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| Authors | De Battisti, Davide; Fowler, Mike S.; Jenkins, Stuart R.; Skov, Martin W.; Bouma, Tjeerd J.; Neyland, Penelope J.; Griffin, John N. |
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RESEARCH ARTICLE

# Multiple trait dimensions mediate stress gradient effects on plant biomass allocation, with implications for coastal ecosystem services

Davide De Battisti[1] | Mike S. Fowler[1] | Stuart R. Jenkins[2] | Martin W. Skov[2] | Tjeerd J. Bouma[3] | Penelope J. Neyland[1] | John N. Griffin[1]

[1]Department of Biosciences, Swansea University, Swansea, UK

[2]School of Ocean Sciences, Bangor University, Bangor, UK

[3]Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research (NIOZ), Utrecht University, Yerseke, The Netherlands

**Correspondence**
Davide De Battisti
Email: davide.de85@gmail.com

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## Abstract

1. The plant economic spectrum (PES) predicts a suite of correlated traits in a continuum from resource conservation to rapid resource acquisition. In addition to competing for resources, plants need to cope with other environmental stresses to persist and reproduce. Yet, it is unclear how multiple strategies (i.e. traits uncorrelated with the PES) affect plant biomass allocation, hindering our ability to connect environmental gradients to ecosystem services.
2. We examined intraspecific dimensionality of leaf and root traits in the salt marsh pioneer species *Spartina anglica* across salinity, redox and sand content gradients, and related them to above-ground and below-ground plant biomass—properties associated with wave attenuation and sediment stabilization in coastal marshes.
3. Through principal component analysis, we did not find support for a single PES trait dimension (strategy), but instead identified four trait dimensions: (a) leaf economic spectrum (LES, leaf analogue of PES); (b) fine roots-rhizomes; (c) coarse roots; and (d) salt extrusion. Structural equation modelling showed a shift towards the conservative side of the LES under increasing salinity, while redox had a positive influence on the coarse roots dimension. In turn, these trait dimensions were strongly associated with above-ground and below-ground biomass (BLW biomass) allocation.
4. These results indicate that under high salinity, plants will adopt a conservative strategy and will invest more in BLW biomass. Yet, high sediment redox would still allow plants to invest in above-ground biomass. Therefore, plants' trait-mediated biomass allocation depends on the specific combination of abiotic factors experienced at the local scale.
5. *Synthesis*. Our study highlights the importance of considering multiple ecological strategies for understanding the effect of the environment on plants. Abiotic stresses can influence multiple trait strategy-dimensions, with consequences for ecosystem functioning.

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KEYWORDS
functional traits, intraspecific trait variability, plant economic spectrum, *Spartina anglica*

## 1 | INTRODUCTION

A central tenet in plant trait ecology is the existence of an ecological strategy represented by correlated leaf traits, the leaf economic spectrum (LES), where plants display traits in a continuum from fast to slow resource acquisition (Garnier, Navas, & Grigulis, 2016; Reich, 2014; Reich et al., 1999; Wright et al., 2004). For instance, plants in nutrient-rich habitat have higher SLA (higher leaf area per biomass invested) and leaf nitrogen content (LNC), with consequent higher nutrient acquisition and rapid growth (Reich et al., 1999; Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). Recently, the LES has been expanded to a whole plant economic spectrum (PES), because theory indicates that plants with traits for fast resource acquisition in one organ (e.g. leaf) should also have traits for fast resource acquisition in other organs (e.g. roots; Reich, 2014). As an example, subarctic plants growing in fertile soil have higher SLA coupled with higher specific root length, that is longer fine roots per biomass invested (Freschet, Cornelissen, Logtestijn, & Aerts, 2010). The PES is, therefore, an ecological strategy adopted by plants to compete for (acquisitive side) or store (conservative side) resources for optimal growth in a given environment (Reich, 2014; Wright et al., 2005).

Changes along the PES are important because they can track environmental (abiotic) changes, which consequently affect ecosystem functions (Lavorel et al., 2013; Suding et al., 2008). For instance, addition of nutrients to the soil drives a shift in traits of plant communities along the LES towards the rapid acquisitive side, for example increases in SLA and LNC (Freschet, Kichenin, & Wardle, 2015; Jager, Richardson, Bellingham, Clearwater, & Laughlin, 2015). In turn, changes in traits along the PES can influence plant biomass allocation, with higher investment in the below-ground portion for plant at the conservative side of the spectrum (Freschet et al., 2015). Plant above- and below-ground biomass (BLW biomass) can have important consequences for ecosystem functions and services. In salt marshes, for example, these properties have been related to wave attenuation and sediment stabilization respectively (Bouma et al., 2013; Bouma, Vries, & Herman, 2010; Ford, Garbutt, Ladd, Malarkey, & Skov, 2016; Lo, Bouma, Belzen, Colen, & Airoldi, 2017), which are crucial determinants of the capacity of salt marshes to provide the service of coastal protection (Barbier et al., 2011; Bouma et al., 2014; Costanza et al., 2008). Therefore, traits along the PES could be used to investigate the indirect effect of abiotic stress on ecosystem properties (e.g. biomass allocation), which can have strong implications for ecosystem functions and services (e.g. coastal protection; Figure 1a).

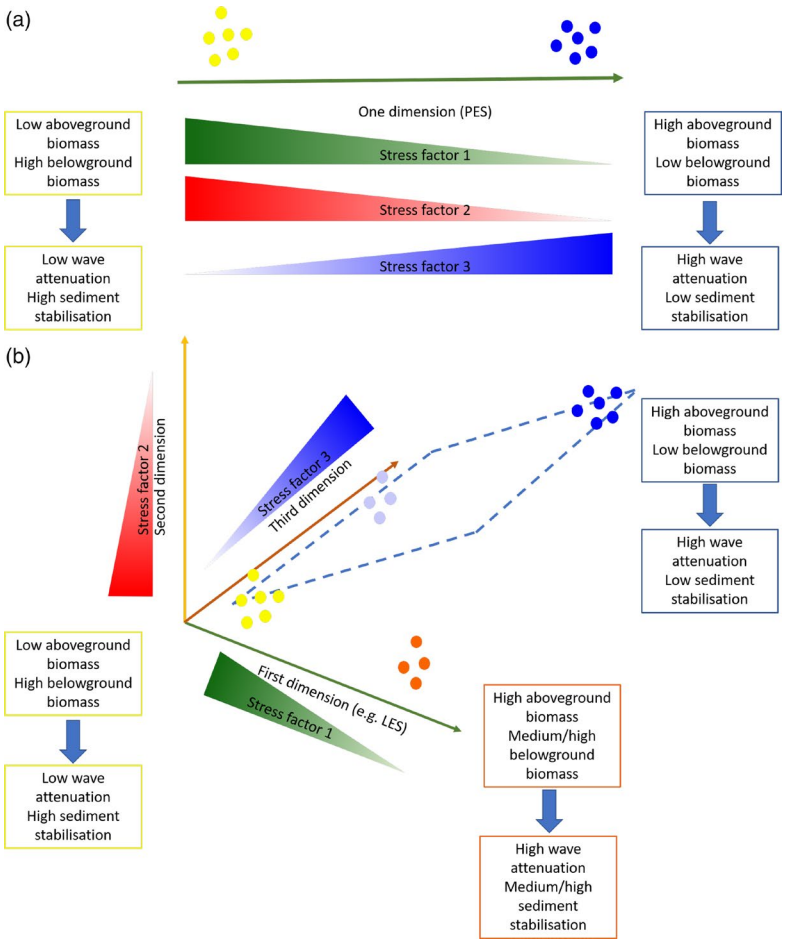



**FIGURE 1** Panel (a) illustrates low dimensionality of ecological strategies (e.g. plant economic spectrum [PES] only) and its hypothesized effect on ecosystem properties (i.e. biomass allocation), with implications for ecosystem functions. Here, different types of stress determine a shift of plant traits along the PES (e.g. shift from blue to yellow dots), consequently affecting the above- to below-ground biomass allocation, with implications for ecosystem functions (e.g. lower wave attenuation; yellow dots). Panel (b) demonstrates the effect of multiple ecological strategies on ecosystem properties under several environmental stresses. Here, different stress types affect different strategies (trait dimensions). As an example, an increase in stress factors 1 and 2 determines changes from high above-ground to below-ground biomass allocation (high wave attenuation and low sediment stability; blue dots) to similar above-ground biomass but also higher below-ground biomass investment (increased sediment stability but still maintaining similar wave attenuation capacity; orange dots) [Colour figure can be viewed at wileyonlinelibrary.com]

While the traits along the PES relate to resource utilization, plants also need to cope with abiotic stresses to successfully survive and reproduce. For instance, aquatic plants show higher SLA to increase gas exchange and ensure optimal photosynthesis when submerged (Mommer, Lenssen, Huber, Visser, & Kroon, 2006; Mommer, Wolters-Arts, Andersen, Visser, & Pedersen, 2007; Pierce, Brusa, Sartori, & Cerabolini, 2012), while in salt marshes, plants have lower SLA and higher leaf dry matter content (LDMC) to reduce evapotranspiration and maintain osmotic balance under salinity stress (Richards, Pennings, & Donovan, 2005). Furthermore, low SLA could reduce drag forces on plants experiencing wave action by minimizing frontal area and high LDMC can enhance resistance to drag forces by strengthening leaf tissue (Bornette & Puijalon, 2011; Bouma et al., 2005, 2010 Heuner et al., 2015). Yet, not all traits related to stress resistance necessarily always align with the PES, because changes in traits adopted to resist a particular stress might not be linked to resource acquisition/conservation (Pan, Cieraad, & Bodegom, 2019). As an example, in wetlands plants elongate their stems to maintain air contact, ensuring adequate oxygen supply to all plant tissues (Adams & Bate, 1995; Colmer, 2003; Nishiuchi, Yamauchi, Takahashi, Kotula, & Nakazono, 2012). Plant height is not related to the economic spectrum (Laughlin, Leppert, Moore, & Sieg, 2010; Westoby, Falster, Moles, Vesk, & Wright, 2002), thus, flooding and/or waterlogging stress could elicit a response in plant traits which does not involve a shift along the PES, but could still affect ecosystem properties (biomass allocation). Consequently, a suite of correlated traits related to stress resistance could lead to multiple ecological strategies (Jager et al., 2015; Laughlin, 2014) that, in turn, could have a complex effect on ecosystem properties and, thus, on ecosystem functions/services (Figure 1b; Westoby et al., 2002).

Most studies investigating stress-traits-function linkages have focused mainly on resource stress (nutrients and light gradients; e.g. Freschet et al., 2015; Kramer-Walter et al., 2016) and single-dimension economic spectra (both LES and PES; Diaz et al., 2004; Freschet, Aerts, & Cornelissen, 2012; Lavorel & Garnier, 2002; Suding et al., 2008; Wright et al., 2004, 2005). Therefore, the extent to which environmental stresses affect the multidimensionality of ecological strategies in plants, and the consequent effect of these strategies on ecosystem properties, remains poorly understood. Strong abiotic stress gradients make salt marshes ideal systems to investigate the importance of multiple ecological strategies in determining ecosystem properties, with implications for ecosystem services. For instance, salinity can affect leaf morphology and physiology (Adams & Bate, 1995; Colmer & Pedersen, 2008; Naidoo, Somaru, & Achar, 2008), leading to a reduction in above-ground biomass (ABV biomass; Crain, Silliman, Bertness, & Bertness, 2004). This biomass decrease along salinity gradients plays a critical role for geomorphological changes in salt marshes (Bouma et al., 2009, 2010, 2013). Moreover, low redox potential in the sediment (a proxy for waterlogging) can affect root production, morphology and biomass, which plays a significant role in below-ground carbon storage and sediment stabilization (Bouma, Nielsen, Hal, & Koutstaal, 2001; De Battisti et al., 2019; Ford et al., 2016; Wang et al., 2017). Thus, changes in traits that reduce both ABV and BLW biomass production could be detrimental for several ecosystem functions and services.

Like other vegetated coastal ecosystems (e.g. mangrove and seagrass beds), monospecific stands can dominate large areas of salt marshes, implying that intraspecific trait variability is likely an important driver of ecosystem functions (Hughes & Lotterhos, 2014; Hughes & Stachowicz, 2004; Hughes, Stachowicz, & Williams, 2009). Thus, here we focused on trait variability of *Spartina anglica*. Using this species as a model, we aimed to improve our understanding of the dimensionality and environmental drivers of intraspecific trait variability. We hypothesized that traits (both above-ground and below-ground) that are related to resource acquisition (PES, Table 1) and traits related to plants' stress resistance (Table 1) will be represented on different dimensions, leading to multidimensionality in ecological strategies. Furthermore, through a structural equation modelling (SEM) approach, we investigated the direct and indirect effect of abiotic stress on ecosystem properties through their effect on the strategy-dimension(s) (Figure 1). Finally, we discuss the

**TABLE 1** Abiotic and biotic variables measured in this study. In bold, traits considered to belong to exclusively to resource acquisition/conservation or stress resistance

| Abiotic variables | Resource acquisition/ conservation | Stress resistance | Unit |
|---|---|---|---|
| Salinity | | | ppt |
| Redox | | | mV |
| Sand | | | % (in weight) |
| Above-ground traits | | | |
| Leaf area (LA) | Yes | Yes | $cm^2$ |
| Specific leaf area (SLA) | Yes | No | $cm^2/g$ |
| Succulence | No | Yes | — |
| Excreted salts | No | Yes | mg/g |
| Leaf dry matter content (LDMC) | Yes | Yes | mg/g |
| Leaf N content (LNC) | Yes | Yes | % |
| Leaf C/N ratio | Yes | Yes | — |
| Above-ground biomass (ABV biomass) | — | — | G |
| Below-ground traits | | | |
| RMF | Yes | Yes | % (in weight) |
| Below-ground Biomass (BLW biomass) | — | — | G |
| Specific root length of fine roots (SRLf) | Yes | No | m/g |
| Fine roots | Yes | No | % (in weight) |
| Coarse roots | No | Yes | % (in weight) |
| Rhizomes | Yes | Yes | % (in weight) |

possible consequences of multidimensionality in ecological strategies for coastal protection, a key ecosystem service in our saltmarsh study system.

## 2 | MATERIALS AND METHODS

### 2.1 | Site description

Three salt marshes were selected along a salinity gradient in each of two estuaries in South Wales (UK), the Taf and the Loughor (Figure 2). Seven 1 m × 1 m plots were established in the *S. anglica* zone in each marsh. Abiotic and biotic variables (both above-ground and below-ground) were sampled from each plot, for a total of 42 replicates (6 marshes × 7 plots per marsh; Table 1).

### 2.2 | Above-ground traits

At the end of the growing season, prior to *S. anglica* senescence (October 2016), we collected samples for leaf traits (Table 1) and above-ground peak biomass for a total of 42 replicates for each trait. From each 1 m × 1 m plot, 15 fully grown leaves were collected. Within 24 hr, five of the 15 leaves were rehydrated in deionized water for half an hour, scanned with a flatbed scanner (Epson Perfection, V550 Photo; black and white, 1,200 dpi) and dried at 70°C for 48 hr. Leaf area (LA) was calculated using ImageJ software (Schindelin et al., 2012); SLA and LDMC were calculated according to standard protocols (Pérez-Harguindeguy et al., 2013). For each trait, we took the mean of the values from the five rehydrated leaves per plot. After drying, five leaves from the same plot were pooled together, ground and the percentage of nitrogen (%N) and carbon (%C) present in the leaf, as well as the ratio of carbon to nitrogen (C/N), were measured with a PDZ Europa 2020 isotope ratio mass spectrometer interfaced with an ANCA GSL elemental analyser.

Succulence was measured in another five leaves from each plot according to Tabot and Adams (2013). Fresh mass (FM, g) was measured followed by drying at 70°C for 48 hr. Leaves were then reweighed for dry mass (DM, g). Succulence was calculated as the ratio between leaf moisture content (FM – DM) and leaf DM.

Extruding salts for coping with salinity imposes an energetic cost on plants (Flowers & Colmer, 2008). Thus, plants' energetic expenditure in extruding more salts under higher salinity might have a negative effect on biomass production. To measure salt extrusion, five leaves were placed in 50 ml of deionized water for 30 min, after which total dissolved solutes (p.p.m.) were measured with a portable metre (Hanna instruments, HI98129) and readings were converted to mg as follows: mg = (p.p.m. × 50 ml)/1,000 ml (Tabot & Adams, 2014). After conversion, salt extrusion was standardized per unit of leaf FM.

Overall, SLA can uniquely be related to resource acquisition/conservation (Westoby et al., 2002); excreted salts and succulence uniquely related to stress resistance (Tabot & Adams, 2013, 2014); and LDMC, LNC and leaf C/N to both resource acquisition/

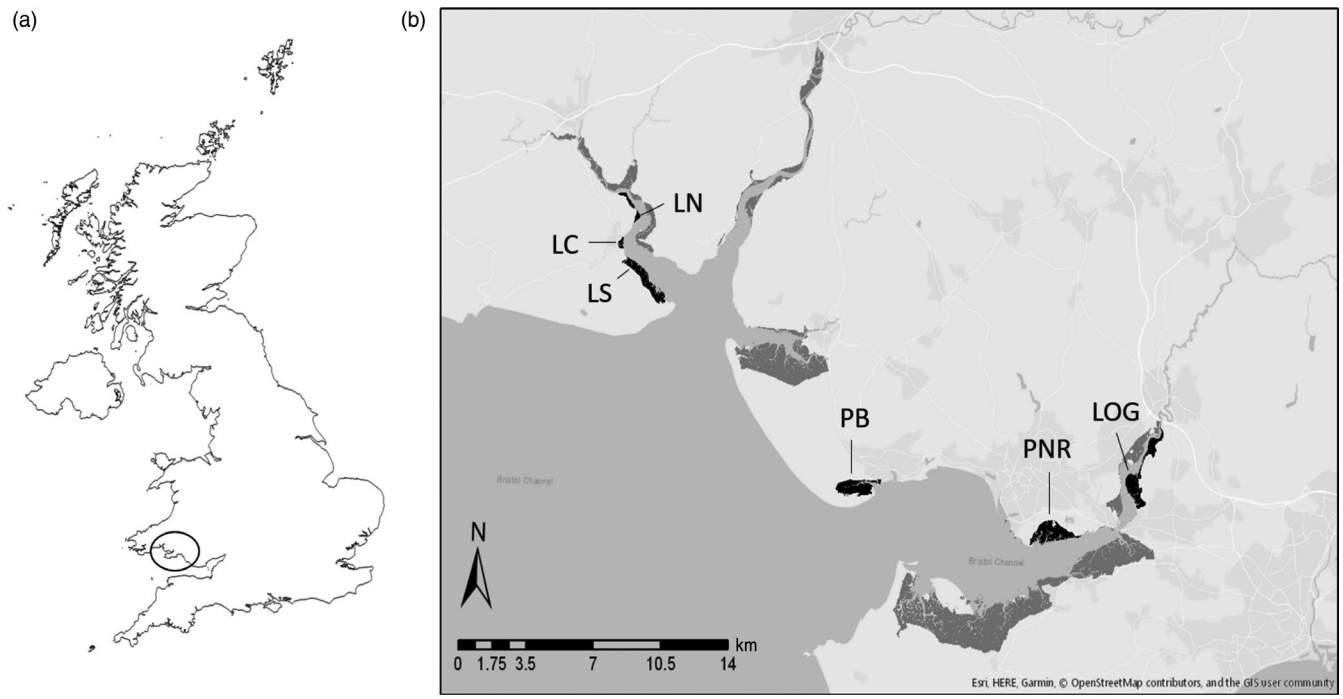



**FIGURE 2** Location of the study sites, in south Wales, UK (indicated by circle in panel a). Panel (b), shows a close up of the circle from panel (a). Marshes sampled are highlighted in black, in dark grey other marshes in the estuary; from the mouth to the head of the estuary, the position of Pembrey (PB), Penrhyn Gwyn (PNR) and Loughor (LOG) marshes in the Loughor estuary (lower side panel) and Laugharne South (LS), Laugharne Castle (LC) and Laugharne North (LN) marshes in the Taf estuary (left side panel)

conservation and stress resistance (Garnier et al., 2016). Thus, we expect that the trait uniquely related to resource acquisition (SLA) will load on one dimension (the economic spectrum dimension), the traits uniquely related to stress resistance (excreted salts and succulence) will load on a second dimension, while the traits related to both resource acquisition and stress resistance (LDMC, LNC and leaf C/N) will load either on the economic spectrum dimension or on the stress dimension.

We sampled peak ABV biomass at the end of the growing season (October 2016) after plants have reached their highest seasonal biomass (Hemminga, Huiskes, Steegstra, & Soelen, 1996). ABV biomass was collected from each plot within a 25 cm × 25 cm quadrat and subsequently dried at 70°C for 72 hr.

## 2.3 | Below-ground traits

In October 2016, with a spade we dug a small hole in the centre of each plot and with a knife we collected a 500 $cm^3$ sediment sample (5 cm × 5 cm area to 20 cm depth) within the hole, for each of the 42 replicates. Samples were brought to the laboratory and stored at 4°C until being processed for root trait measurements (Table 1). Samples were gently washed with warm water to remove sediment and plant roots were collected with a sieve of 1 mm mesh diameter. The below-ground portion of plants was divided into (a) rhizome, (b) coarse roots (>1 mm in diameter) and (c) a mixture of fine roots (<1 mm in diameter) and dead plant material. Fine roots were defined using a 1 mm threshold in diameter (Freschet & Roumet, 2017) to obtain roots mainly involved in nutrient absorption, although we acknowledge that some transport roots might have been included (McCormack et al., 2015). The fine roots present in the samples were calculated based on the proportion of fine roots present in three subsamples of ~1 g fresh material.

A subsample of fine roots was selected and scanned with a flatbed scanner (Epson Perfection, V550 Photo; black and white at 1,200 dpi) and root length was measured with the software Rootnav (Pound et al., 2013). Root diameter was measured for 10 randomly selected roots per scanned images using ImageJ (Schindelin et al., 2012). Specific root length of fine roots (SRLf) is linked to resource acquisition (Freschet & Roumet, 2017) and was calculated according to Pérez-Harguindeguy et al. (2013). All root materials (both scanned and un-scanned) were dried at 70°C for 48 hr (Pérez-Harguindeguy et al., 2013). Root mass fraction (RMF) is related to both resource acquisition and stress resistance (Freschet & Roumet, 2017) and was calculated as the ratio of root biomass (rhizomes excluded) over total plant biomass (ABV plus BLW biomass). We also calculated the percentage by mass of fine roots, coarse roots and rhizomes present in the BLW biomass. Fine roots and rhizomes are related to a plant's capacity to acquire resources and store resources, respectively, while coarse roots can be beneficial for oxygen transport to roots under waterlogged conditions (Armstrong, Wright, Lythe, & Gaynard, 1985; Colmer & Flowers, 2008). BLW biomass was calculated as the sum of rhizomes, coarse roots and fine root biomass. The ABV to BLW biomass ratio indicates a trade-off in biomass investment between shoots and roots and was calculated (Freschet et al., 2015; Hemminga et al., 1996). Collectively, for root traits we considered two traits uniquely related to resource acquisition/conservation (SRL and % of fine roots), one trait uniquely related to stress resistance (coarse roots) and two traits related to both resource acquisition/conservation and stress resistance (RMF and % of rhizomes).

Traits related to resource acquisition (SRLf and % of fine roots) are expected to load on the economic spectrum dimension, while coarse roots (a trait related to stress resistance) are expected to load on a second dimension. Furthermore, we expect that RMF and % of rhizomes, which relate to both resource acquisition and stress resistance, will load either on the economic spectrum dimension or on the stress dimension.

## 2.4 | Abiotic variables

Three main abiotic stressors for salt marsh plants were considered in this study: salinity, sediment redox (a proxy for waterlogging; Armstrong et al., 1985) and sediment sand content (a proxy for nutrient availability; Minden, Andratschke, Spalke, Timmermann, & Kleyer, 2012). Sediment samples for measuring abiotic variables were collected from plots on three spring tides over July–September 2016 to minimize the influence of variation in tide heights and weather. Mean plot values were used for further analysis. MacroRhizones (www.rhizosphere.com) were inserted to 15-cm depth, the porewater extracted and sampled for salinity (Hanna instrument, HI98129). Redox potential was measured at 5-cm soil depth (Hanna instruments, HI 98120). Sediment samples were collected on two of the spring tides, using a 10-cm deep, 2.5-cm diameter core; sediment was oven-dried for 72 hr at 70°C and subsequently burnt in a furnace at 440°C for 18 hr (Feagin et al., 2009). After combustion, sediment samples were sieved to separate the clay-silt fraction (<53 μm), fine sand (53–250 μm), coarse sand (250–1,000 μm) and very coarse sand (>1,000 μm; Denef et al., 2001).

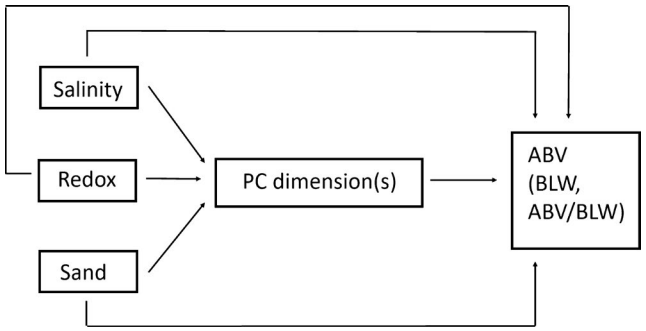



**FIGURE 3** Conceptual model of the hypothesized relationship between variables. Principal component (PC) dimensions are the dimensions retained and extracted from the principal component analysis, with eigenvalues >1. Here, only one dimension has been represented for clarity. ABV, above-ground biomass; BLW, below-ground biomass; ABV/BLW, above- to below-ground biomass ratio

**TABLE 2** Explanation of the causality of paths in the structural equation modelling (SEM). Principal component (PC) dimensions were obtained from the principal component analysis

| Stress factor | Hypothesized effect on plant strategy-dimensions | Hypothesized effect on ecosystem properties |
|---|---|---|
| Salinity | Morpho-physiological adaptations alter economic spectrum traits (e.g. low SLA and high LDMC) and increase salt extrusion (first and fourth PC dimensions)[a] | At high salinity, traits shift towards the conservative side of the plant economic spectrum (PES) reducing investment in above-ground biomass, but increasing investment in below-ground biomass (low above- to below-ground biomass ratio) |
| Redox | Sediment anoxia (low redox) induces aerenchyma production, increases root size and reduces nutrient uptake capacity (first, second and third PC dimensions)[b] | At low redox, traits shift to the conservative side of PES, increase in storage organ and aerenchyma, determine more investment on below-ground biomass, lower above-ground biomass and lower above to below-ground biomass ratio |
| Sand content | Nutrient availability shifts traits towards the slow/fast side of the PES and alters root/shoot biomass allocation (first and second PC dimensions)[c] | At low nutrients, traits shift to the conservative side of the spectrum and the increase in root mass fraction determines higher investment on the below-ground biomass, lower investment in above-ground biomass and lower above- to below-ground biomass ratio |

[a]Richards et al. (2005), Naidoo et al. (2008), Adams and Bate (1995), Minden and Kyler (2012) and Flower and Colmer (2008).
[b]Armstrong et al. (1985), Bouma et al. (2001), Colmer (2003) and Colmer and Flower (2008), Justin and Armstrong (1987).
[c]Freschet et al. (2010) and Freschet et al. (2015).

## 2.5 | Statistical analysis

First, principal component (PC) analysis (PCA) was used to investigate the presence of the plant economic spectrum at the intraspecific level, that is, whether leaf and root traits related to resource acquisition correlated on a single dimension, and whether traits related to stress resistance were loading on different dimensions. All variables were *z*-scale transformed. According to Kaiser's rule, we retained PC dimensions with eigenvalues >1 (Jager et al., 2015; Laughlin, 2014; Appendix, Figure A1). Second, piecewise structural equation models (SEM; Lefcheck, 2016) were used to understand the direct and indirect effects of the main salt marsh abiotic stressors or their proxies (salinity, redox and sand) on ABV biomass, BLW biomass and the ABV/BLW biomass ratio, through their effect on the retained PC dimensions (Figure 3). The causal links reported in the a priori SEM model (Figure 3) are based on the pre-existing knowledge (Grace, 2006; Shipley., 2016) of the effect of abiotic factors on plant traits and plant biomass and the effects of traits on plant biomass (see Table 2 for the explanation of causal paths and related references). Marsh site was considered as a random factor in the mixed effect models (LME4 package; Bates, 2010) used in the SEM analysis. Response variables were log transformed to meet linear model assumptions where appropriate. All the analyses were carried out in R (R Core Team, 2018).

## 3 | RESULTS

Plant traits (see Appendix, Figure A2 for traits variability along the estuaries) showed high dimensionality, with the first four PC axes (dimensions), accounting for ~70% of trait variability (Table 2). The first PC dimension captured the LES, with LDMC and leaf C/N ratio trading-off with SLA, LA and LNC (Figure 4; Table 3). Yet, RMF and SRLf were only weakly correlated with the first PC dimension (Table 3), failing to support a PES at the intraspecific level for *S. anglica*. On the second PC dimension rhizomes traded-off with both fine roots and leaf succulence (Figure 4a; Table 3; Table A1), suggesting that plants with higher capacity to absorb nutrients (fine roots) can invest in more succulent leaves but need less storage organs (rhizomes). Interestingly, coarse roots were not associated with the same dimension as rhizomes and fine roots, but loaded on a separate (third) dimension, together with leaf C/N and LNC (Figure 4a; Table 3). Thus, on the third dimension, plants with higher leaf C/N and lower LNC produced more coarse roots. The fourth dimension was mainly represented by a trade-off between salt extrusion and SLA (Figure 4a; Table 3).

Structural equation models showed that salinity and redox had a significant negative effect on the LES and a significant positive effect on coarse roots dimensions respectively (Figure 4b; Table 4). Thus, plants shifted towards the conservative end of the LES with increasing salinity and invested more in coarse roots with higher redox values. Furthermore, only redox had a significant positive direct effect on BLW biomass (Figure 4b), indicating that plants invest more in below-ground tissue in oxygenated sediment.

Regarding the effect of PC dimensions on ecosystem properties, the coarse roots and salt extrusion dimensions had a positive significant effect on ABV biomass (Figure 4b) and the LES dimension had a strong, significant, negative effect on BLW biomass (Figure 4b). Consequently, on the one hand, plants with more coarse roots and higher salt excretion invested more in ABV biomass and, on the other hand, plants on the acquisitive side of the spectrum invested less in the BLW biomass. Yet, because these two dimensions are orthogonal, this result indicates that plants that invest more in

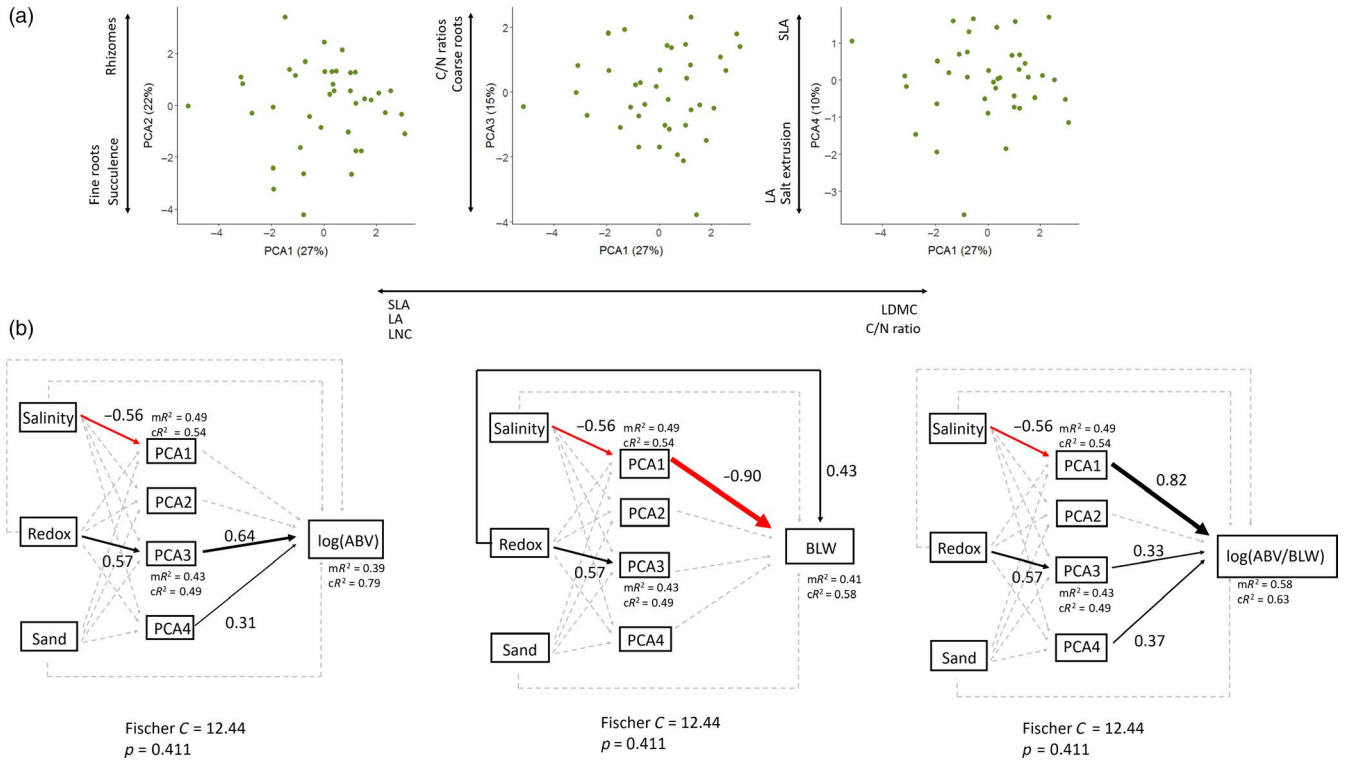



**FIGURE 4** Panel (a), principal component analysis of above-ground and below-ground traits within *Spartina anglica*. SLA, leaf area (LA), leaf dry matter content (LDMC), leaf C to N ratio (C/N), percentage of leaf N (LNC), root mass fraction (RMF), specific root length of fine roots (SRLf), percentage of coarse roots (coarse roots), percentage of fine roots (fine roots). $N = 39$. Panel (b), Structural equation model (SEM) for *S. anglica* of the effect of PCA dimensions (extracted from the PC trait analysis) and environmental factors on above-ground biomass (ABV biomass), below-ground biomass (BLW biomass) and above-ground–below-ground biomass ratio (ABV/BLW ratio). standardized coefficients are shown where significantly different from 0 (for unstandardized coefficients see Appendix, Figure A4). Random term, Marsh, omitted for clarity. Marginal $R^2$ ($mR^2$), conditional $R^2$ ($cR^2$). $N = 38$. Fisher C and $p$ values of the SEMs are the same because the only variable that changes between models is the ecosystem property investigated (ABV, BLW or ABV/BLW ratio) [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 3** Principal component analysis of trait variability for *Spartina anglica*. Specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), leaf C to N ratio (C to N), leaf N content (LNC), root mass fraction (RMF), specific root length of fine roots (SRLf), percentage of coarse roots (coarse roots), percentage of fine roots (Fine roots), percentage of rhizomes (Rhizomes). $N = 39$. PCA trait loading values showing a significant difference from 0 are formatted in bold text (based on critical values for Pearson's correlation coefficients at $\alpha = 0.05$)

| *Spartina anglica* | First axis | Second axis | Third axis | Fourth axis |
|---|---|---|---|---|
| Proportion of variance | 0.26 | 0.21 | 0.15 | 0.10 |
| Cumulative variance | 0.26 | 0.48 | 0.62 | 0.72 |
| Trait loading | | | | |
| LA ($cm^2$) | **0.364** | 0.238 | 0.177 | **0.380** |
| SLA ($cm^2/g$) | **0.368** | | −0.255 | **−0.418** |
| LDMC (mg/g) | **−0.463** | −0.154 | | 0.312 |
| Succulence | 0.255 | **0.371** | 0.242 | 0.254 |
| Salt excretion (mg/g) | −0.286 | | −0.267 | **0.501** |
| LNC (g) | **0.355** | −0.232 | **−0.329** | 0.185 |
| C/N ratio | **−0.348** | 0.205 | **0.463** | −0.131 |
| SRLf (m/g) | 0.241 | −0.179 | 0.253 | 0.171 |
| RMF (%) | −0.251 | 0.214 | −0.252 | **−0.386** |
| Fine roots (%) | | **0.540** | −0.285 | |
| Coarse roots (%) | | | **0.468** | −0.167 |
| Rhizomes (%) | | **−0.558** | 0.149 | |

ABV biomass (more coarse roots) could still invest in BLW biomass if they are on the conservative side of the LES. Furthermore, the LES, salt extrusion and coarse roots dimensions had significant positive effects on the ABV/BLW biomass ratio (Figure 4b). Plants at the acquisitive end of the LES (high values on the first dimension) invested less in BLW biomass, consequently increasing the ABV/BLW

**TABLE 4** Effect of abiotic factors (salinity, redox and sand content) and principal component analysis (PCA) dimensions on above-ground biomass (ABV biomass), below-ground biomass (BLW biomass) and above-ground–below-ground biomass ratio (ABV/BLW ratio) in the structural equation modelling (SEM) submodels for *Spartina anglica*. The effect of environmental factors on principal component (PC) dimensions has been omitted for BLW biomass and ABV/BLW biomass ratio for clarity. Random term, Marsh, omitted for clarity. Marginal $R^2$ ($mR^2$), conditional $R^2$ ($cR^2$). $N$ = 38

| Response | Predictors | Standardized coefficients | *SE* | *p* | $mR^2$ | $cR^2$ |
|---|---|---|---|---|---|---|
| PCA1 | Salinity | −0.559 | 0.053 | **0.001** | 0.49 | 0.54 |
| | Redox | 0.116 | 0.003 | 0.454 | | |
| | Sand | −0.159 | 0.017 | 0.263 | | |
| PCA2 | Salinity | −0.177 | 0.065 | 0.359 | 0.05 | 0.05 |
| | Redox | 0.085 | 0.004 | 0.694 | | |
| | Sand | 0.009 | 0.021 | 0.960 | | |
| PCA3 | Salinity | 0.257 | 0.045 | 0.133 | 0.43 | 0.49 |
| | Redox | 0.569 | 0.002 | **0.003** | | |
| | Sand | −0.299 | 0.014 | 0.067 | | |
| PCA4 | Salinity | −0.079 | 0.050 | 0.716 | 0.04 | 0.42 |
| | Redox | −0.262 | 0.002 | 0.232 | | |
| | Sand | −0.124 | 0.013 | 0.509 | | |
| log(ABV biomass) | Salinity | −0.119 | 0.018 | 0.524 | 0.39 | 0.79 |
| | Redox | 0.128 | 0.001 | 0.527 | | |
| | Sand | 0.278 | 0.004 | 0.068 | | |
| | PCA1 | 0.289 | 0.047 | 0.118 | | |
| | PCA2 | 0.215 | 0.033 | 0.069 | | |
| | PCA3 | 0.644 | 0.052 | **<0.001** | | |
| | PCA4 | 0.307 | 0.053 | 0.002 | | |
| BLW biomass | Salinity | −0.177 | 0.081 | 0.365 | 0.41 | 0.58 |
| | Redox | 0.429 | 0.004 | **0.045** | | |
| | Sand | −0.159 | 0.022 | 0.341 | | |
| | PCA1 | −0.905 | 0.222 | **<0.001** | | |
| | PCA2 | −0.076 | 0.156 | 0.552 | | |
| | PCA3 | −0.114 | 0.257 | 0.508 | | |
| | PCA4 | −0.182 | 0.247 | 0.189 | | |
| log(ABV/BLW biomass) | Salinity | −0.012 | 0.039 | 0.945 | 0.58 | 0.63 |
| | Redox | −0.241 | 0.002 | 0.191 | | |
| | Sand | 0.134 | 0.011 | 0.377 | | |
| | PCA1 | 0.816 | 0.112 | **<0.001** | | |
| | PCA2 | 0.187 | 0.078 | 0.116 | | |
| | PCA3 | 0.329 | 0.131 | **0.047** | | |
| | PCA4 | 0.371 | 0.119 | **<0.01** | | |

Significant values are in bold.

biomass ratio, while a higher presence of coarse roots and higher salt extrusion increased ABV biomass, increasing the ABV/BLW biomass ratio.

## 4 | DISCUSSION

In this study we showed that in a system with many strong stress factors, plants employ multiple ecological strategies at the intraspecific level, possibly leading to complex effects on ecosystem functions. Therefore, our study highlights that researchers need to consider multiple abiotic stressors and plant ecological strategies simultaneously, to fully understand the direct and indirect effects of the environment on ecosystem functions.

### 4.1 | PES at the intraspecific level

In contrast to our hypothesis, we did not find support for a PES at the intraspecific level based on the PCA. According to the PES, SRLf, or RMF, should be positively coordinated with SLA and LNC on the same axis (Freschet et al., 2015; Reich, 2014). In contrast, other studies showed a lack of alignment of root traits with above-ground traits along the PES, but indicated that root traits are

multidimensional (Kramer-Walter et al., 2016; Wang et al., 2018; Weemstra et al., 2016). This multidimensionality could arise from the heterogeneity of resource distribution in the soil and the several functions provided by the root system (Bardgett, Mommer, & Vries, 2014; Freschet et al., 2017; Weemstra et al., 2016). Furthermore, in contrast to above-ground traits (e.g. SLA), few data exist for root traits (e.g. SRL) to support the links between traits and resource acquisition (Weemstra et al., 2016). In our study, neither RMF nor SRLf was represented along the PES, which clearly differs from PES predictions. Also, none of the root characteristics considered (rhizomes, coarse and fine roots) were strongly correlated with the first axis in the PCA (PES), further indicating the absence of a PES for *S. anglica*. Therefore, our study supports the multidimensionality view of the root system for handling multiple functions (e.g. nutrient acquisition and stress resistance; Bardgett et al., 2014; Freschet & Roumet, 2017; Weemstra et al., 2016). More studies are needed to fully elucidate the extent of dimensionality in root traits and how these traits (or dimensions) covary with above-ground traits (i.e. the PES).

In our study, we did find evidence for an LES at the intraspecific level, as indicated by the loading of SLA, LDMC, LNC and leaf C/N ratio on the first PC dimension. The LES has found strong support on local to global scales (Díaz et al., 2016; Gross et al., 2013; Lavorel & Garnier, 2002; Wright et al., 2004) and from intraspecific to community levels (Fajardo & Siefert, 2018; Siefert et al., 2015; Suding et al., 2008). This high conservation of the LES across spatial and organizational scales likely reflects the high specificity of the leaf organ for resource acquisition (light and $CO_2$) and the homogeneity of distribution of these resources in the environment (Weemstra et al., 2016; Westoby & Wright, 2006). Thus, our study adds to a growing body of the evidence on the usefulness in considering the LES for understanding the effect of a changing environment on plant traits.

## 4.2 | Effect of the abiotic environment on trait dimensions

In line with our hypothesis, traits related to stress resistance gave rise to multiple dimensions of trait coordination, or ecological strategies. Our result is in accordance with the previous findings where, across species, the consideration of multiple (three to six) trait dimensions increased the ability to correctly predict community assemblages (Laughlin, 2014). This multidimensionality likely arises from plants' need to cope with different stresses at the same time (e.g. fire, storms, frost; Laughlin, 2014; Pan et al., 2018). Here, we showed that high ecological dimensionality (four dimensions) also exists at the intraspecific level, within the range found across species, resulting from *S. anglica's* need to cope with multiple stresses (salinity and redox).

Salinity had a strong negative effect on the LES (first dimension) but, surprisingly, had no effect on salt extrusion and succulence. In an experimental study, *S. anglica* had higher salt secretion at salinities over 35 ppt (Adams & Bate, 1995). Thus, it is possible that in our study salinity (mean 33.3 ± *SD* 0.74 ppt, Appendix, Figure A3) was not strong enough to significantly increase salt extrusion. Also, in contrast to experimental studies, the regular washing effect of the tide possibly reduced the build-up of salts in the sediment and the consequent salinity stress experienced by plants. Moreover, we would have expected a negative effect of salinity on leaf C/N because previous studies in European marshes suggest that plants in the lower marsh have high leaf N (Minden et al., 2012; Minden & Kleyer, 2011), due to N-based compounds (e.g. proline and glycinebetaine) employed to maintain osmotic balance (Slama, Abdelly, Bouchereau, Flowers, & Savouré, 2015; Tabot & Adams, 2012, 2013, 2014). In contrast, we found that leaf C/N ratio increased with salinity at the intraspecific level. Smaller, thicker leaves (high LDMC and C/N ratio) are known to reduce evapotranspiration and maintain osmotic balance under salinity stress (Naidoo et al., 2008; Qiu, Lin, & Guo S, 2008; Tounekti, Abreu, Khemira, & Munné-Bosch, 2012). Overall, it is possible that physiological adaptations in *S. anglica* (e.g. production of osmolytes, salt extrusion) are constitutive of the species (Flowers & Colmer, 2008; Slama et al., 2015), but within-species morphological adaptations are employed for coping with salinity (e.g. decrease in SLA). It also possible that some traits related to stress adaptation, i.e. salt extrusion, succulence and osmolyte production, are less plastic than other traits, i.e. C/N ratio. Thus, future research should investigate a wider salinity gradient and array of species to understand to what extent different plant traits can cope with salinity stress.

Most studies on root traits have focused on fine roots alone, although the importance of the whole root system to perform several functions is well recognized (Bardgett et al., 2014; Freschet et al., 2017). In our study, considering different root compartments allowed us to detect the multidimensional nature of the root system and its importance for coping with the abiotic environment. Wetland plants increase root diameter with aerenchyma tissue to increase oxygen transport to the root tips under waterlogged condition (low redox; Colmer & Flowers, 2008; Justin & Armstrong, 1987; Nishiuchi et al., 2012). Consequently, we expected more investment in coarse roots (third dimension) at lower redox values. In contrast to this expectation, we found that plants invested more in coarse roots with increasing redox. This result indicates that, although a generally wide root diameter with respect to some other species (Bouma et al., 2001) allows *S. anglica* to colonize the lower marsh, very low redox still negatively affects root production, in particular the amount of coarse roots. This is also supported by the direct positive effect of redox on the BLW biomass (Figure 4b), indicating an amelioration of abiotic conditions with increasing redox potential. Interestingly, coarse roots loaded on a different dimension than fine roots and rhizomes (Table 3). Under waterlogged conditions, plants can switch to a fermentation metabolism, which requires high carbohydrate reserves (Colmer & Flowers, 2008). Thus, having root compartments (rhizomes, coarse and fine roots) on different dimensions could be beneficial in waterlogged sediment (low redox) because plants could reduce the investment in coarse roots, cutting down energetic costs, but maintain the same investment in rhizomes and fine roots (acquisition and storage of resources).

### 4.3 | Ecosystem service implications of plant multiple ecological strategies along abiotic stress gradients

Structural equation modellings highlight that considering multiple ecological strategies of plants could enhance our ability to explain variability in ecosystem functioning. Our results indicate that, consistently with the LES theory, *S. anglica* plants growing at the conservative end of the LES (first dimension) would strongly invest in BLW biomass (Freschet et al., 2010, 2015). Furthermore, in well-aerated sediments (high redox) plants would produce many coarse roots (third dimension), allowing an higher soil exploration (Freschet & Roumet, 2017; Garnier et al., 2016) with an associated investment in ABV biomass. Previous studies demonstrated the capacity of BLW biomass to stabilize the sediment (De Battisti et al., 2019; Ford et al., 2016; Lo et al., 2017) and that of ABV biomass to attenuate wave energy (Bouma et al., 2010, 2013; Möller et al., 2014; Möller & Spencer, 2002). Therefore, our study suggests that, at estuary mouths (high salinity), *S. anglica* plants shift towards the conservative side of the LES, investing more in BLW biomass and possibly enhancing sediment stability (Figure 5). Interestingly, the orthogonality of the trait-dimensions (ecological strategies) implies that areas of sediment high redox in marshes at the estuary mouths would still allow plants to invest in ABV biomass and possibly maintain plants' ability to reduce wave energy (Figure 5). Therefore, our study suggests that the net effect of abiotic factors (salinity and redox) on ecosystem functions (wave attenuation and sediment stabilization) mediated by plant traits will likely depend on the specific combination of environmental stressors experienced by plants.

Although in our study the causal links between abiotic factors, traits and biomass allocation are grounded on the a priori knowledge of the system, as with any non-experimental study, the results should be interpreted with a degree of caution. Focusing on a single species in the pioneer zone allowed us to account for environmental variability by measuring three main stressors: salinity, redox (a proxy for sediment anoxia related to inundation frequency; Armstrong et al., 1985) and sand content (a proxy for low nutrient availability; Minden et al., 2012). Importantly, we were also able to account for variation among marshes in unmeasured variables such as land-use history by including marsh identity as a random factor in our analyses. Yet, it is still possible that other stressors not measured here, such as within-marsh variation in disturbance history, might have influenced traits or biomass allocation. Moreover, although we found evidence for multidimensionality in plant trait strategies, we focused on a single species. Therefore, future studies should investigate the

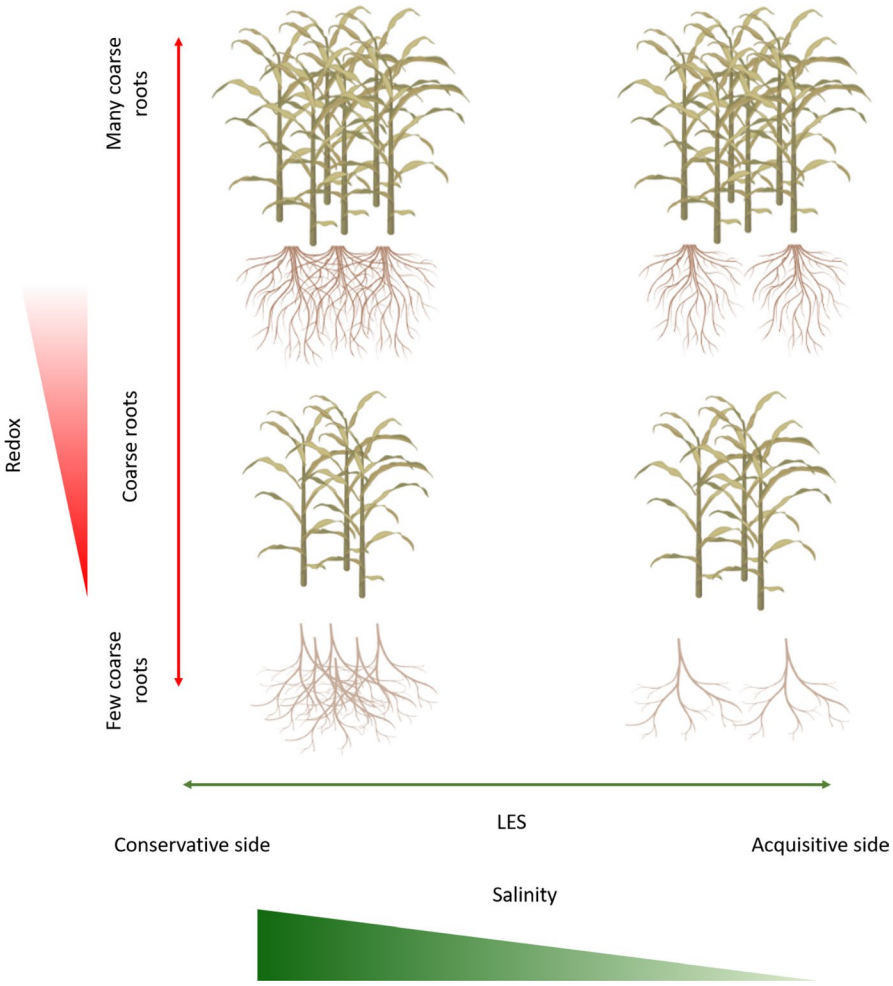



**FIGURE 5** Schematic representation of our main findings. Our study species, *Spartina anglica*, responds to both salinity and redox factors, but employing different suite of traits. This leads to multiple orthogonal traits dimensions (ecological strategies) which have a complex effect on plant biomass investment and thus, possibly on ecosystem functions and services. For instance, under higher salinity plants shift towards the conservative side of the spectrum (left side images), investing more in below-ground biomass and thus possibly increasing sediment stability. On this side, if plants grow under high sediment redox then plants would invest more in coarse roots (upper left images), consequently investing more in above-ground biomass and thus possibly maintaining the capacity to reduce wave energy [Colour figure can be viewed at wileyonlinelibrary.com]

dimensionality of trait strategies across multiple species and using a combination of observational and experimental approaches. Despite the limitations of our study, the key, novel aspect of this work is to highlight that multiple suites of correlated traits (ecological strategies) do not necessarily align with the PES (or LES) but can still have a strong influence on ecosystem functioning and services.

## 5 | CONCLUSIONS

Our study highlights the importance of multiple ecological strategies at the intraspecific level for driving ecosystem properties. Here, we found support for the LES, but not for the whole-plant spectrum. The lack of a PES likely arises from plants' need to cope with multiple environmental stresses, which also increases dimensionality in plant ecological strategies (Pan et al., 2018). Indeed, our study showed that changes in environmental factors can affect trait expression in different dimensions, leading to a complex, integrated effect on ABV and BLW biomass production and, thus, possibly on ecosystem functions. This is of particular importance in coastal ecosystems where large monospecific stands can be crucial for maintaining ecosystem functions and resilience. Overall, we suggest that adopting a multidimensional strategy perspective would increase our ability to more accurately predict changes in ecosystem functions compared to a unidimensional economic spectrum. Future research should focus on the role of multidimensionality in plant ecological strategies for driving ecosystem properties at different scales of organization (e.g. community level) and in different ecosystems.

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### AUTHORS' CONTRIBUTIONS

D.D.B. and J.N.G. developed the idea and led the writing of the manuscript; D.D.B. performed field work, laboratory work and data analysis; J.N.G. and M.S.F. contributed to data analysis; M.S.F., S.R.J., M.W.S., T.J.B. and P.J.N. contributed to writing the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

### DATA AVAILABILITY STATEMENT

The dataset has been made available on figshare https://doi.org/10.6084/m9.figshare.12005508.v1 (De Battisti, 2020).

### ORCID

*Davide De Battisti* https://orcid.org/0000-0001-7847-0414

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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