Long-Term Monitoring of Coupled Vegetation and Elevation Changes in Response to Sea Level Rise in a Microtidal Salt Marsh

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Abstract Tight interplays between physical and biotic processes in tidal salt marshes lead to self-organization of halophytic vegetation into recurrent zonation patterns developed across elevation gradients. Despite its importance for marsh ecomorphodynamics, however, the response of vegetation zonation to changing environmental forcings remains difficult to predict, mostly because of lacking long-term field observations of vegetation evolution in the face of changing rates of sea level rise and marsh vertical accretion. Here we present novel data of coupled marsh elevation-vegetation distribution collected in the microtidal Venice Lagoon (Italy) over nearly two decades. Our results suggest that: (a) despite increasing absolute marsh elevations (i.e., above a fixed datum), vertical accretion rates across most of the studied marsh were not high enough to compensate for relative sea-level rise (RSLR), thus leading to a progressive marsh drowning; (b) accretion rates ranging 1.7–4.3 mm/year are overall lower than the measured RSLR rate (4.4 mm/year) and strongly site-specific. Accretion rates vary largely at sites within distances of a few tens of meters, being controlled by local elevation and sediment availability from eroding marsh edges; (c) vegetation responds species-specifically to changes in environmental forcings by modifying species-preferential elevation ranges. For the first time, we observe the consistency of a sequential vegetation-species zonation with increasing marsh elevations over 20 years. We suggest this is the signature of vegetation resilience to changes in external forcings. Our results highlight a strong coupling between geomorphological and ecological dynamics and call for spatially distributed marsh monitoring and spatially explicit biomorphodynamic models of marsh evolution.

Plain Language Summary Salt marshes are important ecosystems currently threatened by changes in environmental forcings. We analyzed the coupled elevation-vegetation response to relative sea-level rise in a marsh located within the Venice lagoon (Italy) by using accurate on-site measurements collected between 2000 and 2019. We found that the marsh elevations above a fixed datum increased over the study period. However, marsh sites were found to be gradually drowning, because sediment deposition on the marsh surface did not balance the increase in relative mean sea level. We also found that the response of halophytic vegetation to relative sea-level rise is species-specific. In addition, we showed that vegetation species are distributed according to a specific sequence with increasing elevations and that such sequence remained stable for nearly two decades. This suggests that vegetation species can endure rising relative sea levels, at least temporally, without significantly modifying their distribution despite marsh gradual drowning.

1. Introduction

Tidal salt marshes are characteristic biogeomorphic features of tidal landscapes, typically found at elevations ranging between mean sea level (MSL) and mean-high water level (MHWL) and therefore regularly inundated by tides (Murray et al., 2022). Salt marshes form critical transitional environments between marine and terrestrial landscapes that provide highly valuable ecosystems by hosting high biodiversity, supporting significant primary productivity, attenuating wave action along the coast, and filtering nutrients and pollutants (Barbier et al., 2011; Costanza et al., 1997). Salt marshes also serve as important carbon sinks due to their ability to sequester and store large amounts of organic blue carbon (Chmura et al., 2003). However, salt-marsh ecosystems are currently disappearing at alarming rates all over the world, being threatened by a

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lack of mineral sediment supply, direct wave attacks, increasing anthropogenic pressures, and rising relative sea levels (A. D'Alpaos et al., 2011; Horton et al., 2018; Jankowski et al., 2017; Tognin et al., 2021). In particular, rates of sea level rise have been accelerating in the 21st century, posing a serious threat to marsh survival.

Previous analyses have documented that marshes can keep pace with local sea-level rise, up to a threshold rate, through coupled deposition of mineral and organic sediments (A. D'Alpaos et al., 2011; Kirwan et al., 2010). Beyond this threshold rate, which depends on local conditions such as sediment supply and tidal range, marsh vulnerability is controlled by the imbalance between the rates of marsh vertical accretion (R_{acc}) and relative sea-level rise (RSLR), the latter being the sum of rates of local land subsidence and eustatic SLR relative to a fixed datum (A. D'Alpaos et al., 2011; Day et al., 1998). Salt-marsh survival in the face of RSLR is intimately related to the ability of halophytic (i.e., salt-tolerant) species that colonize the marsh platform to adapt to sea-level-driven changes in edaphic properties and environmental stresses. Halophytic species play a key role in the eco-morphodynamic evolution of salt marshes, due to their influence on erosional and depositional patterns (A. D'Alpaos et al., 2007; Kirwan & Murray, 2007; Mariotti, 2020; Morris et al., 2002). Several studies emphasized that vegetation can facilitate marsh survival by reducing water flow velocity and related sediment erosion, mitigating lateral retreat due to wave attack, and increasing marsh vertical accretion through organic matter deposition (A. D'Alpaos, 2011; A. D'Alpaos et al., 2007; Kirwan & Murray, 2007; Morris et al., 2002).

The distribution of salt-marsh vegetation is strongly intertwined with marsh geomorphology, with individual halophytic species living and thriving only within a narrow elevation range that represents the species' realized ecological niche (often referred to as the vegetation realized distribution; Finotello et al., 2022; Pennings & He, 2021; Silvestri et al., 2005). Such an organization leads to the formation of vegetation patches dominated by a single species or characterized by typical species associations, a pattern known as *zonation* (Pennings et al., 2005; Silvestri et al., 2005; Yang et al., 2020). Halophyte zonation can be considered the result of vegetation adaptation to abiotic factors (e.g., edaphic properties and hydrodynamic stresses) and biotic interactions (e.g., inter-specific competition and facilitation mechanisms) (A. D'Alpaos et al., 2007; Finotello et al., 2022; Pennings & He, 2021; Pennings et al., 2005). The observed marsh bio-geomorphic zonation patterns are therefore the signature of multiple stable states, generated by competing vegetation species adapted to different elevation ranges (Da Lio et al., 2013; Marani et al., 2013). The sequence of vegetation distributions across marsh elevations observed from direct field surveys has been the critical ingredient to developing numerical models aimed at simulating marsh ecomorphodynamic evolution, under the assumption that such sequence holds stable over decadal or even longer timescales (Da Lio et al., 2013; A. D'Alpaos et al., 2007; Kalra et al., 2021; Kirwan & Murray, 2007; Kirwan et al., 2016; Morris, 2006; Morris et al., 2002). This assumption, however, is mostly based on realized vegetation distributions derived from field observations that are often limited to one single field observation and seldomly encompass more than a few years.

It thus remains unclear whether sequences of vegetation distributions will remain stable in the face of RSLR over decadal time scales, or if they will rather change due to RSLR-induced modifications of environmental stresses and biotic interactions (e.g., Morris, 2006; Pennings & He, 2021). This knowledge gap is mostly due to a persisting lack of detailed, long-term, spatially extensive field observations and analyses on the response of salt marshes to changing relative sea levels, in particular in terms of coupled evolution of vegetation distributions and marsh topography. Such a lack of empirical observations has so far undermined our ability to properly estimate marsh vulnerability to RSLR, a task that is especially urgent concerning salt marshes found in microtidal environments, which are supposedly highly vulnerable to rising relative sea levels due to lower accretion rates compared to their meso- and macro-tidal counterparts (A. D'Alpaos et al., 2011; Ganju et al., 2017; Kirwan & Guntenspergen, 2010). To contribute to filling this knowledge gap, here we analyze combined changes in topographic elevations and vegetation distributions observed in the microtidal salt marsh of San Felice (Venice lagoon, Italy) over nearly two decades.

This paper is organized as follows. In the next section, we provide an overview of the study area and describe both data and methods. Then, in the third section (Section 3) we analyze changes in marsh elevation and the related vegetation distributions, with reference to both an absolute datum and the local relative mean sea level at San Felice. The fourth section (Section 4) contains ample discussions regarding the vulnerability of the studied marsh and the response of halophytic vegetation to RSLR. The paper ends with a set of final remarks.

2. Materials and Methods

2.1. Geomorphological Setting and Study Area

The Venice lagoon (Italy) is the largest lagoon in the Mediterranean Sea (Figure 1a) with a total area of about 550 km^2. The lagoon is characterized by a semi-diurnal tidal regime, with an average tidal range of about 1.0 m and maximum spring tidal oscillations of approximately 1.5 m (Roner et al., 2016; Tommasini et al., 2019). The lagoon is connected to the Adriatic Sea by the inlets of Lido, Malamocco, and Chioggia from North to South. Both freshwater and sediment inflows are nowadays practically negligible as a consequence of major river diversions operated between the sixteenth and the nineteenth centuries (L. D'Alpaos, 2010). The lagoon has experienced a significant decrease in salt-marsh area, which has accelerated since the beginning of the last century, due to combined natural and anthropogenic processes, among which one should recall human-induced reductions of fluvial sediment supply, the construction of jetties at the inlets, the excavation of large navigable channels, and the increase in the rate of RSLR (A. D'Alpaos et al., 2010; Day et al., 1998; Finotello et al., 2023; Tommasini et al., 2019).

In the present work, we focus on the San Felice (SF) marsh (Figures 1a and 1b), which is located in the northern and best naturally preserved part of the lagoon (Marani et al., 2003; Roner et al., 2016). Our study area is delimited by the San Felice and Spacco Tralo channels to the South and East, respectively, and by a shallow tidal flat to the North (Figure 1b). An extensive network of branching and meandering channels cut through the SF marsh. These channels exert primary controls on marsh ecomorphodynamics, serving as the main conduits for the propagation of tides, as well as for the distribution of mineral sediments and nutrients across the marsh (Roner et al., 2016). The total marsh area at SF decreased significantly in the last century, due to the inner pond enlargement and, above all, wave-induced erosion of the marsh's outer margins (Day et al., 1998; Tommasini et al., 2019).

The SF marsh hosts most of the typical halophytic vegetation species found in the Venice Lagoon, such as *Salicornia Veneta* (hereafter "*Salicornia*"), *Spartina Maritima* (hereafter "*Spartina*"), *Limonium Narbonense* (hereafter "*Limonium*"), *Sarcocornia Fruticosa* (hereafter "*Sarcocornia*"), and *Juncus Maritimus* (hereafter *Juncus*) (Belluco et al., 2006; Yang et al., 2020). Previous field campaigns highlighted a pronounced vegetation zonation as a function of local marsh topographic elevation, with *Salicornia* and *Spartina* usually encroaching lower elevations, *Limonium* being more widespread in areas with moderate elevations, and *Sarcocornia* and *Juncus* preferring the highest marsh portions (Silvestri et al., 2005).

2.2. Field Measurements of Marsh Topography and Vegetation Species Distributions

Over the last two decades, seven distinct topographic surveys were carried out at SF in the years 2000, 2002, 2003, 2004, 2006, 2013, and 2019 (see Table 1 and Figures 1d–1f). During each survey, geographic positions and soil elevations were measured through a total station with a high precision (order of 1 mm). All the surveys were referred to the national Istituto Geografico Militare (IGM) datum, corresponding to the mean sea level measured at the Genova gauging station in 1942 and for this reason also known as the "Genova 1942" datum. Data points in 2000, 2013, and 2019 were evenly distributed over the marsh, whereas data in 2002, 2003, 2004, and 2006 were collected mostly within homogeneous vegetation patches (Figures 1d–1f).

Aiming to monitor the evolution of vegetation cover across marsh topographic gradients, we focused specifically on data collected along 10 fixed transects, each originating on the marsh boundary and ending in either inner marsh portions or at minor creek edges. Five transects (Transects 1–5 in Figure 2a) were surveyed in 2013 and 2019, while the other five transects (Transects 6–10 in Figure 2a) were surveyed twice in 2000 and 2019, respectively. Moreover, to explore the spatial variability of marsh vertical displacements, we subdivided the SF marsh into three distinct sectors (Sectors I, II, and III in Figure 1b). Within each sector, a patch area characterized by high data-point density (Figure 2b) was analyzed to estimate marsh vertical accretion rates. Additionally, a subset of paired points (Figure 2c) derived from the 2000 and 2019 surveys was also used to analyze marsh topographic changes in Sector III. Specifically, we paired data by constructing a buffer zone with a radius of 5 m around each data point collected in 2000 and associating each point with the corresponding 2019 data falling within such a buffer zone. The number of data included in each patch and paired-point set is listed in Table 2. The statistical significance of differences in IGM elevation of each studied transect, patch, or set of paired points was tested by means of one-way ANOVA tests performed using the Origin 2018 software. Local accretion rates
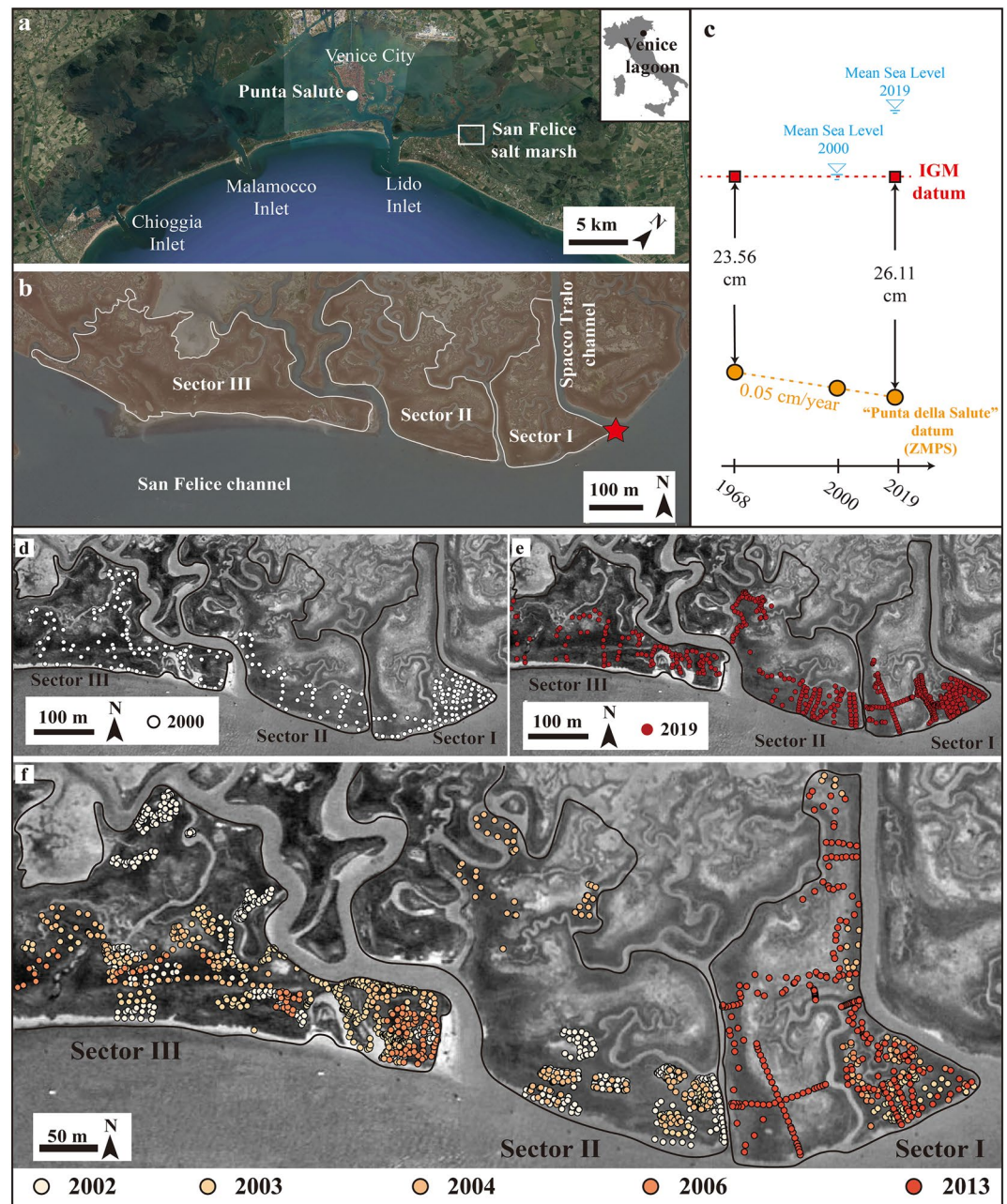
Figure 1. Geomorphological setting and study area. (a) Aerial view of the microtidal Venice lagoon (Italy) (image © Google/Landsat). The locations of the "Punta della Salute" tidal gauge, as well as of the San Felice salt marsh are also highlighted. (b) A close-up aerial view of the San Felice salt marsh, with indications of the major surrounding channels. The subdivision of the marsh into the three separate Sectors analyzed in this study is also highlighted. The red star denotes the crossover point of marsh boundaries along the San Felice and Spacco Tralo channels (image © Google/Landsat). (c) Sketch illustration of the increasing elevation difference between the official Italian "Istituto Geografico Militare" (IGM) datum, which remains fixed through time, and the subsiding local datum of "Punta della Salute" (ZMPS). The elevations of mean sea level (MSL) in the years 2000 and 2019 are also shown, with reference to the IGM datum. (d, e) Positions of data points collected in 2000 and 2019. (f) Positions of data points surveyed in the years 2002, 2003, 2004, 2006, and 2013. The base map of panels d, e, and f is a satellite IKONOS image (red band, central wavelength = 666 nm) acquired in 2006.

(R_{acc} [mm/year]) for each studied transect, patch, or paired-point set, were estimated based on linear regression performed on the average values of topographic data (referenced to the IGM datum) measured at different years. The R_{acc} estimation was carried out through the Matlab R2022a software.

Table 1
Number of Data Points Surveyed in Different Years and Different Sectors of the San Felice Salt Marsh

Marsh sector	Year of survey						
	2000	2002	2003	2004	2006	2013	2019
Sector I	88	–	82	–	30	138	284
Sector II	51	247	93	76	–	–	104
Sector III	99	335	332	149	120	–	108

Data regarding marsh vegetation distributions associated with each topographic survey were also available, which allowed us to relate changes in marsh elevation and vegetation distribution across topographic gradients. Vegetation fractional abundance (i.e., the relative area occupied by a given species, including bare soil) was estimated using the standard Braun-Blanquet visual method, which records the presence of individual species in an area of about 1 m^2 and provides results in the range from 0% to 100% at 10% resolution (Silvestri et al., 2005). The number of times that each species was surveyed is listed in Table 3. Notably, because only limited points (<3) in each Sector were covered by *Juncus*, the latter species was not included in the analyses as we could not track its evolution in sufficient detail. The statistical significance of differences in vegetation preferred elevations (referenced to the IGM datum) in different years was tested by one-way ANOVA tests performed using the Origin 2018 software. Finally, we also computed the rate of change in the preferred absolute elevation (R_c) at which each species was found based on linear regression performed using Matlab R2022a on IGM elevation data measured during different surveying campaigns.
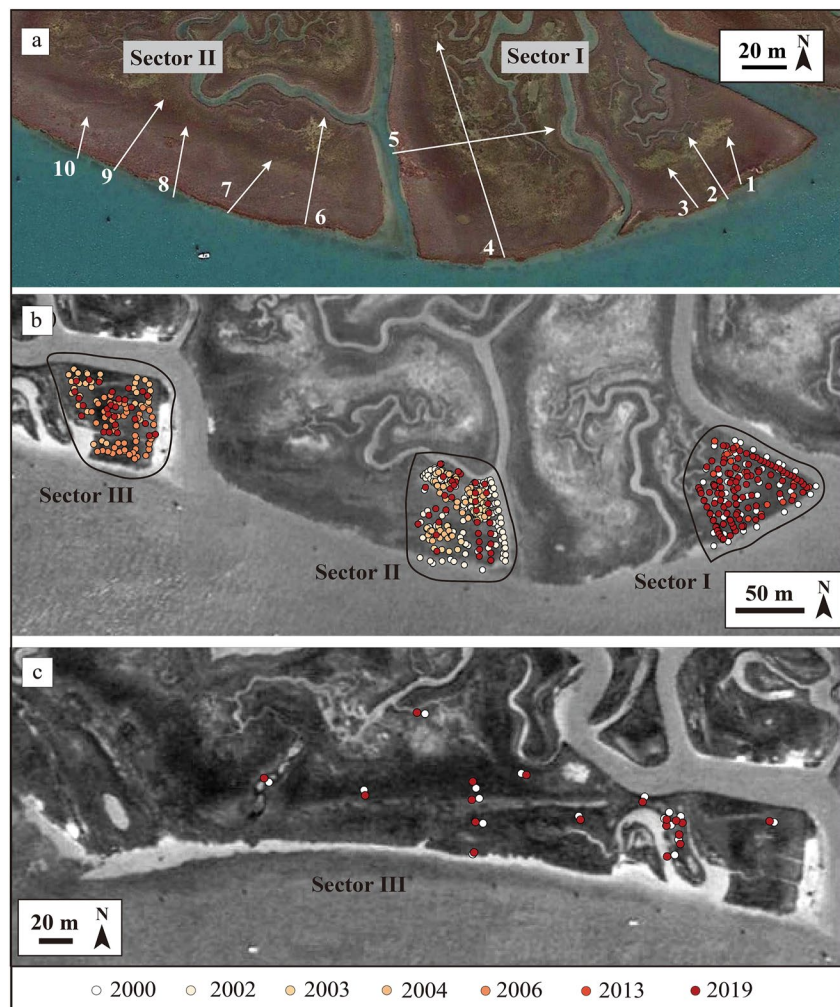
Figure 2. Highlights of different types of data used for the analyses. (a) Positions of coupled elevation-vegetation data collected along fixed transects within Sector I and Sector II (image ©Google/Landsat). (b) Positions of coupled elevation-vegetation data collected within marsh patches characterized by a high spatial density of data points (image © IKONOS). (c) Positions of paired sets of coupled vegetation-elevation data points derived from the surveys carried out in the years 2000 and 2019. Data were paired based on spatial proximity (see Section 2).

Table 2
Number of Data Points Contained in the Transect, Patch, and Paired-Point Data Sets in Different Years and Different Sectors of the San Felice Salt Marsh

	Transect data				Patch data										Paired-point data	
Marsh sector	Sector I		Sector II		Sector I				Sector II					Sector III		Sector III	
Year of survey	2013	2019	2000	2019	2000	2013	2019	2000	2002	2003	2004	2019	2004	2006	2019	2000	2019
Number of data points	73	71	21	21	48	49	97	18	129	57	40	36	42	56	27	17	18

2.3. Changes in Relative Mean Sea Level

Changes in mean sea level (i.e., the average sea level observed over a long period above a fixed datum, hereinafter MSL) within the Venice lagoon were computed based on water level measurements performed by a widespread network of tide gauges managed by the Venice Municipality (https://www.comune.venezia.it/it/archivio/1653). Tidal gauges measure water levels referred to the local, historical datum of Punta della Salute ("Zero Mareografico di Punta della Salute," ZMPS hereinafter; see https://www.comune.venezia.it/it/content/riferimenti-altimetrici). While the elevation of ZMPS was 23.56 cm below the IGM datum in 1968 (Figure 1c), recent remote sensing observations suggested that such differences increased at an average rate of about 0.05 cm/year (Figure 1c) due to natural and human-induced subsidence in Venice (Da Lio et al., 2018; Tosi et al., 2018). Therefore, the elevation of ZMPS in 2019 was approximately equal to 26.11 cm below the IGM datum (Figure 1c). Variations in relative mean sea level (RMSL, i.e., the algebraic sum of observed local soil subsidence and MSL changes) at the Punta Salute (PS) tidal gauge station (Figure 1a) are used here to represent RMSL changes in the San Felice marsh, due to its proximity to the PS gauge (Figure 1a). Indeed, differences in subsidence rates between these two sites (PS and San Felice) are negligible (Da Lio et al., 2017; Tosi et al., 2018) and high-resolution hydrodynamic numerical modeling (Tognin et al., 2022; Tommasini et al., 2019) suggests that water level differences between the two sites are negligibly small (order of 1 cm).

RMSL in the lagoon is influenced by fluctuations in MSL due to storm events and waves over short time scales (order of days; Mel et al., 2014), astronomic forcings over longer timescales (order of 1–10 years; Valle-Levinson et al., 2021), and by subsidence resulting from human activities at even longer time scales (order of decades to centuries; Tosi et al., 2018), thus displaying annual and interannual fluctuations around a general trend. Numerical modeling has documented that marsh elevations, and the related accretion rates, are unable to record the above recalled annual or interannual fluctuations in RMSL, but can track changes in the general trend of RMSL within a few decades (A. D'Alpaos et al., 2011; Kirwan & Murray, 2008). Hence, in order to properly analyze the effects of changes in RMSL on marsh surface and halophytic vegetation response at the San Felice site, we proceeded as follows. First, to ensure consistency with topographic survey data, we referred water levels measured at PS, originally referenced to the ZMPS datum, to the stable IGM datum by accounting for the elevation difference between the ZMPS and IGM datums in 1968 (23.56 cm), as well as for the subsidence rate (0.05 cm/year) of the ZMPS datum. Second, to represent the general trend of RMSL, rather than focusing on annual fluctuations to which marsh topography cannot adapt (A. D'Alpaos et al., 2011; Kirwan & Murray, 2008), we assumed linear changes in RMSL during the study period (i.e., from 2000 to 2019) and computed the RMSL of each year on record. Then, we referred the measured marsh platform elevations to the RMSL corresponding to the year when the topographic survey was performed, to determine whether marsh vertical accretion rates were able to compensate for RSLR. Finally, we used the approximated RMSL of each studied year to determine the realized vegetation distributions across marsh topographic gradients and to reconstruct potential changes in the preferred elevation range occupied by each halophytic species.

3. Results

3.1. Changes in Relative Mean Sea Level and Marsh Elevation

Our analyses highlight statistically significant changes in RMSL at the San Felice marsh over the studied period, with an average rate of RSLR estimated equal to 4.4 ± 1.5 mm/year based on linear regression of annual RMSL data (Figure S1 in Supporting Information S1). Such a rising trend in RMSL was resembled by data regarding marsh topographic elevation. Specifically, Figure 3 shows increasing marsh elevations relative to the IGM datum for all the marsh sectors, although with different rates. Indeed, vertical accretion rates (R_{acc}) range between 1.7 and 2.2 mm/year in Sector I (Figures 3a and 3d), with larger values being observed both in Sector II (R_{acc} = 3.4–4.3 mm/year; Figures 3b and 3e) and Sector III (2.4–2.9 mm/year; Figures 3c and 3f). We evaluate the statistical significance of changes in marsh elevation distributions, and therefore of the computed accretion rates, by means of a one-way ANOVA test performed at the standard significance level $\alpha = 0.05$ (Figure 3). Results suggest that marsh topographic changes and accretion rates are overall significant, except for those measured along the study transects in Sector I and for paired points in Sector III (p-value $> \alpha$; Figure 3).

Despite the observed general increase in marsh absolute elevation, however, field data suggest that marsh elevations referenced to RMSL have been consistently decreasing during the studied period (Figure 4), as a consequence

Table 3
Number of Data Points Surveyed for Each Vegetation Species in Different Years and Different Sectors of the San Felice Salt Marsh

	Year of survey																				
	2000			2002			2003			2004			2006			2013			2019		
	Marsh sector																				
Vegetation Species	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Salicornia	–	–	–	–	–	–	–	–	–	–	–	–	23	–	–	23	–	–	48	13	12
Spartina	18	11	15	–	87	68	47	17	50	–	24	37	–	–	–	27	–	–	33	5	12
Limonuim	46	24	36	–	100	206	–	68	149	–	38	125	–	–	55	77	–	–	170	81	59
Sarcocornia	51	36	56	–	174	211	31	65	126	–	38	56	–	–	98	62	–	–	185	79	75

of R_{acc} being typically lower than the average rate of RSLR (4.4 ± 1.5 mm/year). The analysis of individual transects in Sector I (transects 1–5, Figure S2 in Supporting Information S1) and Sector II (transects 6–10, Figure S3 in Supporting Information S1) confirms the above general trend. Data from individual transects in Sector I (Figure S2 in Supporting Information S1) show that while marsh elevations referred to the IGM datum did not display notable changes in time (consistent with the average accretion rate of 1.7–2.2 mm/yr described above), marsh elevations referenced to RMSL decreased in time, thus suggesting marsh inability to keep pace with rising relative sea levels. In contrast to transects in Sector I, transects in Sector II display a notable increase in marsh elevations referenced to the IGM datum (Figures S3a–S3e in Supporting Information S1). Hence, marsh elevations appear to remain stable relative to RMSL. This suggests that marsh sites in Sector II can cope with rising relative sea levels (Figures 3b and 3e; Figures S3f–S3j in Supporting Information S1), their average accretion rate
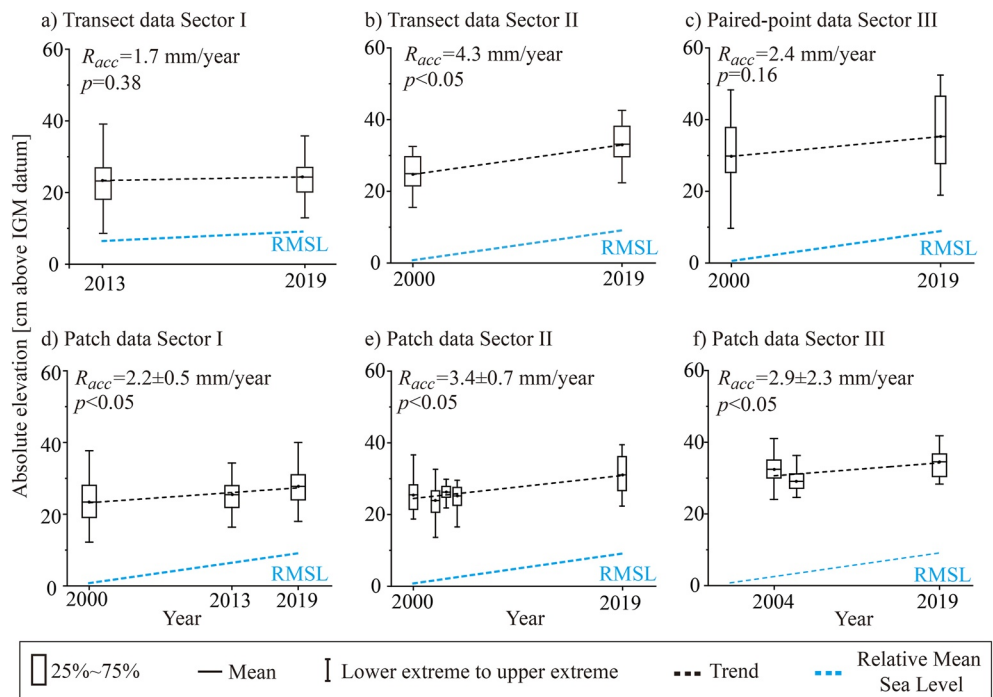

Figure 3. Box whisker plots of absolute marsh elevation distributions measured in different years with reference to the fixed IGM datum. (a, b) Elevation data measured along fixed transects in Sector I and II; (c) Elevation data measured at paired-data points in Sector III; (d–f) Elevation measured within patches with high data density in all the analyzed Sectors. Dashed blue lines in each panel represent the Relative Mean Sea Level referred to the IGM datum. The average value of marsh vertical accretion rate (R_{acc}) for each set of data is also shown, with R_{acc} being computed as the slope coefficient of the linear regression performed on average marsh elevations in different years. Finally, the statistical significance of differences between distinct elevation distributions shown in each panel was tested by means of one-way ANOVA, and the resulting p-values are shown in the corresponding panel.
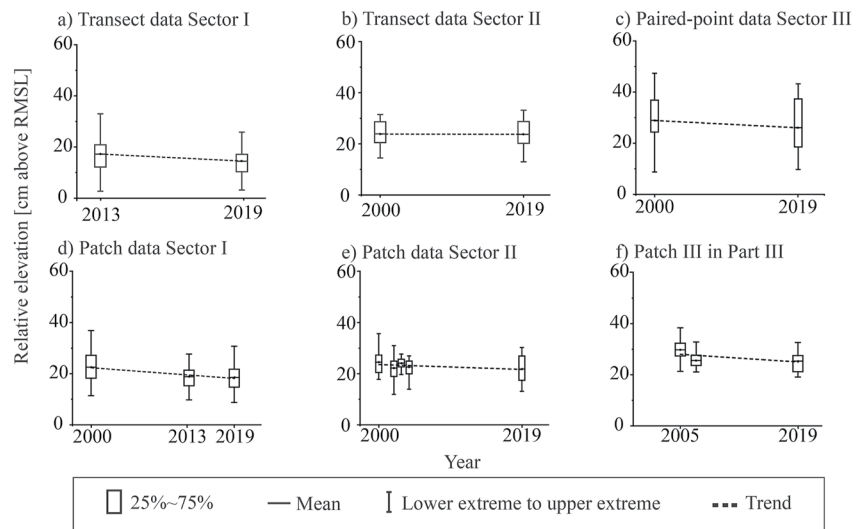
Figure 4. Box whisker plots of relative marsh elevation distributions measured in different years with reference to the relative mean sea level (RMSL). (a, b) Elevation data measured along fixed transects in Sector I and II; (c) Elevation data measured at paired-data points in Sector III; (d–f) Elevation data measured within patches with high data density in all the analyzed Sectors.

(3.4–4.3 mm/yr) being quite close to the observed rate of RSLR (4.4 ± 1.5 mm/yr). Data from individual transects also highlight that marsh elevations generally decrease with increasing distance from the nearest channel edge (Figures S2 and S3 in Supporting Information S1), thereby shaping a characteristic concave-up profile with higher elevations along marsh edges and lower areas in the innermost marsh portions. Such a concave-up profile has been observed earlier by several authors and is likely a consequence of the reduced ability of tidal flows to carry suspended mineral sediments to the marsh interior and to locations further away from the major tidal channels and creeks (Coleman & Kirwan, 2019; A. D'Alpaos et al., 2021; Rinaldo et al., 1999a, 1999b; Roner et al., 2016).
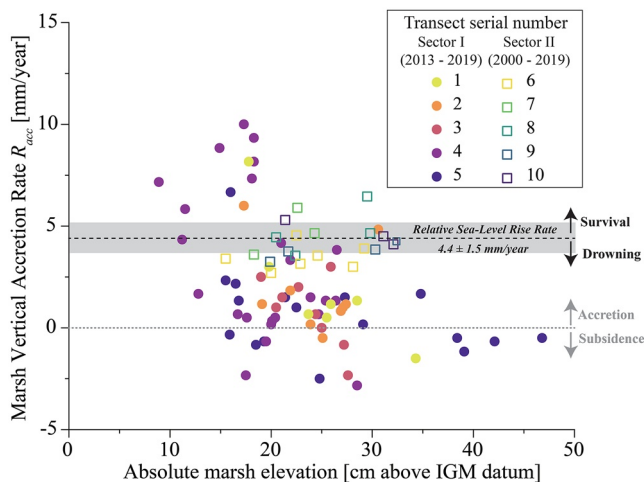
Elevation measurements at individual marsh sites allowed one to analyze the dependency of accretion rates (R_{acc}) on marsh geomorphology. Figure 5 shows that R_{acc} generally decreases with increasing elevations, indicating that coupled rates of organic and inorganic sediment deposition are higher at sites with lower elevations. A few marsh sites, characterized by high marsh elevations and located in transects within Sector I (filled dots in Figure 5), displayed a temporal decrease in elevation relative to the IGM datum, likely due to local subsidence (Da Lio et al., 2018; Tosi et al., 2018). On the one hand, this might suggest that enhanced R_{acc} in the lower marsh portions is likely to balance elevation loss caused by subsidence. On the other hand, however, when comparing accretion rates with the average rate of RSLR (i.e., 4.4 ± 1.5 mm/year), it becomes clear that most of the sites in Sector I could not keep pace with RSLR and are likely to drown. In contrast, data from individual transects in Sector II (empty squares in Figure 5) suggest higher chances of marsh survival, since accretion rates tend to match the rate of RSLR, consistent with our previous observations (Figures 3 and 4).

Figure 5. Changes in marsh vertical accretion rates (R_{acc}) as a function of local absolute marsh elevations. Solid dots represent R_{acc} measured from transects in Sector I, whereas hollow squares denote data derived from transects in Sector II. The dotted gray line highlights the null accretion state ($R_{acc} = 0$ mm/year), with data points falling above and below this line experiencing active accretion and subsidence, respectively. The dashed black line and gray shadow area indicate the average rate of relative sea-level rise (4.4 ± 1.5 mm/year), with points falling above (below) such a line being (not being) able to cope with rising relative-sea levels.

3.2. Changes in Vegetation Distribution Across Marsh Elevations

The available field data allowed us to analyze the realized distributions (i.e., realized ecological niches) of halophytic vegetation species, that is, the relative frequency at which each species encroaches marsh sites found at a given topographic elevation (Kuhn & Zedler, 1997; Levine et al., 1998; Pennings & Bertness, 2000; Snow & Vince, 1984). In agreement with earlier
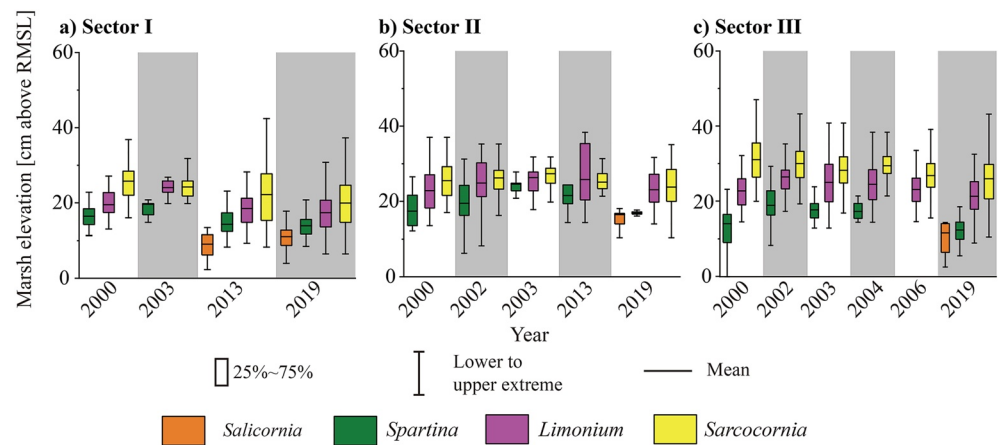
Figure 6. Box whisker plots of realized vegetation distributions referred to the Relative Mean-Sea Level (RMSL), observed in different years for Sector I (a), Sector II (b), and Sector III (c) at the San Felice salt marsh.

literature findings (Morris et al., 2005; Mudd et al., 2009; Redfield, 1972; Silvestri et al., 2005), our analyses suggest that each species is characterized by a maximum potential for presence and growth at a given optimal elevation, with different species confined to relatively narrow elevation ranges. This gives rise to a pronounced ecological zonation according to local marsh elevation, with *Salicornia* typically encroaching the lowest marsh portions, *Spartina* occupying slightly higher elevations compared to *Salicornia*, *Limonium* being found at even higher elevations, and *Sarcocornia* colonizing the uppermost parts of the marsh (Figure 6) (Belluco et al., 2006; Finotello et al., 2020). Realized vegetation distributions of different species and in different years are summarized in Figure 6 for all the three studied Sectors, with elevations being referred to the RMSL rather than to a fixed topographic datum. Despite individual species being preferentially found at different elevations in different years, our data show that the sequence in vegetation zonation remained consistent through time with *Salicornia, Spartina, Limonium, and Sarcocornia* being found at progressively higher elevations with reference to RMSL. It is also worthwhile noting that individual halophytes display distinct realized distributions in different marsh sectors, the latter being however quite proximal to each other and separated by just a few hundred meters.

Temporal changes in realized distributions of individual species in distinct marsh sectors are shown in Figure 7, with reference to the IGM datum. Data suggest that the realized distributions tend to shift upmarsh as sea levels rise, with individual species being found at progressively higher elevations relative to the IGM datum. The rate at which such upmarsh migration occurs (R_c), computed by linearly interpolating the mean values of vegetation distributions through time, appears to be strongly species-specific (see Table 4), with a minimum and maximum value of $R_{c_{MIN}} = 1.5 \pm 0.3$ mm/year and $R_{c_{MAX}} = 3.6 \pm 1.1$ mm/year observed for *Sarcocornia* in Sector I and *Limonium* in Sector II, respectively. Once R_c is compared to the average rate of RSLR, data indicate that Sector II stands the highest chance of keeping up with the current RSLR, with *Sarcocornia* and *Limonium* being the species more likely to be able to track RSLR by migrating upmarsh. However, if one considers vegetation distributions referenced to the RMSL (Figure 8), it clearly emerges that the preferred elevation at which individual species are found tends to either decrease in time (Sector I, Figures 8a–8d; Sector III, Figures 8h–8j) or remain approximately constant (Sector II, Figures 8e–8g). Our vegetation records along transects in Sector I (Figure S2 in Supporting Information S1) show that, despite the possible occurrence of species replacements and transitions between vegetated and unvegetated states, local vegetation underwent only minor changes over the studied period, suggesting vegetation persistence despite decreasing elevations relative to the mean sea level. Similar results can be drawn based on transect vegetation data collected in Sector II (Figure S3 in Supporting Information S1), where vertical accretion rates are more sustained and the marsh is likely to better cope with RSLR.

The available records of vegetation-cover evolution also allow one to analyze changes in species assemblages through time, highlighting the absence of the annual *Salicornia* species until 2004. The latter species was instead consistently recorded between 2006 and 2019 in Sector I and in all Sectors in 2019 (Table 3; see also Figures 6–8), pointing to a possible initial encroachment event and later successful colonization in the period 2004–2006. In addition, the perennial *Spartina* was virtually absent in 2006 in all Sectors, despite being sparsely present in all the previous years, thereby potentially suggesting a significant dieback event. Notably, the observed
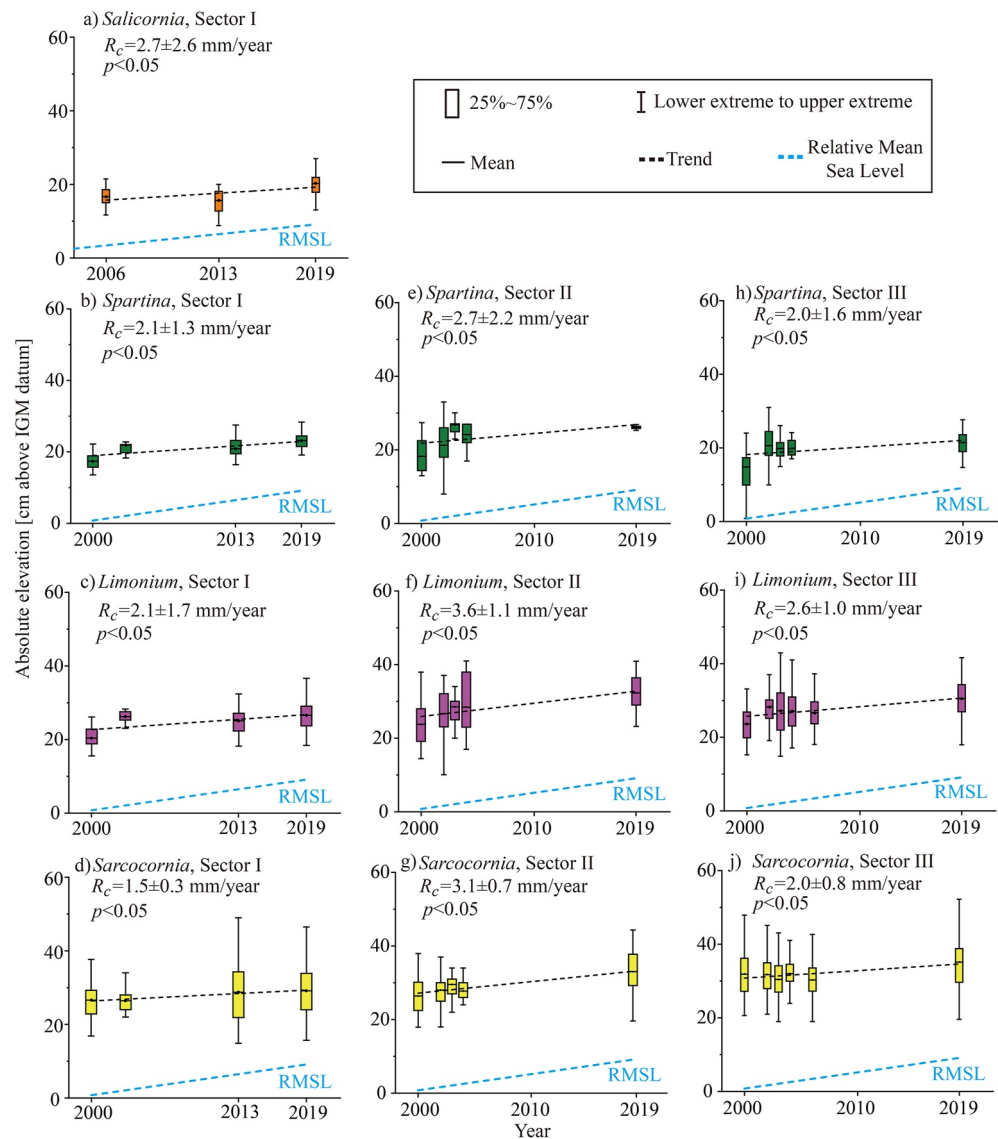
Figure 7. Temporal evolution of realized vegetation distributions computed based on absolute marsh elevation (i.e., referred to the fixed IGM datum) observed for different species and in different Sectors of the San Felice salt marsh. The average rate (R_c) at which each species changed its preferred (i.e., average) elevation in different Sectors is also shown in the corresponding panel, with R_c being computed as the slope coefficient of the linear regression performed on the average elevation of species distributions in different years. Finally, the statistical significance of differences between distinct vegetation distributions shown in each panel was tested by means of one-way ANOVA, and the resulting p-values are shown in the corresponding panel.

changes in species assemblages prior to 2006 are consistent with earlier findings by Belluco et al. (2006), thus supporting the validity of the analyses we presented in this work.

4. Discussion

4.1. Salt-Marsh Vulnerability to Rising Sea Levels

Our measurements of marsh platform elevation (Figure 3) show that all the monitored marsh Sectors increased their absolute elevations (above the fixed IGM datum) during the study period, albeit with distinct vertical

Table 4
Rate of Changes (R_c) in the Preferred (Average) Vegetation Elevation of Each Species Between the Years 2000 and 2019

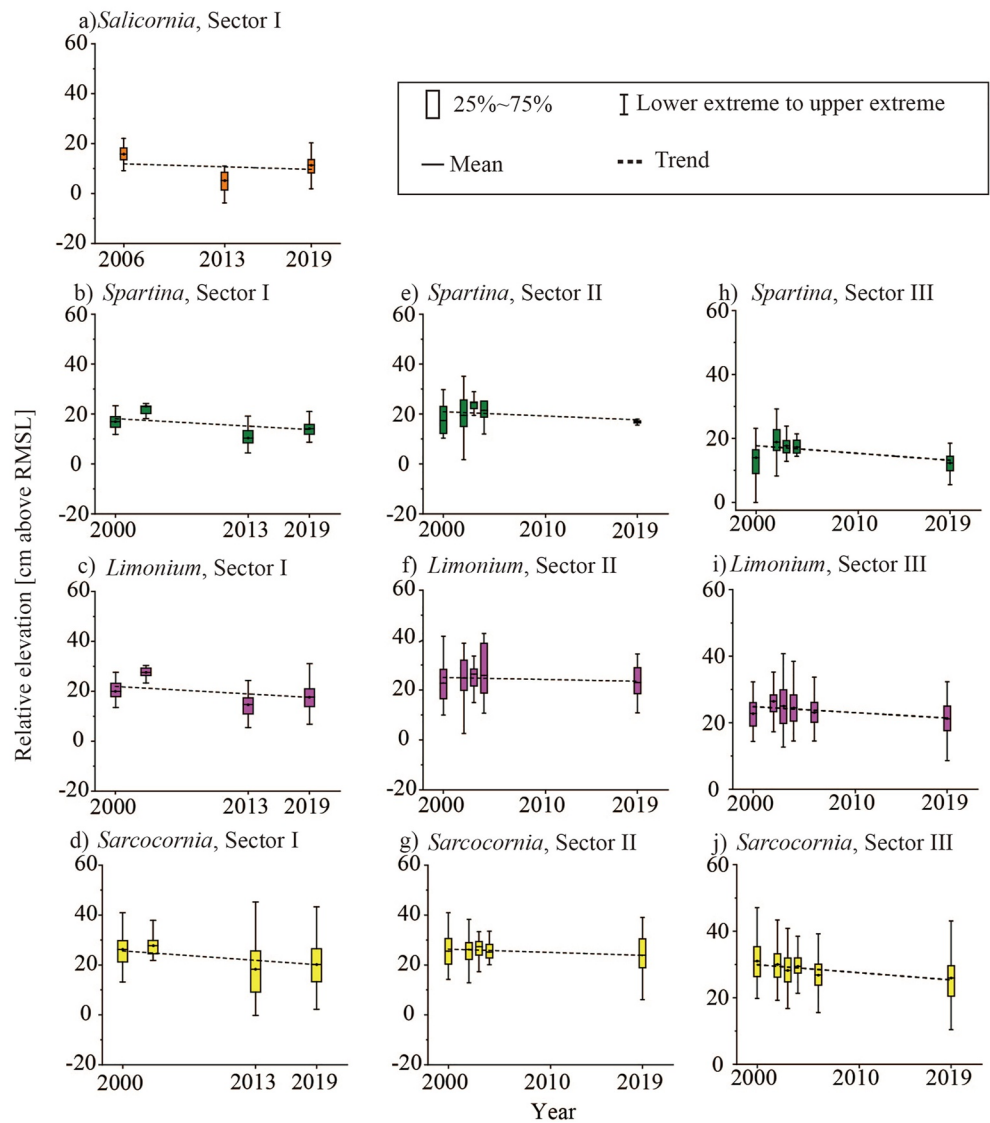|	Sector I	Sector II	Sector III	Rate of RSLR (mm/year)
Salicornia	2.7	–	–	4.4
Spartina	2.1	2.7	2	
Limonium	2.1	3.6	2.6	
Sarcocornia	1.5	3.1	2	

Figure 8. Temporal evolution of realized vegetation distributions computed based on relative marsh elevation (i.e., referred to the Relative Mean-Sea Level, RMSL) observed for different species and in different Sectors of the San Felice salt marsh.

accretion rates (R_{acc}) in each Sector (R_{acc} = 1.7–2.3 mm/year in Sector I; R_{acc} = 3.4–4.3 mm/year in Sector II; R_{acc} = 2.4–2.9 mm/year in Sector III). Hence, accretion rates appear to be strongly site-specific, displaying significant variations even among sites separated just by a few hundred meters. In particular, marsh elevation measurements along the studied transects suggest that R_{acc} increases with decreasing marsh elevation (Figure 5), likely because organic production is typically higher in the lower marsh portions, thus enhancing vertical accretion through organic matter deposition (Janousek et al., 2020; Morris et al., 2002; Roner et al., 2016). Finally, one might wonder why significantly higher R_{acc} is observed in Sector II compared to Sectors I and III (Figure 3). We interpret this data in relation to the higher rate of marsh-edge lateral retreat (ζ_L) that characterizes Sector II, where ζ_L = 0.39 ± 0.16 m/year, in comparison to both Sector I (ζ_L = 0.29 ± 0.08 m/year) and Sector III (ζ_L = 0.11 ± 0.12 m/year; see Figure S4 in Supporting Information S1). Sediments eroded from the marsh boundary can be redistributed over the marsh platform by waves and tides, thus helping the marsh to vertically keep pace with RSLR while retreating horizontally (Hopkinson et al., 2018; Mariotti & Carr, 2014; Priestas et al., 2015). However, quantitative descriptions of the link between marsh boundary retreat and vertical deposition are still lacking, thus calling for spatially extensive field observations and modeling to facilitate the analysis of future marsh ecomorphodynamic evolution (e.g., Kalra et al., 2021).

Notwithstanding generalized marsh vertical accretion, the majority of marsh sites in our study area lost elevation with respect to the RMSL, because the sum of mineral and organic sediment deposition was not enough to counterbalance the ongoing RSLR, the latter being in the order of 4.4 ± 1.5 mm/year on average. This suggests that the San Felice marsh experienced a submergence trend over the monitoring period. Possible explanations for such a drowning trend include (a) accelerating rate of RSLR, with the present-day value of 4.4 ± 1.5 mm/year being significantly higher than the average RSLR rate (about 3.5 mm/year) observed in the Venice lagoon over the last century (Carbognin et al., 2004; Marani et al., 2007); (b) the relatively low concentration of suspended sediment ($C_0 \approx 10$ mg/L on average) in the Venice lagoon waters (Venier et al., 2014), which is mostly caused by diversion of major freshwater rivers to the open sea (Marani et al., 2007; Tommasini et al., 2019); and (c) the microtidal regime that characterizes the lagoon, which is known to limit marsh resilience to changing rates of RSLR and sediment supply (A. D'Alpaos et al., 2011; Ganju et al., 2017; Kirwan & Guntenspergen, 2010). The observed drowning trend is likely to continue in the upcoming years, since the mean sea level is projected to rise further and the supply of mineral sediment to the marsh platform will be further reduced by the activation of the mobile floodgates designed to protect Venice city from flooding during storm-surges (see thorough discussions in Tognin et al., 2022, 2021). This calls for mitigating and restoring interventions aimed at enhancing mineral sediment supply by, for example, redirecting rivers into the lagoon or artificially adding sediments that could be later reworked and redistributed by waves and tides.

Overall, our analyses highlight the need of assessing marsh vulnerability to rising relative sea levels with reference to the current, local value of RMSL, rather than by referring to a fixed, absolute datum. This is because marsh drowning can occur even if the absolute elevation of the marsh platform increases through time, since the rate of marsh vertical accretion might be not enough to counterbalance the rate of RSLR due to coupled eustatism and soil subsidence.

4.2. Vegetation Response to Rising Relative Sea Levels

Changes in realized vegetation distributions demonstrate that halophytes tracked the increase in marsh absolute elevation by shifting their preferred habitat toward higher marsh portions (relative to the IGM datum), in this way modifying the typical range of elevations within which each species is observed (Figure 7). Nevertheless, the species-specific rates (R_c) at which distinct species are found to migrate upmarsh are consistently lower than the average rate of RSLR (4.4 ± 1.5 mm/year) over the study period, thus indicating that realized vegetation distributions shifted toward lower elevations with reference to RMSL (Figure 8). Such a loss of relative marsh elevation is expected to increase physical (abiotic) stresses on marsh vegetation, mostly due to enhanced salinity as well as flooding frequency and duration (i.e., hydroperiod), thus producing relevant changes in the marsh community assemblages and zonation patterns (Pennings & Bertness, 2000; Pennings & He, 2021). This is because an inherent tradeoff typically exists between plant competitive and stress-tolerance abilities, such that competitively superior species (e.g., *Limonium* and *Sarcocornia*) occupy the more elevated, least stressful marsh portions of the marsh and displace competitively inferior, highly stress-tolerant plants (e.g., *Spartina* and *Salicornia*) to the lower, more stressful portions of the intertidal frame (see Pennings & He, 2021, and references therein). Therefore, in the case of San Felice, one would expect *Spartina* and *Salicornia* to expand their optimal range of elevation at the expense of *Limonium* and *Sarcocornia* as a result of the observed decreasing marsh elevation relative to the mean sea level. On the contrary, instead, we did not observe consistent replacements of dominant species along our studied transects (Figures S3 and S4 in Supporting Information S1), suggesting that vegetation can tolerate the deterioration of physical conditions and persist in its original position even in the face of RSLR. As a consequence, the observed shift of halophytic species toward higher (absolute) elevations did not alter the pre-existing vegetation zonation across marsh topographic gradients (Figure 6). In fact, our data highlight that halophytic species are distributed according to a typical sequence with increasing elevations, and that such a sequence remained consistent over the 20-year studied period (Figure 6). To our best knowledge, consistency of salt-marsh zonation sequence over a period of nearly two decades had never been observed to date and is of critical importance to inform and test ecomorphodynamic models aimed to reproduce marsh evolution in highly biodiverse settings characterized by multi-species assemblages (Brückner et al., 2019; Da Lio et al., 2013; A. D'Alpaos et al., 2007; Finotello et al., 2022; Marani et al., 2013).

Among the variety of processes that may contribute to the persistence of vegetation in spite of RSLR, it is worth recalling that biotic interactions in tidal marshes depend strongly on local population density, as well as on

habitat quality and size (Bertness & Ellison, 1987; Bouma et al., 2009). Hence, pre-existing and spatially dense marsh perennials, which reproduce mostly vegetatively rather than by seedling, have competitive advantages in colonizing available bare patches produced by local vegetation dieback (Bertness & Ellison, 1987; Bullock et al., 2017; Finotello et al., 2022). Moreover, species-specific physiological traits, such as tissue porosity and tissue O_2 status, also contribute to vegetation tolerance to the RSLR-related increase in hydroperiod and salinity (Pellegrini et al., 2017). All the above-recalled processes allow halophytes to respond to RSLR by persisting in their original position, rather than by rapidly modifying their preferred habitat through competitive displacement (Strain et al., 2017). Within our studied marsh, halophytic vegetation appears capable to tolerate the deterioration of physical conditions caused by RSLR rate in the order of a few millimeters per year through biotic interactions and improvement in soil aeration (Marani et al., 2006; Pennings et al., 2003). Records of vegetation cover along transects in Sector I (Figure S2 in Supporting Information S1), where the marsh is likely subjected to drowning and did not display relevant species replacement over 6 years (2013–2019), confirm this speculation.

However, there should clearly exist a critical threshold in the rate of RSLR beyond which vegetation species, or at least some of them, cannot persist in their original position and are destined to be replaced. Whether such replacement will lead to the disappearance of some species rather than to the synchronous upmarsh migration of all of them is hard to predict. This is because vegetation migration due to geomorphological displacement is affected and possibly limited by several factors, including; (a) the ability of vegetation species to operate as eco-engineers and ameliorate their own habitat conditions through, for example, organic matter deposition and sediment particle capture (Marani et al., 2013); (b) the relative abundance of marsh sites with suitable elevations above RMSL for the establishment of individual species; and, (c) the overall marsh size, that is by definition limited and can change through time as a consequence of marsh expansion, retreat, and fragmentation (e.g., Brückner et al., 2019; Duran Vinent et al., 2021; Finotello et al., 2022; Kirwan & Gedan, 2019; Marani et al., 2011; Murray et al., 2022). With specific reference to the analyzed San Felice salt marsh, the ongoing loss of elevation with respect to RMSL is likely to reduce the relative extent of high-marsh areas, thereby limiting the rate (R_c) at which vegetation can move upmarsh. This might contribute to explain the reduced values of R_c (relative to the RSLR rate) that we observed from our data.

In view of the above, we speculate that in the near future, in the San Felice marsh *Limonium* and *Sarcocornia* will still occupy positions higher than those preferred by *Spartina* and/or *Salicornia* even if the rising trend in RMSL will continue. However, if RSLR will accelerate beyond a critical threshold value—due to, for example, increasing eustatic sea level rise or enhanced soil subsidence—or if mineral sediment supply will be further reduced, some halophytic species will not be able to survive and will likely disappear, leading to a decrease in biodiversity. In this scenario, the species with higher tolerance to waterlogging and other abiotic stresses, such as *Spartina* and *Salicornia*, are the most likely to persist. Although earlier studies carried out in mid-latitude marshes worldwide support our hypothesis by documenting the migration of lower-marsh species into the high marsh due to accelerating RSLR (e.g., Donnelly & Bertness, 2001), further research efforts and evidence from coupled long-term monitoring and numerical modeling will be needed to support these speculations. Indeed, predicting the ecomorphodynamic evolution of tidal wetlands is not a straightforward task, as several factors can lead to critical changes in community assemblages.

First, sudden, possibly temporary changes in environmental conditions, and time lag in the ecosystem response to such changes, could affect the evolution of species assemblages through time. For example, the temporary absence of *Spartina* observed in San Felice between 2004 and 2006 was likely due to a dieback event associated with the heat wave that stroke the Mediterranean Sea in 2003 (García-Herrera et al., 2010).

Second, the successful establishment of alien, potentially invasive species can also determine changes in biotic interactions and the resulting marsh vegetation zonation, thereby affecting the evolution of the whole marsh ecosystem. Salt marsh encroachment by *Salicornia* at San Felice in 2006, with offsprings likely arriving from neighboring marshes where *Salicornia* was already abundant (Silvestri et al., 2005), altered vegetation zonation by forcing existing lower-marsh species to adapt to higher and relatively narrower elevation ranges.

Finally, increases in atmospheric CO_2 and nutrient levels due to, for example, coastal eutrophication, are likely to change biotic interactions between salt-marsh halophytes and their resultant zonation across environmental stress gradient (Johnson et al., 2016; Ratliff et al., 2015). In particular, stress-tolerant species might become dominant competitors under high nutrient levels, thereby affecting competitive outcomes (Emery et al., 2001), whereas

enhanced atmospheric CO_2 concentrations can significantly increase the threshold rate of RSLR that initiates marsh submergence (Ratliff et al., 2015).

All the above-described processes contribute to explaining why the rate (R_c) at which realized vegetation distributions move across marsh topographic gradients varies significantly from species to species, possibly suggesting species-specific response and adaptation mechanisms to changing relative sea levels.

As a concluding remark, some limitations in the analyses presented in this study need to be recalled. An important source of uncertainty is that the position and number of surveyed marsh points change from year to year, except for data coming from fixed measuring transects (Figure 2a). This might have affected the accuracy of the estimated marsh accretion rates and vegetation elevation changes, thus calling for further field observations. Another limitation of our approach is associated with the fact that, although the number of in situ observations is large (2,237 in total), our surveys did not cover the whole marsh extent. Our analyses showed differential marsh vulnerability and vegetation response to RSLR even at adjacent sites, suggesting that marsh community assemblages and their response to RSLR are likely to be extremely site-specific (e.g., Silvestri et al., 2005). This calls for large-scale observations of marshes found in distinct locations. However, field observations of the type considered in the present study are time- and resource-consuming. Recent developments in mapping marsh vegetation and elevation through multi- or hyper-spectral and lidar-derived data (Pinton et al., 2021; Yang et al., 2020) can facilitate marsh monitoring, reducing research costs while increasing the spatial and temporal resolution of data. This will lead to a significant improvement in our understanding of ecomorphodynamic processes that shape tidal marshes, with relevant implications for the conservation and restoration of these valuable ecosystems.

5. Conclusions

We analyzed the coupled elevation-vegetation response to changes in RMSL in the microtidal San Felice salt marsh (Venice lagoon, Italy) by using accurate measurements of marsh topographic elevation and vegetation cover, derived from 7 distinct surveys carried out between 2000 and 2019. Such a unique data set spanning nearly two decades allowed us to highlight that the studied marsh responded to rising mean sea levels by increasing its absolute elevations (i.e., relative to a fixed datum in time) through vertical accretion driven by joint organic and inorganic sediment deposition. However, a declining trend in marsh elevations was found with reference to the relative mean sea level (RMSL), which accounts both for eustatic sea level rise and soil subsidence. Thus, it emerged that the studied marsh underwent drowning overall. The rate of such drowning is however strongly site-specific due to significant variations in marsh vertical accretion rates (range 1.7–4.3 mm/year) even at neighboring sites located just a few tens or hundreds of meters apart. Differences in vertical accretion rates are likely related to local conditions, such as differential supply rates of mineral sediments and changes in local marsh topography, with accretion rates increasing with decreasing marsh elevations.

Vegetation species tracked marsh vertical accretion by shifting their realized distributions toward higher marsh portions, such that a given species is preferentially observed at progressively higher elevations with reference to a fixed datum. While halophytes migrated upmarsh following species-dependent rates, these migrations rates were found to be consistently lower than the average rate of RSLR (4.4 ± 1.5 mm/year), thus indicating that realized vegetation distributions have actually shifted toward lower elevations with reference to RMSL. Although such a loss of relative elevation should increase abiotic stresses due mostly to longer waterlogging periods and favor lower-marsh species that are typically the best stress tolerators, we did not observe significant replacements of dominant species across our measuring sites. In fact, a sequential species zonation as a function of marsh elevation was consistently found, with *Salicornia*, *Spartina*, *Limonium*, and *Sarcocornia* observed at progressively more elevated marsh sites. We observed for the first time the consistency of sequential vegetation zonation in the face of RSLR over nearly two decades, suggesting that such consistency is a signature of vegetation resilience to changes in environmental forcing. While several biotic processes can aid vegetation species to persist in their original position despite RSLR, we argued that a critical threshold should exist in the rate of RSLR beyond which halophytes are no longer able to cope with enhanced abiotic stresses caused by rising relative sea levels. Hence, beyond said threshold, individual species could survive only by rapidly modifying their preferred habitat and colonizing new marsh portions through competitive displacement, with those species not able to adapt to new environmental conditions going extinct.

Our observations altogether point to an intimate interdependency between geomorphological and ecological dynamics in tidal salt marshes and call for the need to consider local marsh elevations referenced to RMSL when

assessing marsh vulnerability to RSLR. Spatially distributed monitoring of coupled salt-marsh elevation and vegetation evolution will be needed in the future to expand the results presented in this study and properly inform and test ecomorphodynamic models of marsh evolution, in this way highlighting potentially different adaptability of both individual halophytic species and entire marsh ecosystems to rising relative sea levels.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

- Data—Field data of marsh surface elevations and vegetation distributions are freely available at https://figshare.com/s/f4593b121a21bbe795b4. The tidal gauge data are freely available from the website of Venice Municipality (https://www.comune.venezia.it/it/archivio/1653).
- Software—Linear fittings were carried out by using Matlab software version R2022a (MathWorks, 2022); Statistical tests and figure plots were performed in Origin software version 2018 (OriginLab Corporation, 2018, Northampton, MA, USA).

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