Bioinvasion by Spartina patens alters sediment biogeochemical functioning of European salt marshes

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Abstract Bioinvasions pose undeniable threats and trigger changes in salt marsh ecosystem functioning. In Mediterranean and Atlantic marshes, the invasion by S. patens contributed to added competitive pressure to native middle-upper marsh species such as H. portulacoides. The introduction of a new and aggressive non-indigenous species (NIS) is a game-changer for the marsh biogeochemical functioning. In the present study we explored effects of this bioinvasion on an array of different extracellular enzymatic activities (EEA) of salt marsh sediments colonized by NIS and native plant species and its impacts on the biogeochemical functioning of a large estuarine ecosystem. In H. portulacoides there was an evident control of the extracellular enzymatic activities (EEA) by the sediment physic-chemical traits, but these relationships were weaker and fewer in number when compared to the EEA and the sediment abiotic traits in the sediments colonized by S. patens. This indicates a prevalence of a plant effect over abiotic traits in controlling EEA. Disruption in biogeochemical functioning was evident in the sediments colonized by S. patens, with clear enzymatic activity peaks during spring and summer and with significantly higher values of several EEA during autumn and winter. These led to an acceleration of necromass decomposition processes and thus to reduced marsh storage and remediation capacity. Spartina patens also showed increased phosphatase, urease, and protease activity contributing to increased release of the inorganic phosphorous and nitrogen (ammonia) into the system. Higher activity of carbon-based substrates decomposition allied to an increase in dehydrogenase activity (proxy to microbial abundance and respiration), will lead to an inevitable decrease in the carbon sink capacity of the sediments and reduction of the blue carbon storage ecosystem service. The sulfatase activity in the S. patens rhizosediments also showed a significant decrease during autumn, leading to reduced production of sulfate, sulfides and increased metal bioavailability. All these changes amount to a loss of the sink capacity of the system, in terms of eutrophication reduction through organic nitrogen and
phosphorous retention, carbon sink due to the acceleration of the decomposition processes and decreased metal remediation capacity. Thus, the present work highlights the need to control this invasive species not only to prevent potential reductions in floristic diversity but also to prevent the loss of key biogeochemical services, that can impact the entire estuarine system.

Keywords  Biogeochemical cycling · Extracellular enzymatic activity · Non-indigenous species · Salt marshes

Introduction

Salt marshes are among the most productive ecosystems on the planet, as key areas not only for wildlife habitat but also providing important functions and services, such as erosion and flood control, water quality maintenance (via assimilation and filtration), carbon sequestration and storm protection (Himes-Cornell et al. 2018; Adams 2020; Duarte et al. 2021; zu Ermgassen et al. 2021). These ecosystem services are provided by the halophyte vegetation that colonizes estuarine habitats. These plants can cope with the harsh physico-chemical environment and are resilient to submersion, increased salinity, low oxygen rhizosphere concentrations and high thermal amplitudes (Colmer and Flowers 2008; Flowers and Colmer 2008). Importantly, these plants also produce large amounts of biomass (Caçador et al. 2009; Duarte et al. 2010), sequestering considerable amounts of carbon and nutrients and acting as carbon sinks (Sousa et al. 2008, 2010). Nevertheless, these plants also generate large amounts of detritus (Duarte et al. 2010, 2014b) that supply the surrounding food webs (Nordström et al. 2014; Fonseca et al. 2019), but these detritus are also stored in the sediments as necromass, prone to microbial decomposition (Benner et al. 1984; Newell 1993; Lillebø et al. 1999; Duarte et al. 2008), a key process for biogeochemical cycling in estuarine systems. These microbial-mediated processes are influenced by various factors, including abiotic features (Valiela et al. 1985; Duarte et al. 2008, 2014a), anthropogenic impacts (Windham et al. 2004; Duarte et al. 2013a), and vegetation type (Duarte et al. 2012; Menon et al. 2013; Rietl et al. 2016), and thus any change at this level will have impacts on the system biogeochemical functioning, namely in terms of biomass recycling and nutrient regeneration (Tobias and Neubauer 2019; Bulseco et al. 2020). These decomposition processes are mediated by the activity of microbial extracellular enzymes, especially active in the rhizosphere of these halophyte species, that promote microbial activity through rhizosphere oxygenation and carbon substrate supply (Duarte et al. 2008; Chaudhary et al. 2018).

Several enzymes are present in these rhizosediments, aiming to decompose different necromass components, being enrolled in the key biogeochemical cycles of carbon (e.g., peroxidases, phenol oxidases and N-acetylglucosaminidase and β-glucosidases), nitrogen (e.g., proteases and urease), phosphorous (e.g., phosphatases) and sulfur (e.g., sulfatases), on which the whole estuarine ecosystem functioning is dependent (Duarte et al. 2008; Freitas et al. 2014; Li et al. 2019). Thus, the evaluation of these extracellular enzymatic activities (EEA) and the associated biogeochemical cycling processes can provide insights into the ecosystem necromass recycling functions (Duarte et al. 2012; Bulseco et al. 2020). Peroxidase and phenol oxidase are two oxidoreductases that participate in the oxidation of organic matter (by opposition to the hydrolytic activity of most of the abovementioned enzymes). These enzymes mediate key ecosystem functions of lignin degradation, humification, carbon mineralization and dissolved organic carbon export (Sinsabaugh 2010). Peroxidases are enzymes that use H₂O₂ as an electron acceptor, known for their role in depolymerizing lignin (Sinsabaugh 2010). Phenol oxidases enzymes that oxidize phenolic compounds using oxygen (Sinsabaugh 2010), and thus are linked with the phenolic recalcitrant organic matter decomposition in sediments. The activity of these enzymes is highly important for a more complete assessment of the C biogeochemical cycling in soils. Protein degradation is an ubiquitous capacity of almost all microorganisms in soils, and is frequently linked to ammonium release and thus to N biogeochemical cycling (Alef and Nannipieri 1995). Similarly, urease activity is also linked to ammonium generation in soils, although in this case from the hydrolysis of urea, hydroxycurea and semicarbazid, and thus the evaluation of its activity, coupled to protease activity, provides additional insights on the N biogeochemical cycling (Alef and Nannipieri 1995). Phosphatases catalyse the hydrolysis of phosphate esters and are the most important class of enzymes directly related
Bioinvasion by *Spartina patens* alters sediment…

Vol.: (0123456789)

3219

Bioinvasion by *Spartina patens* alters sediment…

**Bioinvasion by Spartina patens alters sediment…**

The biogeochemical cycling of organic phosphorous forms into inorganic and phytoavailable P forms (Alef and Nannipieri 1995). β-glucosidase is the more prominent disaccharides hydrolytic glucosidase in soils, being also the typical limiting step in the cellulose decomposition processes in soils (Alef and Nannipieri 1995). Disaccharides are rich in carbon and abundant in vegetated sediments due to plant activity, β-glucosidase activity is thus key for assessing the carbon biogeochemical cycling in sediments.

N-acetylglucosaminidase are also known as chitobiases and are essential enzymes for the degradation of chitin homopolymer, the major organic constituent in the exoskeletons of insects, crustaceans and many fungi (Alef and Nannipieri 1995). Since salt marshes are the habitat of several crustacean species that live in sediment burrows (Fonseca et al. 2019), these enzymes provide insights on the decomposition of the necromass generated by the organisms, which is directly linked with C and N biogeochemical cycling. Sulfatases catalyze the hydrolysis of organic sulfate esters being therefore essential for sulfur mineralization and bioavailability for example for plants (Alef and Nannipieri 1995).

Beyond the well-known anthropogenic impacts to which these ecosystems are exposed (e.g. pollution, land claiming, eutrophication), nowadays Mediterranean salt marshes are also prone to a new stressor: non-indigenous species (NIS) bioinvasions (Windham and Ehrenfeld 2003; Dibble et al. 2013; Ge et al. 2015; Baumel et al. 2016; Duarte et al. 2018). More specifically, salt marsh invasion by NIS *Spartina* species (Zhong-Yi et al. 2004; Li et al. 2009; Strong and Ayres 2013; Baumel et al. 2016; Duarte et al. 2018) has been reported to have significant impacts on salt marsh ecosystems, both in terms of floristic biodiversity losses (Zhong-Yi et al. 2004; Li et al. 2009; Borges et al. 2021) and in terms of changes in the services provided by these ecosystems, such as its natural remediation capacity, provided by both halophytes and the microbial communities associated to its rhizospheres (Anjum et al. 2014; Paredes-Páliz et al. 2018; Couto et al. 2018; Megonigal and Neubauer 2019; Human et al. 2020). *Spartina patens* has been reported in several salt marshes along the Mediterranean and Atlantic coasts (SanLeon et al. 1999; Baumel et al. 2016). This species has a high tolerance to salinity (Duarte et al. 2015b), thermal extreme events (Wu et al. 1998; Duarte et al. 2016), and a tremendous tolerance to anthropogenic stressors such as heavy metal pollution (Lin and Mendelsohn 2008), being capable of colonizing the entire upper-middle marsh elevation gradient, making it a formidable competitor against native flora (Bertness and Shumway 1993; Brewer et al. 1998; Duarte et al. 2015a). Nevertheless, its invasion potential in European populations is reduced due to its lack of production of viable seeds, thus making its spread reduced to a local scale by vegetative propagation (Castillo et al. 2017). The *Spartina* genus (also known as cordgrasses) is one of the most successful halophytes, being present in a wide range of latitudes across the globe, highlighting the plasticity and adaptive capacity of these species (Bortolus et al. 2019; Borges et al. 2021).

Due to its aggressive colonization, mostly due to its high photosynthetic rates and large biomass production (Castillo et al. 2017), colonization by *Spartina patens* of the middle-upper areas of Mediterranean and neighboring Atlantic saltmarshes will inevitably reduce the colonization area of the native *Halimione portulacoides*, the prevalent species present in the region (Caçador et al. 2013; Borges et al. 2021; Duarte and Caçador 2021). Therefore, it is key to evaluate how the NIS *S. patens* is potentially changing the biogeochemical cycling processes in salt marshes. Hence, the present work aims to depict the effects of this bioinvasion on the EEA of salt marsh sediments where this NIS occurs in comparison with the EEA in the rhizosediments colonized by the native *H. portulacoides* and evaluate its impacts on the biogeochemical functioning of a large estuarine ecosystem. This will allow to understand if *S. patens* colonization also affects the biogeochemical functioning of the invaded marshes, beyond its negative and recognized impacts.

**Material and methods**

**Sample collection**

Sampling occurred in April 2012 (Spring), August 2012 (Summer), November 2012 (Autumn) and January 2013 (Winter) in the Hortas salt marsh (Tejo Estuary, Portugal, Fig. 1). The Hortas salt marsh is a young undisturbed salt marsh located within the Tejo Estuary Natural Reserve and thus provides
an anthropogenic interference-free context (Duarte et al. 2015a). Sediment cores were collected in pure stands of *S. patens* and neighboring pure stands of *H. portulacoides*. Each pure stand was considered as an experimental unit (replicate). Five stands were considered for all samplings and all five stands from each species were chosen considering their similar position along the marsh to minimize elevation-driven differences. PVC tubular cores were used to collect sediment samples and sliced in the field. The depth between 5 and 8 cm depth was always used as in previous studies this was found to be the layer with higher microbial activity and root density (Duarte et al. 2008, 2009). Sliced sediment samples were placed in refrigerated bags and transported to the laboratory, where they were frozen at -20 °C until analysis. According to previous works (Wallenius et al. 2010), when the soil enzymatic activity may not be performed immediately, sample freezing is the best option with small impacts (<20%) in the activity of EEA in loamy clay organic soils.

### Rhizosediment physic-chemical characterization

Sediment relative water content (RWC) was determined by drying sediment samples at 60 °C until constant weight. Organic matter was determined by the loss on ignition (LOI) method, by burning 1 g of airdried sediment at 550 °C for 3 h. Values of pH were measured in the field in freshly sliced sediment samples using a HANNA pH/mV (HI 9025) probe. Carbon and nitrogen content (%) were determined in dried pulverized sediment samples using a Flash EA 1112 Series elemental analyzer coupled online via Finningan conflo III interface to a Thermo delta V S mass spectrometer.

### Rhizosediment extracellular enzymatic activities

All enzymes and samples were assayed within 2–3 working days following sample collection in order to limit possible sample storage effects. All enzymatic determinations were carried out with colorimetric...
methods and the absorbances were read on a TECAN Absorbance Microplate Reader (SPECTRA Rainbow). Dehydrogenase activity (DH) was determined using the triphenyltetrazolium chloride (TTC) method according to Kazemi et al. (2017), immediately after sampling upon arrival to the laboratory. Briefly, approximately 5 g of fresh sediment were incubated with 5 ml of TTC solution (1%). Samples without the substrate were also prepared with 5 ml Tris–HCl buffer (100 mM) instead of the TTC solution. Incubation was performed at 30 °C for 24 h. After incubation, 40 ml of acetone were added to each tube to stop the reaction and extract the formed coloured compound (Triphenyltetrazolium formazan, TPF). The tubes were shaken and kept in the dark for 2 h and centrifuged at 14,000 × g for 15 min, at 4 °C. The clear supernatant absorbance was read at 546 nm and compared with a standard curve for TPF.

Phenol oxidase (FOX), peroxidase (POX), N-acetyl-glucosaminidase (NACET), phosphatase (PHO), β-glucosidase (GLU) and sulfatase (SULF) were assayed according to Ravit et al. (2003) with minor modifications as described in Duarte et al. (2008) and Freitas et al. (2014). Briefly, 75 ml of sodium acetate buffer (pH 5) was added to 5 g of fresh sediment and mixed for 1 min to obtain the sediment slurry. The substrates (5 mM) used were p-nitrophenyl-N-acetyl-d-glucosaminate, p-nitrophenyl-phosphate, p-nitrophenyl-glucoside and p-nitrophenyl-sulphate, respectively, for N-acetylgalactosaminidase, phosphatase, β-glucosidase and sulfatase. Two millilitres of each substrate were added to 2 ml of slurry and incubated at 30 °C with gentle agitation for 30 min (phosphatase), 60 min (sulfatase and β-glucosidase) and 2 h (N-acetylgalactosaminidase). After incubation, samples were centrifuged at 6,530 × g for 15 min at 4 °C, and 0.2 ml of 1 N NaOH was added to stop the reaction and reveal the p-nitrophenol (pNP) formed. The absorbance of the supernatant was read at 410 nm. The activity was expressed as μg of pNP released per gram sediment dry weight per hour. Phenol oxidase and peroxidase were assayed using 5 mM L-DOPA (1,3,4-dihydroxyphenylalanine) as substrate. Two millilitres were added to 2 ml of slurry (adding 0.1 ml of 0.3% H2O2 for peroxidase assay) and were incubated for 60 min in both enzymes. After incubation, samples were centrifuged at 6,530 × g for 15 min at 4 °C. The absorbance of the supernatant was read at 460 nm and the absorbance of phenol oxidase was subtracted from the absorbance of total peroxidase to obtain the real value for peroxidase activity alone. The activity is expressed as μmol L-DOPA oxidized per gram sediment dry weight per hour. Protease (PROT) activity was assayed according to Ladd et al. (1976). Briefly, 1 g of fresh sediment was incubated with 5 ml of Tris (tris-hydroxymethyl-aminomethane) buffer (0.05 M, pH 8.1) and a 2% (w/v) casein solution, for 2 h at 50 °C. After incubation, the reaction was stopped with 1 ml of trichloroacetic acid 17.5% (w/v) and centrifuged at 14,690 × g for 15 min, at 4 °C. For photometric analysis, 1 ml of supernatant was added to 1 ml of Folin–Ciocalteu’s phenol reagent (0.2 N) and 2.5 ml alkali reagent, and left to stand for 90 min. The absorbance was measured at 700 nm and compared with the calibration curve for tyrosine. The activity was expressed as μg tyrosine equivalents per gram sediment dry weight per hour.

Urease (URE) activity was assayed according to Aşkın and Kızılkaya (2006). Briefly, approximately 2 g of sediment were incubated with 3.75 ml of citrate buffer (50 mM, pH 6.7) and 5 ml of urea 10% (w/v). Samples without the substrate were also prepared to subtract the citrate-extractable ammonia. The incubation was made at 37 °C for 3 h. After this period the samples were centrifuged at 4000 × g for 15 min, at 4 °C. One ml of supernatant was diluted to a final volume of 10 ml with distilled water. This solution was used for ammonia determination using the iodophenol-blue method (Aminot et al. 1997). Ammonia concentrations were read at 630 nm and urease activity expressed as μmol NH4 formed per gram of sediment fresh weight per hour.

Statistical analysis

The seasonal patterns of the sediment physico-chemical features and extracellular enzymatic activities were already evaluated and discussed in previous papers (Duarte et al. 2008, 2009, 2015a), and thus the statistical analysis of the present work focused only on a season by season comparison between the variables measured in the sediments colonized by H. portulacoides and S. patens. All statistical analyses were computed in R-studio (2021.09.0 Build 351). Due to the lack of normality and homogeneity of variance of the data, non-parametric tests were used for testing statistical differences between samples. Differences among rhizosediments colonized by
each of the surveyed species were evaluated through Kruskal–Wallis tests, performed using the ‘ggsignif’ package. Principal Component Analysis was performed using the ‘ggfortify’ package. Spearman correlations were attained using the ‘corrplot’ package. A statistical significance level at $p < 0.05$ was considered in all tests.

### Results

#### Rhizosediment physic-chemical characterization

Regarding the sediment relative water content (Fig. 2), significant differences between the sediments of the two analyzed species were only observed in winter, with the rhizosediments colonized by *S. patens* presenting lower RWC values. On the other hand, the pH values of the sediments colonized by this NIS showed higher values than the ones measured in *H. portulacoides* rhizosediments during the spring season. In terms of rhizosediment organic matter content (here evaluated through the loss on ignition, LOI), these were found to be substantially higher in the area colonized by *H. portulacoides* during spring, summer and winter, when compared to *S. patens* rhizosediments. Rhizosediment total carbon and nitrogen contents were found to be higher during all seasons in the sediments colonized by the NIS *S. patens* when compared to *H. portulacoides* rhizosediments. Analyzing the C/N ratio, the opposite trend was observed, with the sediments colonized by *H. portulacoides* showing higher values of this ratio during all seasons, in comparison with *S. patens* rhizosediments.

#### Rhizosediment extracellular enzymatic activities

Regarding the extracellular enzymatic activities (EEA) of the analyzed rhizosediments, several significant differences could be observed (Fig. 3).

![Figure 2](image-url)  
**Fig. 2** Physic-chemical characteristics (RWC, relative water content; LOI, organic matter express as loss on ignition; C, total carbon content; N, total nitrogen content; C/N, carbon to nitrogen ratio) of the rhizosediments colonized by the native *H. portulacoides* (HP) and the NIS *S. patens* (SP), across seasons (values are given as mean and standard deviation of 5 replicates per species per season). Significant differences between sites are represented by asterisks (Kruskal–Wallis multiple comparisons test, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)
Dehydrogenase EEA (DH) differed between rhizosediments of the two surveyed species only during Summer, with the rhizosediments colonized by NIS S. patens presenting significantly lower values of activity of this enzyme. On the other hand, Peroxidase EEA (POX), showed significantly higher activity levels during winter in the rhizosediments colonized by S. patens, when compared to the sediments from the native congener. During summer and autumn, phenol oxidase (FOX), was more active in the rhizosediments colonized by S. patens, in comparison to the ones colonized by H. portulacoides. During winter the inverse trend was observed. Regarding phosphatase activity (PHO), it was significantly higher in the rhizosediments colonized by S. patens when compared to the sediments collected in H. portulacoides monospecific stands. The hydrolase β-glucosidase (GLU) was more active during summer and winter sampling in the sediments colonized by S. patens. This same trend was found for N-acetylglucosaminidase (NACET),
with this enzyme also showing higher activities in the sediments colonized by *S. patens* during spring. Analyzing sulfatase EEA (SULF), it was more active in the rhizosedsimals colonized by the native *H. portulacoides* during the autumn season when compared to the rhizosedsimals colonized by the NIS *S. patens*. During this season, protease activity (PROT) also showed higher activity levels in the rhizosedsimals colonized by *S. patens*, in comparison to its native congener. Finally, urease (URE) was more active during all seasons in the rhizosedsimals colonized by the NIS *S. patens*.

**Rhizosediment biogeochemical profiles**

The relationships between the extracellular enzymatic activities and the sediment physic-chemical traits in the rhizosedsimals colonized by *H. portulacoides* (Fig. 4A) and by *S. patens* are highlighted in Fig. 4A, B, respectively. In the rhizosedsimals colonized by *H. portulacoides*, all enzymes, except for protease and urease, showed significant correlations with the analyzed physic-chemical traits. Specifically, the relative water content was negatively correlated with dehydrogenase (DH), peroxidase (POX) and phenol oxidase (FOX) activities. The two latter enzymes also showed a significantly negative correlation with the sediment pH, total carbon and nitrogen. Sediment organic matter showed a positive and significant correlation with dehydrogenase (DH), peroxidase (POX) and phenol oxidase (FOX) activities, whilst phosphatase (PHO), β-glucosidase (GLU), *N*-acetylglucosaminidase (NACET) and protease (PROT), showed strong negative correlations with the rhizosediment organic matter (LOI). Moreover, sulfatase activity also showed a positive strong correlation with sediment RWC and total nitrogen, and an inverse significant correlation with the rhizosediment C/N ratio. Analyzing these same trends between enzymatic and physic-chemical traits in *S. patens* rhizosedsimals, it was possible to observe that there were fewer and weaker significant correlations (Fig. 4B). Sediment water content (RWC) showed an inverse significant correlation with peroxidase (POX), phosphatase (PHO) and sulfatase (SULF) activities, whilst dehydrogenase (DH) activity was enhanced by RWC. Sediment pH showed very similar relationships with the analyzed EEA, being positively correlated with dehydrogenase (DH) and protease activities, and negatively correlated with peroxidase (POX), phosphatase (PHO), β-glucosidase...
Bioinvasion by *Spartina patens* alters sediment…

(GLU), *N*-acetylglucosaminidase (NACET) and sulfatase (SULF) activities. None of the evaluated EEAs showed any significant correlation with *S. patens* rhizosediment organic matter (LOI). Sediment total carbon was significantly correlated with dehydrogenase (DH) activity and inversely correlated with the peroxidase (POX), phosphatase (PHO) and sulfatase (SULF) activities. *Spartina patens* rhizosediment total N and C/N ratio showed a negative correlation with dehydrogenase (DH) activity. Additionally, the sediment C/N ratio showed a strong positive correlation with phosphatase (PHO), *N*-acetylglucosaminidase (NACET) and sulfatase (SULF) activities.

Analyzing both sediments physic-chemical and enzymatic traits as multivariate biogeochemical profiles (Fig. 5), using a principal component analysis (PCA), several sample clusters were observed. The first PCA biplot showed a clear separation between the sediments colonized by the native *H. portulacoides* and the NIS *S. patens*, with the latter

**Fig. 5** Principal Component Analysis (PCA) of the Extracellular Enzymatic Activities (EEA) (DEH, dehydrogenase; POX, peroxidase; FOX, phenol oxidase; PHO, acid phosphatase; GLU, *b*-glucosidase; NACET, *N*-acetylglucosaminidase; SULF, sulfatase; PROT, protease; URE, urease) and physic-chemical traits (RWC, relative water content; pH; LOI, organic matter content; C, total carbon content; N, total nitrogen content) of the rhizoseds colonized by the native *H. portulacoides* and the NIS *S. patens*, grouped by species A and by species and seasonal period B. Shaded polygons represent the area covered by a group of dispersed points delimited by its furthest points.
associated with the majority of the EEA s analyzed in this study (Fig. 5A). On the other hand, *H. portulacoides* biogeochemical profiles appear highly related to sediment dehydrogenase (DH) activity, relative water (RWC) and organic matter (LOI) contents (Fig. 5A). Analyzing the second biplot which also accounts for seasonal variation, a clear separation of rhizosediments by the colonizing species is also evident, but several seasonal clusters are also observable (Fig. 5B). The seasonal clusters formed by the samples collected from *H. portulacoides* rhizosphere had a lower dispersion (higher similarity) when compared to the seasonal clusters formed by the samples collected from *S. patens* rhizosphere, in all periods considered. The exception to this is the cluster formed by *S. patens* rhizosediment samples collected during winter, which showed a higher degree of similarity among them.

**Discussion**

Bioinvasions trigger undeniable changes in ecosystem functioning of estuarine and coastal ecosystems (Carlton 1996; Chakraborty 2019). Salt marshes are no exception, with *Spartina* bioinvasions occurring all over the globe, leading to significant changes in the wetland systems, namely at the floristic biodiversity level (Daehler and Strong 1996; Zhong-Yi et al. 2004; Li et al. 2009; Baumel et al. 2016; Duarte et al. 2018), and with consequent effects at the ecosystem services level (e.g. Carlton 1996; Ge et al. 2015; Chakraborty 2019; Human et al. 2020). In Mediterranean and Atlantic marshes, invasion by *S. patens* has been putting middle-upper marsh native species such as *H. portulacoides* under increased competitive pressure. Spartina species are characterized by high biomass production due to their highly efficient C4 photosynthetic mechanism, and well-developed rhizomes and radicles that allow them to efficiently capture nutrients (Cheng et al. 2006). But in the Tejo estuary, *H. portulacoides*, a C3 shrub plant, is the most abundant species in the middle-upper marsh (Duarte et al. 2013b). But as *S. patens* generate fewer necromass (48–52% of the total biomass produced) (Vera et al. 2009) compared to the native *H. portulacoides* (Caçador et al. 2009; Duarte et al. 2010), bioinvasions by *S. patens* decrease the necromass input to the system and inevitably affecting the decomposition and biogeochemical cycling process occurring in the salt marsh sediments. This biogeochemical cycling is known to be modulated by the colonizing species (Costa et al. 2007; Duarte et al. 2008; Rietl et al. 2016) along the salt marsh floristic inventory. The introduction of a new and aggressive NIS is a game-changer for the marsh biogeochemical functioning. This is demonstrated when analyzing the relationship between the EEA profiles and the physicochemical characteristics in the sediments colonized by both species. While in *H. portulacoides* there is an evident control of the EEA by the sediment physicochemical traits (high number of significant correlations observed), the number of significant (*p* < 0.05) and strong (*r*² > 0.80) relationships between EEA and the sediment abiotic traits is lower in the sediments colonized by *S. patens*. This indicates a prevalence of the plant effect over the abiotic traits in controlling the extracellular enzymatic activities. In fact, the highly active photosynthetic mechanism present in the C4 *S. patens*, allied to a dense rhizosphere system, promotes oxygen input to the sediments but also the exudation of low molecular weight organic acids (LMWOA), known to stimulate the rhizosphere activity, namely at the microbial level (Mucha et al. 2008, 2010; Duarte et al. 2011). The relationship between the abiotic environment characteristics and enzyme activity is well known (Alef and Nannipieri 1995). Factors such as the pH and organic matter availability (here evaluated through LOI), are known to condition the activity of enzymes. Nevertheless, the plant coverage is known to affect directly enzyme activities not only due to the modulation of the physico-chemical environment (e.g. through proton exudation and consequent medium acidification), but also due to the exudation of LMWOA and signaling molecules that are known to modulate EEA via plant species influence on plant-associated microbial communities (He et al. 2020).

Mediterranean salt marsh necromass production has its peak at the end of the growing season (late summer and autumn), concomitant with the peak extracellular enzymatic activity normally observed in the rhizosediments of the native halophyte species (Duarte et al. 2008, 2009, 2010; Caçador et al. 2009). This allows the system to recycle the organic input from the necromass plants, into inorganic forms bioavailable for the primary producers to incorporate into their biomass in the next growing season (Caravaca...
et al. 2005; Huang and Morris 2005; Freitas et al. 2014; Huang et al. 2015). When observing the enzymatic activity peaks in the sediments colonized by *S. patens*, the onset of biogeochemical functioning disruption is evident. In the sediments colonized by this NIS, the activity peaks occurred during spring and summer (observed e.g. for N-acetylglucosaminidase, urease, phenol oxidase and β-glucosidase activities), evidencing a temporal disruption compared to the seasonal pattern associated with the native species. Moreover, during the cold seasons (autumn and winter) several extracellular enzymatic activities showed significantly higher values in *S. patens* rhizosediments. If on one hand, there is a temporal disruption of the biogeochemical recycling processes, on the other, there is a very active decomposition system occurring during the cold seasons. This completely shifts the marsh biogeochemical functioning. Salt marshes are considered efficient organic matter sinks, retaining large amounts of the so-called blue carbon, nitrogen and phosphorous (Himes-Cornell et al. 2018; Geraldi et al. 2019; Duarte et al. 2021; Asanopoulos et al. 2021), not only due to their high productivity but also due to their low decomposition rates, especially when compared to other terrestrial ecosystems (Pereira et al. 2007). This allows marshes to retain, in the form of recalcitrant organic matter, large amounts of necromass, storing high amounts of carbon and reducing the eutrophication loading of the estuarine systems where they are present (Sousa et al. 2008, 2012; Himes-Cornell et al. 2018; Geraldi et al. 2019; Duarte et al. 2021; Asanopoulos et al. 2021). This extracellular enzymatic activity observed in the sediments colonized by *S. patens* during the warmer seasons (spring and summer) alongside the comparatively higher activity assessed during the cold seasons, has as an ultimate consequence the acceleration of the necromass decomposition processes and thus a reduced marsh storage and remediation capacity (Valiela et al. 1985; Pereira et al. 2007; Duarte et al. 2008).

Analyzing the extracellular enzymatic activity profiles, the abovementioned facts acquire added importance when associated with each of the biogeochemical cycles for which these ecosystems play a key role. Observing *S. patens* rhizosediments, phosphatase activity peaks during winter, with values far above the ones observed in the sediments colonized by the native *H. portulacoides*, points to an enhanced release of the inorganic phosphorous into the system, with potential consequences in the eutrophication degree of the estuary. Previous studies have shown there is also a clear relationship between the phosphatase activity and the inorganic phosphorous generation in the vegetated marsh rhizosediments, with vegetated sediments acting as phosphorus sinks, with the recycling of the organic forms of this element being modulated by the plant species present (Huang and Morris 2005; Freitas et al. 2014; Huang et al. 2015). Thus, this change in colonization promoted by *S. patens* has potential consequences on the ecosystem inorganic phosphorous load. On the other hand, this increase in inorganic phosphorous availability can also improve the system primary production, namely of the halophytic vegetation (Talbi Zribi et al. 2020).

In line with this, it could also be observed a higher urease activity year-round in the sediments colonized by the NIS, as well as a peak of proteasitic activity during autumn. Urease and protease act in the hydrolysis of organic to inorganic nitrogen, the former using urea-type substrates and the latter simple peptidic substrates (Caravaca et al. 2005). These enzymes produce inorganic nitrogen forms, namely ammonia, one of the key compounds, that when in elevated concentrations is responsible for eutrophication in estuarine systems (Domingues et al. 2011). Moreover, this is not the preferred form of inorganic nitrogen assimilable by phytoplankton (Domingues et al. 2011), nor by halophytic vegetation (Stewart et al. 1972), thus no phytoremediation process will filter this increase ammonia concentration, leading to an increase in the eutrophic load of the system and in a worst case scenario, if no ammonia metabolization occurs, to hypoxia events. Nevertheless, it should also be taken into account that ammonia oxidation and denitrification processes present an important role in salt marsh N biogeochemistry, and thus this can act as counteractive measures to this potential increase in ammonia concentration (Sousa et al. 2012).

Impacts on carbon biogeochemical cycling is also a matter of concern in sediments colonized by *S. patens*. The two oxidoreductases (POX and FOX) showed higher activities in the sediments colonized by the NIS, in more than one of the sampling seasons, along with high values of β-glucosaminidase and N-acetylglucosaminidase. All these enzymes actively participate in the decomposition of carbon-based substrates, namely, phenolic compounds
(e.g., originated from plant lignin decomposition), carbohydrates and chitin exoskeletons (Freeman et al. 2004; Duarte et al. 2008). The increase in these enzymes activities increases the availability of carbon-based respiratory substrates, that end in carbon release from the sediments in the form of CO₂ from bacterial respiration (Alonso-Sáez et al. 2008). Moreover, these carbon decomposition activity peaks in S. patens rhizosediments were concomitant with an increase in the dehydrogenase activity. Dehydrogenase activity is considered to be a proxy of microbial biomass (Kelley et al. 2011). The higher activity of carbon-based substrates decomposition activity allied to this increase in dehydrogenase activity reinforces the need for carbon use for microbial heterotrophic growth and thus a correspondent increase in respiration, with an inevitable decrease in the carbon sink capacity of the sediments and reduction of the blue carbon storage ecosystem service (Himes-Cornell et al. 2018; Duarte et al. 2021; Asanopoulos et al. 2021). Although sulfur storage in salt marshes is not among the most recognized ecosystem services provided by these habitats, changes in its biogeochemistry have tremendous implications in other key services such as metal remediation (Duarte et al. 2008; Wu et al. 2021). Previous studies (e.g., van Hullebusch et al. 2005) indicate that high sulfatase activity promotes the conversion of the sulfate produced by this enzyme into sulfides by sulfate-reducing bacteria (SRB). The sulfides establish chemically stable bonds with heavy metals, maintaining these elements in a reduced form (residual fraction) for extended periods of time (Tabak et al. 2005), thus reducing the heavy metal bioavailable fraction. Previous studies focusing on the metal speciation in the rhizosediments of the NIS S. patens showed that these metals are present in higher proportions in the more bioavailable chemical fractions (lower residual fraction) (Human et al. 2020). Moreover, this reduction in H₂S concentration would lead to the reduction of H₂S plant toxicity (Aroca et al. 2020). This aligns with our present findings. In Autumn, the period of typically higher organic matter recycling activity (Duarte et al. 2008, 2009), the sulfatase activity in the S. patens rhizosediments showed a significant decrease. This would lead to reduced production of sulfate, and consequently lower production in sulfides to reduce the metals present in these sediments into more stable forms (residual fraction) (Tabak et al. 2005; van Hullebusch et al. 2005; Duarte et al. 2008).

**Conclusion**

The threats of invasive species to salt marshes ecosystems are not limited to aboveground space competition processes but also to belowground processes, namely at the biogeochemical cycling level. The expansion of S. patens in Mediterranean marshes has led to the displacement of the native H. portulacoides. With this, there is an evident shift in the sediment’s extracellular enzymatic activities, as well as a significant increase in several enzyme activities, all key processes to recycle organic matter. These biogeochemical profiles appear to be rather controlled by the plant more than by the sediment physico-chemical environment. All these changes lead to a loss of sink capacity of the system, namely in terms of eutrophication reduction and organic nitrogen and phosphorous retention, blue carbon sink due to the acceleration of decomposition processes, and decreased metal remediation capacity allied to reduction in the production of sulfate. Therefore, the present work highlights the need to control this invasive species, not only to prevent potential floristic diversity losses but also to prevent losses of key biogeochemical services, that can affect the entire estuarine system.

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**Data availability** Data available upon reasonable request.

**Declarations**

**Conflict of interests** The authors have not disclosed any competing interests.
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