).

propagules at the ecotone with adjacent dunes (Polo-Ávila et al., 2019). Even so, the greatest seedling densities were recorded together with the maximum covers of the potential source plants for most of the taxa, which may be the consequence of the positive effects of vegetation canopy on seedling establishment. These results partially supported our first hypothesis, which predicted that seedling densities would be positively related to seed densities and adult plant covers. Adult plants can limit evaporation and reduce salinity, facilitating the establishment of seedlings in salt marshes (Bertness and Hacker, 1994; Bruno et al., 2017; Castillo et al., 2021b). We did not find any seedlings from three species present in the marshes studied and in their soil seed banks (Polo-Ávila et al., 2019): 1) *Cistanche phelypaea* (L.) Cout., an holoparasite that develops inside host plant tissues; 2) *Spartina maritima* (Curtis) Fernald., which disperses its moderate numbers of highly viable caryopses (Infante-Izquierdo et al., 2020) over medium-to-long distances (Polo-Ávila et al., 2019); and 3) *Salicornia ramosissima* J. Woods, which is very rare (cover 0.3%) in the study area (Contreras-Cruzado et al., 2017).

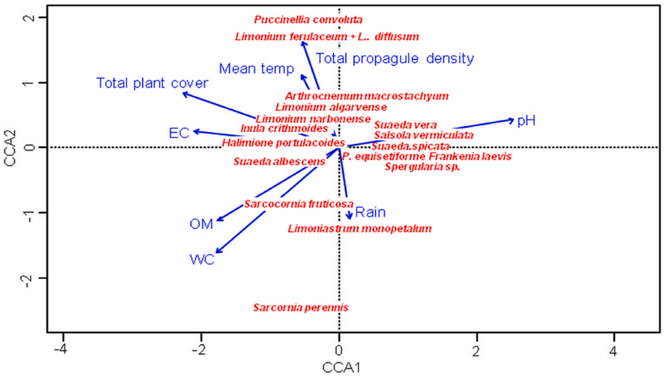

Fig. 5. Ordination diagram of a Canonical Correspondence Analysis (CCA) with environmental conditions (blue arrows) and seedling density of halophyte species growing along the tidal gradient in Ria Formosa (Southwest Iberian Peninsula). Environmental conditions: pH, sediment pH; WC, sediment water content; OM, sediment organic matter; EC, sediment electrical conductivity; Mean temp, mean daily air temperature during the sampling month; Rain, rainfall during the sampling month. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Taxa colonizing the same habitats showed some similarities in their patterns of seedling emergence but they also presented enough temporal differences in seedling presence to configure almost a unique recruitment pattern for each taxa. Sediment characteristics segregated recruitment niches at both extremes of the tidal gradient, and the few species colonizing habitats between these two extremes also showed contrasted spatial recruitment patterns. This was reflected in each taxon exhibiting a unique pattern of seedling density along the intertidal gradient (Fig. 3C). In addition, sequential differences in seedling emergence segregated within high marsh taxa. Therefore, a diverse array of high marsh taxa exhibited seasonal seedling emergence, with each taxon germinating at specific times throughout the year (Fig. 4). Moreover, most of the taxa were able to establish sequential cohorts during most of the year, which would reduce inter- and intra-specific competition (Egan and Ungar, 1999; Lee and Ihm, 2004). This continuous germination strategy was associated to prolonged flowering periods, as in the cases of *S. spicata*, *Frankenia* sp. and *P. equisetiforme* (Castroviejo, 1986–2012), and the ability to germinate along broad salinity ranges in the cases of *Sarcocornia* sp., *I. crithmoides* and *Limonium* species (Muñoz-Rodríguez et al., 2017; Castillo et al., 2021a, 2022). Recruitment niche segregation was reflected in pairwise interspecific correlations between seedling densities that were mainly insignificant, indicating low coincidence between species seedlings. Consequently, seedling densities were always lower than 2100 seedlings m^{-2} in monospecific formations, and lower than 1050 seedlings m^{-2} in multi-specific communities with a maximum of three taxa establishing seedlings together.

Five taxa from low-middle marshes (*Halimione portulacoides, Limonium narbonense*, *Puccinellia convoluta*, *Sarcocornia* sp. and *Suaeda albescens*) presented their highest recruitment on acidic sediments with relatively high salinities, OM and WC. Most of these five taxa are able to germinate along wide salinity ranges, including the salinities recorded in their habitats (Muñoz-Rodríguez et al., 2017; Castillo et al., 2021a). Moreover, the seedlings of *H. portulacoides* and *S. albescens* were associated with areas of high plant cover and low propagule density, where adult plants may facilitate their establishment and where there would be low levels of competition between seedlings (Rubio-Casal et al., 2001). In contrast, the seedlings of *P. convoluta* were mostly associated with areas of high propagule density.

The effects of soil salinity on seed germination and seedling emergence changes across tidal elevations (Watson and Byrne, 2009). In contrast with most of the taxa from low-middle marshes, the majority of the taxa from high marshes (*Frankenia* sp., *Polygonum maritimum*, *Salsola vermiculata*, *Spergularia* sp. and *Suaeda spicata*) exhibited more seedlings on alkaline sediments with low salinities, OM, WC and plant covers (Fig. S2). Alkaline conditions and drought may limit the establishment of seedlings of species from low-middle marshes (Mateos-Naranjo et al., 2008; Li et al., 2010). High marsh taxa behaved as fugitive plants highly tolerant to drought that take advantage of bare patches as refugia from competitors, and were governed by temporally unpredictable opportunity windows for recruitment created by rainfalls that lowered sediment salinity and increased WC (Bertness et al., 1992; NOE and Zedler, 2001b; Goldstein and Suding, 2014; Jiang et al., 2022). In this sense, taxa growing at the upper distribution limit of the tidal gradient showed a clear temporal segregation in their peak seedling densities. Seedlings of *Spergularia* sp., with a persistent seed bank, emerged mostly during March, many months after fruiting in June (Polo-Ávila et al., 2019). Maximum peak of seedling densities of *P. equisetiforme* and *S. spicata* was in May, and *S. vermiculata* in December just after dispersing its fruits (Fernández-Illescas et al., 2010).

The seedlings of six species (*Inula crithmoides*, *Limonium algarvense*, *Limonium ferulaceum-L. diffusum*, *Arthrocnemum machrostachyum* and *Suaeda vera*) colonizing intermediate elevations presented contrasted spatio-temporal patterns in relation to those taxa establishing at the tidal gradient extremes. Increased heterogeneous topography facilitates halophyte establishment in salt marshes (Xie et al., 2019a). In this sense, the seedlings of *I. crithmoides* and *L. algarvense* mostly colonized marshes with low propagule densities. In contrast, *L. ferulaceum-L. diffusum* seedlings were associated to high propagule densities, usually coinciding with concave hollows as we observed in the field and Qiu et al. (2021) reported for *Suaeda salsa* (L.) Pall. in the Yellow River Delta of China. The seedlings of *A. macrostachyum* and *S. vera*, both with permanent seed banks (Polo-Ávila et al., 2019), colonized mostly high marshes with strong seasonal variations in salinity in May–July during high air temperature periods just after dispersal (Fernández-Illescas et al., 2010). The rapid germination of *A. macrostachyum* and *S. vera* took place in opportunity windows with low sediment salinities after rainfalls, avoiding the deleterious effects of high salinities on their seeds (Muñoz-Rodríguez et al., 2017). These results supported our second hypothesis, which predicted that harsh environmental conditions would limit seedling emergence according to flowering, fruiting, dispersal and germination ecology of different taxa.

Our study reveals that environmental variation along the tidal gradient and the pronounced seasonality of the Mediterranean climate create spatiotemporal segregation of recruitment niches for halophytes, supporting our third hypothesis. This would expand the range of successful strategies for seedling establishment, as observed in other stressful environments (Dayrell et al., 2021). The recorded recruitment niche segregation could be altered in the current scenario of climate change and concomitant sea level rise since it depends on changing environmental conditions such as salinity, air temperature and rainfall (Woo and Takekawa, 2012; Zeppel et al., 2014; Zhu et al., 2014; Shan et al., 2018). Small changes in rainfall amount or distribution, inundation and salinity can trigger comparatively large and abrupt changes in different halophytes depending on their ecological niches and local abiotic gradients (Woo and Takekawa, 2012; Janousek and Folger, 2013; Xie et al., 2019b). In the study area, germination of some salt marsh species is very sensitive to salinity (Castillo et al., 2022), and temperatures are increasing at the same time that rainfall is decreasing, especially from January to March (Portela et al., 2019), which would increase salinity just when more seedlings emerge. These environmental changes may compromise the persistence of halophytes with transient seed banks, impacting on their annual recruitment (Ooi, 2012) and affecting plant communities' composition (Callaway and Sabraw, 1994; Lloret et al., 2005). Our results shed light on the importance of recruitment niche segregation to the assembly of plant communities, which is key for understanding their functioning and guiding their management.

CRediT authorship contribution statement

Adolfo F. Muñoz-Rodríguez: Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **María D. Infante-Izquierdo:** Methodology, Investigation, Conceptualization. **Alejandro Polo-Ávila:** Investigation, Conceptualization. **Virgilio Hermoso-López:** Formal analysis. **Francisco J.J. Nieva:** Investigation. **Blanca Gallego-Tévar:** Formal analysis. **Jesús M. Castillo:** Writing – review & editing, Writing – original draft, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108859.

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