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Sea Lavender Reimagined: Keystone Halophytes in Salt Marsh Blue Carbon Dynamics

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Key Points:

- Halophyte species have diverse biomass and soil organic carbon (OC) distribution characteristics
- Belowground biomass and OC content peaks in the middle marsh, while aboveground biomass is highest in the middle to upper marsh
- Sea lavender is adept at enhancing and maintaining blue carbon reservoirs

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Abstract Salt marshes are ecologically and socio-economically valuable intertidal ecosystems that have suffered rapid losses worldwide. As a blue carbon ecosystem (BCE), they are efficient sinks and long-term reservoirs of organic carbon with vital roles in the global carbon cycle. To accurately characterize salt marsh carbon sequestration dynamics, knowledge of halophyte below- and aboveground biomass (BGB, AGB) and their relation to the subsurface organic carbon content (OC) is fundamental, yet only vaguely defined. Herein, the biomass and subsoil dry bulk density (DBD), organic matter (OM), and OC of plots pertaining to seven different halophyte species were analyzed. The volume and partitioning of biomass were found to be species-specific. The difference between the mean AGB in the lower marsh (425 ± 217 g m^{-2}) and the upper marsh (1,616 ± 807 g m^{-2}) was highly statistically significant. BGB, OM, and OC values peaked in the middle marsh zone (5,890 g m^{-2}; 14.5%; 5.4%). DBD was negatively correlated with OM. The BGB, BGB/AGB ratio, OM and OC all had their maxima coinciding with *Sea Lavender*. As a nexus of unique attributes, *Sea Lavender* has remarkable potential as a keystone halophyte capable of enhancing and maintaining blue carbon reservoirs. Overall, these results affirm that the observed distribution of biomass and OC is an artifact of biogeomorphic feedbacks where phytomorphic and physiologic traits interplay with underlying soil chemistry, sediment supply, geomorphology, hydrodynamics and external forcings. This data set elucidates factors underpinning interdisciplinary frameworks focused on intertidal wetlands and the intertwined mechanisms that dictate salt marsh evolutionary trajectories.

Plain Language Summary Located in the intertidal zone, salt marshes support a host of ecosystem services but are vulnerable to human activities and environmental pressures. As a blue carbon ecosystem, they can trap and store organic carbon (OC) in quantities and on timescales significantly greater than terrestrial ecosystems, making them influential in the global carbon cycle. Understanding the complex relationships between abiotic and biotic factors determining carbon sequestration patterns is challenging and can result in inaccurate blue carbon storage estimates. This study examined the biomass distribution, both above- and belowground, for seven different salt marsh species in a Mediterranean lagoon. The soil dry bulk density, organic matter (OM) and OC content were also measured for each of the sample areas. The results showed that above- and belowground biomass and OC content can be specifically linked to the sampling area species. The aboveground biomass was greatest in the upper marsh, while the belowground biomass, OM and OC content peaked in the middle marsh. *Sea Lavender* was found to be located in zones of the marsh highly adept at enhancing carbon sequestration and maintaining carbon reserves. These findings support management frameworks and aid the conservation of salt marshes on a global scale.

1. Introduction

Salt marshes provide vital ecosystem services and are of high ecogeomorphologic and socioeconomic value (Barbier et al., 2011; D'Alpaos & D'Alpaos, 2021). They are formed by vegetated platforms populated by halophytic species (Marani et al., 2013; Silvestri et al., 2005). Salt marshes have a heightened capability to generate, trap, and eventually form long-term reservoirs of organic carbon (OC), hence earning their classification as a blue carbon ecosystem (BCE) (Duarte et al., 2005; Macreadie et al., 2019; McLeod et al., 2011; Trettin & Jurgensen, 2003). The size and health status of salt marsh ecosystems at a worldwide scale have been drastically

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degraded, and they remain vulnerable to the anthropogenic and environmental pressures concentrated in the coastal zone (Day et al., 1999; Rogers & Woodroffe, 2015; Silvestri et al., 2018; Tognin et al., 2021; Valiela et al., 2009). The degradation of salt marshes lessens global carbon reservoirs and liberates stored carbon as greenhouse gases (Campbell et al., 2022; Pendleton et al., 2012; Seyfferth et al., 2020). Thus, alongside other beneficial factors, sustainable salt marsh conservation and restoration can be considered a facet of climate change mitigation strategies and carbon emission offset approaches (Lovelock & Duarte, 2019; Macreadie et al., 2021).

Salt marshes are problematic to monitor in a repeatable and spatially explicit way which is not only standardized but also quantitatively validated. This is due to several factors. The extensive inaccessible zones which salt marshes inhabit; the impediments intrinsic to traversing quagmires; the fine-scale reliefs of topography and vegetation; the recurrent tidal inundations; and the accentuated intricacy of the salt marsh environment, rife with inextricable biogeomorphic feedbacks. As a result of these attributes, in situ data is sparse and remote sensing acts as a lynchpin for monitoring and measuring salt marsh parameters such as vegetation biomass. There have been a variety of studies using remote sensing to map the distribution and biomass of halophytic canopies (e.g., Belluco et al., 2006; Blount et al., 2022; Curcio et al., 2023, 2024; Du et al., 2019; Eon et al., 2019; Silvestri et al., 2003; Silvestri et al., 2005; Tang et al., 2022; Yang et al., 2020; Yang et al., 2023). Yet, as salt marshes inhabit a dynamic terrain poised in the intertidal zone, precisely determining the morphology and predicting above- and belowground plant biomass (AGB, BGB) at an ecosystem scale persists as a challenge (Blount et al., 2023; Curcio et al., 2022). Particularly as biomass estimates are often validated by only a limited number of in situ samples across a narrow spectrum of salt marsh species in restricted geographic locations.

It has been established that within salt marshes, carbon sequestration is spatially variable and dependent on a variety of factors (e.g., Carrasco-Barea et al., 2023; Castillo et al., 2008; Puppin, Tognin et al., 2023, 2024; Roner et al., 2016; Yousefi Lalimi et al., 2018). Furthermore, the composition and structure of the halophytic vegetation's AGB and BGB can influence the carbon sequestration capacity (Carrasco-Barea et al., 2023; Kirwan & Guntenspergen, 2012; Puppin, Tognin et al., 2023, 2024; Sousa et al., 2017) and salt marsh vegetation zonation is driven by a conglomerate of abiotic and biotic factors (Pignatti, 1966; Silvestri et al., 2005; A. D'Alpaos, 2011; Marani et al., 2007, 2013; de los Santos et al., 2022), including competition (Finotello et al., 2022; Marani, Belluco, et al., 2006, Marani et al., 2013; Morris, 2006; Pellegrini et al., 2018; Pennings et al., 2005). While the spatial variability of OC and its drivers in salt marshes has been extensively studied (e.g., Kirwan & Mudd, 2012; Maxwell et al., 2023; Puppin et al., 2024; Seyfferth et al., 2020; Spivak et al., 2017; Van De Broek et al., 2016; Vittori Antisari et al., 2017), more studies are required to have a deeper understanding of the dominant plant and soil controls. This would reduce the substantial uncertainties in predictions of carbon sequestration in a changing environmental context and improve the efficacy of salt marsh conservation and sustainable management. Thus, data sets addressing species efficiency in sequestering carbon through biomass production would provide a foundation for efficacious monitoring and modeling of key salt marsh parameters.

To investigate variability in the AGB-BGB empirical relationship, its species dependency, and how this relates to salt marsh blue carbon reservoirs, an in situ aboveground and belowground biomass data set was acquired in the Venice Lagoon (Italy). The data includes, for each species plot: (a) the magnitude and ratio of aboveground and belowground biomass and; (b) the soil organic matter (OM) and OC content and dry bulk density (DBD). The focus was on the interrelations between key carbon sequestering halophyte species (i.e., *Sea Lavender*), sedimentology, geomorphology and how these can inform conservation and modeling of carbon sequestration in salt marshes from regional to global scales. Halophyte vegetation zonation patterns are often composed of typically occurring associations of species due to shared adaptations to stressful environments, facilitative and competitive relationships and, at times, ecological succession (Pellegrini, 2016; Pellegrini et al., 2018; Pignatti, 1966). The composition of intermixed species assemblages is a spatiotemporally dynamic qualitative measure that can have multiple definitions. As further described in the method, this study focuses on sampling plots with quantitatively defined compositions of seven different species typical of the Venice lagoon (Table 1).

2. Materials and Methods

2.1. Study Site

This research focused on the extensive yet vulnerable salt marshes of the Venice Lagoon (Italy). The Venice Lagoon is 550 km^2 in extent, and it is a barrier island lagoon system with three inlets to the Adriatic Sea. The unchanneled portions of the lagoon have a mean depth of 1.0–1.5 m, a semidiurnal microtidal regime, and a tidal

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Table 1
Halophyte Species Plots in Order From Low to High Marsh Zone Predominance

Ref.	Pignatti (1966) species association	Species dominant in sample plot	Surface coverage	Marsh zone	Typical occurrence observed
1	*Salicornietum venetae*	*Salicornia spp.*	*Salicornia* ≥ 30%	Low marsh	Preference for channel banks or abandoned channel beds, as well as low inner marsh, greater density and homogeneity in the first cases.
2	*Not applicable*	*Spartina anglica*	*S. anglica* ≥ 90%	Low inner marsh	Invasive species are expanding in the inner marsh pools, consistently immersed dense homogeneous patches
3	*Spartinetum strictae*	*Spartina maritima*	*S. maritima* = 20–70%	Lower inner marsh	Bordering the inner marsh pools, consistently immersed, at times sparse, homogenous patches
4	*Limonietum venetum*	*Limonium narbonense*	*Limonium* ≥ 80%	Lower-middle marsh	Omnipresent in the middle marsh, becoming sparser at the extremities toward the lower or upper marsh
5	*Limonietum venetum*	*Sarcocornia fruticosa*	*Sarcocornia* ≥ 80%	Middle-upper marsh	Frequent in the middle marsh with more dense, homogenous patches in the upper marsh
6	*Limonietum venetum/ Juncetum maritimi*	*Juncus maritimus*	*Juncus* ≥ 80%	Middle-upper marsh	More homogeneous in areas at higher elevations, distinct patches formed within the marsh
7	*Staticeto-Artemisietum coerulescentis*	*Inula crithmoides*	*Inula* ≥ 50%	Upper marsh	On narrow raised marsh platform edges which border the marsh channel network

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Figure 1. Study area location in (a) Italy; (b) Venice Lagoon and; (c) San Felice salt marshes. Images contain Copernicus Sentinel-2B data (20210905) and ArcGIS base map World Imagery.

range of approximately 1.0 m (A. D'Alpaos et al., 2013; Silvestri et al., 2018). The study site, referred to herein as San Felice, includes 0.5 km^2 of salt marsh, located in the north-eastern sector of the lagoon adjacent to the San Felice channel (Figure 1). A widespread and longstanding anthropogenic presence has transformed the lagoon system regime, causing substantial alterations to biogeomorphologic and hydrologic dynamics (e.g., Silvestri et al., 2018) as well as a negative sediment balance (Carniello et al., 2009). Environmental forcings, now amplified by climate change, are coupled with the influence of human occupation on this system. During the last centuries, the coverage of Venice's salt marshes has plummeted by about 76%, leaving an enduring salt marsh extent of approximately 43 km^2 (Carniello et al., 2009; L. D'Alpaos, 2010). The marsh area loss rate is not uniform across the lagoon. The studied salt marshes are located in the northern zone, which experienced relatively less intense lateral erosion rates (Bendoni et al., 2016; Day et al., 1998; Marani et al., 2011; Tommasini et al., 2019).

The most common halophyte species in the San Felice salt marshes are *Salicornia spp. (Saliconia), Limonium narbonense* (*Limonium*), *Sarcocornia/Salicornia fruticosa* (*Sarcocornia*), *Juncus maritimus* (*Juncus*), *Pucinellia palustris* (*Pucinellia*), *Inula crithmoides* (*Inula*), *Halimione portulacoides* (*Halimione*), *Aster tripolium* (*Aster*), *Suaeda maritima* (*Suaeda*), *Arthrocnemum macrostachyum* (*Arthrocnemum*), *Spartina maritima/Sporobolus maritimus* (*S. maritima*) (Pignatti, 1966; Silvestri et al., 2005), and of late, the non-local variant *Spartina anglica/ Sporobolus anglicus* (*S. anglica*) (Yang et al., 2020). Generally, these halophyte species follow marked vegetation zonation patterns that display abrupt transitions or wide ecotones as a result of morphology, competition, tidal regime and edaphic characteristics (Belluco et al., 2006; Marani, Zillio, et al., 2006, Marani, Belluco, et al., 2006; Pellegrini, 2016; Pellegrini et al., 2018; Pignatti, 1966; Puppin, Roner, et al., 2023, Puppin, Tognin et al., 2023; Silvestri et al., 2003). *S. anglica* is a vigorous species whose spread has the potential to alter the current biomorphodynamics (Wong et al., 2018).

2.2. Field Data Collection and Processing

The majority of the data set was acquired during two late summer sampling campaigns carried out in 2021 and 2023. In total, AGB, BGB, OM via Loss on Ignition (LOI), OC and DBD were measured or derived at 53 sampling sites. Three of these were taken during early spring in 2023 due to field campaign time constraints. Based on field observations across seasons and other literature from the lagoon (e.g., Scarton et al., 1998), seasonality should not significantly impact the BGB measurements within the scope of the study. The plots were

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geolocated with an autonomous Real-Time Kinematic Differential Global Positioning System (accuracy: horizontal 8 mm + 0.5 ppm; vertical 15 mm + 0.5 ppm), and based on these values, the mean elevation was calculated for each species plot set. The elevations were measured in meters relative to the Italian Military Geographic Institute (Istituto Geografico Militare; IGM) geodetic datum, and the working coordinate system was EPSG:32633. The sampling campaign was designed to capture the large range of biogeomorphological conditions which occur across the study site. Thus, for the purposes of this analysis, the plot sites were split across the seven dominating halophyte species present in the Venetian marsh vegetation mosaic. Salt marsh vegetation assemblages (or associations) in the Venice lagoon have been historically a subject of in-depth studies by eminent botanists, and are usually characterized by the presence of one or more dominant species (e.g., Pignatti, 1966). This definition of species percentage cover, however, is qualitative in nature. To satisfy the need for quantitative plot classes in our study, we subsampled these associations into specific plot types, each with a large majority of certain species. In some cases, our plots were strictly monospecific vegetative plots (i.e., *S. anglica*), while for others, where it is impossible to locate monospecific areas, the largest possible percentage species coverage was specified for the focus species (i.e., *Limonium* $\geq$ 80%). Furthermore, in the case of the *S. maritima* plots, a wider range of percentage cover was permitted as this species has undergone a dieback phase and is no longer as prevalent at the site (Yang et al., 2023). Table 1 quantitatively defines our seven species plot types in regard to: the surface coverage of the dominant species in the plot; the area of the marsh which they occupy; and Venice Lagoon species associations they fall within (Pignatti, 1966). *Limonietum venetum* was identified by Pignatti (1966) as the most diffuse species association in the lagoon salt marshes, and in this work, three of the investigated species plots fall within it: *Limonium, Sarcocornia,* and *Juncus* (associations referenced as 4, 5, and 6 in Table 1).

The AGB of all species present was harvested within a 20 cm by 20 cm area at each sample plot. Observations of maximum vegetation height, species composition, species abundance (surface percentage coverage) and ground elevation were made on site prior to collection. In the laboratory, the AGB samples were dried in an oven at 70°C for at least 72 hr until a constant dry weight was reached. The BGB sample cores were collected using a PVC corer (8 cm internal diameter) at the same location where the AGB was gathered. The BGB cores were divided into 10 cm vertical sections, reaching at least a total depth of 30 cm below the salt marsh surface. The cores were divided into 10 cm sections with the intention that changes in root composition and density with depth could be tracked. Each BGB 10 cm section was processed separately in the lab. To isolate the roots and rhizomes from the sediment and foreign objects, these samples were washed with water over two stacked woven stainless steel sieves (1 mm and 500 μm). Once cleaned and sorted into categories according to size (e.g., sieve class), type (e.g., intact roots with stem base) and species of root biomass, the BGB was placed in aluminum trays and dried in the oven using the same protocol as described for AGB above. The dry biomass weight was calculated in terms of dry weight areal density (g m^{-2}). AGB is the sum of all aboveground plant material, both dead and alive, harvested within the plot. The BGB is the sum of all roots and rhizomes present in each 10 cm section, and the BGBT (total belowground biomass) was calculated as the sum of BGB over the full 30 cm depth.

Additional core samples, 4 cm in diameter and at least 10 cm in length, were also collected within each sample plot, and these were used to derive DBD as well as OC and OM content via the LOI method. Prior to being ground to an even grain size, these samples were segmented into 5 cm (2023 data) or 10 cm (2021 data) vertical sections. These subsets were dried in the oven at 60°C for 72 hr (or longer if the weight did not stabilize). Approximately 7 g of each of the ground samples were placed in crucibles, which were then transferred to a muffle oven as per the LOI analysis methodology (375°C for 16 hr (Puppin, Tognin et al., 2023, Puppin et al., 2024; Roner et al., 2016)), with LOI calculated as:

$$\mathrm{LOI} = 100 - \mathrm{Ash} \tag{1}$$

OC was calculated using the equation introduced by Craft et al. (1991), specifically calibrated for the Venice Lagoon environment (Craft et al., 1991; Puppin, Tognin et al., 2023, Puppin et al., 2024):

$$\mathrm{OC} = 0.37\ \mathrm{LOI} + 0.0024\ \mathrm{LOI}^2 \tag{2}$$

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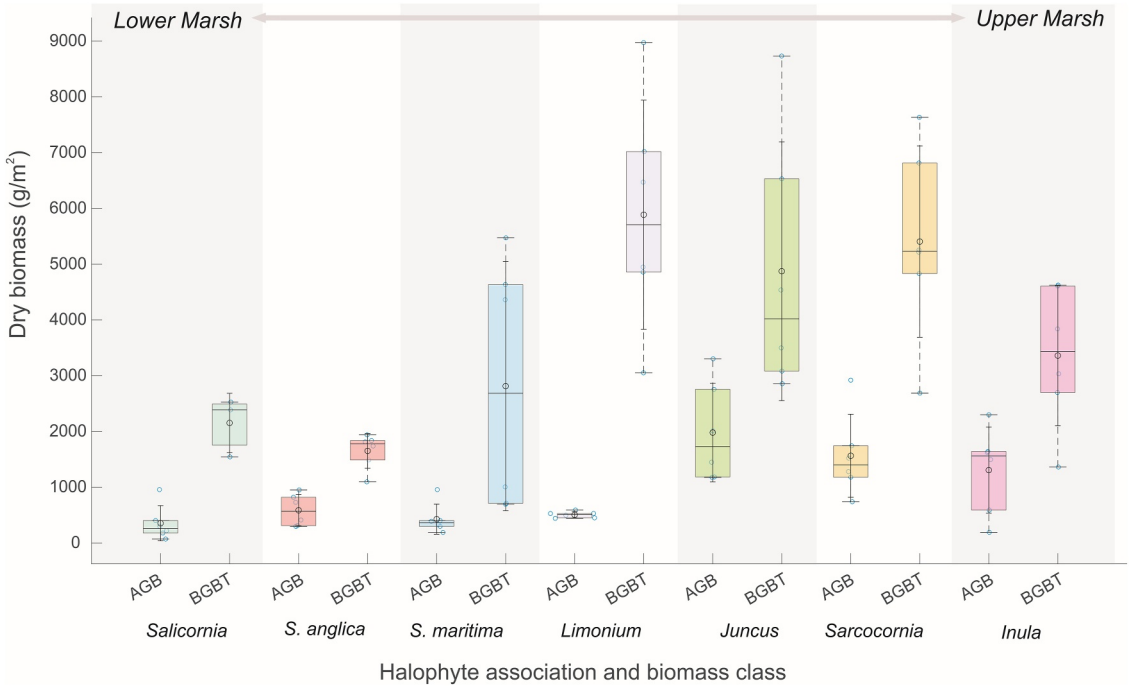

Figure 2. Above- and total belowground dry biomass (AGB; BGBT; g m^{-2}) color-coded for each species class and ordered from low to high marsh based on the species plot mean elevation. Each species data set is based on at least 6 plots.

The dry bulk density (DBD; g cm^{-3}) was derived as:

$$\mathrm{DBD} = \frac{M_d}{V} \tag{3}$$

Where M_d (g) is the dry mass, and V is the wet volume (cm^3) of the sample.

Each species group data set was based on at least six sample plots, and the statistical analysis of the results included the calculation of the mean, median and standard deviation. The statistical significance of the difference between the different species data set groups (i.e., *p-value*) was calculated. The normality of the data set was first checked using the Shapiro-Wilk test, then either a One-Way ANOVA (post hoc: pairwise Tukey's Test) or a non-parametric Kruskal-Wallis test (post hoc: Dunn's Test) was applied to analyze the variance. The strength of correlations between variables (i.e., AGB and BGB) was evaluated with R^2 and *p-values*.

3. Results

3.1. Halophyte Biomass

The AGB and the BGB for the total 30 cm depth (BGBT) of the seven plant species are presented in Figure 2. Further detail relating to the elevation distribution of these plots is included in Section 3.2 (Figure 4b). The plots with the greatest AGB were dominated by *Inula*, *Sarcocornia*, and *Juncus.* These occur in the middle to upper mash zones, with *Inula* restricted to the raised levees bordering the channels (Pignatti, 1966; Silvestri et al., 2005). These three species also have the greatest variance of AGB values (Figure 2). The AGB mean and variance are also lower in the middle to lower marsh zone, where *Limonium*, *S. maritima*, *S. anglica*, and *Salicornia* predominate. The latter three are usually found fringing the inner marsh ponds, sparsely vegetated areas of the low inner marsh or abandoned channel beds (Pignatti, 1966; Silvestri et al., 2005; Yang et al., 2023).

As the mean elevation increases, the mean AGB slightly increases from 293 ± 237 g m^{-2} (*Salicornia*) until the transition zone between *Limonium* and *Juncus* is reached, at which point there is a sudden increase in the mean AGB from 449 ± 96 g m^{-2} to 1,979 ± 885 g m^{-2}. *Juncus* plots have the greatest AGB out of all the species classes, *Sarcocornia* and *Inula* have slightly lower ranges of AGB, with means of 1,564 ± 746 g m^{-2} and

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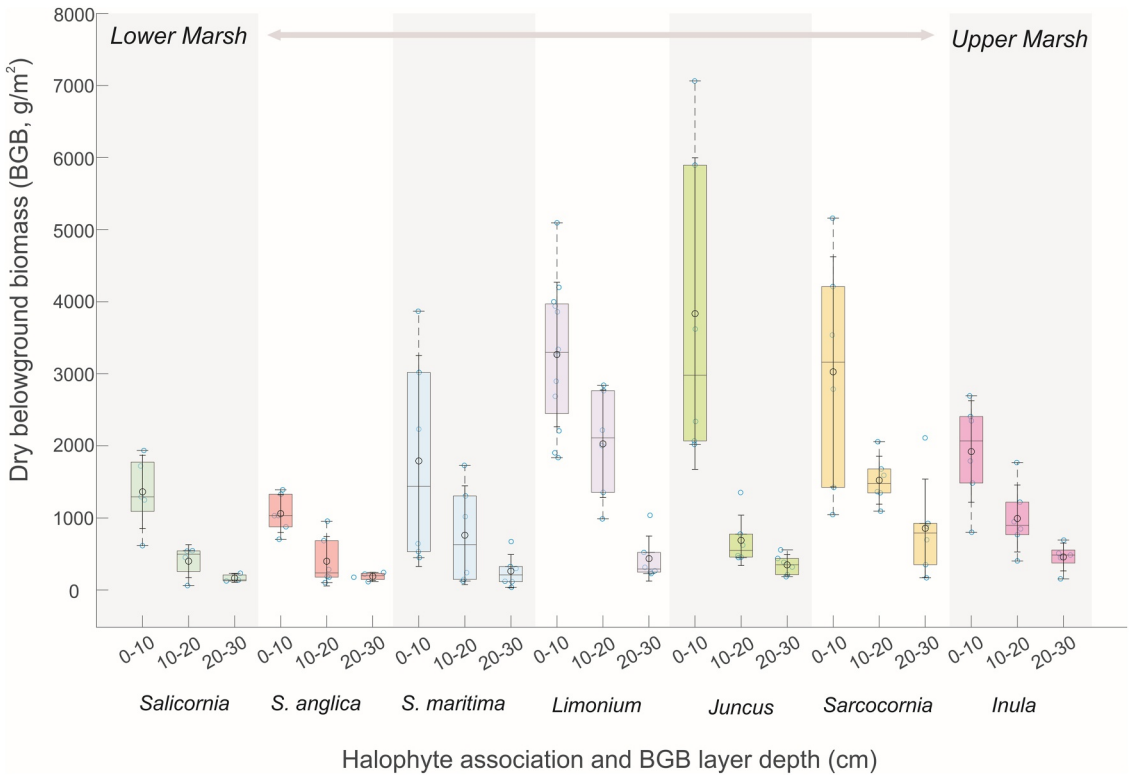

Figure 3. Mean belowground dry weight biomass (BGB; g m^{-2}) is presented for each 10 cm section of the 30 cm core analyzed for each vegetation species class. Classes are color-coded and ordered by increasing mean marsh elevation. Each species plot set is based on at least 6 sample plots.

1,307 ± 774 g m^{-2}. For all species classes, the total BGBT (30 cm core) was more than three times larger than the associated AGB values, and the greatest mean BGBT magnitudes occurred in the middle marsh (*Limonium* 5,885 ± 2,054 g m^{-2}). It is of note that while the other middle marsh species, *Juncus* and *Sarcocornia,* maintained BGBT mean values that were only slightly lower than those of *Limonium* (4,873 ± 2,320 g m^{-2}, 5,406 ± 1,716 g m^{-2}, respectively), the mean AGB of *Limonium* is approximately a quarter of the mean AGB for these other species. Like the AGB, the BGBT is at its minimum in the low marsh. *S. anglica* in particular, despite possessing the largest mean AGB of the low marsh species (520 ± 248 g m^{-2}), had the lowest mean BGBT (1,621 ± 352 g m^{-2}). The total belowground biomass of *S. maritima* had the largest variability of all the species as well as the highest mean BGBT of all the low marsh species (2,813 ± 2,234 g m^{-2}), approaching that of *Inula* (3,295 ± 1,289 g m^{-2}).

The variability of the BGB with depth below the marsh surface for each species plot was also analyzed. As with the BGBT, the BGB values for the 0–10 cm, 10–20 cm and 20–30 cm depths, depicted in Figure 3, were not consistent reflections of the aboveground trends on the surface. In all samples, the belowground biomass reduces as the core depth increases. The key differences observable between the species lie in the rate of this decrease with depth and the magnitude and range of the BGB encountered. In the upper marsh, the 0–10 cm BGB values for *Inula, Sarcocornia*, and *Juncus* are linked to their AGB relative magnitudes, but the differences in means and the ranges of magnitude are accentuated. Thus, the decrease in biomass magnitude and range, as the mean elevation rises from middle to upper marsh, is more rapid for BGB than for AGB across these three species. The similarity in trends for AGB and BGB, however, begins to lessen in the lower BGB layers. For depths greater than 10 cm, the sequence of middle to upper marsh species, when ordered from largest to smallest BGB values, alters. *Juncus* transitions from having the greatest BGB values to the least, and *Sarcocornia* has the highest biomass in these lower depths. In the deepest layer, the *Juncus* mean BGB value is ~350 g m^{-2}. Given that in the 0–10 cm layer its mean BGB was the greatest (~3,830 g m^{-2}), *Juncus* displays the most rapid fall in BGB with depth of all the species investigated. In the 20–30 cm zone, the mean BGB can be split into two main groups dictated by surface elevation: low marsh *Salicornia* and *Spartina* species (~160–260 g m^{-2}) and middle to upper marsh species

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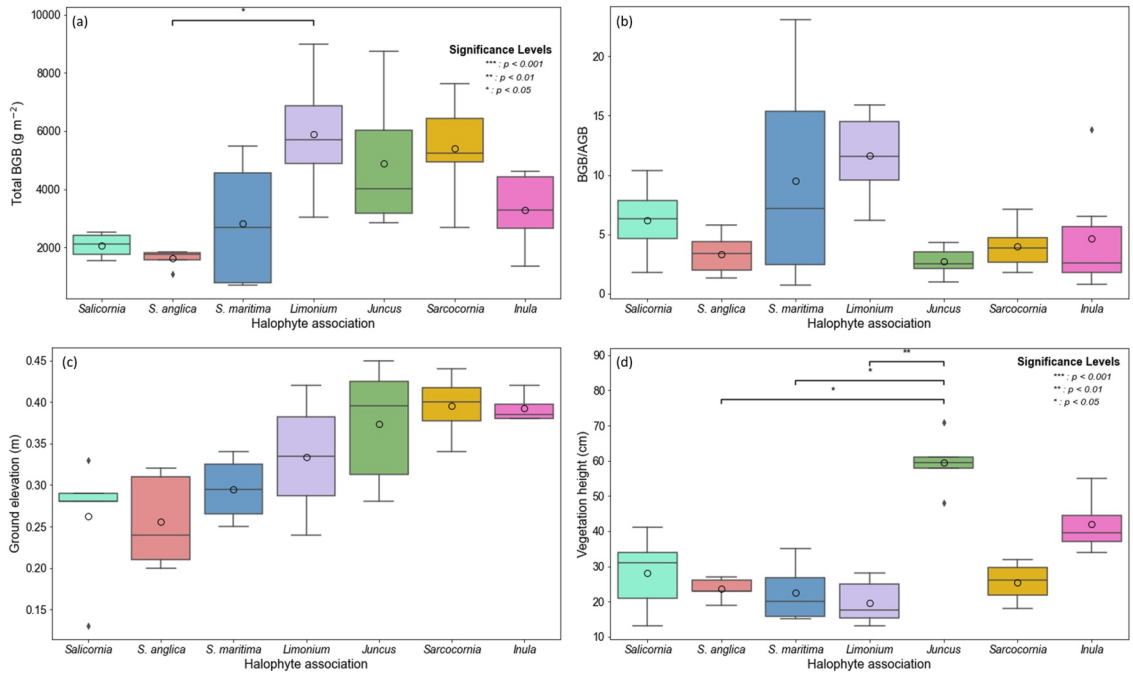

Figure 4. (a) Total dry biomass for each species plot set (AGB + BGBT; g m^{-2}); (b) belowground (BGB) to aboveground biomass (AGB) ratio (based on 0–30 cm BGBT; g m^{-2}) for each species plot set in order of increasing mean elevation. Species plot distributions for (c) ground elevation (meters) and (d) maximum vegetation height (cm). Each species class set is based on at least 6 sample plots, and *p-values* for statistical significance are reported on the graphs.

Limonium, *Juncus*, and *Inula* (~350–460 g m^{-2}). This excludes *Sarcocornia* (~860 g m^{-2}), which, on average, has approximately twice the biomass at the 20–30 cm depth as other middle to upper marsh species.

Pioneer species *Salicornia* and *S. anglica*, which inhabit the lowest areas of the inner marsh, have very similar mean BGB values across the soil layers (~1,060–1,300 g m^{-2} (0–10 cm), ~400 g m^{-2} (10–20 cm), ~170 g m^{-2} (20–30 cm)) even though their mean AGB values are ~293 g m^{-2} and ~520 g m^{-2} respectively. Excluding the 20–30 cm layer, *S. maritima* has BGB data split into two clusters, one with lower values, closer to *Salicornia* and *S. anglica,* and the other with higher values, closer to the distribution of *Limonium*. While the AGB in the low to middle marsh zone shows a slight increase with increasing mean elevation, the BGB behavior only mirrors this slight increase in the 20–30 cm layer. In the upper layers, contrastingly, there is a notable increase in BGB when progressing from low to middle marsh, starting at *S. maritima* and peaking at *Juncus* (0–10 cm layer) or *Limonium* (10–20 cm layer). In the middle upper marsh, this trend is reversed by a downward curve in the BGB starting with *Juncus* and reaching a minimum at *Inula.* (0–10 cm layer). Hence, while the AGB has a sudden stepped increase with increasing elevation at the transition from *Limonium* to *Juncus*, the BGBs sketch an inverted curve trend in the upper 0–20 cm layer, which peaks at *Limonium.*

Overall, based on the sum of AGB and BGBT, the *Sarcocornia* has the greatest mean total biomass surficial density (6,969 ± 2,006 g m^{-2}), however, it is closely followed by the *Juncus* (6,853 ± 2,727 g m^{-2}) and *Limonium* (6,392 ± 2,081 g m^{-2}; Figure 4a). *Limonium* has the greatest mean BGBT (5,885 ± 2,054 g m^{-2}), followed by *Sarcocornia* (5,405 ± 1,716 g m^{-2}) and *Juncus* (4,873 ± 2,320 g m^{-2}). This is despite *Juncus* having the highest BGB levels in the first 10 cm layer (~3,830 g m^{-2}), because both *Sarcocornia* and *Limonium* have relatively higher magnitudes of BGB stored in the second and third core layers. The most statistically significant differences between total biomass are between these three species and *S. anglica* (*p-values* <0.01–0.05). The link between AGB and BGB is directly related to the species present. *Limonium* has a remarkably high surficial density of BGB compared to AGB. To further illustrate this phenomenon, the total BGB (0–30 cm) to AGB ratios for each species plot class are presented in Figure 4b below. The middle to high marsh species (*Inula*, *Juncus* and *Sarcocornia*) tend to have lower ratios with a mean of 2.7–4.7, while the lower to middle marsh species—excluding *S. anglica* (3.3)—have higher BGB/AGB ratio values ranging from a mean of 6.2 ± 3.6 (*Salicornia*) to a mean of 11.6 ± 3.7 (*Limonium*). In addition, excluding *S. anglica*, the ratios for the lower marsh species are

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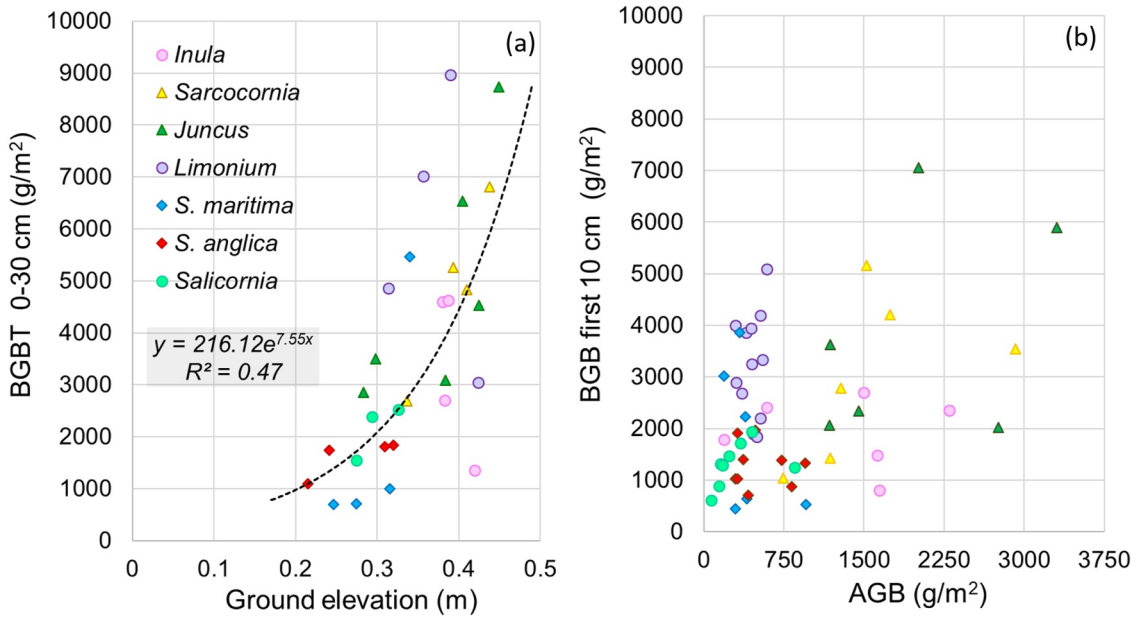

Figure 5. (a) Ground elevation (m) versus total belowground biomass (BGBT—30 cm depth; g m^{-2}) classed by species plot class with exponential trendline (*p-value* <0.001); (b) aboveground biomass (AGB; g m^{-2}) versus belowground biomass (BGB; g m^{-2}) of top 10 cm classed by species coverage.

notably more variable, particularly regarding *S. maritima* (9.5 ± 9.1). While upper-middle marsh species can, on average, retain nearly quadruple as much biomass in the first 30 cm of soil as above ground, certain middle marsh species like *Limonium* are capable of retaining, on average, twelve times the amount of belowground biomass as aboveground. It is of note that *Limonium* is capable of storing unexpectedly large volumes of biomass below ground, given its unprepossessingly sparse aboveground biomass. No significant relationship was found between the species mean BGB ratio (Figure 4b), platform elevation (Figure 4c), and vegetation maximum height (Figure 4d).

The distribution of species class elevations (Figure 4c) was aligned with the field observations of species distribution. The species observed to frequently co-exist in associations (*Sarcocornia*, *Juncus*, and *Limonium*) do indeed occur at overlapping elevation ranges with means descending in elevation (0.40 ± 0.04 m; 0.37 ± 0.07 m; 0.33 ± 0.07 m; mean ± SD). *Inula* has the smallest elevation range (0.39 ± 0.02 m), situated at the high elevations of the marsh, while *Salicornia* is capable of occupying the lowest elevations (0.26 ± 0.08 m) alongside *S. anglica* and *S. maritima* (0.26 ± 0.06 m; 0.30 ± 0.04 m). These mean elevations encompass only 14 cm of vertical change, and the greatest adjacent species mean elevation difference (4 cm) occurs between *Juncus* and *Limonium*. When comparing the mean maximum vegetation height of the species (Figure 4d), it can be seen that the sudden increase in the AGB observed when passing from *Limonium* to *Juncus* aligns with a sudden statistically significant increase in mean vegetation height (from 20 ± 6 cm to 60 ± 7 cm; *p-value* = 0.002). For other species, such as *Sarcocornia,* however, the relatively large magnitude of AGB is not reflected in the canopy height (26 ± 6 cm). Hence, although the AGB trend does link to the physiological traits of species, the key determining trait is not canopy height for all species. Excluding *Juncus,* the vegetation height follows a concave pattern, with the lowest mean vegetation height occurring in the middle marsh with *Limonium*.

The relationship between elevation and halophyte biomass can further illuminate the relationship between biomass and geomorphology. The relationship between BGBT and ground elevation can be fitted with a statistically significant exponential trendline (Figure 5a; $R^2 = 0.5$; *p-value* <0.001). This correlation within species is particularly strong for *Limonium*, *Juncus*, *Sarcocornia*, and *Salicornia.* Whereas, for *S. maritima* and *S. anglica,* the trend is weaker, and their BGBT seems only slightly to increase with a rising elevation. When viewed alone, *Inula* BGB exhibits stochastic variability, with no systematic change within a narrow range of elevations. Next, we examined the relationship between AGB and the BGB of the top 10 cm of soil, where most of the live roots are located (Figure 5b). When considering the variation within the species plots, for *S. maritima*, *S. anglica,* *Limonium,* and *Inula,* there is little evidence of a relationship between the AGB and BGB due to large random

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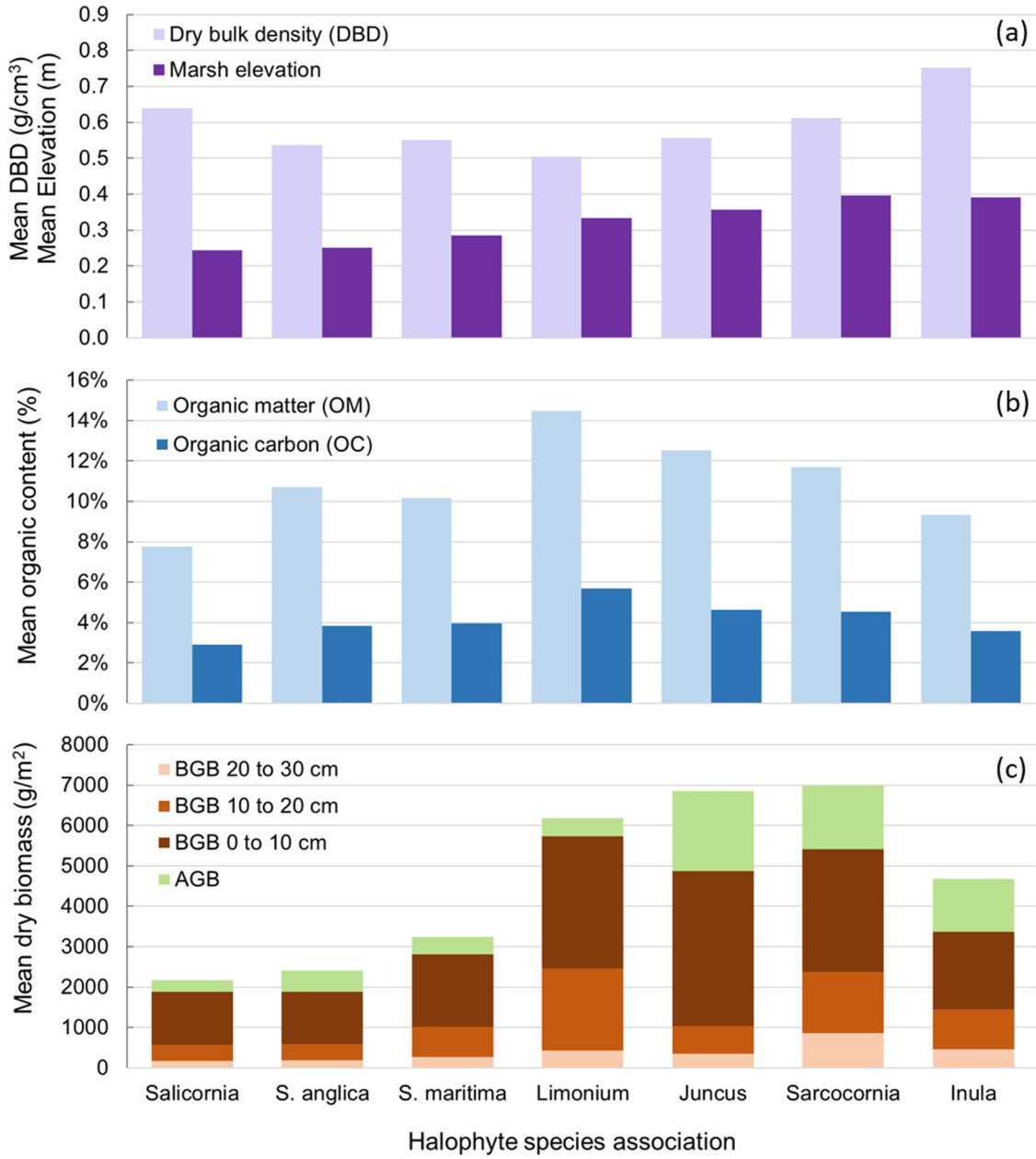

Figure 6. For each species plot set: (a) mean elevation (m) and mean dry bulk density of top 10 cm subsoil (DBD; g cm^{-3}); (b) mean organic matter (OM/LOI; %) and mean organic carbon of top 10 cm topsoil; and (c) mean aboveground biomass (AGB; g m^{-2}) and belowground biomass (BGB; g m^{-2}) for each 10 cm sublayer.

variability. A key difference in the behavior of these species is that the BGB in *Limonium* varies greatly, while the AGB remains fairly constant. Whereas for the other species in this category, especially *Inula*, there is a greater breadth of variability in the AGB axis. For *Salicornia*, *Sarcocornia,* and *Juncus,* the BGB in the first 10 cm tends to increase alongside the AGB. While this relationship is notable for *Salicornia*, in the case of *Juncus* and *Sarcocornia,* the experimental observations are affected by scattering, and having six sampling points prevents the identification of a clear deterministic dependence.

3.2. Sedimentary Organic Matter and Carbon

In the cores, the DBD increased with depth, whereas water content, OM and OC decreased with depth. The DBD from the top 10 cm soil section was lowest in low-middle marsh zones and was greatest adjacent to channel edges

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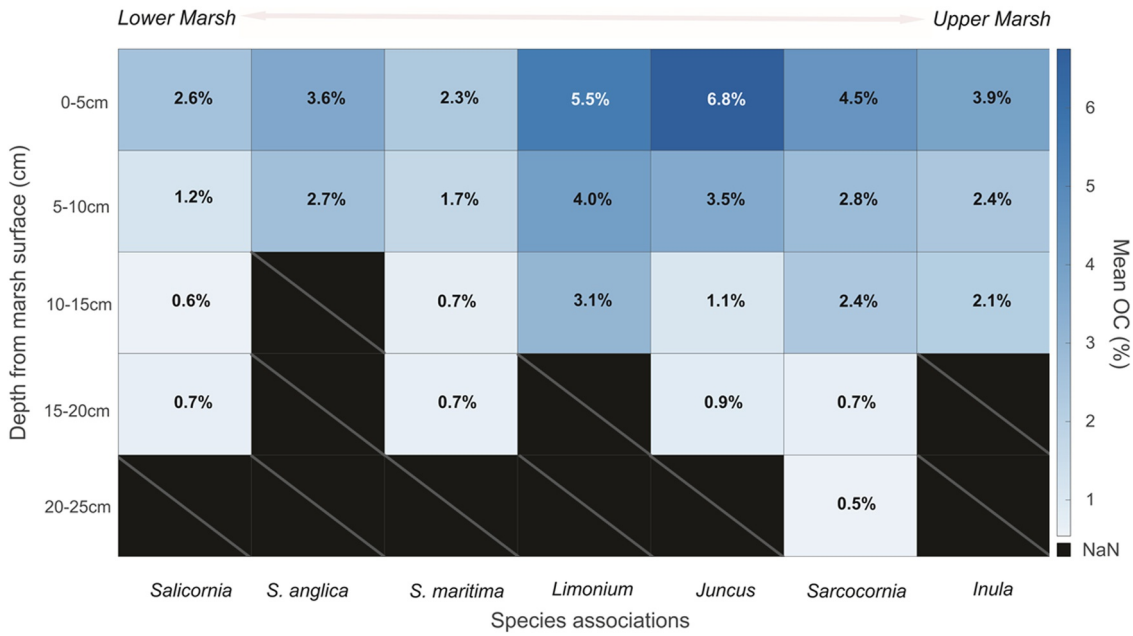

Figure 7. Species plot set mean organic carbon content (OC; %) data from 2023 plotted by depth (cm) from the surface in 5 cm layers.

(Figure 6a). When proceeding from middle to the upper marsh, the DBD increased with increasing elevation. The largest variations in DBD were observed in *Salicornia* and *S. maritima,* as in the OM and OC values (Figure 6b). Concerning platform elevation and tidal influence, the DBD—and vegetation heights exclusive of *Juncus*—follow a reverse trend to OM and OC. Thus, there is an inverse proportional relation between these factors. The mean lowest DBD, AGB, and vegetation height, as well as the highest BGB and OM and OC content, are located within the *Limonium* patches (0.50 ± 0.08 g cm^{-3}; 20 cm; ~5,890 g m^{-2}; 14.5%; 5.4%) (Figure 6c). The two species at the extremities of the marsh elevation—*Salicornia* and *Inula*—differ slightly in the sedimentary parameters, the latter maintaining on average a slightly higher DBD (0.75 ± 0.13 g cm^{-3} vs. 0.64 ± 0.3 g cm^{-3}) and OC content (3.5 ± 0.7% vs. 2.9 ± 1.8%). This occurs despite *Inula*'s total mean biomass being more than twice that of *Salicornia*.

The relationship between LOI (OM) and depth was analyzed for each sample plot from 2023 using 5 cm thick layers of the cores, while the 2021 data was analyzed using 10 cm thick sections. The relation between OC and depth from the surface (Figure 7) visibly concords with the BGB results. *Juncus* has a rapid decrease in OC with increasing depth from the surface. In the low marsh, the OC starts at lower values on the surface but then decreases at a slower rate with depth. The species *Inula, Limonium*, and *Sarcocornia* tend to start in the middle to high range of observed OC at the surface and then decrease less rapidly than *Juncus.* Hence, on average, they maintain higher OC values by the end of the core depth. The OC values across the range of species start to align at a depth of around 20 cm with an OC of 0.6%–0.7%. The OC densities in the top 10 cm were species dependent and ranged from 0.016 g cm^{-3} to 0.26 g cm^{-3}.

4. Discussion

4.1. North Adriatic Lagoon Context

Recent Venetian studies have focused on salt marsh DBD, OC and OM distribution (e.g., Puppin, Tognin et al., 2023, Puppin et al., 2024; Roner et al., 2016). Previous halophyte AGB and BGB samples in the Venice Lagoon are sparse (e.g., Caniglia et al., 1978; Day et al., 1999; Scarton et al., 1998). The majority are of *Sarcocornia* dominated plots, but also include some from *Salicornia*, *S. maritima, Limonium*, and *Juncus*. In the Marano and Grado Lagoon, located in the North Adriatic eastwards of the Venice Lagoon, there have also been measurements of *Limonium*, *Sarcocornia*, and *Halimione* biomass as well as OC (e.g., Cingano, 2021; Pellegrini, 2012; Vuerich et al., 2024). The marsh maturity, position on the lagoon-system gradients, the species and sampling methodologies are not uniformly consistent across all studies, so some variation between results is

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inherent. In particular, the previous biomass studies tend to focus on a single species, which is more comparable to our plot classes, where species coverage is defined as >80% (Table 1). Furthermore, in the Marano and Grado Lagoon, the Pellegrini (2012) AGB data is calculated at an individual plant level, which can only be indicatively compared with our AGB plot areal densities. Where feasible, pre-existing biomass data, including both dead and live matter, relating specifically to peak biomass, were selected to increase the comparability with our data set.

4.1.1. Plant Biomass

In the low marsh zone, the AGB peak biomasses of *Salicornia* previously recorded in the Venice Lagoon were 307.2 g m^{-2} (Day et al., 1999) and 640.9 g m^{-2} (Scarton, 2006), while our study has an AGB of 293.3 ± 236.7 g m^{-2} (mean ± SD). The AGB value of Scarton (2006) is twice the magnitude of the mean found in our study, but despite having higher species coverage (>80%), its AGB is less than the maximum value in our data set (848 g m^{-2}; 30%). Only Day et al. (1999) measured BGB in the Venice Lagoon for *Salicornia* (100 g m^{-2}), which was notably less than what was found in our study (2,074.0 ± 462.0 g m^{-2}) and could be linked to discrepancies in vegetation coverage and biomass extraction methodologies. The *Salicornia* BGB/AGB ratio from the previous data sets is much lower (0.3), in comparison to our ratio of (6.2 ± 3.6). Regarding *S. maritima,* in our study, the mean AGB was 427.5 ± 270.3 g m^{-2} while previous AGB values from the Venice Lagoon were 662.4 g m^{-2} (Day et al., 1999), 830.9 g m^{-2} (Scarton et al., 2000) and 478.2 g m^{-2} (Scarton, 2006). Thus, our AGB results fall within the lower end of the *S. maritima* AGB biomass range previously identified within the Venice Lagoon. Again, only Day et al. (1999) reported a BGB value of 2,221 ± 1,778 g m^{-2}, which is 30% less than the mean of our study (2,813.0 ± 2,234.0 g m^{-2}). Since *S. maritima* forms patches often extensively intermixed with other species (e.g., *Limonium*), the mean BGB/AGB ratio derived from our study is large, yet highly variable (9.5 ± 9.1). Thus, even though Day et al. (1999) derived a lower ratio (3.4), this remains within the range found herein.

Moving on to the middle marsh zone, the previous Venice Lagoon data relating to the AGB of *Limonium* ranged from 226 to 239 g m^{-2} (Scarton, 2006; Scarton et al., 2000) up to 512.8 ± 252.1 g m^{-2} (Day et al., 1999). Our data (449.3 ± 95.6 g m^{-2}) aligns more with the latter and thus sits in the higher range of the previous AGB values in the Venice Lagoon. As for the BGB and BGB/AGB ratio in the Venice Lagoon, Day et al. (1999) (3,421.0 ± 1,999.0 g m^{-2}; 6.7) is within the lower range of results from our study (5,885.3 ± 2,054.3 g m^{-2}; 11.6 ± 3.7). The Marano-Grado *Limonium* indicative AGB values (~336 ± 182 g m^{-2}) are in the lower-middle range of the Venetian AGB samples. The Marano-Grado BGB (2,628.2 ± 1,678.5 g m^{-2}) is on average in the lower range of the Venetian data. However, the *Limonium* BGB values within the Marano-Grado data set do reach 5,990 g m^{-2}, which is close to the mean of the Venetian *Limonium* BGB estimates. The indicative Marano-Grado median biomass-based BGB/AGB ratio (~9.4) of *Limonium* aligns with the findings in the Venice Lagoon. Out of all the halophyte species patches analyzed in our study, *Limonium* ranks among the species generating the greatest total biomass. Given its low AGB values, its large biomass is driven by having the greatest BGBT and BGB/AGB ratio, as well as the slowest decrease in BGB with depth. A trend which can also be seen in the Marano-Grado data set (Pellegrini, 2012). The data from Marano-Grado also confirms a species-specific AGB-BGB relationship noted in Figure 5b, where *Limonium* has the unique characteristic of maintaining fairly constant AGB while the BGB varies significantly. The other middle to upper marsh species, *Sarcocornia*, *Inula* and *Juncus*, instead tend to have AGB that varies greatly while the BGB stays more constant.

The previous data relating to *Juncus* mean peak AGB values for the Venice Lagoon were 726.6 g m^{-2} (Scarton et al., 2000) and 1,028.3 g m^{-2} (Scarton, 2006). Hence, the previous Venetian AGB values are lower than the AGB results found in our study (1,979.3 ± 884.7 g m^{-2}). No previous measurements of BGB were available for *Juncus* within the Venice or Grado Marano Lagoons. The *Sarcocornia* mean AGB biomass in our study was 1,563.5 ± 745.6 g m^{-2}, which is higher but still within the range of variability of the previous records from the Venice Lagoon, 1,005.3 g m^{-2} (Scarton, 2006), 1,112 g m^{-2} (Scarton et al., 1998, 2002) and 766.9 ± 285.3 g m^{-2} (Day et al., 1999). The Marano-Grado *Sarcocornia* mean indicative AGB data is ~1,042 ± 619 g m^{-2} (Pellegrini, 2012; Pellegrini et al., 2017) and 500–1,500 g m^{-2} (Cingano, 2021; Vuerich et al., 2024), which aligns well with the Venetian results. As for the BGB, which has a mean of 5,405.8 ± 1,715.7 g m^{-2} at our study site, the pre-existing Venetian data have lower values at 4,314 g m^{-2} (Scarton et al., 1998, 2002) and 3,496 ± 2,171 g m^{-2} (Day et al., 1999). Whereas at Marano and Grado Lagoon, the *Sarcocornia* BGB is even lower than samples from the Venice Lagoon (1,136.7 ± 701.1 g m^{-2}) (Pellegrini, 2012; Pellegrini et al., 2017). In addition, the total biomass values of the pre-existing Venetian *Sarcocornia* data sets, inclusive of Caniglia et al. (1978), tend to be

Table 2
Mean Organic Subsoil Carbon Content (OC%) and Species Class Elevation (m) in Two North Adriatic Lagoons

Source	Location	*Salicornia*	*S. anglica*	*S. maritima*	*Limonium*	*Juncus*	*Sarcocornia*	*Inula*
OC (%)								
This Study	Venice (SF)	2.9 ± 1.8	3.7 ± 1.9	3.8 ± 2.1	5.4 ± 1.1	4.6 ± 1.7	4.4 ± 0.9	3.5 ± 0.7
Puppin et al. (2024)	Venice	5.4 ± 0.9	–	–	8.4 ± 1.2	3.0 ± 1.0	5.2 ± 2.4	2.3 ± 0.6
Pellegrini (2012)[a]	Marano/Grado	–	–	–	5.4 ± 1.4	–	4.7 ± 2.1	–
Elevation (m; m.s.l.)								
This Study	Venice (SF)	0.26 ± 0.08	0.26 ± 0.06	0.30 ± 0.04	0.33 ± 0.07	0.37 ± 0.07	0.40 ± 0.04	0.39 ± 0.02
Puppin et al. (2024)	Venice	0.27 ± 0.07	–	–	0.38 ± 0.05	0.31 ± 0.04	0.34 ± 0.08	0.47 ± 0.06
Marani et al. (2013)	Venice	–	–	0.18–0.22	0.20–0.32	0.28–0.52	0.26–0.46	–
Scarton (2006)	Venice	0.17 ± 0.07	–	0.23 ± 0.07	0.24 ± 0.01	0.28 ± 0.05	0.37 ± 0.08	–
Silvestri et al. (2005)	Venice (SF)	–	–	0.18 ± 0.07	0.23 ± 0.05	0.30 ± 0.10	0.28 ± 0.06	0.31 ± 0.06

Note. SF refers to San Felice marsh study site. [a]Mature marshes' average OC% over the top 15 cm of soil profile and OM and OC derived using ECS 4010 Elemental Combustion System (Costech) instead of LOI. OC values of this study and Puppin et al. (2024) are averaged over 10 cm and derived via LOI as per stated in the methodology.

lower than our values (6,969.3 ± 2,005.7 g m^{-2}). Nevertheless, due to characteristic division between above and belowground biomass, the BGB/AGB ratio of our study (4.0 ± 1.9) aligns well with that of the other Venetian data sets (3.9–4.6) (Day et al., 1999; Scarton et al., 1998, 2002). While at Marano and Grado Lagoon, the indicative BGB/AGB ratio is lower (1.7 ± 2.0), indicating more investment in AGB relative to BGB.

Finally, existing biomass data sets from the Venice and Grado-Marano lagoons did not include plots dominated by *Inula* (AGB: 1,306.5 ± 773.8 g m^{-2}; BGB: 3,295.0 ± 1,289.2 g m^{-2}) and *S. anglica* (AGB: 520.2 ± 247.7 g m^{-2}; BGB: 1,620.8 ± 352.3 g m^{-2}). The lack of data for *S. anglica* in these lagoons is expected, given that it has only recently become established (Wong et al., 2018). Another common species present in the North Adriatic marshes is *Halimione*. *Halimione* was not included in our study due to its scarcity within our study area, however, an AGB sample was collected in 2023 (2,189.9 g m^{-2}). This sample aligned well with the peak mean *Halimione* AGB (2,140.4 ± 356.3 g m^{-2}) measured by Scarton (2006) in three marshes in the Venice Lagoon. The Venetian *Halimione* AGB values are closer to the higher values of AGB for *Juncus* and *Sarcocornia* in our study. *Halimione* data from Marano and Grado Lagoon, however, has a low BGB of 714.2 ± 589.5 g m^{-2} paired with a lower indicative AGB, an almost 1:1 ratio (Pellegrini, 2012; Pellegrini et al., 2017). Overall, in the north Adriatic lagoon context, our biomass data set tends to have slightly higher values of AGB and notably higher values of BGB. Although differences in biomass sampling methods can introduce some variability in results, the tendency for greater root biomass investment observed in the San Felice salt marsh across diverse species could also be indicative of higher levels of tidally induced stress (Carrasco-Barea et al., 2023; Groenendijk & Vink-Lievaart, 1987; Scarton et al., 1998; Schubauer & Hopkinson, 1984; Sousa et al., 2008). Although an indicator of stress, this does not necessarily entail imminent salt marsh vegetation collapse or erosion vulnerability, more likely signaled by rapidly increasing BGB/AGB ratio and low BGB values (e.g., Turner et al., 2004; Bass et al., 2022).

4.1.2. Marsh Belowground Organic Matter and Carbon

DBD, OC and OM were spatially variable in the topsoil layer, markedly influenced by biogeomorphological factors, subsoil characteristics and hydrologic conditions (depth and frequency of inundation) across elevations (Puppin, Roner, et al., 2023, Puppin, Tognin et al., 2023; Silvestri et al., 2005). Previous studies of salt marsh elevation, OM, DBD, and OC within the Venice lagoon and elsewhere provide a contextual frame for the results of this study. Puppin et al. (2024) measured OC (10 cm) for *Inula, Sarcocornia*, *Juncus*, and *Limonium* in the Venice lagoon, with equivalent vegetation coverage percentages and elevations. These have a similar range across the species as in our study (Table 2). The Marano and Grado Lagoon mean mature marsh OC (15 cm) values for *Limonium* and *Sarcocornia* were highly convergent with our OC (10 cm) values at San Felice (Table 2; Pellegrini, 2012). Furthermore, in the Ria Formosa Lagoon (Portugal) and Cádiz Bay (Spain),

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monospecific stands of *S. maritima* and *Sarcocornia perennis* also had surficial layer OC values close to the Adriatic Lagoons' *S. maritima* and *Sarcocornia* surficial OC values, despite geographic and geomorphologic differences (Carneiro et al., 2024; Jiménez-Arias et al., 2020; Martins et al., 2021). Additionally, these studies and our data fall within the dominant range of global-scale non-species-specific salt marsh OC content (Maxwell et al., 2023).

Our results showed that the OM values in the top 10 cm are at a minimum in the sparse low marsh (*Salicornia*: 7.8 ± 4.5%) and on the channel edges (*Inula:* 9.3 ± 1.6%). The OM is slightly higher in the middle-upper marsh (*Juncus*: 12.5 ± 4.1%; *Sarcocornia*:11.7 ± 2.3%) and the inner low marsh (*S. maritima*: 10.2 ± 5.2%; *S. anglica*: 11.3 ± 3.4%). The OM peak was within the lower-middle marsh (*Limonium*: 14.5 ± 2.9%). At the San Felice marsh, both Roner et al. (2016) and Puppin et al. (2024) investigated the variation of DBD and OM (within the top 5 and 10 cm of soil, respectively). In these studies, the DBD was maximum at the edge of the San Felice Channel, and as the distance from the main channel increased, the DBD values rapidly decreased to 0.5–0.8 g cm^{-3}. Values in line with the DBD in our study and at other Venetian marshes (Puppin et al., 2024). The OM followed a reverse trend to DBD, rising away from the channel, likely linked to greater deposition rates of inorganic sediment along the channel and a tendency for organic deposits to increase with lessening hydrodynamic energy exposure (Bass et al., 2022; Martins et al., 2021). The OM of Roner et al. (2016) was on average 6.2% near the San Felice Channel and around 17.3% across the inner marsh. Whereas Puppin et al. (2024) had OM values of 3.0% near the channel, increasing in the middle marsh (24.1%), then reducing again in the lower marsh (13.4%). In the southern part of the lagoon, middle marsh OM (10 cm) was reported as 19% by Scarton et al. (2002). These spatial distributions of OM across the marsh zones are consistent with our findings and with the regional and global context (Li et al., 2018; Maxwell et al., 2023; Pellegrini, 2012).

On the vertical axis, the DBD increases with depth, while the OM, OC, and BGB contents lessen at different rates alongside depth, depending on the species present and the position on the platform (Figures 6 and 7). This behavior also occurred in the Marano and Grado Lagoon (Pellegrini, 2012; Pellegrini et al., 2017). In our study, at a depth of 15–20 cm, there was a confluence of OC values at approximately 1%, irrespective of the species coverage. For the same salt marsh, a similar phenomenon at 20 cm depth was also found by Puppin, Roner, et al. (2023), Puppin, Tognin et al. (2023), Puppin et al. (2024), as well as at other Venetian marshes by Pignatti (1966). However, this particular OC trend within the soil profile is a local biogeomorphic history artifact in the salt marshes of the central-northern region of the Venice Lagoon, rather than a consistent profile across all the lagoon marshes (Puppin, Tognin et al., 2023; Scarton et al., 2002). In addition, iron oxide precipitation granules co-occurred with woody fragments at different depths depending on the species and were completely absent within the sulphide-rich *Spartina spp*. cores. This testifies to the presence of redox gradients with *S. maritima* located in the most reducing anoxic subsoil (Bezzi, 2013; Pellegrini, 2012, 2018; Seyfferth et al., 2020).

In addition, the negative proportional relationship between DBD and OM (LOI) (%) observed in our study ($R^2 = 0.8$) aligns well with the global scale salt marsh power function model proposed by Morris et al. (2016) (Figure 8a). At the lagoon scale, the Venice Lagoon DBD and OM data from Puppin, Tognin et al. (2023) and Puppin et al. (2024) generally follow the Morris et al. (2016) model (Figure 8a) and other Venetian studies are in accordance that OM is inversely proportional to DBD (Carneiro et al., 2024; Roner et al., 2016; Scarton et al., 2002; Yousefi Lalimi et al., 2018). An unexplored stratum of interpretation regarding the DBD and OM model is from the vegetation composition perspective. Our results show that, depending on the species and its position on the marsh platform gradient, the relationship between DBD and OM begins to significantly deviate after 5% OM is surpassed (Figure 8b). When transitioning from the high marsh to the low marsh, the DBD starts to decrease more rapidly in comparison to the rate of increasing OM. The Morris et al. (2016) global model is more representative of our middle marsh DBD and OM trends. Hence, at our site, it underpredicts the OM content of the high marsh and overpredicts the OM content of the low marsh. Overall, the observed species-associated subsoil spatial heterogeneity and variability in the DBD-OM relationship are driven by factors affecting the generation, decay and sequestration of OM, notably tidal flooding and its interplay with plant functional traits and biogeochemistry (e.g., Moffett et al., 2010; Moffett & Gorelick, 2016; Pellegrini et al., 2018; Pont et al., 2002; Puppin, Roner, et al., 2023, Puppin et al., 2024; Schwarz et al., 2015; Serrano et al., 2020; Van De Broek et al., 2016), which should be accounted for when analyzing salt marsh blue carbon stocks.

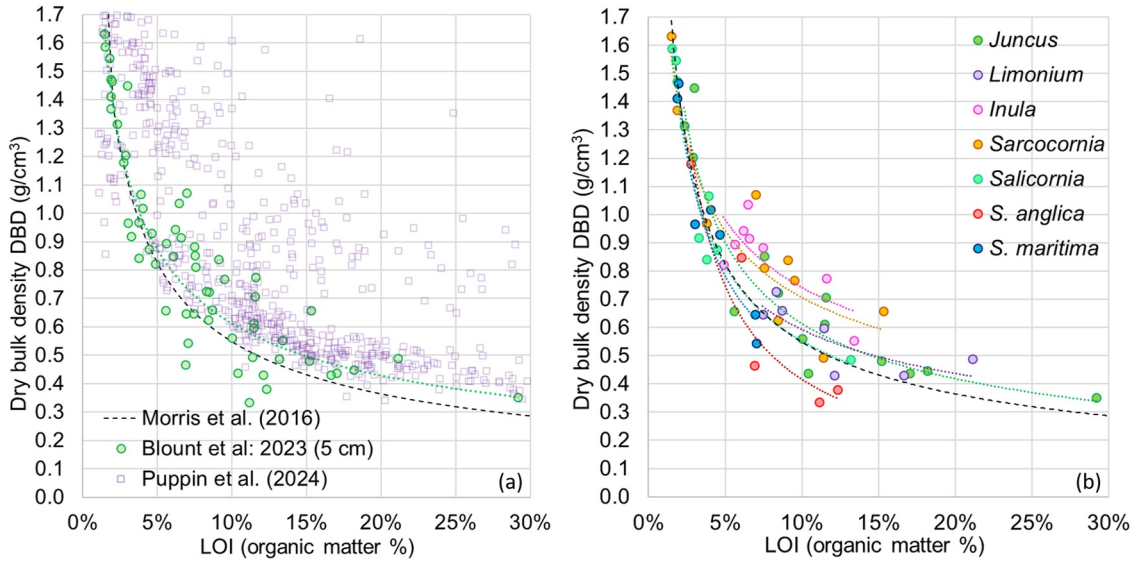

Figure 8. Dry bulk density (DBD; g cm^{-3}) versus Loss on Ignition organic matter (%) 5 cm layers 2023 data set with (a) the trend line Morris et al. (2016) and data from Puppin et al. (2024); (b) Species classes and the trend line Morris et al. (2016).

4.2. Implications for Blue Carbon Dynamics

4.2.1. Predicting Variability

Salt marsh halophytes are autogenic engineers, inextricably engaged in a dialog with their environment and its fluctuations (Castillo et al., 2008; Da Lio et al., 2013; Jones et al., 1994; Marani et al., 2013; Schwarz et al., 2015). Biotic and abiotic interactions dictate halophyte species' presence, biomass, as well as soil OC distribution (e.g., Contreras-Cruzado et al., 2017; Moreno et al., 2020; Pellegrini et al., 2018; Sousa et al., 2008). Capturing the form of the link between biophysical factors and blue carbon in a globally generalizable mode has been consistently challenged by the presence of ephemeral factors and multiscale heterogeneity. Salt marsh elevation is well-known to be linked with the distribution of OC stock (Chmura et al., 2003; de los Santos et al., 2022). As a proxy, elevation is useful as it unites a variety of abiotic and biotic variables, particularly tidal flooding gradients (Yousefi Lalimi et al., 2018; de los Santos et al., 2022). We found that while AGB, BGB and OC are non-linearly linked to elevation via vegetation zonation, it could be perceived only as an aspect of the ensemble driving the distribution (Figures 2 and 5). Nor did we find that vegetation height was notably controlled by elevation, as there were species-specific relationships between plant traits and the resulting biomass density (e.g., Figure 4; Pellegrini et al., 2018). The strongest correlation with elevation was found to be BGBT (R^2 = 0.5; *p-value* <0.001; Figure 5). BGBT increased with rising elevation, with varying levels of sensitivity to elevation amongst the species. This trend has been observed elsewhere and could be related to the potential suppression of root growth at lower elevations due to a combination of stressors encountered in anoxic conditions (Castillo et al., 2008; Hussey & Long, 1982; Li et al., 2018; Mendelssohn & Morris, 2002; Pellegrini et al., 2018). The gradual decrease in total biomass as the elevations rise beyond *Juncus* (Figures 4 and 6) at our site could be credited to increasing stress levels from high soil crust saline concentrations and desiccation (Berger et al., 1978; Mendelssohn & Morris, 2002; Pignatti, 1966). Both these hypotheses reinforce the dominant role of biogeochemistry in sculpting blue carbon reservoirs (Moffett & Gorelick, 2016; Moreno et al., 2020; Vittori Antisari et al., 2017) but do not overwrite the importance of purely halophyte-driven controls (Pellegrini et al., 2018).

Biomass and OC distribution also have links to micro-variations in sedimentation mechanisms and hydrologic processes across the marsh gradient. Particularly as biomass accumulation can be enhanced by higher accretion rates (Castillo et al., 2008) and plant biomechanics can aid OM deposition and retention through mechanisms such as trapping and BGB generation (Bass et al., 2022; Santos et al., 2019; Turner et al., 2004). Furthermore, water and sediment circulations can play a key role in biomass distribution and OM deposition (e.g., Castillo et al., 2008; Schwarz et al., 2015; de los Santos et al., 2022; Vuerich et al., 2024), with flow velocity as a potential key driver of allochthonous OC patterns in salt marsh sediments (Santos et al., 2019). This latter hypothesis pivots

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on the assumption that fine particles rich in OM are more predisposed to be deposited within the inner marsh due to low flow velocities and erosion potential (A. D'Alpaos et al., 2007; Roner et al., 2016; Santos et al., 2019; Martins et al., 2021; de los Santos et al., 2022). Additionally, tidal flooding, sediment water content and OM decay rates have been considered drivers of biomass and OM distribution (Cociancig, 2019; Pellegrini et al., 2018; Vittori Antisari et al., 2017; Yousefi Lalimi et al., 2018). At some sites, OM burial rates are correlated with tidal elevation (Jiménez-Arias et al., 2020). OM decay rates, however, are not strongly dependent on elevation, depth or flooding (Arnaud et al., 2024; Ibañez et al., 1999; Puppin et al., 2023a; Roner et al., 2016) but on occasion, decay and metabolism rates have been related to biomass characteristics and species (Arnaud et al., 2024; Scarton et al., 2002; Spivak et al., 2017). We conclude that elevation, although an important factor, is not a reliable standalone proxy for predicting biomass and carbon sequestration, as previous literature has also noted (Silvestri et al., 2005; de los Santos et al., 2022).

Previous research has demonstrated that OC sequestration rates, microbial metabolisms and hydro-biogeochemical conditions are highly heterogeneous and linked to plant community diversity and functional structure (Li et al., 2018; Pellegrini et al., 2018; Puppin et al., 2024; Serrano et al., 2020; Seyfferth et al., 2020; Spivak et al., 2017). Furthermore, the zonation of species can be used to track changes in salt marsh soil hydrology, salinity and nutrient dynamics (Moffett & Gorelick, 2016; Moreno et al., 2020; Vittori Antisari et al., 2017). Thus, when monitoring and modeling salt marsh blue carbon reservoirs, we suggest that emphasis should be placed on capturing spatiotemporal heterogeneities of biomass and, through this, sedimentary OC. For this to function, it is vital to select complementary halophyte species patch classes wherein the coverage and compositional dominance of species can be consistently quantitatively defined and differentiated (i.e., *S. anglica* vs. *Juncus*). In addition, species which have high phenotypic plasticity and share a wide ecotone with another species can result in a plot class with dualistic and highly variable biomass and OC distributions (e.g., *S. maritima* in our study). Such highly intermixed species classes need to be well constrained to avoid them becoming a source of intrinsic uncertainty errors in biomass and OC estimates. Blue carbon monitoring via species zonation could be further streamlined by prioritizing the precise delineation of the species patches which have the most impact on the sedimentary carbon content due to their high surficial coverage and/or OC content (e.g., *Limonium*).

Overall, considering the multiplicity of interlinked drivers, using species as a proxy for mapping sedimentary OC distribution is a salient approach when sufficient in situ data are available to characterize species patch parameters. The aspects that warrant further investigation, but were out of the scope of this study, are the precise roles of species interactions, soil chemistry, subsurface flow, litter lignin ratios and evapotranspiration on biomass distribution and OC decay rates (Arnaud et al., 2024; Guimond et al., 2020; Marani, Zillio, et al., 2006; Pellegrini et al., 2018; Pont et al., 2002; Seyfferth et al., 2020; Silvestri et al., 2005; Ursino et al., 2004). Furthermore, the dynamics of allochthonous and autochthonous OM inputs in tidal systems are important drivers of sediment OM (Puppin, Roner, et al., 2023, Puppin, Tognin et al., 2023; Roner et al., 2021). As a result of anthropogenic modifications, however, the Venice Lagoon has minimal fluvial or coastal sediment inflows, thus most of the OM we observed is autochthonous at the lagoonal spatial scale (Carniello et al., 2009; Silvestri et al., 2018). Thus, it would be of interest to further investigate the origin and magnitude of allochthonous inputs of OM from different species at this site (Bulmer et al., 2020; Jiménez-Arias et al., 2020; Serrano et al., 2020).

4.2.2. Halophytic Carbon Imprinting

The highest soil OC levels were concentrated within the middle marsh *Limonium* (*Sea Lavender*) dominated patches (Figure 6). Not only at the San Felice marsh, but also at a regional scale in the Venice Lagoon (Puppin, Roner, et al., 2023, Puppin, Tognin et al., 2023, Puppin et al., 2024) and in the Marano-Grado Lagoon (Pellegrini, 2012; Pellegrini et al., 2015, 2017; Vittori Antisari et al., 2017). This overarching halophytic trend is significant at a species level, given that the variability in OC content between salt marshes is affected by marsh geomorphology and maturity, the geographic location within the lagoon system gradients, as well as OM input, source and decomposition characteristics (Carneiro et al., 2024; Carrasco-Barea et al., 2022; Cociancig, 2019; Pellegrini, 2012; Pellegrini et al., 2015, 2017; Puppin, Roner, et al., 2023, Puppin et al., 2024). Ergo, the presence of *Limonium* is linked to increased OM production and retention, hence carbon sequestration. These results point to it being an adept ecological engineer, *sensu* Marani et al. (2013), one which could also increase marsh resilience to sea-level-rise as submergence proceeds from the low marsh toward the middle marsh (Ratliff et al., 2015).

Limonium has a unique relationship between BGB, AGB and elevation (Figure 5). This species, rather than producing more biomass in general as the elevation increases (e.g., *Juncus* and *Sarcocornia*), invests mainly in generating additional belowground biomass. This phenomenon relates to the extensive perennial woody rhizome structures which characterize the *Limonium* species, markedly different from the root systems of the other species encountered. The flowering stems and the rhizome system of *Limonium* have a high density of sclerenchyma fibers, sclereids and thus thick lignified walls which are recalcitrant to degradation and capable of significant anti-erosion mechanical resistance (Arnaud et al., 2024; Bass et al., 2022; González-Orenga et al., 2020; Serrano et al., 2020). The low marsh species (*Salicornia, S. anglica* and *S. maritima*) have fine superficial root structures which do not extend deep into the saturated subsurface, whereas *Juncus* has a dense root mat of fibrous roots, concentrated in the top 10 cm of soil. In contrast, the intensely lignified rhizome systems of *Limonium* persisted throughout the 30 cm core depth, unparalleled by any of the other species examined. Hence, the rhizome and root physiology can be feasibly linked to the observed trends in belowground biomass and OC in the soil of each species plot class (e.g., Figures 6 and 7).

This aspect is salient when modeling blue carbon reservoirs as the lignin levels, C:N ratio and structure found in halophyte biomass vary between species and can result in different rates of decay and persistence of OC in the salt marsh soils (Arnaud et al., 2024; Ibañez et al., 1999; Puppin, Roner, et al., 2023; Scarton et al., 2002; Yousefi Lalimi et al., 2018). *Limonium*'s potential is not restricted to carbon sequestration and reservoir enhancement; it is also a biodiverse halophyte species that can be cultivated as an ornamental or medicinal crop, as well as act as a tolerant heavy metal sink (González-Orenga et al., 2020; Pellegrini et al., 2017). Furthermore, *Limonium* is a genus which is widespread in Mediterranean habitats considered to be vulnerable yet encompassing crucial ecosystem services (Doğan et al., 2020; González-Orenga et al., 2021). It is highly tolerant and competitive in saline conditions, with a strong potential to regenerate salt marshes and withstand increasing levels of salinity due to climate change (Al Hassan et al., 2017). In fact, the colonizing success of the *Limonium* genus can sometimes lead to it being considered an invasive species outside of its natural habitat (Archbald & Boyer, 2014). Furthermore, Pellegrini et al. (2018) and Vittori Antisari et al. (2017) have shown that *Limonium* is capable of modifying the subsoil characteristics, aiding its establishment as well as that of other species through OM generation and lessening soil anoxia. *Limonium'*s ABG structure may also enhance accretion via leaf roughness (Bass et al., 2022). In these modes, *Limonium* has the potential to shape the impact of environmental stressors (i.e., flooding and edaphic conditions) on vegetation distribution and composition in salt marshes.

In addition, our results can provide insights into the niche competitiveness and the effects allochthonous species can have on endemic carbon sequestration dynamics. Allochthonous and non-local variant species *S. anglica* and *S. densiflora* in Europe tend to form dense homogenous patches in the lowest and most stressful elevations on the marsh platform (Bass et al., 2022; Neves et al., 2010; Wong et al., 2018). In the Venice Lagoon, this is often within the shallow inner marsh ponds where competition from endemic species is at a minimum. *Salicornia* predominantly frequents the most minute and extremal parts of the channel network. Whereas, *S. maritima* vegetation is sparser, fringing the inner pond and encroaching on the lower extents of the *Limonium* dominated zones. Despite having a lower BGB/AGB ratio and BGB than *S. maritima*, *S. anglica* has higher levels of OM and OC in the top 10 cm of soil. Similar to those of *Inula,* which has much greater biomass densities and is stationed on the more oxygenated and inorganic sediment rich channel edge. Species can influence salt marsh pond soil biogeochemistry (Spivak et al., 2017). In this case, however, it is likely that the unexpectedly high values of OM and OC in the inner marsh ponds favored by *S. anglica* are due to enhanced fine sediment OM deposition as well as reduced carbon oxidation rates in highly anoxic environments (Puppin, Roner, et al., 2023; Roner et al., 2016; Seyfferth et al., 2020; Yousefi Lalimi et al., 2018). Although their spatiotemporal success is dependent on the ambient conditions of each site, allochthonous *Spartina spp*. are endowed with an elevated capacity to draw on resources and compete intensively with endemic species for dominance in both the aboveground and belowground realms (Li et al., 2018; Neves et al., 2010). This can have cascading ecological, chemical and physical effects, including rewriting plant functional trait diversity, stress gradient modulated intra and inter-species interactions, and sediment deposition dynamics (e.g., via hydraulic roughness and root physiology (Bass et al., 2022; Schwarz et al., 2015)). Thus, since OC decay sequestration rates vary spatially according to specific halophyte species, invasive species can change carbon sequestration dynamics of salt marshes by simply altering vegetation extent, composition and zonation gradients.

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5. Conclusions

In our study, patches dominated by seven halophyte species typical of Mediterranean salt marshes—*Salicornia*, *S. maritima*, *S. anglica*, *Limonium*, *Sarcocornia*, *Juncus* and *Inula*—were analyzed. For each species, the magnitude and ratio of BGB and AGB, as well as the relationship between biomass, DBD, OM content (OM/LOI, determined through Loss-on-Ignition) and OC content (OC) were evaluated. The difference between the mean AGB in the lower marsh (425 ± 217 g m^{-2}) and the upper marsh (1,616 ± 807 g m^{-2}) was highly statistically significant. For BGB, OM, and OC, rising elevation caused a convex curve trend, where these values peaked in the middle marsh zone (~5,890 g m^{-2}; 14.5%; 5.4%) and decreased toward the lower and upper marsh. The DBD was negatively correlated to OM with values in the top 10 cm ranging from 0.5 g cm^{-3} to 0.8 g cm^{-3}. The belowground biomass, BGB/AGB ratio, OM and OC have their maxima exactly coinciding with the Sea Lavender (*Limonium*) species plots. Given its lignin-rich slow slow-degrading, and extensive belowground biomass, *Limonium* constructs a robust carbon imprint within the marsh that can long outlast its residence period on the surface. Due to *Limonium's* nexus of unique attributes and its extensive presence in Mediterranean marshes, it has remarkable potential as a keystone salt marsh umbrella genus, one that is adept at enhancing and maintaining blue carbon reservoirs in the face of climate change. Overall, to accurately characterize salt marsh carbon sequestration and storage capacity, it is fundamental to define the underlying patterns of halophyte species above- and belowground biomass and their relation to the sedimentary OC content and soil chemistry. This data set elucidates halophyte species biomass and sequestration variability, factors which underpin interdisciplinary frameworks aspiring to capture the complex mechanisms which dictate the evolution of this fragile ecosystem. Future work is needed to clarify the effects of anthropogenic and environmentally driven halophyte zonation spatiotemporal fluctuations on the deposition, decomposition rate and retention of OM across diverse time scales and marsh ecosystems.

Conflict of Interest

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

Data Availability Statement

The field data used for the analysis presented in the study are available at Research Data UNIPD via https://researchdata.cab.unipd.it/id/eprint/1709 (DOI: 10.25430/researchdata.cab.unipd.it.00001709) with Creative Commons Attribution 4.0.

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Erratum

The originally published version of this article contained a typographical error. The second sentence of the Abstract has been corrected as follows: "As a blue carbon ecosystem (BCE), they are efficient sinks and long-term reservoirs of organic carbon with vital roles in the global carbon cycle." This may be considered the authoritative version of record.

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