LIMNOLOGY
and
OCEANOGRAPHY

Limnol. Oceanogr. 70, 2025, 792–805

doi: 10.1002/lno.12795

RESEARCH ARTICLE

Recovery from drought-induced dieback may lead to modified salt marsh vegetation composition

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Abstract

Salt marshes are vital but vulnerable ecosystems. However, our understanding of disturbance-induced dieback and recovery processes in multi-specific marshes remains limited. This study utilized remote sensing data (2001–2021) to analyze a dieback event and subsequent recovery in the multi-specific San Felice marsh within the Venice lagoon, Italy. A significant dieback of *Spartina maritima* (*Spartina*) was identified in 2003, likely triggered by a drought event and heat stress. This resulted in a conversion of 4.6 ha of marsh predominantly colonized by *Spartina* (fractional cover of *Spartina* > 50%) in 2001 to bare soil in 2003. These bare areas were then gradually encroached by vegetation, indicating the occurrence of the recovery. Despite gradually gaining ground, *Spartina* only dominated 6.4 ha marshes in 2021, significantly lower than its pre-dieback area (21.3 ha). However, other species also encroached on the dieback area, such that the aboveground biomass returned to pre-dieback levels, indicating that the shift in marsh species composition that occurred as a consequence of the event compensated for this ecosystem service. Vegetation recovery, spanning from 1 yr to more than 18 yr, was found to be slowest in areas of lowest elevation. This study provides evidence that dieback and recovery can modify the species composition of multi-specific marshes over decades. These insights contribute to a better understanding of marsh resilience to drought and elevated temperature, both of which are likely to increase in the future.

Salt marshes are crucial transitional zones between land and sea, providing critical ecosystem services, such as coastal protection (Möller et al. 2014), carbon sequestration (Rosentreter et al. 2023), and biodiversity support (White, Vogt, and Arin 2000). However, salt marshes face numerous threats, including rising sea levels (Yang et al. 2023), reduced sediment supply (Blum and Roberts 2009), wave-driven erosion (Marani et al. 2011), and intensified human activities (e.g., Deegan et al. 2012). Loss of vegetated marsh can reduce the marsh's ability to adapt to sea-level rise and undermine its resilience against storms and lateral erosion (Coleman and Kirwan 2019), potentially leading to irreversible shifts to tidal flats.

Climate change-induced stressors, such as rising temperatures and increased drought frequency, have been observed to cause sudden and widespread mortality of the salt marsh cord grass *Spartina alterniflora* in marshes in the Southeastern United States (Alber et al. 2008). These areas were typically recolonized by *Spartina alterniflora* once favorable conditions returned. However, many existing analyses focus on short timeframes, spanning only a few months or years (Alber et al. 2008; Crain, Albertson, and Bertness 2008; Silliman et al. 2012; Yang, Alexander, and Alber 2024). Moreover, *Spartina alterniflora* dieback may create opportunities for other species to encroach on the affected areas, potentially modifying marsh species composition (McKee, Mendelssohn, and Materne 2004), with implications for primary

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Associate editor: Ruth Reef

Data Availability Statement: Fractional cover maps are freely available at: https://figshare.com/s/17a46ecf8b38a53142bc. The binary maps in the years without field surveys are freely available at: https://figshare.com/s/1f3c6d2f2d382167888e.

production, food webs, and other processes. Evaluating dieback and recovery in multispecies marshes, particularly over large scales and long time periods, is important for understanding marsh response to these events and predicting their future dynamics.

In 2003, a dieback event of *Spartina maritima* was reported in marshes in the Venice lagoon and other areas of the Mediterranean (Strain et al. 2017; Wong et al. 2018). This event led to the near disappearance of *Spartina maritima* from some marshes, where it had previously been the dominant plant before the dieback (Belluco et al. 2006). The event was speculated to be triggered by a severe heatwave event and associated drought (Garcia-Herrera et al. 2010; Strain et al. 2017). *Spartina maritima* started to reappear approximately 10 yr after this event (Yang et al. 2023). However, the extent of the dieback and the response of the other salt marsh species present in the system have? not been explored.

In this paper, we explored dieback and recovery of marsh vegetation in the San Felice marsh, a multi-specific salt marsh located in the Venice lagoon (Italy), using a time series of satellite remote sensing data covering the period 2001–2021. The main aims of this study were (i) to document the *Spartina maritima* dieback and its association with drought and (ii) to assess recovery and its long-term effect on species composition and aboveground biomass (AGB).

Data and methods

Study site

This work took place in the San Felice (45°28′N, 12°27′E) salt marsh, a natural marsh located in the northern part of the Venice lagoon (Fig. 1a,b). The Venice lagoon, situated along the northeastern coast of Italy, is the largest lagoon in the Mediterranean Sea with an area of about 550 km^2. This lagoon is characterized by a semi-diurnal tide with an average tidal range of about 1 m. It is connected to the Adriatic Sea through the Lido, Malamocco, and Chioggia inlets. Salt-marsh area in the Venice lagoon has strongly decreased in the last century, mainly because of drowning, wave-induced lateral erosion, and human activities (Silvestri et al. 2018; Tognin et al. 2021; Tommasini et al. 2019). Over the last two decades, the San Felice marsh (Fig. 1b) has experienced a submergence trend, with sea level rise outpacing local accretion (Yang et al. 2023). This has led to the suggestion that waterlogging is a major abiotic stressor in the San Felice marsh (Silvestri, Defina, and Marani 2005), independent of the dieback that is considered here.

This San Felice marsh hosts halophytic vegetation species typical of the Venice lagoon and the Mediterranean climate, including *Salicornia veneta* (hereafter "*Salicornia*"), *Spartina maritima* (hereafter "*Spartina*"), *Limonium narbonense* (hereafter "*Limonium*"), *Sarcocornia fruticosa* (hereafter "*Sarcocornia*") and *Juncus maritimus* (hereafter "*Juncus*") (Silvestri, Defina, and Marani 2005). These species display a distinct elevational sequence, that is, *Salicornia*, *Spartina*, *Limonium*, *Sarcocornia*, and *Juncus* prefer to colonize progressively higher marsh portions (Silvestri, Defina, and Marani 2005; Yang et al. 2023). Note that another *Spartina* genus species, *Spartina anglica* was first reported in this marsh in 2021 (Cuenca Portillo 2022). We did not distinguish between *Spartina maritima anglica* and *Spartina maritima maritima* in this analysis, referring to both as *Spartina*, because *Spartina anglica* did not appear until near the end of our observation period and we could not distinguish between them with remote sensing. However, it is limited in extent, forming sparse and small patches of a few square meters in size (Cuenca Portillo 2022).

Remote sensing data classification

We utilized a series of remote sensing data representing 9 yr between 2001 and 2021 to estimate changes in vegetation cover over time (Table 1). For six of these years (e.g., 2001, 2003, 2006, 2013, 2019, 2021), we had paired field observations that we used to classify vegetation to a species level. For the remaining 3 yr (e.g., 2004, 2007, 2009), we produced a binary classification (vegetated or bare) that allowed us to fill in our estimates for time to recovery. Below we describe the satellite data, initial data processing, field data collection, and classification.

Satellite imagery

Satellite data used in this study were acquired from three different multispectral sensors (IKONOS, QuickBird II, and World-View 2), which vary in terms of both their bands and spatial resolutions. These data were cloud free and were matched as closely as possible to the time of the field surveys (Table 1). Although most data were collected during the summer (June–August), data from 2019 and 2013 were taken in fall (November) and winter (December), respectively, as no other summer cloud-free acquisitions were available for these 2 yr. Data not acquired in the growing season may influence vegetation identification, particularly for annuals such as *Salicornia* that may not be identifiable at all times of year. Tide levels at the time of the data collection can also affect classification accuracy as higher tides (e.g., > 25 cm) can obscure parts of the marsh. As shown in Table 1, tidal levels exceeded 25 cm on four of the nine acquisition dates due to a lack of other cloud-free satellite images taken at lower tidal levels.

We conducted atmospheric corrections, pan-sharpening and georeferencing of each image (Supporting Information). Then, in ArcGIS 10.8, we manually digitized channels that cut through and delimit the San Felice marsh and the inner ponds according to the boundary of vegetation cover for each georeferenced image (Supporting Information Fig. S1a). The channelized area and inner pond were not included in the following procedures, since the analyses were exclusively focused on changes in marsh vegetation.

Field data

Field surveys were conducted in 2001, 2003, 2006, 2013, 2019, and 2021. For all years, regions of interest, a few square

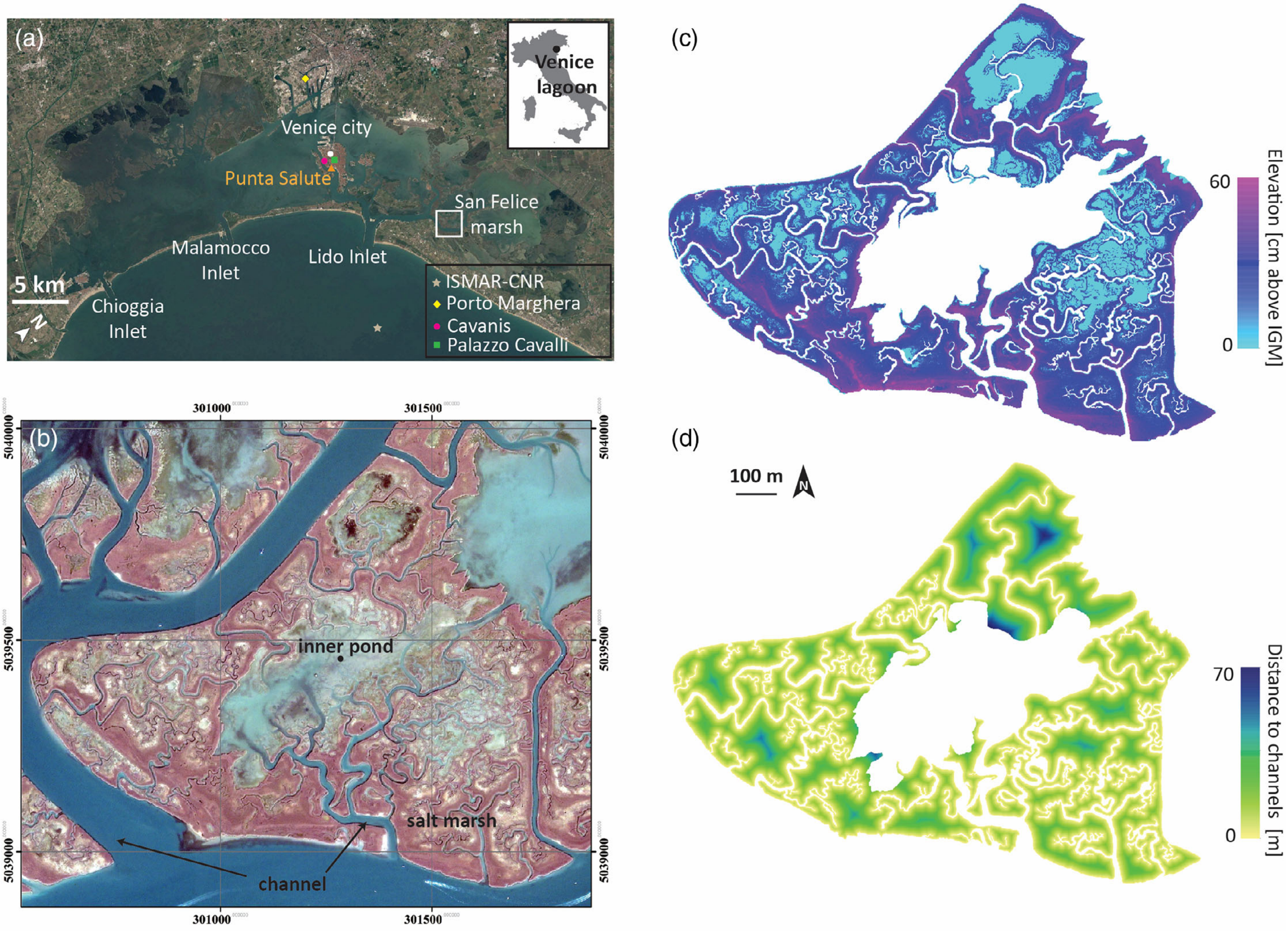


Fig. 1. Research area. (**a**) Aerial view of the Venice lagoon (Italy) (base map © Google TerraMetrics). The locations of the San Felice marsh, as well as sites measuring meteorological data located at Porto Marghera, Cavanis, Palazzo Cavalli, and The Institute of Marine Sciences of the National Research Council of Italy (ISMAR-CNR) stations are highlighted. The location of the Punta Salute tidal gauge is also exhibited; (**b**) zoomed-in aerial view of the San Felice marsh. Examples of different geomorphological features, that is, salt marshes, channels and the inner pond are also indicated. The base map of (**b**) is the combination of red, green, and blue bands acquired by the IKONOS sensor in 2001; (**c**) the Digital Terrain Model of the San Felice marsh, with a reference to the Istituto Geografico Militare (IGM) datum (*see* "Elevation datums" in the Supporting Information for details, Wang et al. 2009); (**d**) an example displaying the distance of each marsh pixel to channels, derived from channel digitization based on Word-View 2 data in 2019.

meters in size, were randomly selected to represent a wide variety of vegetation, including mono- and multi-specific patches. At each site, the relative cover of each species was estimated in the field using the Braun-Blanquet method, which records the presence of each species in 10% intervals between 0% and 100% (Belluco et al. 2006; Roner et al. 2016). The boundaries of the regions of interest were delineated using a differential GPS (Leica CS15 in RTK mode), ensuring a horizontal accuracy better than 3 cm. In 2021, species cover was also estimated based on 1 m^2 quadrats (detail information can be found in the Supporting Information). For all years, the regions of interest were overlayed with the georeferenced remote sensing data in the corresponding year. Pixels entirely falling within them and their spectral properties were used to build a reference dataset for training and validating the classifiers. The total number of pixels utilized to construct the model averaged 3760 per year, and ranged from 2198 to 6234 (Table 1).

Fractional vegetation cover

Fractional cover (i.e., for a sample region, such a pixel, the area, projected onto the horizontal plane, relative vertically projected area occupied by a given species or bare soil, divided by the total area of the sample region) was estimated from satellite data by applying the Random Forest Soft Classification method, which has proven to be robust for estimating

Table 1. Information on remote sensing data: Random Forest Soft Classification to estimate fractional cover of each species; Random Forest Classification to binarily classify the data to vegetated and unvegetated marsh portions; the tidal level above Istituto Geografico Militare datum was calculated by considering the tidal elevation measured by Punda Salute gauge (above Zero Mareografico di Punta della Salute (ZMPS) datum) and the difference between ZMPS and Istituto Geografico Militare datum (*see* "Elevation datums" in Supporting Information).

Classification method	Sensor	Date	Spatial resolution (m)	Number of bands	Flight time (GMT)	Tidal level (cm)	Date of field work	Number of ground truth pixels	Number of classes
Fractional cover estimate	IKONOS	Jun 26, 2001	P: 1.00 m, M: 4.00 m	4	10:00	−45	Oct 31, 2001	2569	6
	QB	Jul 25, 2003	P: 0.72 m, M: 2.88 m	4	9:45	+7	Jul 7, 2023	5649	6
	IKONOS	Aug 31, 2006	P: 1.00 m, M: 4.00 m	4	10:37	+8	Sep 13, 2006	2996	6
	WV-2	Dec 3, 2013	P: 0.50 m, M: 2.00 m	8	10:24	+43	Aug 13, 2013	2914	6
	WV-2	Nov 7, 2019	P: 0.50 m, M: 2.00 m	8	10:23	+45	Oct 19, 2019	6234	6
	WV-2	Jul 29, 2021	P: 0.50 m, M: 2.00 m	8	10:28	+23	Sep 10, 2021	2198	6
Binary classification	IKONOS	Jul 31, 2004	P: 1.00 m, M: 4.00 m	4	10:16	+52	—	3622	2
	IKONOS	Jul 12, 2007	P: 1.00 m M: 4.00 m	4	10:11	+40	—	2342	2
	QB	Jul 25, 2009	P: 0.72 m, M: 2.88 m	4	10:08	+22	—	1894	2

M, multispectral; P, pancromatic; QB, QuickBird II; WV-2, World-View 2.

multispecies vegetation fractional cover in marsh environments (Yang et al. 2020). This method was used to estimate the fractional cover of five vegetation classes (*Salicornia*, *Spartina*, *Limonium*, *Sarcocornia*, and *Juncus*) and bare soil, for a total of six classes.

A separate Random Forest Soft Classification model was developed for each of the 6 yr (2001, 2003, 2006, 2013, 2019, and 2021) and trained independently based on the ground-truthing data collected for that year. In each case, 75% of pixels in the paired ground-truthing dataset were randomly selected for training the fractional cover estimation model and the remaining 25% were used to validate the accuracy of the model. This validation was carried out by using two metrics, root mean square error (RMSE), and the coefficient of determination (R^2).

Binary classification

We obtained satellite data for 2004, 2007, and 2009, to increase the temporal resolution of our analysis of the time to marsh recovery. We did not have field observations for these years and so could not develop vegetation fractional cover estimate models. Instead, we produced a binary classification to classify pixels as either vegetated or bare soil using the Random Forest Classification algorithm (Breiman 2001). Year-specific Random Forest Classification models were developed based on spectral information extracted from randomly selected regions of interest that were visually inspected and classified. Seventy-five percent and 25% of the pixels in the paired spectral information dataset were used for training and testing the accuracy of each Random Forest Classification model's application, respectively. The Confusion Matrix and Overall Accuracy (A), describing the ratio between the number of correctly classified and the total number of validation points of each class, were used to evaluate the performance of the binary classification.

Change analysis

We used the vegetation maps obtained from fractional cover estimates to identify the *Spartina* dieback event and track changes in species composition over time, along with their implications for AGB. As part of this, we evaluated meteorological variables in relation to the event. We also evaluated plant distributions in terms of marsh characteristics (elevation and distance to channels), and their relationship to recovery time.

Spartina dieback event

We analyzed shifts in species composition mainly through the comparison of dominant species maps, which were generated by selecting the species or bare soil with the highest fractional cover values within each pixel. We defined "*Spartina* dieback" as areas that switched from > 50% *Spartina* in 2001 to > 50% bare soil in 2003. Note that this is conservative as *Spartina* was also

Table 2. Accuracy information of the fractional cover estimates for each year.

Species	Metrics	2001	2003	2006	2013	2019	2021
Juncus	R^2	0.83	0.83	0.78	0.93	0.90	0.70
	RMSE (%)	9.76	4.22	8.48	3.04	8.97	13.46
Limonium	R^2	0.72	0.70	0.69	0.86	0.78	0.73
	RMSE (%)	15.88	12.55	17.03	12.47	15.52	13.05
Sarcocornia	R^2	0.78	0.66	0.71	0.58	0.72	0.67
	RMSE (%)	17.15	9.98	17.13	14.03	18.67	13.75
Spartina	R^2	0.94	0.90	—	0.68	0.88	0.82
	RMSE (%)	6.09	4.73	—	11.37	7.07	14.79
Salicornia	R^2	—	—	0.89	0.58	0.65	0.60
	RMSE (%)	—	—	4.74	9.95	11.87	12.76
Soil	R^2	0.91	0.75	0.9	0.95	0.96	0.84
	RMSE (%)	10.42	9.27	8.93	9.47	6.75	11.28

R^2, the coefficient of determination; RMSE, root-mean-square error.

lost in other areas with fractional cover < 50%, and in some places a different species had already encroached by the data acquisition date in 2003 and so the area was no longer bare. We therefore also evaluated changes in fractional cover of all vegetation classes between 2001 and 2003.

In order to assess whether the dieback was associated with drought, we analyzed temporal changes in monthly temperature and precipitation in the Venice Lagoon between 1993 and 2019. In addition, the 3-month Standardized Precipitation Evapotranspiration Index (*see* Vicente-Serrano, Beguería, and López-Moreno 2010) was used to quantify the severity of drought conditions. The details of meteorological data and Standardized Precipitation Evapotranspiration Index calculation is described in the Supporting Information.

Vegetation recovery

We primarily utilized the spatiotemporal variability in the dominant species to track changes in species composition over time. This included focusing specifically on revegetation of the *Spartina* dieback area as well as changes that occurred over the whole study site. Changes in the fractional cover of vegetation were also analyzed. As part of these analyses, we compared the patterns of *Spartina* fractional cover, both before and after the dieback event, in relation to elevation, derived from the Digital Terrain Model (Fig. 1c; vertical accuracy with RMSE = 6.4 cm), and the distance to the nearest channel (Supporting Information Fig. S2), to determine whether there were specific areas in the marsh that were affected by dieback and whether there was a shift in distribution during recovery. The detailed procedure for determining the distance of each marsh pixel to channels is described in the Supporting Information. For each year, the average value of fractional cover of *Spartina* within each elevation interval (5 cm) and distance interval (5 m) was calculated and then made non-dimensional by dividing by the maximum grid value for 2001. Using this 2003 Digital Terrain Model to represent marsh elevation over the entire study period may introduce errors, as marsh elevation can vary due to accretion and subsidence (Yang et al. 2023).

Table 3. Confusion matrix for binary classification performed on images collected in 2004, 2007, and 2009.

		Test pixels		
Year	Classes	Vegetated	Bare soil	Overall accuracy *A*
2004	Vegetated	673	9	0.98
	Bare soil	9	215	
2007	Vegetated	352	6	0.97
	Bare soil	10	187	
2009	Vegetated	330	0	1.00
	Bare soil	0	144	

We also characterized recovery based on binary maps (vegetated or not). This used data from the six vegetation maps in which we classified pixels as vegetated if the combined fractional cover of all vegetation species exceeded 50%, as well as the binary classification maps produced for the other 3 yr (Table 1). We then calculated the "Years to Revegetate" (*Y2R*) a metric commonly used to represent the time span of the recovery in different ecosystems (e.g., van Belzen et al. 2017; White et al. 2022). We combined this with the elevation data to evaluate whether time to revegetate increased at lower elevations, which might be the case if waterlogging is an important stressor (Silvestri, Defina, and Marani 2005). We again used elevation derived from the Digital Terrain Model in Fig. 1c.

Aboveground biomass

We estimated AGB for each year throughout the time series based on empirical data obtained during repeated field surveys conducted in the Venice Lagoon (Scarton, 2006; Supporting Information Table S1). We did this by considering

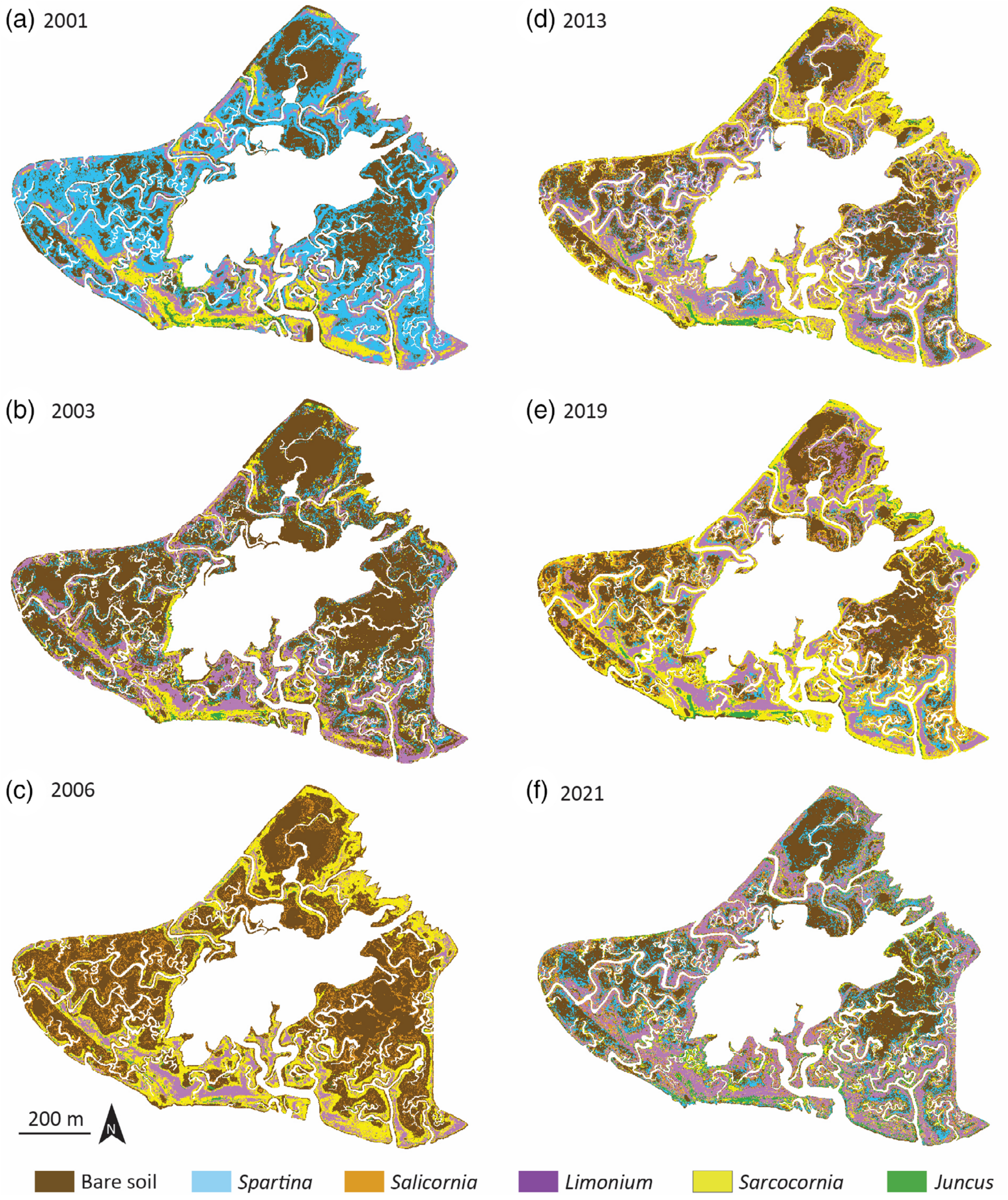


Fig. 2. Dominant species distribution maps.

the species-specific fractional cover of each remote sensing data pixel for a given year and the paired yearly maximum AGB:

$$\mathrm{AGB} = \sum\nolimits_{j} \mathrm{FC}_j \varepsilon_j \tag{1}$$

where ε_j and FC_j are the empirical dry weight (Supporting Information Table S1) and fractional cover of the jth species, respectively. This method accounts for the fact that bare soil does not contribute to AGB. The statistical significance of changes in AGB over time was estimated by using a one-way ANOVA test with the significance level set at 0.05.

Results

Remote sensing data classification

The Random Forest Soft Classification model performed generally well in estimating fractional cover, R^2 values generally exceeding 0.96 and RMSE being below 20% (Table 2). This level of performance supports the use of estimated fractional cover (Supporting Information Figs. S3, S4) for assessing interannual variations in marsh species in the San Felice marsh. The poorest performance occurred for *Sarcocornia* and *Salicornia*. The model performance in 2013 was also generally worse than in other years. We interpret this as being connected to the winter timing of acquisition of these data. However, the performances for most species (*Spartina*, *Limonium*, and *Juncus*) and bare soil were generally very good (with $R^2 > 0.6$ and RMSE < 20%).

The Random Forest binary classification achieved a high accuracy, with more than 97% of pixels within the validation dataset correctly classified (Table 3). The robustness of Random Forest Soft Classification and Random Forest Classification models allowed us to use the vegetated/unvegetated maps (Supporting Information Fig. S5) to analyze marsh recovery.

Spartina dieback event

The dominant species distribution maps (Fig. 2a,b) show that between 2001 and 2003 there was a reduction in *Spartina*-dominated area from 21.3 to 4.4 ha and an increase in soil-dominated area from 15.9 to 30.9 ha (Fig. 2a,b). The widespread disappearance of *Spartina* and increasing exposed bare soil can also be observed from changes in their fractional cover values (Supporting Information Fig. S6a,b). These changes resulted in about 4.6 ha of marsh shifting from predominantly colonized (with fractional cover > 50%) by *Spartina* to bare soil and/or other marsh species (yellow and red areas in Fig. 3a, respectively). All these observations suggest the occurrence of a dieback of *Spartina* in 2003.

In contrast, neither *Limonium*, *Sarcocornia*, or *Juncus* showed widespread reductions in either their dominated areas (Fig. 2) or their fractional cover values (Supporting Information Fig. S6d–f). Note that *Salicornia* was not present in the marsh in either 2001 or 2003 and was not affected.

The *Spartina* dieback corresponded to a severe drought. The lowest Standardized Precipitation Evapotranspiration Index value occurred in 2003, which was during the growing season (Fig. 4). The drought event in 2003 can be attributed to a combination of extremely high temperature and low rainfall (Supporting Information Fig. S7; the annual maximum monthly temperature was 27°C in 2003 as compared to an average max monthly temperature of 15°C over the study period, as well as the second lowest annual total rainfall [584 mm vs. 898 mm]), both of which could negatively affect plant performance.

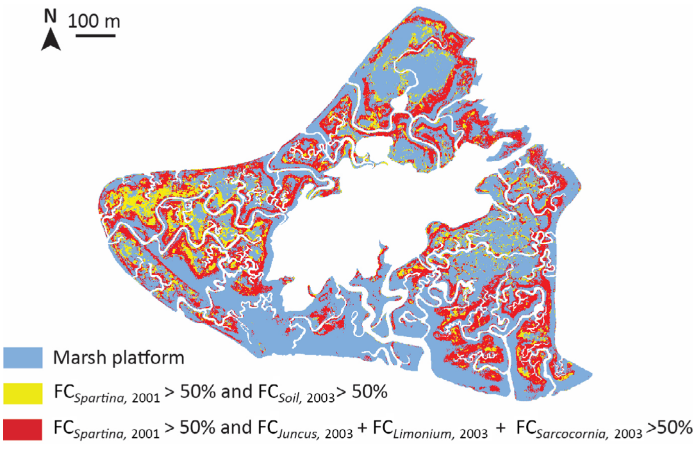


Fig. 3. Dieback area. Marsh portions that shifted from *Spartina* majority (fractional cover of *Spartina* larger than 50%) in 2001 ($FC_{Spartina,2001} > 50\%$) to bare soil majority (fractional cover of soil larger than 50%) in 2003 ($FC_{Soil,2003} > 50\%$), represented by yellow. Marsh portions subjected to the shift from the *Spartina* majority in 2001 to the combined fractional cover of *Limoniuim*, *Sarcocornia*, and *Juncus* being higher than 50% in 2003 ($FC_{Juncus,2003} + FC_{Limonium,2003} + FC_{Sarcocornia,2003} > 50\%$) are displayed as red.

Vegetation recovery

Marsh species composition in 2021 is strikingly different from that in 2001. This is obvious when we focus on the dieback area (yellow area in Fig. 3). By 2021, 45% of these areas still remained bare and only 22% of them were re-dominated by *Spartina* (Fig. 5a). The rest of the area was dominated by *Limonium* (12%), *Salicornia* (15%), *Sarcocornia* (3%), and *Juncus* (2%) in 2021, showing the encroachment of other species. However, the gradual reduction in bare soil area and the general increase vegetated area between 2006 and 2021 (Fig. 5a) indicates the occurrence of the recovery.

The shift in species composition can also be observed across the entire marsh (Fig. 5b). The area dominated by *Spartina* in 2013–2021 (2.7–4.4 ha) was much lower than that in 2001 (21.3 ha). Extensive marsh portions experienced a transition between *Limonium* and *Sarcocornia* dominance (Fig. 5b). In fact, these two species always occur in the same areas of the marsh and display strong interspecific competition (Marani et al. 2006; Silvestri, Defina, and Marani 2005; Yang et al. 2023). Their combined dominated area increased from 13.7 ha (2001) to 25.7 ha (2013) and then decreased to 16.7 ha by 2021, but was still larger than that in 2001 (13.7 ha). The *Juncus*-dominated area in 2021 (3.2 ha) was also larger than that in 2001 (1.2 ha). *Salicornia*, which was absent from the San Felice marsh in 2001 and 2003, appeared in 2006 (5.8 ha) and then maintained its area ranging from 5.3 to 6.8 ha in 2019 and

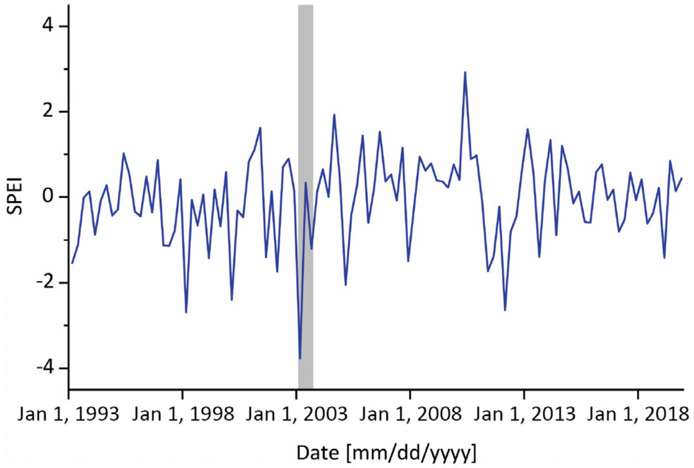
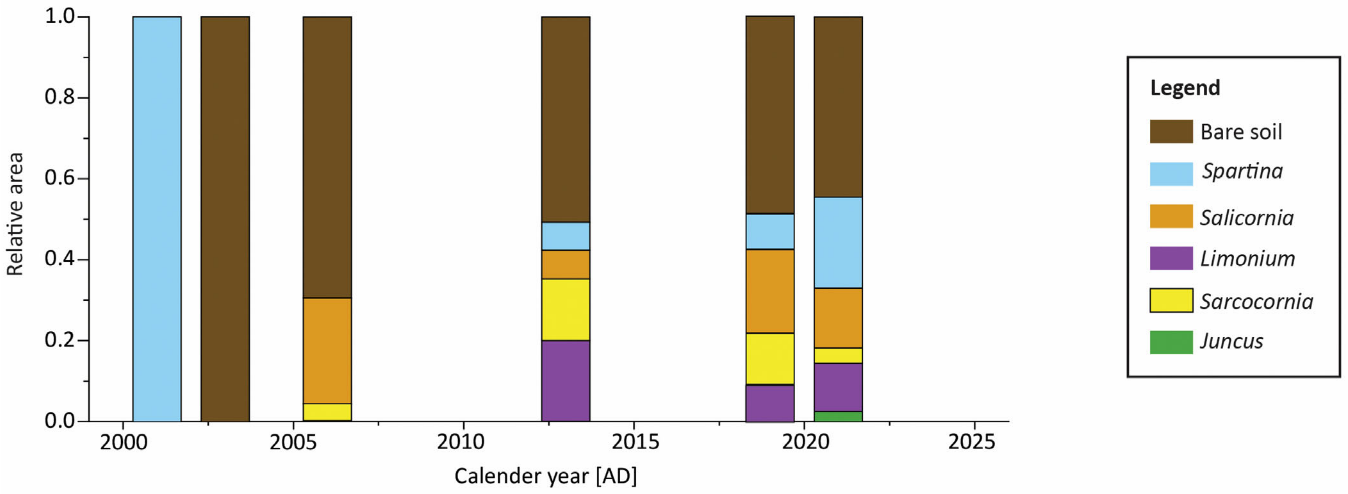
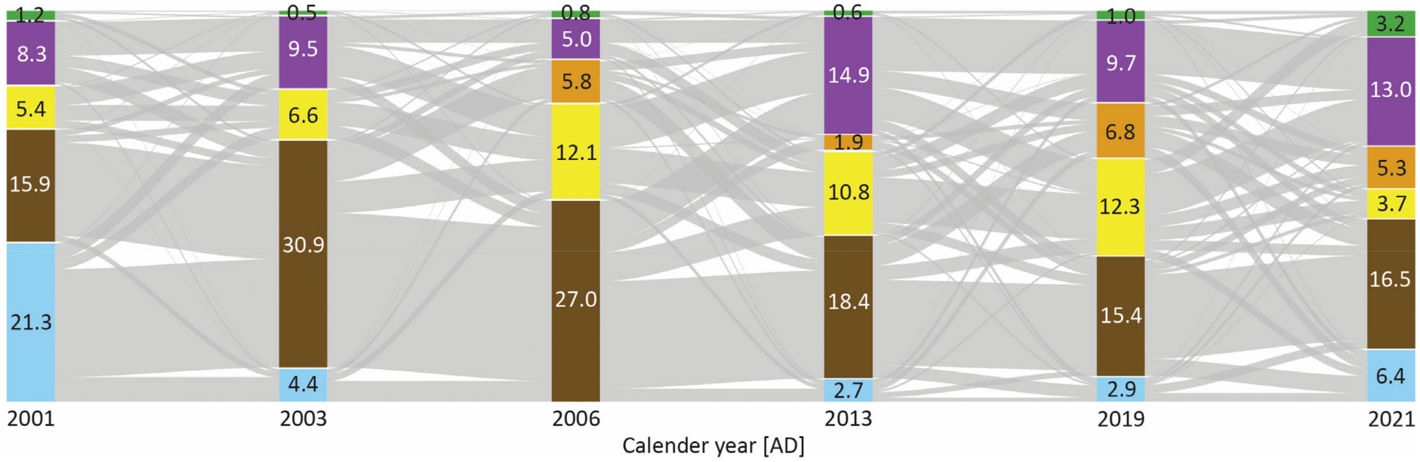


Fig. 4. Temporal variations of the Standardized Precipitation Evapotranspiration Index (SPEI) in the Venice lagoon between 1993 and 2019. The growing season of *Spartina* in 2003 is marked as gray.



(a) Species composition within dieback area



(b) Species composition over the entire marsh

Fig. 5. Changes in the species composition within the dieback area (**a**) and over the entire marsh (**b**). Species composition was represented by the relative area of each dominant species in (**a**) and the true area (in hectares) in (**b**). The transitions between different dominant species over the entire marsh were represented by the gray flows in (**b**).

2021. Note that the low value of *Salicornia*-dominated area in 2013 (1.9 ha, Fig. 6a) may be due to the fact that the WorldView 2 data in 2013 was acquired in December and did not have high classification accuracy (*see* "Methods" section).

Changes in the spatial distributions of *Spartina* and other species were analyzed by examining the standardized fractional cover (the fractional cover made non-dimensionalized by dividing by the maximum grid value of *Spartina* for 2001) across elevation and distance to channels to show the shifts in species distribution in relation to these environmental factors (Fig. 6). Prior to the dieback event in 2001 (Fig. 6a), *Spartina* exhibited the highest standardized fractional cover values at lower elevations (5–30 cm above the Istituto Geografico Militare datum) in two distinct zones with respect to distance from the channel network: the marsh interior, approximately 50–70 m from channels, and in close proximity to channels (0–10 m). A sharp decline in *Spartina* cover is evident due to the dieback (*see* Fig. 6b for 2003), but as it regrew it occupied a similar location in terms of these variables (Fig. 6c,d). Between 2003 and 2021, the combined fractional cover of the remaining species (*Juncus*, *Limonium*, *Salicornia*, and *Sarcocornia*) showed evidence of a shift toward lower elevation areas that had the highest *Spartina* cover values in 2001 (Fig. 6d–f; Supporting Information Figs. S8, S9), where they were not frequently observed prior to the dieback (Fig. 6e). This implies that they encroached on areas previously occupied by *Spartina*, potentially hindering its re-establishment.

The *Y2R* displayed a substantial spatial variation, with some areas revegetating within 3 yr, while others remained bare even after 18 yr (Fig. 7a). When we integrated the marsh elevation (Fig. 1c) with the *Y2R* data, we found a negative correlation (Fig. 4b), indicating that higher marsh areas tended to be revegetated faster.

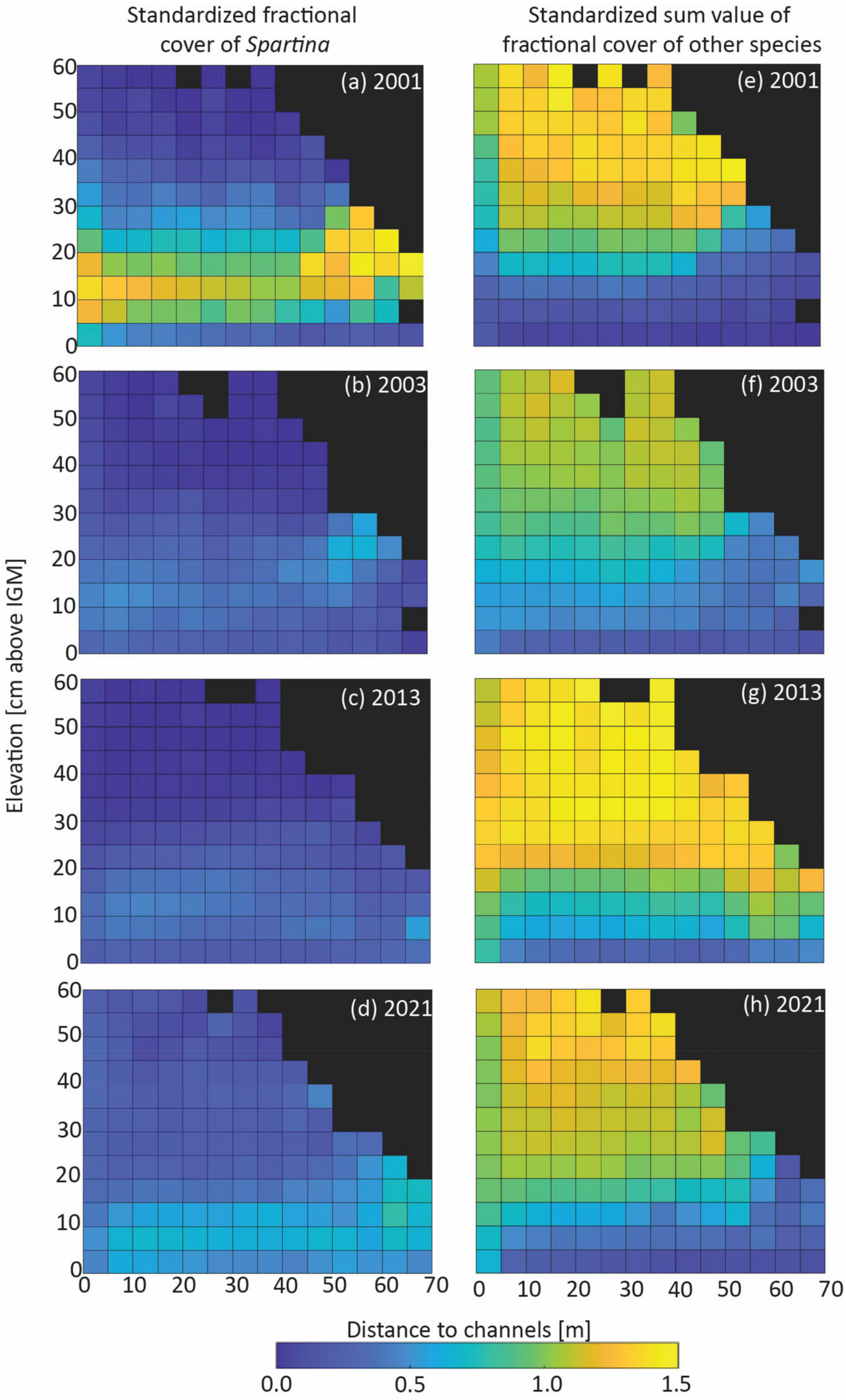


Fig. 6. Distribution patterns of *Spartina* (**a**–**d**) and other species (**e**–**h**) along gradients in elevation and distance to the channel. Grid values are the results of average fractional cover within each grid made non-dimensional by using the maximum value of *Spartina* for 2001. Distribution patterns prior to the dieback (2001), during the dieback (2003), at the middle (2013), and at the end of the observation (2021) were selected to display. IGM represents the Istituto Geografico Militare datum.

Observations from AGB maps (Supporting Information Fig. S10) indicate variations in AGB in response to the dieback and the subsequent recovery. Within the dieback area (Fig. 8a), AGB significantly ($p < 0.05$) decreased from an average of 736 (± 94) g m^{-2} in 2001 to 261 (± 146) g m^{-2} in 2003. By 2013, it had increased to 542 (± 277) g m^{-2}, and

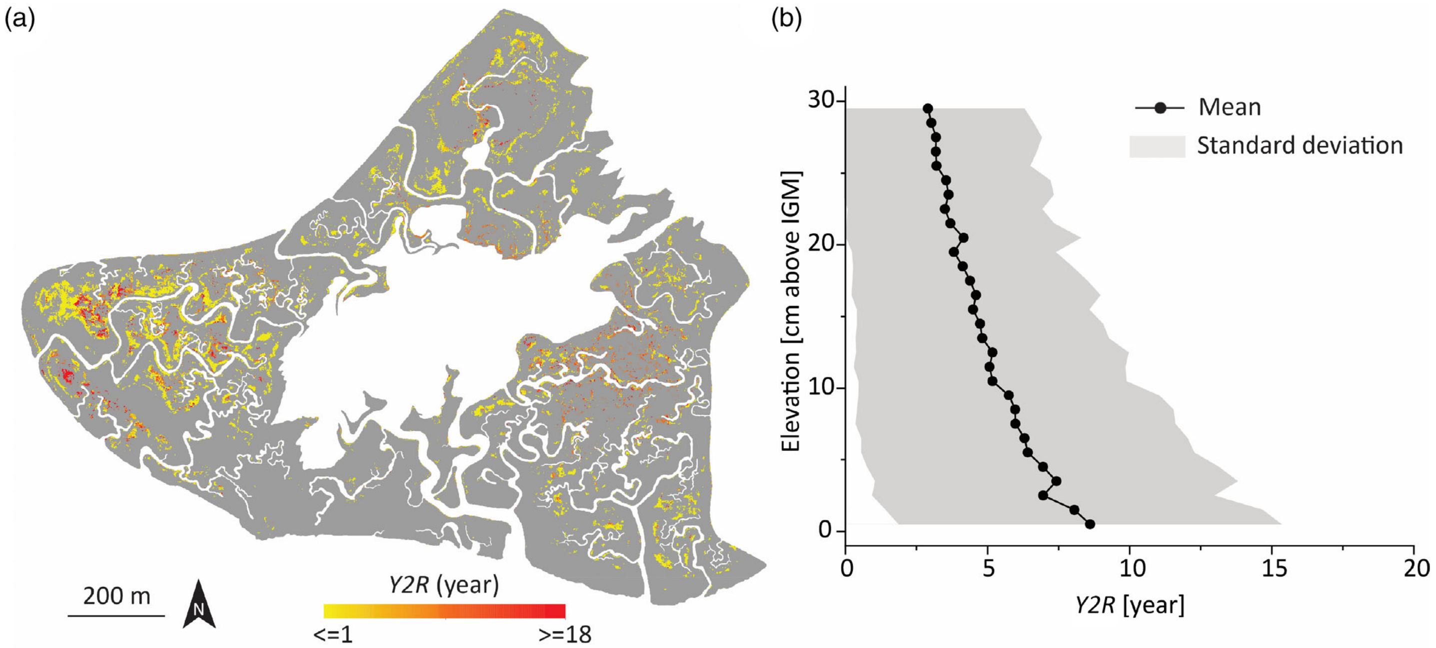


Fig. 7. Year to Revegetate (*Y2R*) within the dieback areas. (**a**) Spatial variation of *Y2R* within the dieback area (yellow area in Fig. 3); (**b**) the relationship between *Y2R* and marsh platform elevations. Gray areas in (**a**) are marsh areas that were not considered dieback areas (*see* “Methods” section), that is, blue and red areas in Fig. 3. IGM represents the Istituto Geografico Militare datum.

remained relatively stable after that. Aboveground biomass for the entire marsh displayed a similar trend (Fig. 8b), with a significant reduction from 690 ($\pm$ 299) to 454 ($\pm$ 173) g m^{-2} between 2001 and 2003 (p-value < 0.05), and a subsequent increase to 611 ($\pm$ 391) g m^{-2} by 2021. Thus, even though *Spartina* did not recover, the expansion of other species allowed AGB to approach pre-dieback levels.

Discussion

This study utilized fractional cover, dominant species, and AGB maps derived from remote sensing data to quantitatively document the 2003 *Spartina* dieback event in the San Felice marsh within the Venice lagoon and the subsequent recovery between 2003 and 2021. It provides evidence that dieback can significantly modify the species composition of a multispecies marsh, which has important implications for marsh response to disturbance.

Spartina dieback event

Based on remote sensing data, we identified a dieback event of *Spartina* in the San Felice marsh in 2003. Our analyses suggest that this dieback event can be attributed to the drought, as a result of the heatwave event. The observed dieback aligns with previous field measurements in the same marsh (Yang et al. 2023) and observations from other marshes within the lagoon (Merloni 2007; Mion et al. 2010; Strain et al. 2017). Our results further support the hypothesis that extreme drought can be one of the main drivers of sudden and widespread mortality of *Spartina* (Garcia-Herrera et al. 2010; Strain et al. 2017). The underlying mechanisms for this dieback likely involve elevated soil temperatures and reduced soil moisture, as documented in previous studies (Strain et al. 2017). The dieback of other *Spartina* species (*Spartina alterniflora*) was also observed in marshes along the Atlantic Ocean during drought (Alber et al. 2008; McKee, Mendelssohn, and Materne 2004; Silliman et al. 2005).

In contrast to *Spartina*, other species displayed varying responses to the drought event. In particular, *Limonium* and *Sarcocornia* showed no apparent mortality in 2003 (Fig. 5b). However, whether *Limonium* and *Sarcocornia* directly benefited from the heatwave itself and the reason for why they did not suffer as *Spartina* did requires further investigation. *Juncus* also exhibited signs of mortality between 2001 and 2003 (Fig. 5b), but its persistence in 2006 suggests a less severe response compared to *Spartina*. These findings underscore the diverse response of halophytic vegetation to drought stress, likely attributed to species-specific physiological traits (Pellegrini et al. 2017; Strain et al. 2017), a topic open to further investigation.

Vegetation recovery

After the dieback event, the dominant vegetation in these areas shifted from *Spartina* to other marsh species (Fig. 5a). We speculate that this widespread transition in vegetation dominance is a consequence of the combined effects of species-specific response to drought and inter-specific competition. Previous observations indicate that the distribution of halophytic vegetation in the San Felice marsh is generally stable, without massive inter-species replacement within a

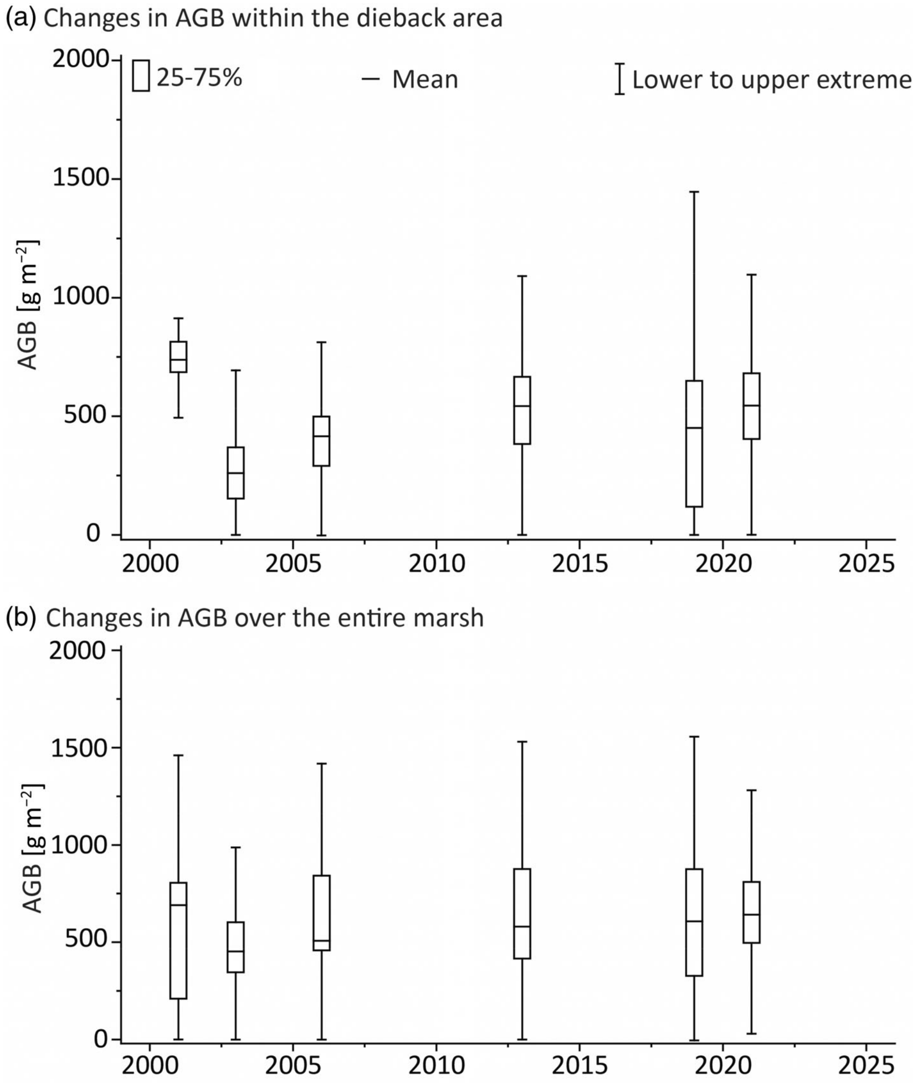


Fig. 8. Changes in aboveground biomass (AGB) within the dieback area (**a**) and over the entire marsh (**b**).

few years (Belluco et al. 2006). We thus suggest that the disturbance (drought/heatwave) noticeably reduced the competitive ability of drought-sensitive species (i.e., *Spartina*; *see* Strain et al. 2017), allowing for the rapid encroachment of more drought-tolerant species (e.g., *Limonium and Sarcocornia*). We did not distinguish between *Spartina maritima* and *Spartina anglica*, as *Spartina anglica* had a minimal presence during the study period. However, we speculate that the dieback event may have facilitated the invasion of *Spartina anglica* (Cuenca Portillo 2022). Further research is needed to investigate the mechanisms of *Spartina anglica* encroachment and whether it occupies the same elevation as *Spartina maritima* on the marsh (Wong et al. 2018).

Our analyses revealed a negative correlation between time to revegetate and marsh platform elevation (Fig. 7b). We interpret this as evidence that intensified physical stress, such as increased inundation frequency and duration at lower elevations, can hinder the recovery process. This is consistent with observations from mono-specific Hellegat and Paulina marshes (van Belzen et al. 2017). Therefore, we suggest that the slowing down of recovery from the disturbance due to waterlogging stress may be an indicator of reduced resilience regardless of species composition.

Effects of disturbance, dieback, and recovery on multispecies marshes

We found that the drought-induced dieback and subsequent recovery significantly modified the species composition of the entire marsh (Fig. 5b) in two primary ways: (1) encroachment of other species into bare areas left by the dieback of *Spartina* (Fig. 5a); and (2) an immediate shift from *Spartina* dominance to other species in areas adjacent to the dieback zones (Fig. 3a). Areas dominated by *Spartina* remained limited even 18 yr after the event, failing to reach its pre-dieback extent (Fig. 5). This contrasts with patterns in *Spartina*-dominated marshes in the southeastern United States, where *Spartina* typically recolonized the same areas during the recovery period (Alber et al. 2008; Ramsey et al. 2014), and suggests that there has been a shift in underlying conditions that allows other species to outcompete *Spartina*. This is an avenue for future study.

To our knowledge, this is the first demonstration that disturbance and recovery can modify the species composition of an entire marsh, confirming previous speculation (e.g., McKee, Mendelssohn, and Materne 2004). Notably, shifts in species composition compensated for the loss of AGB, allowing it to return to pre-dieback levels and maintain the overall ecosystem service. This is consistent with the observations from terrestrial landscapes (Hooper et al. 2005). For example, when climatic variations resulted in loss of some grassland species, unaffected species increased and stabilized total community biomass (Tilman 1996). However, other aspects of plant performance likely varies with species. For example, *Salicornia* produces less below-ground biomass than *Spartina* (Janousek et al. 2016), potentially leading to lower organic sedimentation and a reduction in marsh surface vertical accretion and soil shear strength (e.g., Coleman and Kirwan 2019). Moreover, the loss of *Spartina* may disrupt the food web and energy flow by reducing food sources for certain invertebrates and fish (Nelson et al. 2019). These findings also underscore the importance of considering multispecies dynamics when studying disturbance, recovery, and long-term ecological change.

Implications for climate change

Climate change projections indicate more intense and frequent drought events in this century (Dai 2013), which could also increase the likelihood of *Spartina* dieback. The shift in species composition could further impact marsh vulnerability to erosion and submergence, as the loss of *Spartina* may reduce marsh surface vertical accretion and soil shear strength (e.g., Coleman and Kirwan 2019). In addition, while *Limonium* and *Sarcocornia* encroached on previous *Spartina*-occupied areas, their productivity might be suboptimal due to less favorable elevation conditions (Morris et al. 2002; Yang et al. 2023), potentially resulting in reduced organic sedimentation compared to the pre-dieback state. Given the rapid sea level rise in the Venice lagoon in this century (about 4.4 mm yr^{-1}; *see* Yang et al. 2023), these factors could accelerate marsh loss, particularly in low-lying interior areas where recovery cannot happen immediately (Fig. 7; Supporting Information Fig. S11) and where accretion relies heavily on organic sediments (Da Lio, D'Alpaos, and Marani 2013; Roner et al. 2016). This raises concerns about the future vulnerability of these marshes. Therefore, we emphasize the importance of incorporating drought-related changes in species composition in marsh evolution models to enhance our understanding of marsh vulnerability to climate change and improve the accuracy of predictions regarding the fate of these valuable ecosystems.

Author Contributions

Zhicheng Yang: Conceptualization; formal analysis; data curation; investigation; writing – original draft; visualization; writing – reviewing and editing. Andrea D'Alpaos: Formal analysis; data curation; investigation; writing – reviewing and editing; project administration. Marco Marani: Formal analysis; data curation; investigation; writing – reviewing and editing. Tegan Blount: Data curation. Merryl Alber: Conceptualization; formal analysis; investigation and visualization; writing – reviewing and editing. Brad Murray: Formal analysis; data curation; investigation; writing – reviewing and editing; project administration. Sonia Silvestri: Conceptualization; formal analysis; data curation; investigation; visualization; writing – reviewing and editing; project administration.

Acknowledgments

We thank Davide Tognin, Alice Puppin, Enrica Belluco, and Alvise Finotello for their assistance in field observations and discussions for vegetation distribution. We appreciate comments from Steve Pennings and Clark Alexander about the dieback-recovery. We are grateful for constructive reviews from two anonymous reviewers, the associate editor, and the editor, who were instrumental in improving earlier versions of this manuscript. This scientific activity was performed in the Research Programme Venezia2021, coordinated by CORILA, with contributions from the Provveditorato for the Public Works of Veneto, Trentino Alto Adige, and Friuli Venezia Giulia, provided through the concessionary of State Consorzio Venezia Nuova, Research Line 3.1 (P.I. A.D.). It was also supported by the National Science Foundation under Grant No. 2016068, project title: "Coupled Ecological-Geomorphological Response of Coastal Wetlands to Environmental Change." Z.Y. would like to thank the Fondazione Cariparo, for providing the essential funding for his Ph.D. study. Z.Y. and M.A. are also supported by the Georgia Coastal Ecosystems Long-Term Ecological Research project, which is supported by the National Science Foundation (OCE-1832178). A.D., S.S., and M.M. acknowledge support by the RETURN Extended Partnership and received funding from the European Union NextGenerationEU through the Italian Ministry of University and Research (National Recovery and Resilience Plan, Mission 4, Component 2, Investment 1.3—D.D. 1243, August 2, 2022, PE0000005). M.M. acknowledges funding by the National Biodiversity Future Center, Project No. CN_00000033, MUR Directorial Decree No. 1034.

Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 05 March 2024
Revised 03 November 2024
Accepted 23 December 2024