Invasion mechanisms of Spartina anglica in salt marshes of the Bay of Arcachon and consequences for native vegetation species

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Invasion mechanisms of *Spartina anglica* in salt marshes of the Bay of Arcachon and consequences for native vegetation species

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Mécanismes de l'invasion de la Spartine anglaise dans les prés salés du Bassin d'Arcachon et conséquences pour la végétation native

Spartina anglica est une espèce exotique hybride qui peuple les zones humides littorales. Elle s'est installée dans le Bassin d'Arcachon au cours des années 1980, envahissant fortement les prés salés et les platiers vaseux préalablement occupés par, respectivement, *Spartina maritima* et *Zostera noltei*. Face aux inquiétudes suscitées par cette installation, cette thèse vise à comprendre, par une approche pluridisciplinaire, les mécanismes d'invasion et ses conséquences sur le milieu physique et sur les espèces végétales natives. L'objectif de ce travail est d'étudier l'occupation de niche par *S. anglica* et ses interactions avec deux espèces intertidales natives : *S. maritima* et *Z. noltei*.

L'analyse d'images aériennes et satellitales a montré que, 30 ans après l'invasion, dans une zone densément peuplée par la Spartine native, la zone haute des prés salés a peu changé : la Spartine anglaise a occupé des niches vides et n'a pas remplacé la végétation native. Une expérience de transplantation réciproque et de mesures de biomasses confirment ce résultat, en montrant que l'espèce native offre une résistance à la colonisation de l'espèce exotique. L'expansion de la Spartine anglaise vers les replats de marée de l'intérieur du Bassin serait ainsi liée à sa capacité à tolérer les perturbations physiques, à sa forte plasticité de croissance en milieu oxygéné et riche en nutriments et à son comportement auto-facilitateur. Sa forte capacité d'ingénieur d'écosystèmes semble être liée à son système racinaire très développé, qui améliore l'aération des sols fortement anoxiques.

Les effets de la colonisation par l'espèce exotique des zones intertidales basses à subtidales sur la Zostère naine sont importants sur le long-terme (dizaines d'années). En tant qu'ingénieur d'écosystèmes, la Spartine exotique favorise l'élévation du sol par sédimentation, entrainant une dessiccation du sédiment, peu favorable à la Zostère. Des mesures physiques au sein de patchs de l'espèce exotique suggèrent que l'élévation du sédiment est toutefois lente, surtout liée à une allocation de biomasse spécifique aux racines ainsi qu'à des rhizomes qui permettent de résister à l'érosion.

En termes de gestion et de conservation des prés salés du Bassin d'Arcachon, ces résultats indiquent l'importance de limiter les perturbations physiques et les apports nutritifs qui pourraient rompre la résistance à l'invasion de la Spartine native. Ils supportent aussi l'idée que la Spartine anglaise pourrait être un allié robuste face à l'élévation du niveau de la mer.

Mots clés : Invasions biologiques, ingénieur d'écosystèmes, prés salés, interactions biotiques, interactions biophysiques, Spartine, Zostère

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Invasion mechanisms of *Spartina anglica* in salt marshes of the Bay of Arcachon and consequences for native vegetation species

Spartina anglica is a hybrid exotic cordgrass that inhabits coastal salt marshes. This species arrived in the Bay of Arcachon in the 1980s and since has importantly colonized the salt marshes and tidal flats formerly only occupied by the native *Spartina maritima* and *Zostera noltei*, respectively. This work aims at understanding, with an interdisciplinary perspective, the invasion mechanisms of this exotic cordgrass and the outcoming changes of its introduction in the Bay, both to the physical environment and to the native vegetation. Different approaches were considered in order to assess the niche occupancy by the exotic *Spartina* and its interactions with the native intertidal species, *Spartina maritima* and *Zostera noltei*.

The analysis of aerial and satellite images has shown that, in about 30 years after the invasion, within a zone densely populated by the native *Spartina*, the global high marsh zone did not suffer significant changes with the arrival of the invasive species. *Spartina anglica* did not replace the existent marsh vegetation, it occupied empty niches along the intertidal area instead. Additionally, experimental works of cross transplantation and biomass measurements have corroborated that the native *Spartina maritima* offers resistance to the colonization by the exotic *Spartina*. It was also shown that the invasive occupies the same intertidal niche along the elevation and anoxic gradient than the native. The successful extension of *Spartina anglica* into the mudflat towards the inner Bay was related to its likely ability to tolerate physical disturbances, its strong growth plasticity in nutrient- and oxygen- rich patches and its self-facilitator behaviour. This latter trait is related to its strong ecosystem-engineering ability due to its prominent root system and consequent ability to ameliorate the oxygenation of highly anoxic soils.

The main effect of the exotic *Spartina* species on the seagrass is related to its stronger ecosystem-engineering ability, favouring bed accretion up to levels that are not favourable to *Z. noltei* through enhancement of desiccation stress. However, hydrodynamic and altimetry measurements have shown that the process of bed accretion is slow and, due to the cordgrass' specific preferential biomass allocation to roots, its efficiency is more linked to its resistance to erosion rather than sediment trapping.

The results of this study provide relevant information for the definition of appropriate action and conservation strategies of marsh zones in the Bay of Arcachon, and in particular the importance of limiting physical disturbance and nutrient pollution that could disrupt the biotic resistance of the native cord grass. They also suggest a potentially important role of the exotic species in facing increasing Sea Level Rise.

Keywords: Biological invasions, ecosystem engineering, salt marsh, biotic interactions, biophysical interactions, *Spartina*, *Zostera*

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General introduction

The arrival of a new species into a location often raises substantial concern, mostly for the possible threats it might represent to the local biological diversity. Nonetheless, positive changes in ecosystem services can result from a biological invasion[1]. Either way, a biological invasion represents a learning opportunity on systems' adaptability to change (Crooks 2002) which becomes particularly important in a context of global change. The evaluation of the impact of biological invasions must be carried out at appropriate spatial and temporal scales (Strayer et al. 2006). For instance, the impact of an introduced species can change over the course of time, not only because it acclimatizes to the new location, but also, the hosting environment will evolve and try to adapt to the changes.

The major problem with invasive species is that we still don't always understand the mechanisms of the adaptation of systems to such a change. In particular, the complexity of the subject is related to the fact that invader impacts concern alterations in both biotic and abiotic features of the recipient system (Vitousek 1990; Vitousek et al. 1997). Organisms able to modify biotic conditions are called ecosystem engineers (Jones et al. 1994; Jones et al. 1997; Crooks 2002). In general terms, ecosystem engineering is the creation, destruction or modification of habitats by living organisms either by direct or indirect means (Crooks 2002).

Coastal environments are highly dynamic and chiefly modulated by the physical forces they are subjected to, and represent therefore an excellent scenario for the study of ecosystem engineering cases (Murray et al. 2008). Such systems are often characterized by a plant distribution that tends to follow patterns that are closely linked to the trade-offs between plant competition abilities and stress tolerance (Grime 1977). In particular, in the case of intertidal systems (Figure 1), where plant growth is conditioned by physical stresses (Belliard et al. 2017), ecosystem engineering and positive interactions represent major determinants of community assembly dynamics (Bertness and Callaway 1994; Bruno et al. 2003). Notably, numerous studies have shown that marsh vegetation tends to be structured by positive associations to cope with the constraints of frequent inundation and consequent soil salinity and anoxia (Bertness and Hacker 1994; Bruno 2000; Dethier and Hacker 2005; Pennings et al. 2005).

Salt marshes are extremely productive environments that provide different ecosystem services (Costanza et al. 2008, Barbier et al. 2011), such as water purification, carbon sequestration (Mitsch and Gosselink 2007), provision of nursery, coastal protection from waves and storm surge (Möller et al. 1999, Mendez and Losada 2004, Bouma et al. 2005, Temmerman et al. 2013) and sediment stabilisation (Castellanos et al. 1994, French et al. 1995), and protection against erosion (Vannoppen 2016).

The local processes of interaction between plants and the incident flow (either water or air) have been recognised to propagate to larger scales and to be determinants of landscape development in coastal environments (D'Alpaos et al. 2007, Kirwan and Murray 2007, Temmerman et al. 2007) affecting the species growth and survival on a larger extent, a process known as bio-geomorphodynamics (Corenblit et al. 2008, Murray et al. 2008, Coco et al. 2013).

Biodiversity and the health of coastal systems are being threatened all over the world and these threats gain importance with climatic changes. There is then a pressing need to

[1] Biological invasion is here defined as the process of the arrival of a species into a location where it did not exist historically in time sensu Carlton (1979).

achieve an integrated understanding of how these ecosystems are affected by change, from an interdisciplinary perspective.

Figure 1. *Aerial overview of tidal flats in the Bay of Arcachon (top images). Spartina anglica in the tidal flats (bottom left) and high marsh zone in the Bay of Arcachon (bottom right)*

Intertidal vegetation as ecosystem engineers

The importance of the interactions between living organisms and the environment they inhabit has long been acknowledged. Because the work presented in this thesis is focused on intertidal vegetation, examples herein will mostly concern studies on submerged aquatic vegetation (SAV) in intertidal systems.

More precisely, biologically mediated modifications of the environment can result in the alteration of both chemical and/or physical properties of the soil, that can go from a local to the landscape level. Soil chemistry modification by SAV is mostly related the alteration of resources availability, namely, nutrient uptake and oxygenation (Pennings and Bertness 2001). Most of wetland vegetation is capable of transporting oxygen from the air to the below-ground compartment which is an important asset within frequently inundated environments (Mahall and Park 1976, Maricle and Lee 2002, Koop-Jakobsen et al. 2017). Oxygen transfer underground between the root system and soil, increasing oxygen availability within highly anoxic soils and hence facilitating nutrient uptake by the plants (Lai et al. 2012). Additionally, the ability of SAV to trap sediment and other suspended particles can be an important contribution to the renewal of the soil resources availability.

In general terms, the vegetation influence on the incident hydrodynamic flow and subsequent impact on sediment dynamics can be divided in an above-ground and in a below-ground effect. On one hand, through their above-ground biomass (shoots and leaves), and depending on its density, height and flexibility, plants exert friction on the flow, modifying sedimentation rates. On the other hand, through their root system (below-ground biomass), and also depending on its density and length, they will influence sediment cohesion and resistance to erosion (Figure 2). Most studies concerning the interactions between the vegetation aerial biomass and the hydrodynamic forces, both currents (Christiansen et al. 2000, Neumeier and Amos 2006, Bouma et al. 2013) and waves (Möller et al. 1999, Mendez and Losada 2004, Bouma et al. 2005, Rooijen et al. 2016) have shown effective energy dissipation by vegetation canopies. For field experiments considering *Spartina* vegetation, an effective wave attenuation ability was found, varying between 2 and 7% along 10 m long canopies (Möller 2006) and of 63% along 200 m long canopies (Möller et al. 1999). However, in a flume study, Bouma et al. (2005) have shown that most of the energy reduction can occur within the first 2 m of the canopy. Indeed, also with flume experiments, Möller et al. (2014) have shown that the effectiveness of energy attenuation is inversely correlated to the incident wave height. This reduction of energy to the incident flow usually translates into vertical sediment accretion (Friedrichs et al. 2000, Bouma et al. 2005, Temmerman et al. 2007, 2012). Marsh vegetation that achieves a net positive sediment trapping, increases marsh elevation and has higher chances to cope with increasing rates of sea level rise (Fagherazzi et al. 2013, Kirwan and Megonigal 2013, Kirwan et al. 2016), as long as sediment inputs remain relevant in the system (Nyman et al. 2006, Lauzon et al. 2018).

Nevertheless, studies on vegetation induced flow/sediment interactions have led to contradictory results on the bed-stabilizing effects of SAV (Tinoco and Coco 2018). Such variability is probably depending on the type of vegetation, the presence/absence of other seasonal biological features, and the properties of the sediment, that influence the physical processes, but also, due to field difficulties inherent to the intertidal environment characteristics

(Belliard et al. 2019). Flume studies can represent a good alternative, but they often consider artificial vegetation (Yang et al. 2016, Tinoco and Coco 2014, 2016) which tends to simplify the structures response to the studied processes.

In this sense, despite the already existing extensive work on the subject, there is still a need for a better understanding of the bio-gemorphodynamic processes, namely the complex spatio-temporal behaviour of bed level changes under the action of vegetation and the reciprocal adaptations of the vegetation.

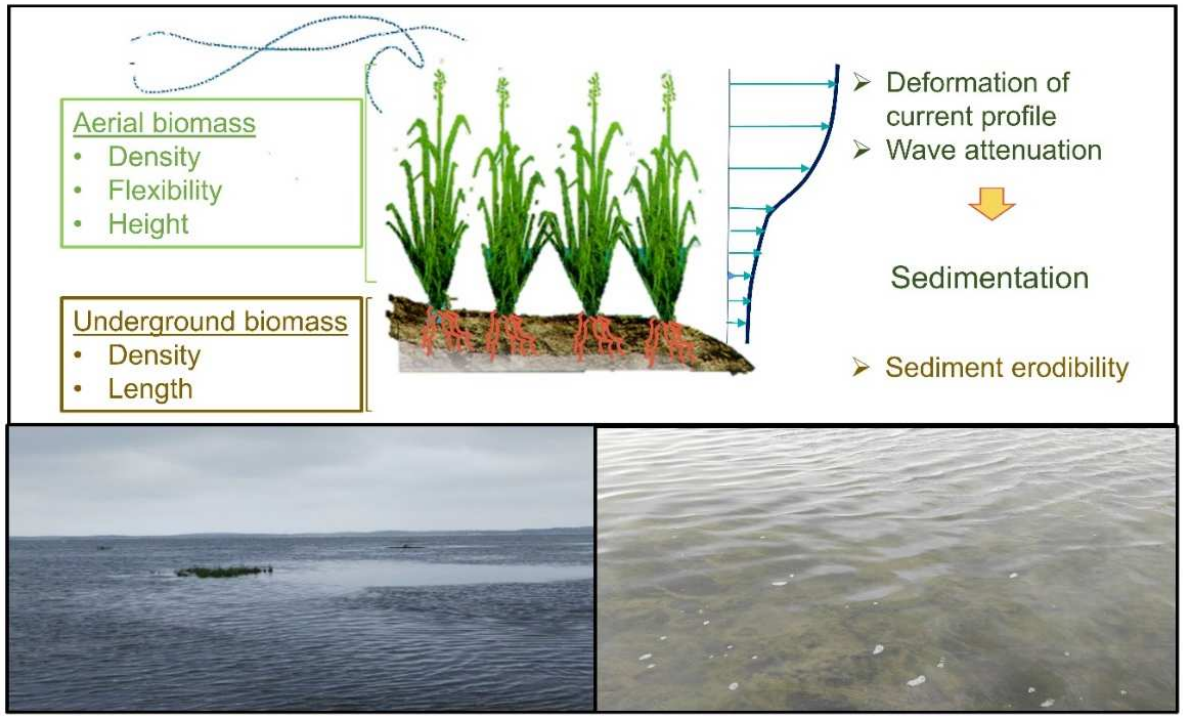

Figure 2. *Schematic representation of biophysical interactions between submerged aquatic vegetation (SAV) and hydrodynamics (top). Images of fluid motion deformation due to the presence of SAV – shadow zone on hydrodynamic flow motion behind Spartina tussock (bottom left) and Zostera noltei meadow oscillating with waves (bottom right).*

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Global evolution of seagrass meadows

There is a general concern on the health of seagrass meadows worldwide, that are strongly affected by coastal development and anthropic eutrophication (Orth et al. 2006, Waycott et al. 2009). As previously mentioned, coastal ecosystems comprise numerous benefits and, in tidal wetlands, the decline of seagrass meadows might lead to considerable consequences at the ecosystem level.

The overall health of seagrass systems seems to be driven by the balance between recruitment capacity and mortality, which is, on its hand, determined by abiotic factors such as light availability, mechanical disturbance and nutrient availability (Marba and Duarte 1995, Auby and Labourg 1996, Orth et al. 2000, Plus et al. 2010, Cognat et al. 2018). In particular, *Zostera* sp. have been shown to follow strong seasonal patterns (Duarte 1989, Auby and Labourg 1996). Within a global change context, there is the possibility that this seasonal behaviour might be affected. At the end of the last century, there was an estimated global loss of seagrass meadows, both from direct and indirect human impacts, of 90 000 ha (Short and Wyllie-Echeverria 1996).

Several studies indicate that the primary cause of seagrass degradation is related to reduction light availability both due to increases in turbidity and nutrient loading (Duarte 2002, Short 2003, Cognat et al. 2018). Such changes in water clarity are often linked to dredging operations (Erftemeijer and Robin Lewis 2006). Indeed, the adaptation to light conditions seems to be species dependent within seagrasses where for example *Zostera noltei* presents a better tolerance to high light conditions comparing permanently submerged seagrasses (Vermaat and Verhagen 1996).

In France, *Zostera noltei* meadows occupied over 6000 ha in the Mediterranean coast, in the Etang de Berre by the middle of the 20th century (Warner 2012). Disturbance through human activities linked to industrial pollution lead to a drastic decrease in *Z. noltei*'s population (Bernard et al. 2007), where perturbations in the haline distribution in the water column were reported to be a major cause (Alekseenko et al. 2017). On the contrary, in Jade Bay, on the German coast of the North Sea, *Z. noltei* beds have been reportedly increasing between the 1970s and 2009 (Singer et al. 2017). Indeed, with a modelling approach, Singer et al. (2017) predicted a good acclimatization of this species to environmental changes related to Sea Level Rise, namely by further extension of colonization on the lower intertidal flat. In the Bay of Arcachon, the trend of *Z. noltei* beds exhibit mostly a decline (Plus et al. 2010 – Figure 3) that is accompanied by an increase in suspended sediment concentrations (SSC) in the Bay (Cognat et al. 2018). This alteration in of SSC can both be a cause for the seagrass decline through the decrease in water clarity and, at the same time, a consequence from *Zostera* meadows regression as this species is known for its important impact on fine sediment retention in the Bay (Ganthy et al. 2013, Kombiadou et al. 2014).

Recently, much effort has been given to seagrass beds restoration and characterization of suitable unvegetated habitats (Valle et al. 2013, Folmer et al. 2016, Suykerbuyk et al. 2016a, 2016b). An important point that has risen from such studies, is the benefice of intraspecific facilitative behaviour through positive feedback mechanisms (van der Heide et al. 2007, 2008). However, these positive feedback loops can be strongly affected by winter reduction of the aboveground biomass (Vermaat and Verhagen 1996) and seed burial (Cabaço et al. 2008).

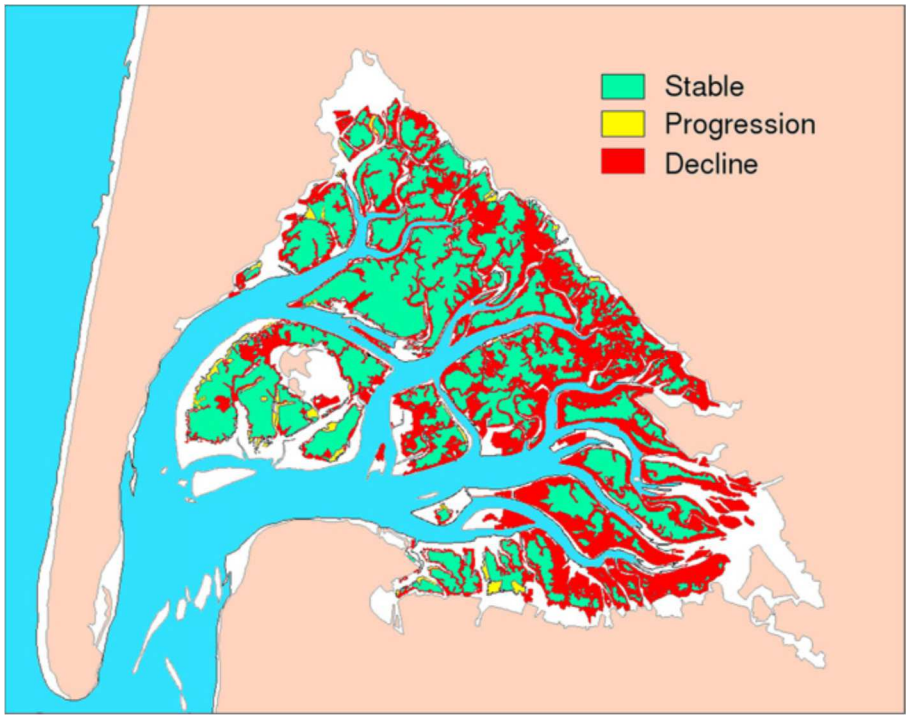

Figure 3. *Evolution of Zostera noltei meadows between 1989 and 2007 in the Bay of Arcachon (Plus et al. 2010).*

Spartina invasions around the world

It has long been known that maritime cordgrasses play an active role in sediment dynamics within estuarine zones. *Spartina* introductions with such purpose go back as early as the sixteenth century (Strong and Ayres 2013), when they were introduced for the stabilization of harbour zones, eroding shorelines and land reclamation (Callaway and Josselyn 1992). *Spartina alterniflora* and *Spartina anglica* are maybe the two most widespread *Spartina* sp. invaders, particularly in the coasts of Australia, western Europe and China.

Specifically, *Spartina anglica* introductions have been reported all over the world, namely in the UK, starting from its place of Origin, in Southampton, the Netherlands (Oenema and DeLaune 1988), in France (Baumel et al. 2001,Cottet et al. 2007), in China (An et al. 2007), in New Zealand (Hubbard and Partridge 1981, Lee and Partridge 1983), in Australia and Tasmania (Sheehan and Ellison 2014) and in the US (Hacker and Dethier 2006, Strong and Ayres 2013). The success of this exotic cordgrass colonization is such that countries like the US, Australia (Hacker and Dethier 2006, Seddon et al. 2000) and China (Sun et al. 2017) have declared *Spartina anglica* as a notorious invasive species.

In the United States, *Spartina* invasion occurred mainly in the Puget Sound, in Washington, where it was introduced in 1961, to stabilize a dyke systems and provide forage for cattle (Hacker et al. 2001). By the late 1990s it covered a surface of marine intertidal habitat of about 3300 ha and 1997 the removal of *S. anglica* in the Puget Sound was designated by the Washington State Department of Agriculture. Despite active control actions, in 2006 it spread into the British Columbia and Canada. Such control measures, both by mechanical and chemical means have similarly been established in Australia (Roberts and Pullin 2006). Still in the US, a popular case for the co-habitation and behaviour of diverse *Spartina* species is the Bay of San Francisco (Callaway and Josselyn 1992, Ayres et al. 1999). Indeed, this is an interesting case study, as the Bay of San Francisco hosts more than 230 exotic species which makes it known as the "world's'" most invaded estuary (Ayres et al. 1999).

In China, three introduced *Spartina* species are estimated to have caused annual economic losses of 2000 million US dollars (Sun et al. 2015). The Chinese population of *Spartina anglica* was first introduced in 1963 in Xinyang Agricultural Experimental Station, Sheyang, Jiangsu and grew to cover 36000 ha by 1985 (Chung 1993). However, in this country, it seems to be *Spartina alterniflora* the most aggressive cordgrass invader. This species was introduced in the Jiangsu Province of China in 1979 to solve erosion issues as well as soil amelioration and dike protection (Quan et al. 2016). During the 1980s and 1990s, the Chinese government increasingly transplanted the exotic species in tidal flats for sediment accretion purposes (Quan et al. 2016). *Spartina alterniflora* was transplanted into Yantze river estuary in the late 1990s and since then it rapidly spread into salt marshes, replacing the native *Phragmites* and *Scirpus mariqueter* (Quan et al. 2011). Concerning *Spartina anglica*, a large decline was verified over the last decade in coastal china, where its general occupation decreased to less than 50 ha (An et al. 2007).

In Europe, a good example of human intervention for land reclamation purposes is the Netherlands where the human influence on salt marsh accretion and extension is considerable and several actions with this purpose have taken place through planting of *Spartina anglica* (Oenema and DeLaune 1988).

At first glance, when it concerns biological invasions, they are commonly seen with mistrust. However, invaders can have different impacts depending on the habitats they invade. In opposition to the theory that strong invaders decrease species diversity, Hacker and Dethier (2006) found increased native plant diversity with the invasion in some habitats while it decreased in others. Even though *Spartina* sp. invasions are mostly known by their success, this is not always the case. For example, in case of *Spartina anglica*, experiments by Dethier and Hacker (2005) have shown that invasions by this species can strongly vary with the habitat and that they are mostly controlled by abiotic factors rather that biotic resistance. Indeed, *Spartina anglica* seems to occupy a wide extent of habitats among which it presents highest abundance in low salinity marshes and mudflats and lowest abundance (lower surface of occupation) in high salinity marshes and cobble beaches (Hacker et al. 2001). In fact, germination success of *S. anglica* seeds significantly increases under low salinity conditions (Dethier and Hacker 2005) which might be a determinant factor for successful rapid spreads of this species.

The history of *Spartina anglica* C. E. Hubbard

Plant species that are newly formed polyploids and that are additionally originated from hybridizations, commonly result in invasive species (Brown and Marshall 1981, Pandit et al. 2006). This is the case of the cordgrass *Spartina anglica* C.E. Hubbard (Ainouche et al. 2004). This species owes its origin to the crossing between the north American species *Spartina alterniflora* Loisel and the European native *Spartina maritima* (Curtis) Fernald, the most ancient *Spartina* species known (Raybould et al. 1991a, 1991b, Thompson 1991, Ainouche et al. 2009). S. alterniflora is a widespread and abundant cordgrass species in north American salt marshes that in the nineteenth century, around 1820, had its seeds accidently transported on shipping ballast and hence introduced in the UK, from Southampton, on the southern coast of the British territory. There, the American species hybridized with its European congener, *S. maritima*, resulting in a F1 sterile hybrid, *S. x townsendii* H. & J. Groves. As a consequence of chromosome doubling of the hybrid species, a new species was born around 1890, *Spartina anglica* C. E. Hubbard (Figure 4).

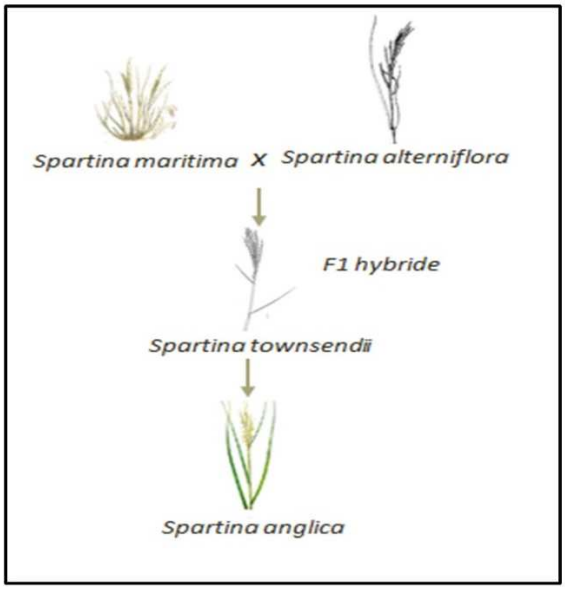

Figure 4. *Illustration of Spartina anglica's direct genealogical origin.*

The introduction of *Spartina anglica* in the Bay of Arcachon and context of the present study

Several *Spartina* species are present in the Bay of Arcachon, namely *Spartina maritima* and *Spartina versicolor (*reported since 19th century), *Spartina alterniflora* (intentionally introduced in the late 1970s), and *Spartina anglica* (appeared in the late 1980s) (Auby 1993, Lafon et al. 2017). Like it occurred with the introduction of *Spartina alterniflora* in the UK, *Spartina anglica's* seeds or plant fragments might have crossed the English Channel, accidently by boat or, simply transported with currents arriving thus in the Baie des Veys, in the French coast, where it was first recorded in 1906 (Baumel et al. 2001, Strong and Ayres 2013). It then progressively spread southward from Brittany along the western coast of France. It was deliberately introduced in the Gironde estuary in 1924 from where it spread to the Bay of Arcachon, where the first records of its presence date from the 1980s (Baumel et al. 2001).

For the management entities, *Spartina anglica* is the only one that raises concerns for its ability to colonize a wide range of the intertidal region and reputation of being a strong invasive species (Le Nindre et al. 2004, Lafon et al. 2017). Marsh vegetation cartography works have reported a strong development of the exotic *Spartina anglica* during the last 20 years, particular in some specific regions of the Bay. Both the wide distribution ability and the recent rapid spread of the exotic *Spartina* have triggered the alarm among local human communities and management entities that started questioning the possibility of this *Spartina* to become a threat for both *Zostera noltei* meadows, the dominant vegetation on the mudflat facing a retreat itself during the recent years and the native *Spartina maritima*, the originally dominant species on the high marsh zones on the borders of the Bay.

The fears regarding native biodiversity as well as concerns for maintenance of navigation access in the Bay and recreational use of the beaches, have lead the local human communities of the Bassin d'Arcachon to join together and form associations to fight the exotic *Spartina*. Because they wanted to lead global and consistent measures all over the Bay, they have recently requested to the environmental commission of the community union (Commission

Environnementale du Syndicat Intercommunal du Bassin d'Arcachon – SIBA) to perform an inventory of the evolution of *Spartina anglica*'s presence in the Bay of Arcachon and the elaboration of official guidelines for the control of the exotic species. Within their study, the total marsh surface in the Bay was estimated to be around 6 Km^2, which corresponds to about 3% of the total surface of the Bay. The inventory on marshes composition in the Bay of Arcachon has indicated the presence of several *Spartina* species including other exotics, such as *Spartina alterniflora*. However, *Spartina anglica* is reported to be the most spatially present species (Lafon et al. 2017).

Study questions

In this context, the study I present here intends at enlightening the understanding the colonization mechanisms of *Spartina anglica* and its interactions with the biotic and abiotic environment it colonizes. More precisely, with this thesis I aim to answer the following specific questions:

(1) What are *Spartina anglica*'s mechanisms of invasion and what is its preferential niche of occupation?

(2) How did the arrival of *Spartina anglica* impact the high marsh zone, previously occupied by the native *Spartina maritima*?

(3) In what extent does the colonization of the mudflat's pioneer zone by *Spartina anglica* affect the foundation species *Zostera noltei*?

Organisation of the manuscript

In order to assess the previous questions a series of field experimental works were carried in the north eastern part of the Bay of Arcachon. This area was specifically chosen for the limited presence of the exotic *Spartina anglica* along with a well-developed marsh dominated by the native *Spartina* which corresponds to early stage conditions of the invasion.

In order to try to understand the mechanisms of invasion and the niche type occupation by the exotic *Spartina*, as well as the global marsh evolution after its arrival, a first assessment was made through remote sensing. In this first chapter I explore the potential of using high resolution satellite images to identify the spectral signal of the two *Spartina* species in question and evaluate the temporal evolution of the marsh zone.

The second chapter is dedicated to the field experimental assessment of the biotic interactions between the native *Spartina maritima* and the invasive *Spartina anglica* as well as the characterization of the preferential occupation niches by the two species along the different levels of the tidal flat. Not only this work is complementary to remotely sensed observations presented in the first chapter but it also enabled a further characterization of the two *Spartina* niches and competitive abilities.

To further understand the nature of the interactions between the two *Spartina* species and how they can be influenced by the proximity of freshwaters inputs and nutrient availability, I present, in chapter 3, the results of field works combining a removal experiment with nutrient availability and environmental measures.

Because of the possibility of an influence of the exotic *Spartina* on the decline of the seagrass *Zostera noltei*, due to a reported wide colonization of the mudflat by the former, on the fourth chapter, I present experimental works on the interactions between the exotic cordgrass and the native seagrass species, which the original colonizer of the inner zones of the Bay. With this work I present an evaluation of the spatio-temporal extent of action of the invasive cordgrass over the seagrass performance.

Finally, in the fifth chapter I compare the two *Spartina* species ecosystem engineering ability to build marsh from the pioneer zone of the tidal flat in order to understand whether the colonization of the tidal flat by invasive *Spartina* can lead to preoccupying changes or not, relatively to the previous vegetation already colonizing the Bay.

I close this manuscript with a synthesis section where I present the general main conclusions of this thesis and perspectives on further investigations that could be performed in order to complement the findings of the works here presented.

CHAPTER 1

Remotely sensed assessment of niche occupation by the invasive Spartina anglica

The early detection of an invasive species and a rapid understanding of its proliferation in space and time might lead to timely management of control actions. In salt marshes, where field access presents considerable difficulties, spaceborne imagery provides a relevant tool to such type of assessment as it can offer large scale overviews consisting of short time frames at relatively low costs. However, species distinction in remote sensing imagery, particularly at small spatial resolutions, remains challenging. In intertidal environments, vegetation tends to follow a natural zonation according to its specific tolerances to the biotic and abiotic factors that characterize the different tidal levels. Besides this natural zonation between species, small scale heterogeneities occur, namely in terms of vegetation species density, mixing between different species or different degrees of sediment and water deposits on the vegetation.

In this chapter, I assess the evolution of salt marshes at Andernos, in the north eastern side of the Bay of Arcachon through remotely sensed imagery in order to understand their response to the establishment of the invasive *Spartina anglica*. This site is particularly suitable for this objective as *Spartina anglica* is present with a low abundance and the vegetation is still dominated by the native *Spartina* species. I first considered a set of aerial images from 1949 to 2016 to understand the long-term dynamics. Then, I explored the potential of using high spatial resolution satellite images to monitor the invasion of *Spartina anglica* in tidal flats of the Bay of Arcachon from an early stage of the invasion. Field reflectance measurements of the two target *Spartina* species and GNSS contours were performed and used as ground truth for pixel classification of the satellite images.

This work was published in the special issue *Remote Sensing of Estuarine, Lagoon and Delta Environments*, under the section Remote Sensing in Geology, Geomorphology and Hydrology of the journal "***Remote Sensing***". The publication is presented in the following section and the main conclusions are subsequently summarised.

Publication: Potential of high resolution Pléiades imagery to monitor salt marsh evolution after *Spartina* invasion

Research article

Potential of high-resolution Pléiades imagery to monitor salt marsh evolution after *Spartina* invasion

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Abstract: An early assessment of biological invasions is important for initiating conservation strategies. Instrumental progress in high spatial resolution (HSR) multispectral satellite sensors greatly facilitates ecosystems' monitoring capability at an increasingly smaller scale. However, species detection is still challenging in environments characterized by a high variability of vegetation mixing along with other elements, such as water, sediment, and biofilm. In this study, we explore the potential of Pléiades HSR multispectral images to detect and monitor changes in the salt marshes of the Bay of Arcachon (SW France), after the invasion of *Spartina anglica*. Due to the small size of *Spartina* patches, the spatial and temporal monitoring of *Spartina* species focuses on the analysis of five multispectral images at a spatial resolution of 2 m, acquired at the study site between 2013 and 2017. To distinguish between the different types of vegetation, various techniques for land use classification were evaluated. A description and interpretation of the results are based on a set of ground truth data, including field reflectance, a drone flight, historical aerial photographs, GNSS and photographic surveys. A preliminary qualitative analysis of NDVI maps showed that a multi-temporal approach, taking into account a delayed development of species, could be successfully used to discriminate *Spartina species (sp.)*. Then, supervised and unsupervised classifications, used for the identification of *Spartina sp*., were evaluated. The performance of the species identification was highly dependent on the degree of environmental noise present in the image, which is season-dependent. The accurate identification of the native *Spartina* was higher than 75%, a result strongly affected by intra-patch variability and, specifically, by the presence of areas with a low vegetation density. Further, for the invasive *Spartina anglica*, when using a supervised classifier, rather than an unsupervised one, the accuracy of the classification increases from 10% to 90%. However, both algorithms highly overestimate the areas assigned to this species. Finally, the results highlight that the identification of the invasive species is highly dependent both on the seasonal presence of itinerant biological features and the size of vegetation patches. Further, we believe that the results could be strongly improved by a coupled approach, which combines spectral and spatial information, i.e., pattern-recognition techniques.

Keywords: biological invasions; coastal wetlands; multi-spectral imagery; NDVI; Pléiades; Pixel classification; salt marsh; *Spartina anglica; Spartina maritima*.

1.1 Introduction

Biological invasions often represent an important source of change in a system. They are mostly perceived as a possible threat to local biodiversity (Vitousek et al. 1997b, Davis 2003, Seabloom et al. 2013, Simberloff et al. 2013). Occasionally, the arrival of a new species can also carry significant benefits to ecosystem services (Crooks 2002, Zarnetske et al. 2010, Schlaepfer et al. 2011, Seabloom et al. 2013). The consequences of biological invasions are usually difficult to predict. Their impact on ecosystems may significantly change in space and time (Strayer et al. 2006) because of a variable adaptive response of the host communities. This response can induce a slowdown of the invasive species (IS) proliferation or, conversely, a sudden rapid expansion. The detection and mapping of the earliest stage of IS development and expansion often turns out to be the best strategy for anticipating and controlling their impact (Bustamante et al. 2016, Correll et al. 2018).

Due to the frequency of physical disturbance, tidal flats and salt marshes present a high susceptibility to biological invasions (Hacker et al. 2001). This vulnerability particularly increases with human pressure (Early et al. 2016). These systems are characterized by complex interactions between geomorphological patterns and ecological structures (Marani et al. 2004) and present a highly dynamic and extensive character, which, being associated with access difficulties, make remote sensing an appealing monitoring tool (Silvestri et al. 2003, Belluco et al. 2006, Klemas 2011).

Several studies have already demonstrated the strong potential of using optical satellite imagery in mapping intertidal vegetation (Marani et al. 2004, Thomson et al. 2004, Barillé et al. 2010, Zuo et al. 2012, Correll et al. 2018), and particularly, for the monitoring of biological invasions (Zhang et al. 2004, Li et al. 2010, Ouyang et al. 2013). Intertidal vegetation follows a natural spatial zonation, according to its tolerance to the different tidal levels (Chapman 1964, Pennings and Callaway 1992). This natural zonation represents an advantage for remote sensing assessment, because it provides a clear physical separation between different species. Vegetation tends to grow in patches of clearly demarcated borders, presenting a relative homogeneity from a radiometric point of view, and the meadows of each species tend to be constant in time (Silvestri et al. 2003). However, despite the relative intra-patch homogeneity, different degrees of vegetation cover and mixing can occur when the pixel size increases (Silvestri et al. 2003, Adam et al. 2010). The environmental background noise, due to the soil characteristics, water and biofilm, then generates a significant per-pixel variability of the upwelling radiative signal (Silvestri et al. 2002). Further, there is also a significant time dependency on plant phenology that can largely influence species differentiation in spaceborne imagery (Silvestri et al. 2002, Ouyang et al. 2013, Clint Slatton et al. 2008, Sun et al. 2016).

For these reasons, it is essential to select the most suitable satellite on the basis of instrumental characteristics. Especially, remotely sensed multispectral satellite missions can provide data with significantly different temporal, spatial and spectral resolutions (Adam et al. 2010, Mouw et al. 2015). The selection of one resolution over the other needs to be weighted according to the objectives, as current orbiting sensors cannot yet provide simultaneous high temporal, spectral and spatial resolutions (Hill et al. 2014). For instance, Belluco et al. (Belluco et al. 2006) compared multispectral and hyperspectral remote sensing data efficiency in mapping salt marsh vegetation in the Venice lagoon (Italy). They showed that spatial resolution

affected the pixel classification accuracy in a much more important way than spectral resolution and that hyperspectral data can contain largely redundant information. Consequently, they suggested that, for such studies, preference should be given to spatial, rather than spectral, resolution. However, a possible way to overcome these limitations is through the combination of images from sensors, providing different spatial and spectral products by the application of pan-sharpening techniques (Garzelli et al. 2004, Akula et al. 2012). The application of such techniques enables one to simultaneously take advantage of panchromatic (higher spatial resolution) and multispectral (higher spectral resolution) images. The identification and differentiation of vegetation species is commonly based on a similarity in pixel clustering, using supervised or unsupervised methods (Belluco et al. 2006, Carter et al. 2009, Li et al. 2010, Correll et al. 2018, Sun et al. 2016). Better results are most frequently obtained using supervised classification techniques (Zak and Cabido 2002). However, in the case of muddy coastal zones, to achieve good results, these methods may require extensive and impracticable ground truth verifications.

Even with the current advances in remote sensing products and techniques, the differentiation of individual intertidal species, an important aspect in the assessment of biological invasions, is still a difficult (Correll et al. 2018) and usually comprises large errors and confusion with other features. In this study, we aim to assess the potential of multispectral images, acquired by the Pléiades-1 satellite constellation, in order to discriminate the invasive cordgrass, *Spartina anglica*, from the remaining marsh vegetation in the Bay of Arcachon (SW Atlantic coast of France). The evaluation exercise is based on NDVI maps and the use of pixel classification methods—either supervised (Random Forests) or optimized unsupervised (simulated annealing) approaches—applied to Pléiades images, which were acquired in different seasons. Any advances in the accurate identification of the different salt marsh structures will enable a better understanding of the mechanisms and extent of colonization by invasive species and allow for the monitoring of its evolution, facilitating an early intervention if needed.

1.2. Study Site

The Bay of Arcachon is located in the South-western French Atlantic coast (Figure 1.1). This coastal lagoon is separated from the open ocean by the Cap Ferret sand spit. Its main flow entrance is divided into two channels, with sandy banks and shoals between them (Allard et al. 2009). The presence of a mouth bar and inter-channel banks limits the internal propagation of external ocean waves. Therefore, inside the lagoon, waves are mainly wind generated and fetch limited, especially by the presence of the "Ile aux Oiseaux". Wind speed and wind direction vary seasonally; they are variable and weak during summer and mostly westerly or northerly in winter, reaching speeds > 10 m/s. Tides are semidiurnal, ranging from 0.8 m during neap tides to 4.5 m during spring tides (Cayocca 2001), and the high tide surface can reach an area of 174 km^2, mainly composed of a network of narrow channels, which is reduced to 40–50 km^2 at low tide (Plus et al. 2009). The main source of freshwater is the Leyre river in the South-east, and the Porge Canal in the North. The total freshwater input represents less than 1% of the tidal prism (Plus et al. 2009).

For this study, we chose to consider a study area located on the intertidal zone at Andernos (Figure 1.1), on the north-eastern side of the Bay. The particularity of the marsh in this zone is that, even though it presents a stable niche of native vegetation, there is a significant presence of the exotic *Spartina* in small random patches. This is representative of an initial stage of the invasion and is an ideal scenario for our objective of identifying this species from its early stage of territory occupation.

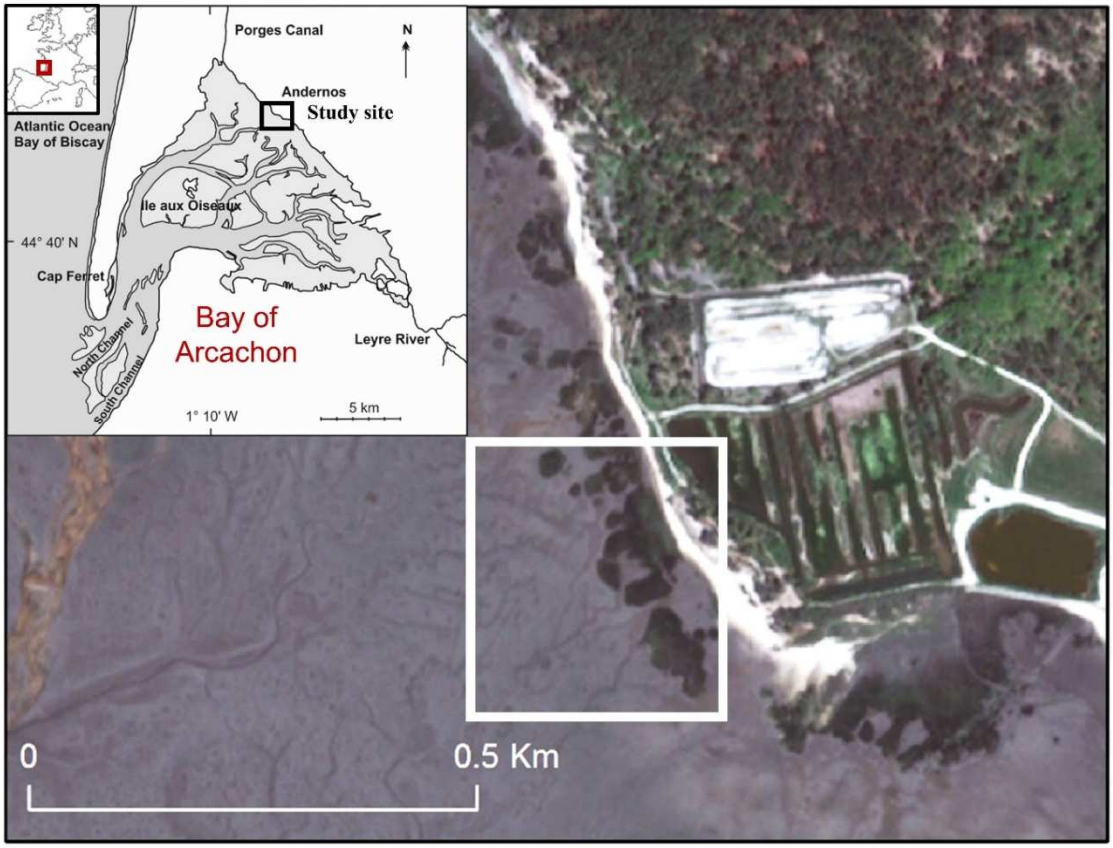

Figure 1.1 *Location of the Andernos' salt marshes (white rectangle) in the* ***s****tudy site (Bay of Arcachon, SW France).*

1.2.1. Vegetation in the Bay of Arcachon

In the Bay of Arcachon, low elevations of the tidal flat (slikke) are mainly colonized by the seagrass, *Zostera noltei*, whereas the margins of the lagoon (schorre) are occupied by typical salt marsh vegetation (Figure 1.2a), principally *Spartina* sp. (*Spartina maritima*—Figure 1.2b–e and *Spartina anglica*—Figure 1.2f–j). The arrival of the invasive species, *Spartina anglica*, in the 1980s (Baumel et al. 2001) provoked concern regarding threats to local species diversity and, especially, the eventual replacement of the native *Spartina* (*Spartina maritima*) by its exotic congener. Even though *Spartina* species constitute the dominant vegetation type in the marsh zone, there are many other species, such as *Salicornia spp.*, *Juncus gerardii*, *Limonium vulgare*, *Halimione portucaloides*, and *Puccinellia maritima* (Soriano-Sierra 1992, Labourg et al. 1995) (Figure 1.2k–m). Usually, there is a well-defined separation between different vegetation species, but different degrees of mixture, as well as different degrees of density within the same type of vegetation, can also occur.

More than other marsh species, the invasive *Spartina anglica* has the particular ability to spread to offshore positions within the tidal flat, at the inner side of the lagoon. For this reason, the vegetated inner tidal flat zone was included, with the intention of identifying the isolated *Spartina anglica* patches that might occur in this zone.

Seasonal differences in the intertidal vegetation's development and phenology can help to determine their identification and discrimination using remotely sensed images (Ouyang et al. 2013, Clint Slatton et al. 2008). Notably, *Spartina maritima* is a species known for its continuous growth and absence of significant seasonal die-back (Pierce 1983). In the Bay of Arcachon, this was verified by Proença et al. (Proença et al. 2019), who estimated a very low productivity for this species at different intertidal levels. On the contrary, the congener *Spartina anglica* presented a strong aerial productivity of aerial biomass, which means that it suffers from a strong die-back during winter, and it completely recovers during the growing season, particularly during summer, due to its exploitative growth strategy, which is better than that of the native. An important difference concerning the phenology of growth is also observable, with a maximum of growth during spring for the native and during summer for the exotics (Appendix A). Additionally, the cordgrasses seem to present some sensitivity both to continuously high and continuously low temperatures, expressed as a color change to yellow/brownish shades during summer and winter seasons, respectively. The seagrass, *Zostera noltei*, was also found to present a pronounced seasonality. Auby and Labourg (Auby and Labourg 1996) found a minimum aboveground biomass for this species between November and February and minimum shoot lengths in springtime. The maximum aboveground biomass was measured between June and August, but high values of shoot length were found during Fall. Concerning algae, several species can be found in the Bay at different times of the year (Castel et al. 1996). According to these authors, in the inner parts of the Bay, there is a strong presence of the green alga, *Monostroma obscurum*, that tends to decline during the period between March and September. However, they found that a clear seasonal trend is difficult to predict.

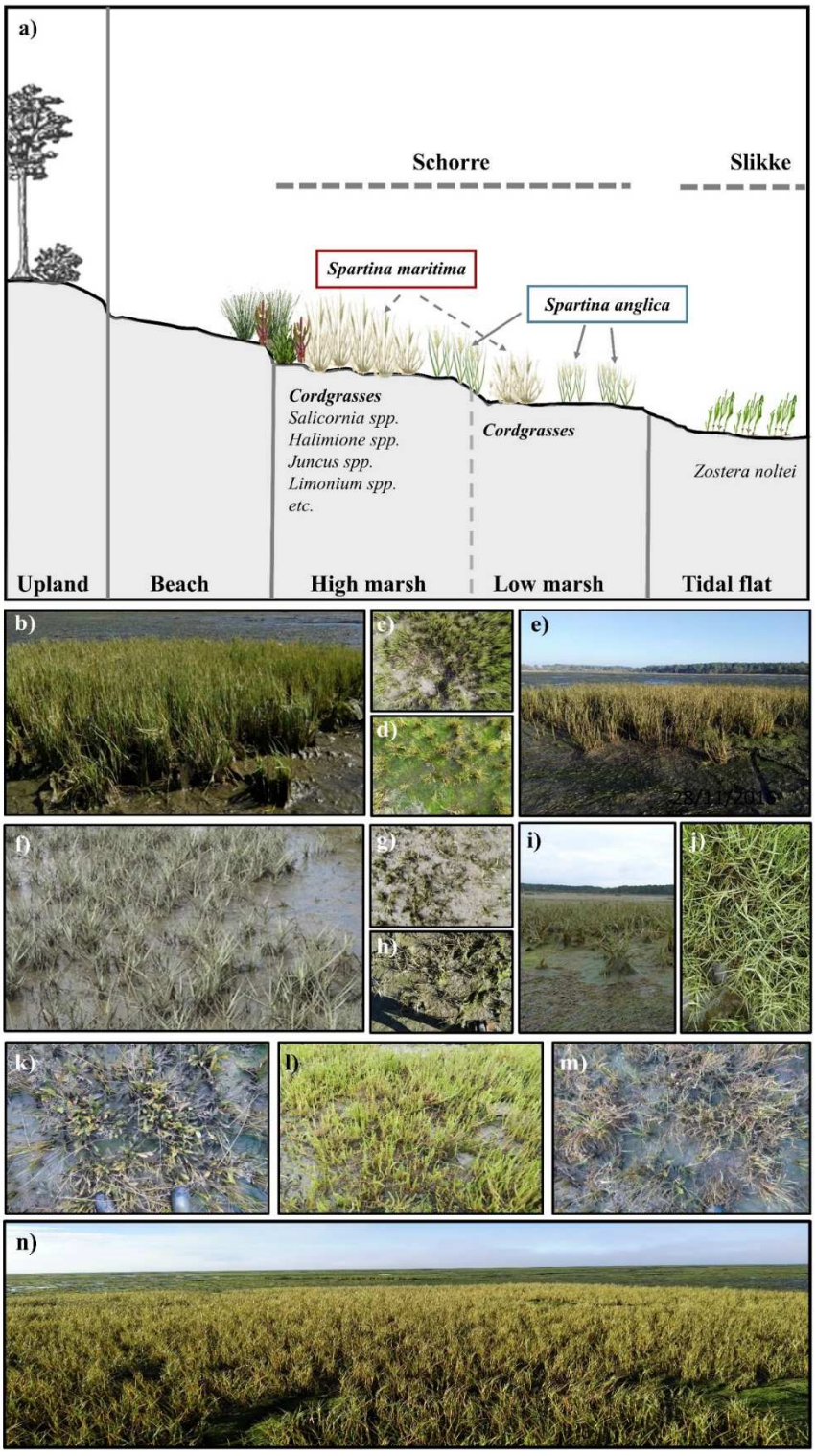

Figure 1.2. *Characterization of vegetation in the Bay of Arcachon.* ***a)*** *Schematic representation of the typical distribution of intertidal vegetation along the tidal gradient;* ***b)*** *dense green meadow of Spartina maritima;* ***c)*** *transition from a dense to a sparse Spartina maritima meadow;* ***d)*** *Spartina maritima with homogenous seaweed (Ulva) coverage;* ***e)*** *brownish dense meadow of Spartina maritima;* ***f)*** *sparse green meadow of Spartina anglica;* ***g)*** *sparse withered meadow of Spartina anglica;* ***h)–i)*** *Spartina anglica with thick algae coverage;* ***j)*** *dense green meadow of Spartina anglica;* ***k)*** *Halimione;* ***l)*** *Salicornia;* ***m)*** *mix of diverse vegetation; and* ***n)*** *dense Spartina maritima meadow with vegetated tidal flat, both due to well-developed Zostera noltei meadows and a strong presence of algae deposits in the background.*

1.3. Datasets and Methods

In this study, we used five high-resolution multispectral (MS) images, acquired by the Pléiades-1 satellite constellation, aerial and drone photographs, centered on the study area, Global Navigation Satellite Systems (GNSS) data, collected as ground truth validation, radiometric measurements of the features likely to appear in the classifications and georeferenced photographs.

1.3.1. Aerial Photographs

The aerial photograph dataset was obtained from French National Institute for Geographic and Forestry Information (IGN) database, and it comprised 41 orthorectified images, taken between 1934 and 2004, with a spatial resolution ranging from 0.10 to 0.85 m. From this dataset, 31 photographs were selected, based on visual evaluation, for their quality and potential for exploitation. They were then georeferenced. A subsection of the study zone was then extracted, and polygons of the identifiable *Spartina* meadows were obtained, distinguishing between the two species based on the GNSS data and georeferenced ground photographs. The number of identified *Spartina* patches (polygons) is variable, depending on the year and quality of the photograph. In order to consider the error associated with the visual determination of the *Spartina* meadows' limits, three replicates of polygons were drawn for each patch. We then used the polygon surface of the three replicates to estimate the mean surface and standard deviation error of each patch.

The most recent aerial photograph was taken during a drone flight that was performed on 21 June 2016 over the study zone. We used a DJI Phantom 2 drone, equipped with a GoPro Hero 4 Black Edition, mounted on a DJI Zenmuse H3-3D gimbal to counterbalance unwanted camera rotations and absorb vibrations. The flight was performed at a very low altitude, 30 m, in order to obtain high-resolution images. Ground control points were taken over the study area and georeferenced using a GNSS system. The image dataset was aligned by a structure-from-motion algorithm through Agisoft Photoscan software, from which we obtained a 3D model that was optimized and georeferenced using the ground control points. Finally, a high-resolution (5 cm) orthophotography was extracted from the 3D-model. This high-resolution orthophotography was used both as a reference image and ground truth for the validation of feature identification in the satellite images.

1.3.2. GNSS Data

A field campaign was carried out on 26 October 2016 to determine the extent of the difference between plant species present in the study site using a differential Global Navigation Satellite Systems (DGNSS) technique. Two GNSS stations, composed of Leica GR25 receivers and AR10 antennae, were installed, one on the shore, as a base station, and a second one, mobile, carried in a backpack. The maximum distance between the two stations never exceeded 300 m during the field campaign. The GNSS station operated at multi-frequencies (L1, L2, L5) on multi-constellation signals. They were acquiring GNSS (GPS and GLONASS) data at a sampling rate of 1 Hz.

The RTK open-source program package (version 2.4.2) (Takasu 2009, Takasu and Yasuda 2009) was used to process the GNSS raw data. This freeware is available at:

http://www.rtklib.com/. The satellite coordinate product provided the GNSS orbit and clock offset data used in this study, which were made available by the International GNSS Service (IGS) at ftp://cddis.gsfc.nasa.gov/gps/products/. We also used the Antenna Exchange Format (ANTEX) file (igs08_wwww.atx), made available by the International GNSS Service (IGS—https://igscb.jpl.nasa.gov/igscb/station/general/igs08.atx), which provides a precise and consistent set of phase center offset (PCO) and variation (PCV) values for both satellites and receivers' antennae, taking into account these corrections. As the two stations were continuously acquiring data at both the L1 and L2 frequency bands, GNSS data were processed in ionosphere-free mode, with tropospheric corrections from the Saastamoinen model, and solid Earth and pole tides, followed by ocean tide loading, were applied (Frappart et al. 2016).

1.3.3. Radiometric Measurements

On July 21 2016, a field campaign was conducted in the study area to collect radiometric measurements, associated with the different types of substrate. Hyperspectral measurements were performed in the 400–900 nm spectral range (every 3 nanometres) from two radiometrically-calibrated TriOS-RAMSES sensors. The radiance sensor pointed downward to measure the upward signal of the substrate ($L_u(\lambda)$, $W.m^{-2}.sr^{-1}.nm^{-1}$), while the irradiance sensor pointed upward to measure the downward irradiance ($E_d(\lambda)$, $W.m^{-2}.nm^{-1}$). Radiance and irradiance measurements were performed simultaneously, as recommended in Reference (Duggin and Philipson 1982). The remote sensing reflectance ($R_{rs}(\lambda)$, sr^{-1}) was then calculated as the ratio of $L_u(\lambda)$ to $E_d(\lambda)$. Note that, for brevity, we do not include the reference to the spectral dependency in the following text. Several features were chosen according to the different aspects of the vegetation of interest found within the study zone. For each feature, a run of 10 radiometric measurements was performed for three different targets in order to compute the average spectrum of R_{rs}.

Finally, in order to compare the field data with the Pléiades data, the in situ R_{rs} spectra were spectrally transformed using the spectral response function (SRF) of the Pléiades-1A and -1B bands in order to make them compatible with the spectral characteristics of the sensors. The SRF-corrected R_{rs} spectra (R_{rs_SRF}) were computed as follows:

$$R_{rs\_SRF}(\lambda_0) = \frac{\int R_{rs}(\lambda) SRF(\lambda) d\lambda}{\int SRF(\lambda) d\lambda} \quad (1)$$

where λ_0 represents the central wavelength of the different MS bands of Pléiades.

1.3.4. High Resolution Pléiades Images

Standard orthorectified Pléiades images, acquired on five dates (25 April 2013, 3 August 2016, 6 October 2016, 24 Mai 2017 and 7 October 2017—Table 1.1), were used to determine the vegetation type in the study area. The Pléiades satellite constellation (Pléiades-1A was launched on 17/12/2011 and Pléiades-1B on 02/12/2012) acquired PAN (wavelength in the 470–830 nm range) images, with a ground sampling distance of 0.7 m in the nadir direction, which were resampled at 0.5 m and in four MS bands—blue (B: 430–550 nm), green (G: 500–620 nm), red (R: 590–710 nm), and Near-Infrared (NIR: 790–940 nm)—at a spatial resolution of 2 m and over a swath width of 20 km at nadir.

Table 1.1. Pléiades satellite data set information.

Satellite	Acquisition Date	Season	Acquisition Time (UTC)	Time of Low Tide (UTC)
Pléiades-1A	25/04/2013	Spring	11h15	12h04
Pléiades-1A	03/08/2016	Summer	11h15	12h45
Pléiades-1A	06/10/2016	Autumn	11h23	14h59
Pléiades-1B	24/05/2017	Spring	11h04	11h06
Pléiades-1A	07/10/2017	Autumn	11h08	13h27

1.3.5. Pre-processing of the Pléiades Images

All images were not provided in the same coordinate system. Therefore, all images were first re-projected in the Universal Transverse Mercator (UTM), Zone 30 North—World Geodetic System 1984 (WGS84). Radiometric calibration and atmospheric correction were then applied to each image in order to convert the Level 1 (L-1) images, provided in digital counts (DC), to images in the surface reflectance values. Then, the surface reflectance was divided by π to obtain R_{rs}. Atmospheric corrections were performed using the optical calibration module from OTB – Monteverdi software (Inglada and Christophe 2009), converting all images to the top of the canopy reflectance. Both sun and viewing angles (elevation and azimuth), as well as the calibration coefficients (gain/biases and solar illuminations), were obtained from the images' metadata files. The applied aerosol model was chosen, depending on the corresponding season of each image, following the methods in Reference (Bru et al. 2017). The atmospheric pressure, aerosol optical thickness and ozone and water content values were obtained from NASA's Aerosol Robotic Network (AERONET) for the Arcachon station at the corresponding acquisition time of the satellite image. The atmospheric corrections in the blue band (B) present the highest residual errors. For this reason, and because the B-band does not provide useful additional information in the identification of vegetation, this band was removed from all images.

For each image, we computed the Normalized Vegetation Index (NDVI, (Rouse et al. 1974)) as:

$$NDVI = \frac{R_{rs}(\lambda_{NIR}) - R_{rs}(\lambda_R)}{R_{rs}(\lambda_{NIR}) + R_{rs}(\lambda_R)} \quad (2)$$

Other indexes proposed in the literature for assessment of vegetation cover were tested, but they did not present significant differences relative to the NDVI. The NDVIs were also estimated for the field reflectance data, and the values obtained for each species were compared to the ones estimated from the satellite images. Based on the analysis of the NDVI maps, for each image, we performed a prior assessment of their capability of identifying the different types of habitats and species using classification methods.

1.3.6. Pixel-based Classification

To attempt to identify the two types of *Spartina* and differentiate them from each other, we tested pixel classification algorithms, using both unsupervised and supervised approaches.

Unsupervised methods provide the advantage of being more flexible (Hutchinson 1986), and this approach was considered with a view to extending the vegetation mapping to the entire Bay. Unsupervised approaches recognize patterns of spectral response using cluster analysis techniques. The resulting classification must be analyzed to regroup and label the classes using ground truth information. Even if there is a perspective of the long-term monitoring of salt marshes of the entire Bay, in this work, we will only focus on the results for the study zone.

Pixel-based unsupervised classification was performed using the Simulated Annealing Algorithm (Bertsimas and Tsitsiklis 1993), a probabilistic method to find the class centers,

which minimizes the cumulated distance from every pixel to their center of class in the spectral space. This is a non-linear algorithm that, with the appropriate parameters, provides a converged solution to the global optimized minimum. To improve the search for the best solution, a start temperature (a control parameter that determines the range of the initial search for the solution) is given, and its decrease, with the number of iterations, corresponds to a decrease in the probability of the acceptance of a worse solution than that previously found.

For the supervised classification approach, we considered different supervised classifiers, where preliminary tests showed that all techniques provided similar results. For this reason, we further proceeded with the Random Forests (RF) classifier (Breiman 2001), which is indicated in the literature as a suitable algorithm, when using a high number of variables and small training sets (Silvestri et al. 2003, Correll et al. 2018). When applying the RF classifier, the classification map is accompanied by an accuracy map, which contains the indicator of the confidence degree of the classification. More precisely, the RF classifier is composed of a set of different individual base classifiers (decision trees). Each tree makes a decision, and the final decision corresponds to the majority vote. The degree of confidence is obtained as the percentage of the individual classifiers that provide a decision equivalent to the final one.

Pixel classification was performed on the three-band MS images. Supervised classification was performed using MATLAB ® on a standard personal computer, an Intel ® Core ™ i5-4690 processor at 3.50 GHz, with 8 Go memory. For images with dimensions of 281 × 300 at a 2 m resolution, the algorithm's computation time was under 5 minutes. As for the unsupervised classification, the simulated annealing algorithm was written in Fortran. It ran on a bi-socket server using AMD Opteron processors at 2.30 GHz, and it was parallelized on 24 cores using the OpenMP library. The longest computation was approximately 10 minutes.

All image processing steps are summarized in Figure 1.3.

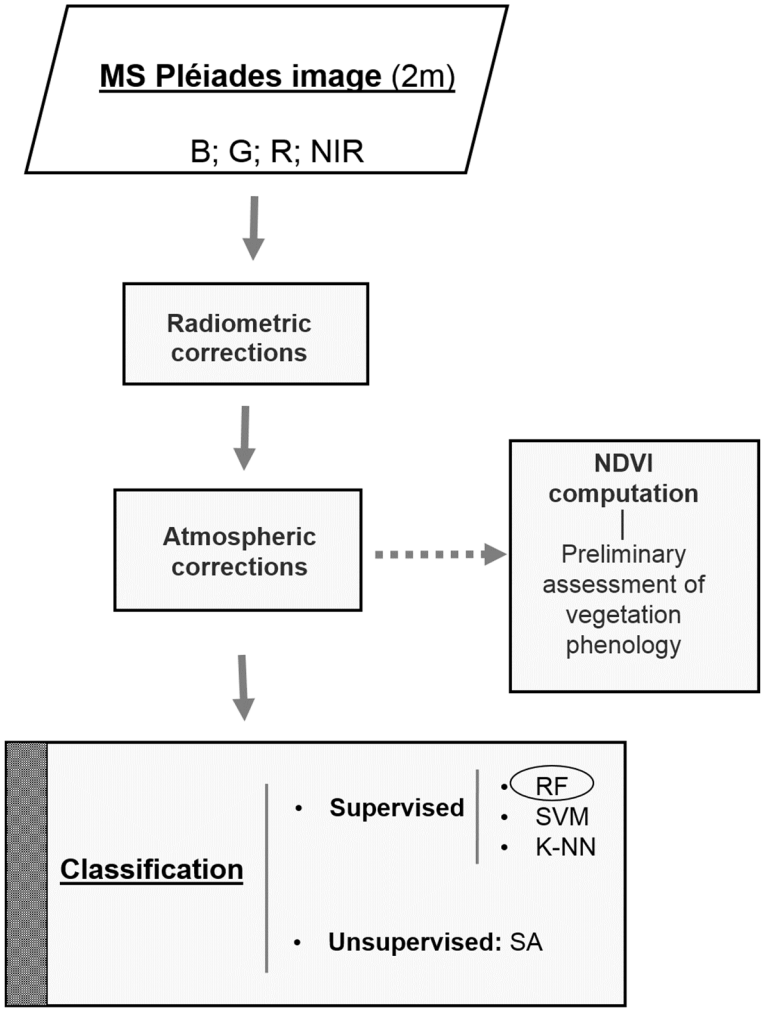

Figure 1.3. *Flow chart of the image processing steps.*

1.4. Results and Discussion

1.4.1. Spectral Signature of Vegetated Structures

Figure 1.4 shows the mean R_{rs} spectra of different characteristic substrate types, collected at the study site on July 21, 2016. The spectral signature of the two *Spartina* species is very clearly distinguishable from other benthic habitat types. This difference is particularly obvious for dense and green *Spartina* meadows, without biofilm or sediment. Their R_{rs} spectra display a narrow peak center at around 550 nm and a sharp increase in the signal between the red and NIR bands, which is associated with high R_{rs} values over 780 nm. Further, *Spartina anglica* and *Spartina maritima* are also spectrally distinguishable. In green wavelengths, *Spartina anglica* shows a more pronounced peak than *Spartina maritima*, while in the red and NIR bands, *Spartina anglica* shows higher R_{rs} values than *Spartina maritima*. For instance, the R_{rs} value is 0.013 sr^{-1} and 0.004 sr^{-1} at 650 nm, and 0.071 sr^{-1}, and 0.042 sr^{-1} at 840 nm, respectively (Table 1.2). The NDVI, obtained from in situ Rrs, also indicates a significant difference between *Spartina anglica* and *Spartina maritima*, with a value of 0.69 ± 0.02 and 0.83 ± 0.03, respectively.

Table 1.2. Mean (standard deviation) values of field hyperspectral, field SRF-corrected Pléiades, and Pléiades remote sensing reflectance (sr^{-1}) in the Green, Red, and NIR bands, and in the NDVI pseudo-band for the same dense and green *Spartina anglica* and *Spartina maritima* patches (see Figure 1.6). Field data were acquired on 21 July 2016, and the Pléiades image was acquired on 3 August 2016.

Spectral Band (nm)		Field R_{rs} (sr^{-1})		Field R_{rs_SRF} (sr^{-1})		Pléiades R_{rs} (sr^{-1})	
		S. maritima.	*S. anglica*	*S. maritima*	*S. anglica*	*S. maritima.*	*S. anglica*
Green	**560** **500–620**	0.007 ± 0.002 -	0.019 ± 0.003 -	- 0.006 ± 0.004	- 0.017 ± 0.004	- 0.015 ± 0.001	- 0.018 ± 0.001
Red	**650** **590–710**	0.004 ± 0.002 -	0.013 ± 0.004 -	- 0.005 ± 0.006	- 0.014 ± 0.005	- 0.007 ± 0.001	- 0.009 ± 0.001
NIR	**840** **740–940**	0.042 ± 0.008 -	0.071 ± 0.007 -	- 0.039 ± 0.009	- 0.064 ± 0.010	- 0.029 ± 0.003	- 0.034 ± 0.003
NDVI	$\frac{NIR - Red}{NIR + Red}$	0.83 ± 0.03	0.69 ± 0.02	0.77 ± 0.05	0.64 ± 0.04	0.60 ± 0.074	0.57 ± 0.061

However, field measurements show a high variability of the spectral signatures of both *Spartina* species, depending on phenology, vegetation cover, biofilm and sediment deposition. For instance, the algae deposition on *Spartina maritima* causes a significant decrease in NDVI (0.54 instead of 0.83) due to an increased signal in the red and a decreased signal in the NIR. On the other hand, the sediment deposition on *Spartina anglica* shows a negligible impact on the radiometric signal in the red, but a strong impact in the NIR, which is responsible for a moderate decrease in NDVI (from 0.69 to 0.61).

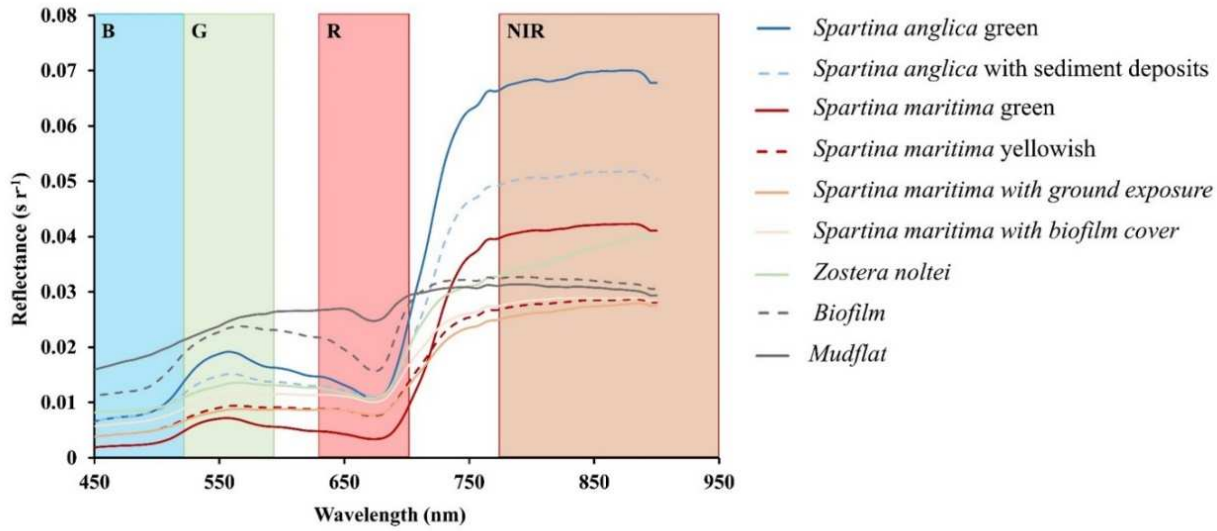

Figure 1.4. *Mean field remote sensing reflectance (sr^{-1}) spectra of different characteristic substrate types, collected in the study site on July 21, 2016. Colored spectral bands are associated with the blue (B), green (G), red (R), and near-infrared (NIR) channels of the Pléiades-1 satellite images.*

Figure 1.5 provides the R_{rs} values in the green, red and NIR channels for the MS Pléiades images, acquired on 3 August 2016. The images zoom in on the *Spartina anglica* and *maritima* meadows, sampled during the field campaign conducted on 21 July 2016. MS images exhibit a high intra-patch variability of their spectral signatures, as previously observed using field observations. This variability is directly related to the spatial heterogeneity of the ground cover percentage in the meadows of *Spartina species*. In order to compare field and satellite remote sensing reflectances, we computed the field SRF-corrected R_{rs} from Eq.1 (Table 1.2). A general smoothing effect on R_{rs_SRF} due to the wide Pléiades spectral bands can be noted. However, small differences were recorded between R_{rs_SRF} and R_{rs}. The lowest and highest relative differences were found in the red band for *Spartina anglica* (7%) and *Spartina maritima* (22%), respectively.

A comparison of the satellite and field SRF-corrected R_{rs} shows that they exhibit a similar general spectral behavior, but with significant differences in the magnitude and spectral shape. For instance, the NDVI values associated with *Spartina maritima* were 0.77 and 0.60 for R_{rs_SRF} and Pleiades R_{rs}, respectively. Further, it is worth noting that the difference between the *Spartina maritima* and *Spartina anglica* NDVI values is significantly lower in the satellite data (0.03) than in the field data (0.13). This reduced capability of discriminating *Spartina maritima* from *Spartina anglica* using satellite observations may be related to the scaling factor (Silvestri et al. 2002). Due to the small scale of the *Spartina* meadow and high spatial heterogeneity of the vegetation cover, the lower the spatial resolution, the lower the radiative contribution of *Spartina* to the per-pixel R_{rs} and the higher the contribution of the soil background signal.

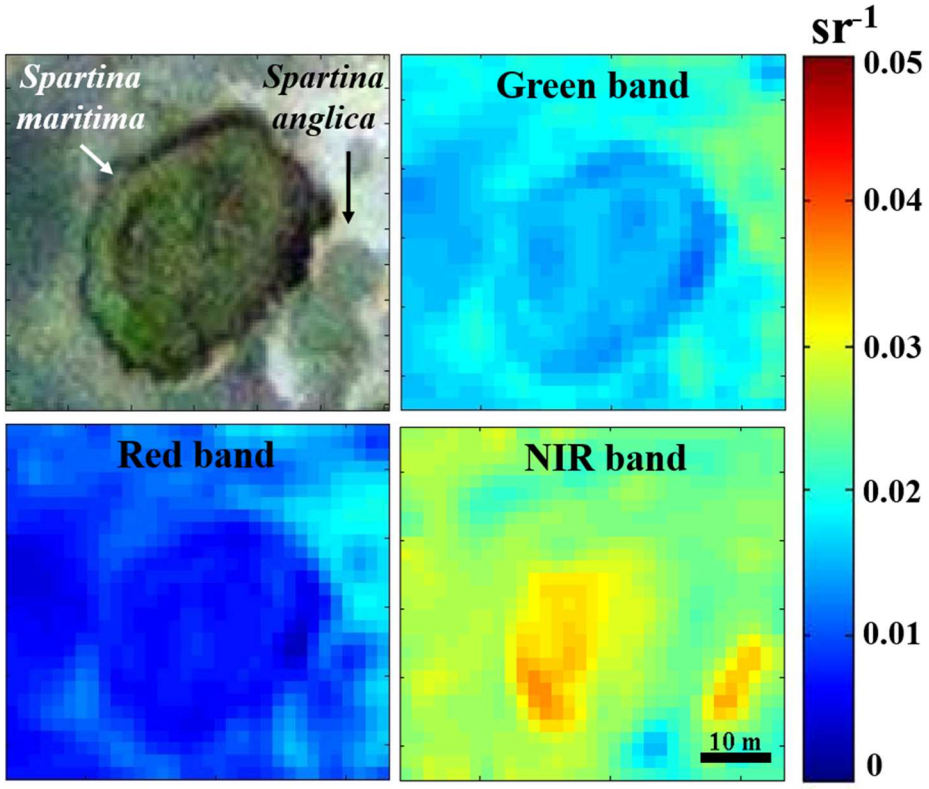

Figure 1.5. *Remote sensing reflectance (sr^{-1}) values in the green (500–620 nm), red (590–710 nm) and NIR (740–940 nm) bands for the multi-spectral Pléiades images, acquired on 3 August 2016. The images zoom in on the well-identified Spartina anglica and maritima meadows (see red and blue boxes on the image of 2016, Figure 1.4).*

Maps of the NDVI were generated for the five different dates of the Pléiades images (Figure 1.6). This index highlights strong seasonal changes, which appear to be primarily related to species phenology and the ephemeral presence of itinerant biological structures (e.g., the presence of biofilm and algae). The global high marsh zone can be clearly identified from the other types of habitat, particularly during spring (April and May), when the NDVIs of *Spartina* sp. vegetation show particularly higher values than sand and sediment. The results also highlight both seasonal and inter-annual variations of the NDVI signal for the *Spartina* vegetation. The NDVI does not, by itself, seem to be sufficient to differentiate the two *Spartina* species, as they present values of the same order of magnitude (Table 1.2). However, due to a small phase shift in their respective seasonal development, which generates considerable differences in aerial biomass density and color (Figure 1.2b–j), autumn appears as the best period to discriminate the two species, where average NDVI values for *Spartina anglica* and *Spartina maritima* are 0.8 and 0.9, respectively. Previous studies have already shown the advantages of a temporal assessment of marsh species identification using this index (Sun et al. 2017, Sun et al. 2018). For instance, Sun et al. (Sun et al. 2017), considering the monthly NDVI of multiple marsh species in the middle coast of Jiangsu, found important temporal windows that made the species distinguishable.

Further, relevant information regarding the general intertidal vegetation presence during the growing season can be withdrawn from this parameter. In particular, remarkable differences appear between both spring images (April 2013 and May 2017). The NDVI values for both intertidal and supratidal vegetation are above 0.8 for the first date and much lower for the second one, ranging from 0.3 to 0.6. This indicates that potentially significant meteorological differences might have occurred within the four years, affecting the vegetation development, namely, in terms of temperatures and sunlight availability. However, such analysis goes beyond the scope of the present study, and further correlations with meteorological data would need to be conducted. For the image corresponding to the beginning of August 2016, at the peak of summer, NDVI values are no longer at their maximum, which could possibly be related to a particularly hot summer, during which high temperatures were reached. A relative senescence of the vegetation during this period was observed during field verifications, which is probably the reason for the marsh vegetation NDVI values being under 0.8 during this period of the year. Finally, for both fall images (2016 and 2017), not only the marsh vegetation structure shows particularly high NDVI values, but there is also the presence of a large vegetated cover over the tidal flat. This is probably related to the fact that, by this time of the year (October), temperatures have not yet significantly decreased, and vegetation growth is still occurring, for the seagrass in particular (Auby and Labourg 1996). Indeed, it seems that this corresponds to an optimum period for *Zostera noltei* meadows to colonize the intertidal flat. Additionally, field inspections on this date allowed us to verify that this corresponds to a particularly favorable period for algae that considerably cover a large part of the tidal flat surface. Several deposits of such algae were also found to be hooked on to the stiff marsh vegetation, which might also affect its spectral signal (Figure 1.2d,h,i). It is then important to note that the presence of biological deposits can significantly affect the NDVI of the target marsh vegetation, and eventually, alter the typical values presented by the *Spartina* species.

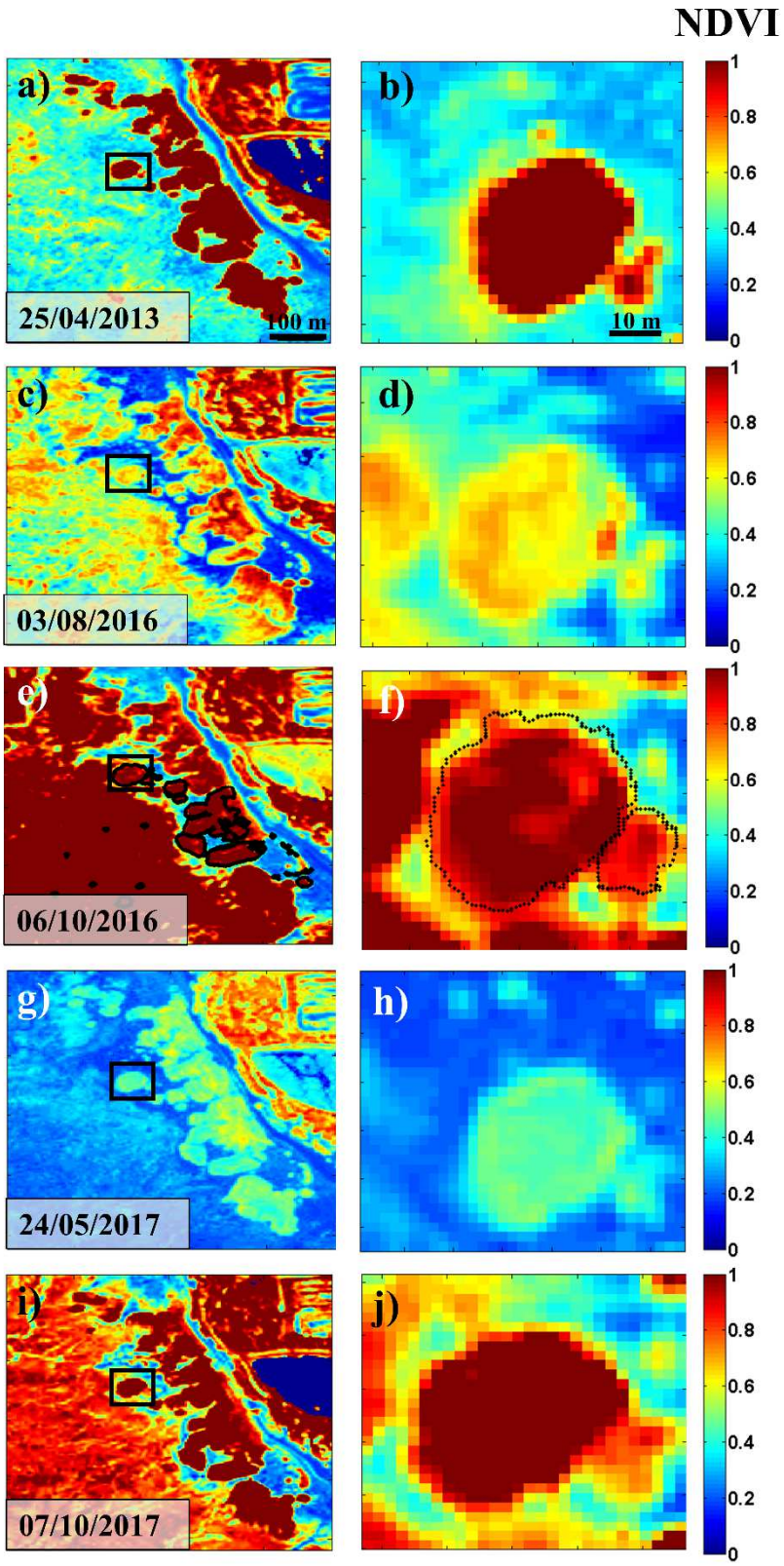

Figure 1.6. Comparison of the NDVI computed from the Pléiades images for the five considered dates, **a) – b)** 25 April 2013, **c) – d)** 3 August 2016, **e) – f)** 6 October 2016, **g) – h)** 24 May 2017, and **i) – j)** 7 October 2017. For each date, the image zooms in on the well-identified, small and invasive *Spartina anglica* and large native *maritima* meadows (right panel—see legend in Figure 1.5). Black contours on the image acquired on 6 October 2016 correspond to the field ground truth GNSS vegetation contours.

1.4.2. Long-Term Evolution of the High Marsh Zone and Ground Truth Data Validation

The long-term temporal evolution of the study area, as viewed through aerial photographs (Figure 1.7), shows that its marsh surface has been relatively stable, especially since the 1980s, the period from which the high marsh zone presents a configuration similar to what can be observed on the present date. Indeed, the most significant changes occurred between 1949 and 1979, the period of remarkable expansion of the high marsh vegetation, dominated by the European native, *Spartina maritima*.

The main marsh structure (identified by the red square in the 2016 image in Figure 1.7) presented a growth of 5700 m^2 (± 85 m^2) between 1949 and 2016. The expansion of this patch seems to have progressively increased over time. For instance, its surface was enlarged by 563 ± 124 m^2 between 1985 and 1993, which is more than twice its growth between 1949 and 1958 (236 ± 67 m^2). Between 2004 and 2016, the patch surface increased by 1613.4 (± 80 m^2).

Considering the exotic *Spartina anglica*, although its presence in the Bay of Arcachon dates from the 1980s, within our dataset, the most identifiable *S. anglica* patch in the study area (blue rectangle in 2016 image—Figure 1.7) has only been visible since 1993. This is the only patch that can be monitored, and it presented a growth of 100 ± 2 m^2 between 1993 and 2016.

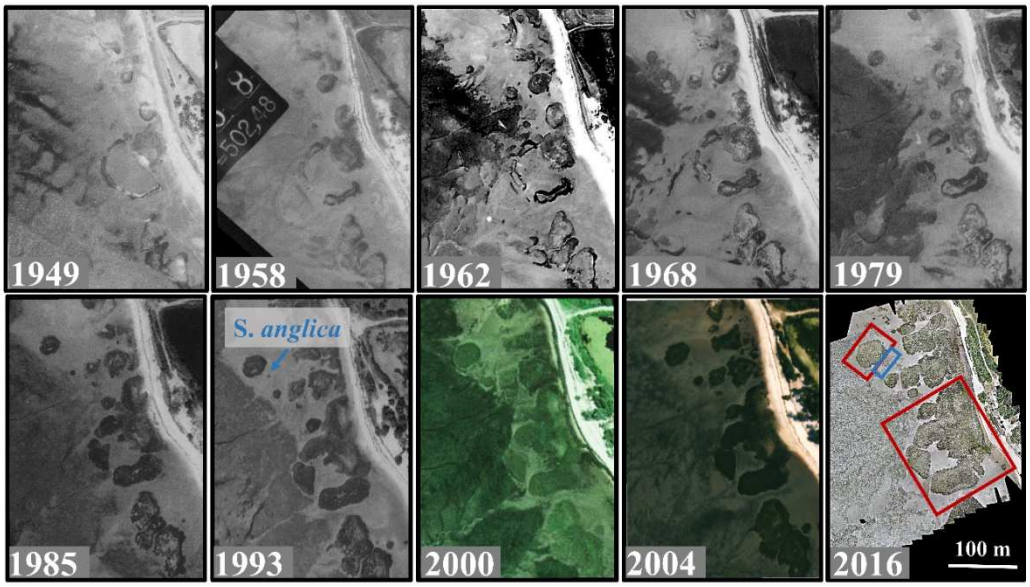

Figure 1.7. Salt marsh evolution at the study site of Andernos between 1949 and 2016. Dates up to 2004 correspond to airborne aerial photographs, and the image from 2016 was acquired by drone. Two zones of *Spartina maritima* dominance are indicated by red boxes, and *Spartina anglica* dominance patches are indicated by the blue box in the drone image. The bigger red box corresponds to the patch considered in the text as the main marsh structure. The appearance of the invasive *Spartina* is indicated in the 1993 image by the blue arrow.

Hence, in this area of the Bay of Arcachon, the most significant changes in marsh evolution are associated with vegetation patch growth (occasionally followed by the merging with neighbor patches). This patch growth and subsequent merging is most remarkable for the native *Spartina*. For the exotic *Spartina anglica*, we notice the appearance of new patches that seem

to mostly occupy empty niches within the higher marsh zone or over the tidal flat (Figure A1). Therefore, apart from growth, there are no major inter-annual (or even inter-seasonal) changes in patch vegetation dominance. Our ground truth data (drone flight, GNSS data, georeferenced photographs and a regular monitoring of this site from 2015 up to 2018 within the scope of the complementary studies) for patch species identification showed that this is a relatively stable site, and no major changes have recently occurred. This provides a correct validation for the images from 2016 (Figure 1.8). Comparing these field data with the oldest image from our dataset (2013), a good match is observed with the knowledge of species composition and patch positions from the most recent data. For this reason, we consider that our ground truth data are also valid for the image of April 2013.

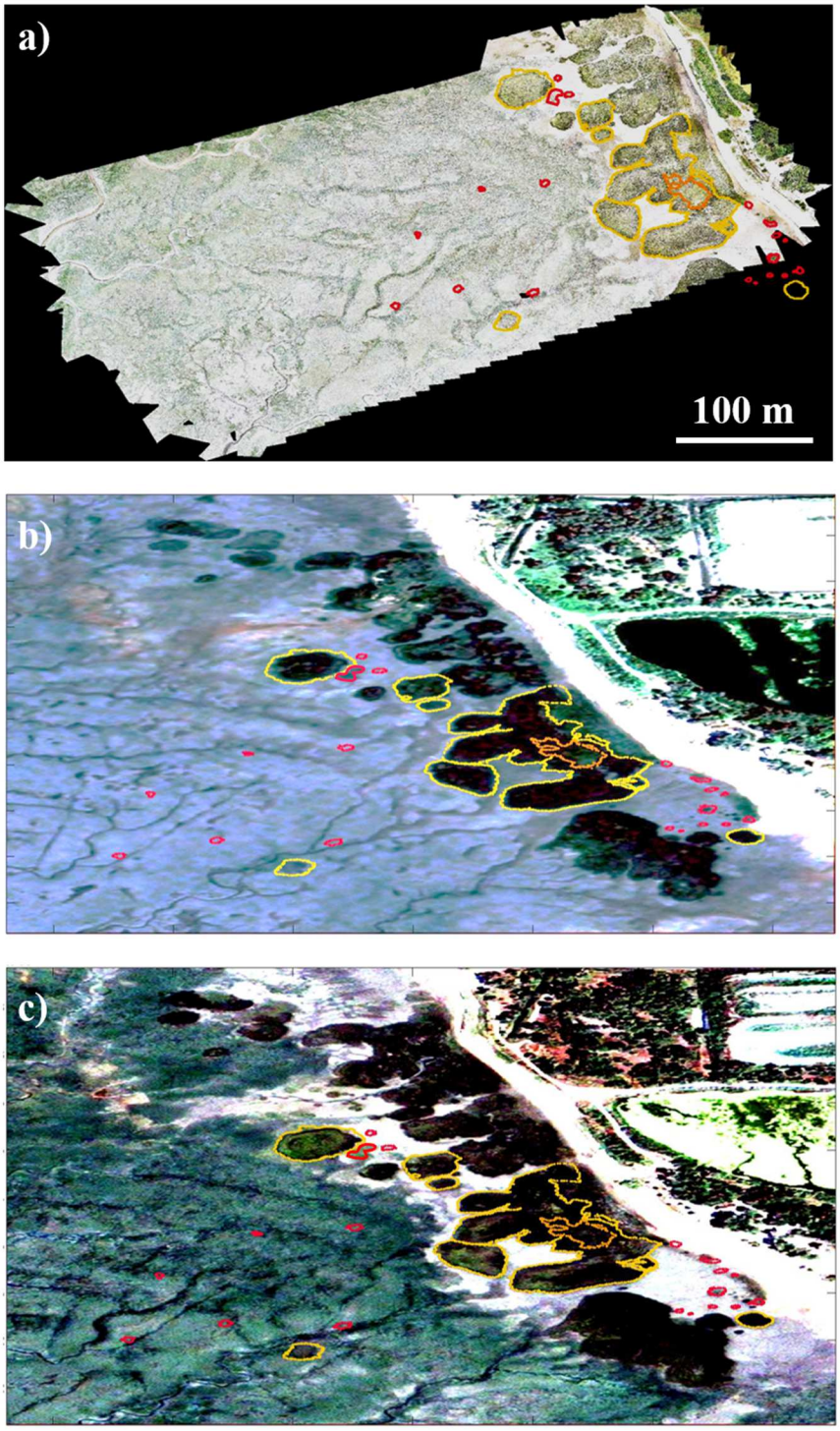

Figure 1.8. Overlay of field GNSS marsh vegetation contours (26 October 2016) over **a)** the drone image (21 June 2016); **b)** the Pléiades image from 25 April 2013; and **c)** the Pléiades image from 10 October 2016. Yellow contours correspond to patches dominated by the native *Spartina maritima,* red contours correspond to patches of the invasive *Spartina anglica*, and the orange contour delineates an intrusion zone of other types of vegetation. Image a is displayed in true color, while images b and c correspond to a RGB composite, with independent contrast enhancements to highlight the vegetated features of interest.

1.4.3. Pixel Classification Using Unsupervised and Supervised Methods

Several pixel classification algorithms were applied for each of the five dates of MS Pléiades images, with the aim of identifying the dominant marsh species in the Bay of Arcachon, *Spartina maritima* and *Spartina anglica*, and monitor the changes resulting from the invasion of the latter.

Concerning the supervised classification, as previously mentioned, after preliminary tests with several classifiers, we proceeded with Random Forests, both because it is a commonly used classifier, and it provided slightly better results than the other tested classifiers. For all classes, we considered the same number of training zones, maintaining, as much as possible, a balanced number of pixels per training zone, depending on the size of the feature representative of the class. For the image of April 2013, this balance was relatively difficult to achieve, as the presence of the invasive *Spartina* was particularly reduced in the study zone at this date. For the simulated annealing algorithm, since it is an unsupervised method, it is important to note that the algorithm class color attribution is done randomly, and class colors need to be re-assigned by the user in order to achieve an agreement between different season images and a match with the previously considered supervised classification results. Different tests were performed for each image, considering the influence of the algorithm's parameters, number of iterations, start temperature (a parameter associated with the initial range of search for pixel clustering), number of classes and transformation coefficient in order to estimate the position of the class center. Very similar results were obtained for the classifications, with differences under 5% for each class from one run to the other. Field surveys have shown that the meadow vegetation dominance did not change at the considered timescale. Therefore, the alteration of the spectral signatures and consecutive class attribution by the algorithm was mostly influenced by the seasonal appearance of transient biological features or the vegetation's phenology. It is then necessary to perform a post-classification analysis to provide the best color match between images of different seasons.

Both the unsupervised and supervised pixel classifications of the overall images allowed for an accurate identification of the global high marsh zone, including all species. However, single-feature identification (species differentiation) remained difficult, and the degree of accuracy was strongly dependent on the presence of noise induced by episodic events or short-term perturbations that can alter the species spectral signal (Figure 1.9; Table 1.3). Such difficulties in the isolation of spectral features due to the presence of water and a high humidity at low marsh levels were also found, in (Li et al. 2010), in the realization of supervised classifications of Landsat images. Given the variability of field reflectance for one matching feature (Figure 1.6), such a result was not completely unexpected, and this was shown by the significant differences between classifications for all dates. We observed that the larger the noise induced by seasonal perturbations, the larger the variability of the classification within the patches, particularly considering the results obtained using the unsupervised classification algorithm.

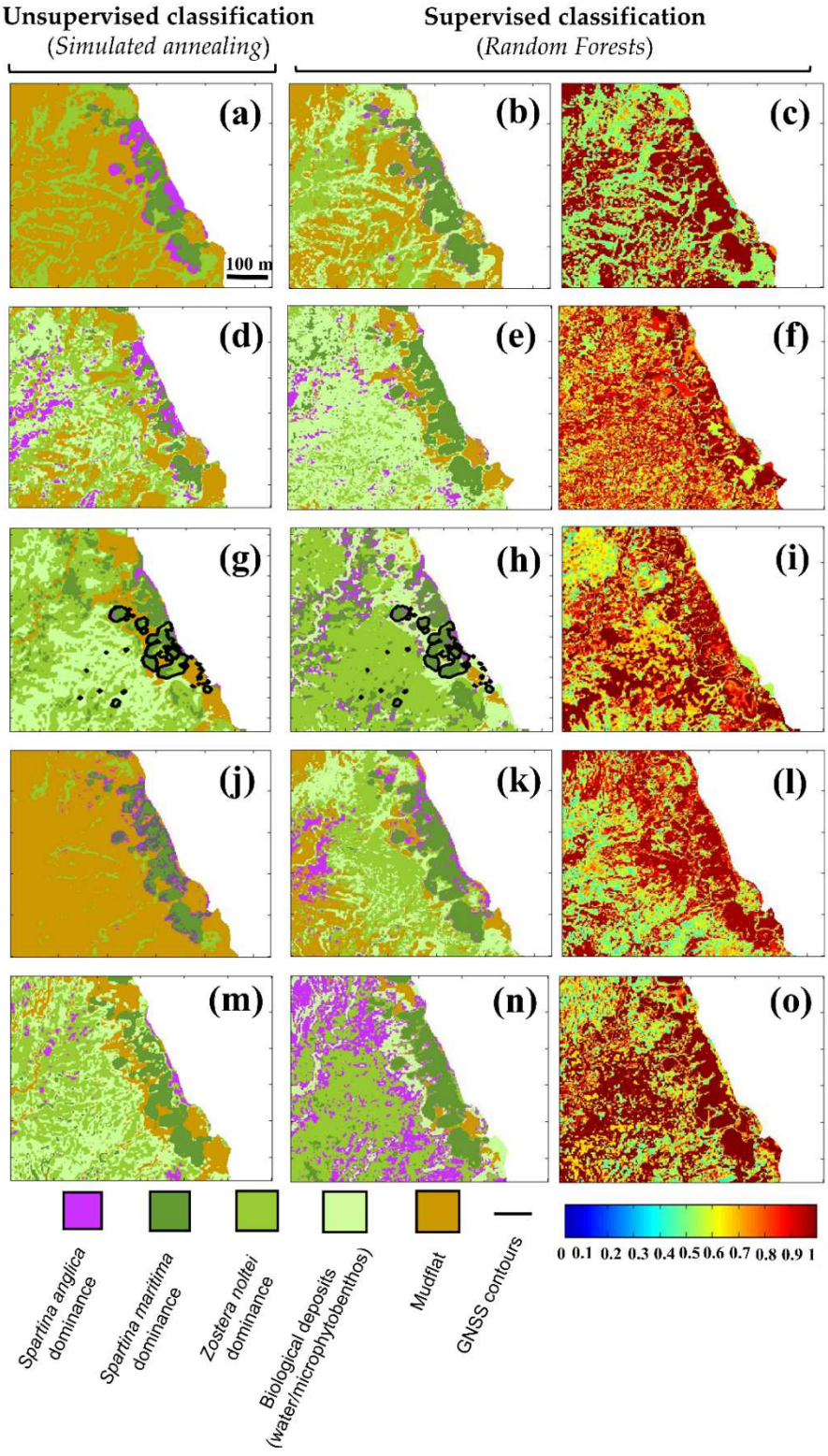

Figure 1.9. Pixel classification using the unsupervised method, Simulated annealing (left panel), with the supervised method, Random Forests (central panel), and classification accuracy maps for the supervised classification (right panel). **(a) – (c)** 25 April 2013, **(d) – (f)** 3 August 2016, **(g) – (i)** 6 October 2016, **(j) – (l)** 24 May 2017, and **(m) – (o)** 7 October 2017. Black contours on the image acquired on 6 October 2016 correspond to the field ground truth GNSS vegetation contours. Color bar indicates the confidence level of class attribution in the accuracy maps.

Table 1.3. Accuracy metrics from the supervised Random Forests classification on the five dates of 3-band (G, R and NIR) multi-spectral Pléiades images. Class assignment: C1- *Spartina anglica*, C2 – *Spartina maritima*, C3 – slikke vegetation dominated by *Zostera*, C4 – mudflat, and C5 – biological deposits (algae/microphytobenthos).

	April 2013					August 2016					October 2016					May 2017					October 2017				
Overall accuracy	0.87					0.66					0.79					0.85					0.56				
Kappa index	0.81					0.56					0.72					0.8					0.46				
Average accuracy	0.69					0.72					0.79					0.83					0.6				
Class accuracy	C1: 0.64 C2: 0.93 C3: 0.97 C4: 0.88 C5: 0.037					C1: 0.9 C2: 0.96 C3: 0 C4: 1 C5: 0.76					C1: 0.72 C2: 0.88 C3: 0.96 C4: 0.39 C5: 0.98					C1: 0.85 C2: 0.74 C3: 0.98 C4: 0.96 C5: 0.64					C1: 0.53 C2: 0.78 C3: 0.39 C4: 0.35 C5: 0.92				
Confusion matrix (in %)	64	0	36	0	0	90	0	0	3	7	72	8	0	0	20	85	2.5	10	2.5	0	53	0	47	0	0
	2	93	0	0	5	0	96	0.4	0	3.6	10.5	88.5	0	0	1	14	74	11	0	1	6	78	15	0	1
	1	0	97	0	2	0	26	0	0	74	0.2	3.8	96	0	0	0.4	0	98	0	1.6	60	0	39	0	1
	0	0	0	88	12	0	0	0	100	0	0	0	0	39	61	0.4	0	2.4	96	1.2	5	0	0	36	59
	0	0	18	78	4	0	22	2	0	76	1	0	0	1	98	0.5	7	28	0.5	64	0	0	0	8	92

Globally, the *Spartina maritima*-dominated patches were identified well with the supervised classifier but comprised a high variability in class assignment, depending on the density of the meadow and the presence of biological debris with the unsupervised one. Small, scattered patches of the invasive *Spartina anglica* extending over the tidal flat were difficult to identify because of both the variety of interference signals and the small dimensions of the meadows towards the interior of the bay. A comparison of the ground truth of the dominant vegetation, identified through the GNSS contours, acquired on October 2016, and the corresponding classified vegetated features in the Pléiades images provided the rate of correctly classified pixels for the two *Spartina* species, obtained with an unsupervised classifier. Overall, patches of *Spartina maritima* dominance were identified well with the supervised classifier, with a percentage of correctly identified pixels of 74% for the image of May 2017, which increased to 96% for that of August 2016. With the supervised classifier, the strong presence of ephemeral biological perturbation on some dates (August and October) did not significantly affect the accuracy of the identification of the native species, and it was always over 74%. Using the unsupervised classification method, the correct classification of the native *Spartina* species attained 93% and 80% for the images of April 2013 and October 2017, respectively. The identification of the invasive *Spartina anglica* proved to be much more difficult, using both the supervised and unsupervised classifiers. Considering the results obtained using the supervised classifier, the identification of the ground truth patches was fairly successful, with accuracies ranging from 53% to 90% for the images acquired in October 2017 and August 2016, respectively. However, this class was frequently mistaken for the extensive zones of the vegetated mudflat (*Zostera*), particularly within the image from October 2017, and we obtained an overestimation of the areas assigned to the invasive *Spartina*. Belluco et al. (Belluco et al. 2006) also found similar uncertainties in the identification of *Spartina species* that would be confused with the typical spectral signature of soil containing microphytobenthos, which contains significant quantities of chlorophyll. Indeed, the mudflat zone can either be vegetated

in different density degrees by seagrasses or present deposits of itinerant features, like algae and microphytobentos, of several sorts. The combined presence of all these features provides complex spectral signatures that can be difficult to characterize. Thus, in this case, the only assurance we have that they do not correspond to the same species is field knowledge. We are confident that such a strong extrapolation could be reduced by increasing the number of ground truth samples of this species. Additionally, the accuracy maps of the classifications obtained for all dates (Figure 1.9–right panel) shows that regions classified by a higher uncertainty degree (accuracy uncertainty under 60 %) correspond to channels and zones in the tidal flat, where the mixing of features is high (vegetated and un-vegetated mud, water with microphytobenthos, sediment with different degrees of humidity, etc.). Considering the accuracy metrics provided in Table 1.3, only images corresponding to Springtime (April 2013 and May 2017) provide a Kappa index of 0.8, reinforcing that the lower level of biological noise within these images positively affects the performance of the classifier.

With the unsupervised algorithm (Figure 1.9), on the other hand, the correct classification of meadows dominated by the *Spartina anglica* species was between 10% and 25%. Such a low performance in the identification of the invasive species is probably primarily due to the fact that we consider several patches of small dimensions (2–4 m diameter). Secondarily, pixels within meadows of this species were often mistaken for pixels classified as vegetated mudflat and water with microphytobenthos, which is most likely due to the fact that *Spartina anglica* vegetation cover tends to be reduced outside of the growing season. Thus, there is a high ground exposure within zones colonized by this type of vegetation, which significantly affects its radiometric signal. However, when considering only patches of larger dimensions (5–10 m diameter), the identification increases to 69.5% for the unsupervised classification of the image acquired on May 2017.

The comparison of field species reflectance is measured in the NIR and Green bands (Figure 1.6; Table 1.2), and the classification results reveal an overall satisfactory class distinction, especially concerning the distinction of the native *Spartina maritima* from the remaining vegetation. Since, in the considered area, the presence of *Spartina anglica* was mostly reduced to isolated patches towards the inner bay or to zones of mixed vegetation in the higher marsh, the identification of the invasive species was not evident, particularly in images with a higher noise level. Considering the image of April 2013, where the vegetation did not yet present a strong seasonal development, several individual *Spartina anglica* patches presented a spectral signal under 0.01 sr^{-1}, which is much lower than the radiometric measurements. Indeed, the phenology of this species is rather late, and at this time of the year, the plants were still withered, and the meadows presented a very low density. Other studies (Silvestri et al. 2003, Belluco et al. 2006) have also shown the interference of visible soil within vegetation in its reflectance, significantly lowering it. The classification of the native *Spartina*, on the contrary, provides center class values in the range of the radiometric field measurements, between 0.02 and 0.04 sr^{-1} (NIR band), mostly depending on the meadow density. The better accuracy of the classification for the native *Spartina* was not so unexpected, considering that this species presents a much earlier development than that of the invasive congener.

The pixel-based classification allowed for the estimation of a surface of the main *Spartina maritima* patch of 5685.5 m^2, whereas with the manual identification of the patch, a surface of 5378.17 (± 87) m^2 was obtained for the year of 2013. Considering the monitored patch of

Spartina anglica, followed in the long-term aerial photographs, we obtained a surface of 67.25 m^2, using the supervised classification, and 74.31 (± 1) m^2 using manual identification for the same date.

1.5. Conclusions

Technological evolutions of HSR multispectral satellite sensors greatly facilitates ecosystems' monitoring capability at an increasingly smaller scale. In order to make progress in the knowledge of biological invasion dynamics in salt marsh environments, we evaluated the potential of Pléiades images to assess salt marsh evolution, after a biological invasion, and discriminate the native species *Spartina maritima* from the invasive species *Spartina anglica* for the study site of the Arcachon Bay (South-west France). Different techniques for land use classification were investigated, and their performance was evaluated using a large set of ground truth data. As expected, the supervised methods exhibit, on average, better results than the unsupervised algorithms. Moreover, in this study, we demonstrated that classification accuracy is highly dependent on two main factors, which are the size of vegetation patches and the species phenology.

Pléiades images provided a robust and consistent identification of the global marsh zone. We showed that, in the Bay of Arcachon, the arrival of the exotic species was relatively controlled and did not lead to significant changes in the marsh composition, which remained dominated by the native *Spartina* species. On the other hand, distinguishing between species remains challenging, particularly when considering small features, such as the invasive species at an early stage of the invasion, which represents relevant information concerning invasion control issues. Our results showed that the current pixel classification methods applied to Pléiades images provide a poor performance, when the order of magnitude of the *Spartina* sp. meadow size is lower than 10 m. However, lags in plant phenology provide temporal windows, making species distinction possible. The results highlight that a high-performance classification requires good knowledge of the field conditions and the vegetation's development. The biggest challenge is revealed to be the dissociation of established vegetation from ephemeral biological features. In periods of low biological productivity, the level of biological noise can be significantly reduced, and hence the success in species differentiation increases. Thus, the seasonal interference of other biological features and stages of development of the target vegetation can alter its spectral signature or influence the exposure of the colonized environment (bare ground).

In the Bay of Arcachon, the two congener *Spartina* species present a phenology lag, where their spectral signature is considerably different between Autumn and early Spring. The strong presence of algae between late Spring and Autumn shortens this temporal window of remotely sensed assessment. We found that a suitable time frame for the remote sensing exploitation of the *Spartina* species distinction should be between late winter and early spring, when *Spartina anglica* is still withered enough to be differentiated from *Spartina maritima*, and algae blooms have not yet occurred.

The current pixel classification methods are highly sensitive to environmental noise. We highlight here that the consideration of particular temporal windows might be crucial for an improved assessment of the different types of marsh vegetation. Additionally, 2-meter spatial

resolution data still generate significant uncertainties in the identification of vegetation patches characterized by a decametric scale. In order to better perform the identification of the invasive species, it will be necessary to evaluate the pan-sharpened products of HSR sensors, provided by Pléiades or WorldView 3 and 4, as well as coupled approaches based on pixel classification and pattern-recognition techniques.

Appendix A – Quarterly monitoring of *Spartina anglica* and *Spartina maritima* biomass in the Bay of Arcachon between 2014 and 2015.

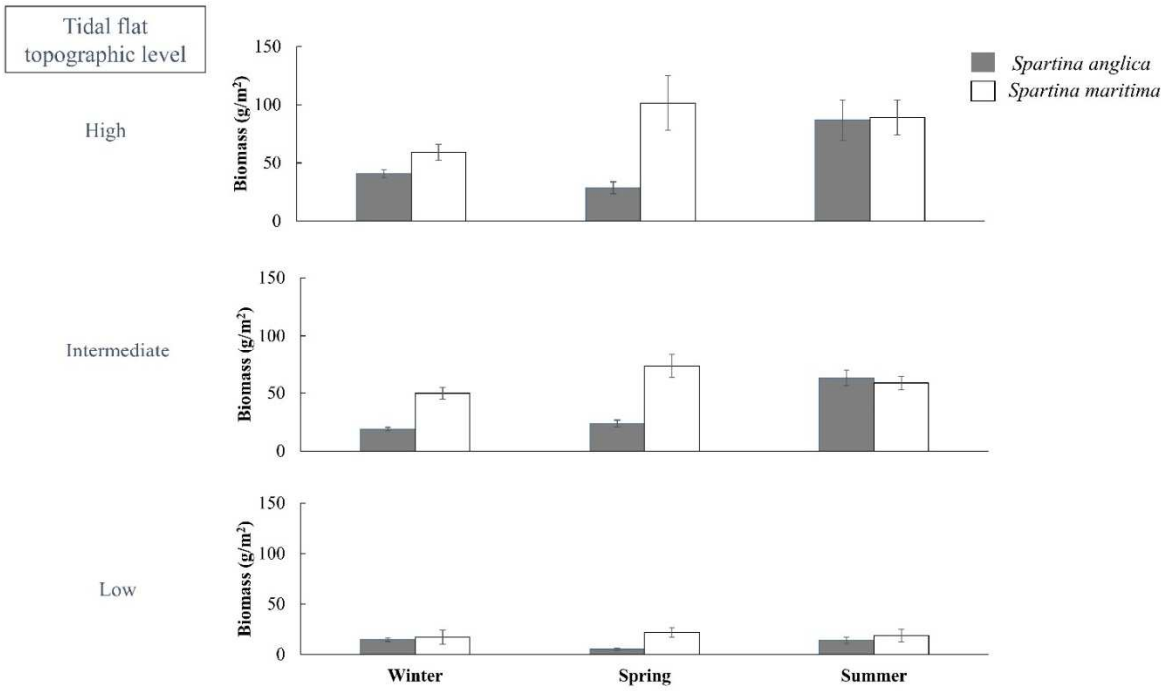

Figure A1. Seasonal biomass (winter, spring and summer) of *Spartina anglica* (dark bars) and *Spartina maritima* (white bars) at three tidal flat relative topographic levels.

References

Adam, E. et al. 2010. Multispectral and hyperspectral remote sensing for identification and mapping of wetland vegetation: a review. - Wetlands Ecol Manage 18: 281–296.

Akula, R. et al. 2012. An efficient PAN sharpening technique by merging two hybrid approaches. - Procedia Engineering 30: 535–541.

Allard, J. et al. 2009. A synthesis of morphological evolutions and Holocene stratigraphy of a wave-dominated estuary: The Arcachon lagoon, SW France. - Continental Shelf Research 29: 957–969.

Auby, I. and Labourg, P.-J. 1996. Seasonal dynamics of *Zostera noltii hornem*. In the Bay of Arcachon (France). - Journal of Sea Research 35: 269–277.

Barillé, L. et al. 2010. Increase in seagrass distribution at Bourgneuf Bay (France) detected by spatial remote sensing. - Aquatic Botany 92: 185–194.

Baumel, A. et al. 2001. Molecular investigations in populations of *Spartina anglica* C.E. Hubbard (Poaceae) invading coastal Brittany (France). - Molecular Ecology 10: 1689–1701.

Belluco, E. et al. 2006. Mapping salt-marsh vegetation by multispectral and hyperspectral remote sensing. - Remote Sensing of Environment 105: 54–67.

Bertsimas, D. and Tsitsiklis, J. 1993. Simulated Annealing. - Statist. Sci. 8: 10–15.

Breiman, L. 2001. Random Forests. - Machine Learning 45: 5–32.

Bru, D. et al. 2017. Atmospheric correction of multi-spectral littoral images using a PHOTONS/AERONET-based regional aerosol model. - Remote Sensing 9: 814.

Bustamante, J. et al. 2016. Hyperspectral sensors as a management tool to prevent the invasion of the exotic cordgrass *Spartina densiflora* in the Doñana Wetlands. - Remote Sensing 8: 1001.

Carter, G. A. et al. 2009. Remote Sensing and Mapping of Tamarisk along the Colorado River, USA: A Comparative Use of Summer-Acquired Hyperion, Thematic Mapper and QuickBird Data. - Remote Sensing 1: 318–329.

Castel, J. et al. 1996. Eutrophication gradients in coastal lagoons as exemplified by the Bassin d'Arcachon and the Etang du Prévost. - Hydrobiologia 329: ix–xxviii.

Cayocca, F. 2001. Long-term morphological modeling of a tidal inlet: the Arcachon Basin, France. - Coastal Engineering 42: 115–142.

Chapman, V. J. 1964. Coastal vegetation. - Pergamon Press; Macmillan.

Clint Slatton, K. et al. 2008. Modeling temporal variations in multipolarized radar scattering from intertidal coastal wetlands. - ISPRS Journal of Photogrammetry and Remote Sensing 63: 559–577.

Correll, M. D. et al. 2018. Fine-scale mapping of coastal plant communities in the Northeastern USA. - Wetlands: 1–12.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. - Oikos 97: 153–166.

Davis, M. A. 2003. Biotic globalization: does competition from introduced species threaten biodiversity? - BioScience 53: 481.

Duggin, M. J. and Philipson, W. R. 1982. Field measurement of reflectance: some major considerations. - Applied Optics 21: 2833–2840.

Early, R. et al. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. - Nat Commun 7: 12485.

Frappart, F. et al. 2016. High rate GNSS measurements for detecting non-hydrostatic surface wave. Application to tidal bore in the Garonne River. - European Journal of Remote Sensing 49: 917–932.

Garzelli, A. et al. 2004. Pan-sharpening of multispectral images: a critical review and comparison. - IGARSS 2004. 2004 IEEE International Geoscience and Remote Sensing Symposium 1: 84.

Hacker, S. D. et al. 2001. A marine plant (*Spartina anglica*) invades widely varying habitats: potential mechanisms of invasion and control. - Biological Invasions 3: 211–217.

Hill, V. J. et al. 2014. Evaluating light availability, seagrass biomass, and productivity using hyperspectral airborne remote sensing in Saint Joseph's Bay, Florida. - Estuaries and Coasts 37: 1467–1489.

Hutchinson, C. F. 1986. Land remote sensing technology and methodology. - Climatic Change 9: 149–166.

Inglada, J. and Christophe, E. 2009. The Orfeo Toolbox remote sensing image processing software. - 2009 IEEE International Geoscience and Remote Sensing Symposium 4: IV-733-IV–736.

Klemas, V. 2011. Remote sensing of wetlands: case studies comparing practical techniques. - Journal of Coastal Research: 418–427.

Labourg, P. J. et al. 1995. Evolution récente de la végétation intertidale du Delta de l'Eyre.

Li, J. et al. 2010. Invading cord grass vegetation changes analyzed from Landsat-TM imageries: a case study from the Wanggang area, Jiangsu coast, eastern China. - Acta Oceanol. Sin. 29: 26–37.

Marani, M. et al. 2004. Tidal landforms, patterns of halophytic vegetation and the fate of the lagoon of Venice. - Journal of Marine Systems 51: 191–210.

Mouw, C. B. et al. 2015. Aquatic color radiometry remote sensing of coastal and inland waters: Challenges and recommendations for future satellite missions. - Remote Sensing of Environment 160: 15–30.

Ouyang, Z.-T. et al. 2013. Spectral discrimination of the invasive plant *Spartina alterniflora* at multiple phenological stages in a saltmarsh wetland. - PLoS One in press.

Pennings, S. C. and Callaway, R. M. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. - Ecology 73: 681–690.

Pierce, S. M. 1983. Estimation of the non-seasonal production of *Spartina maritima* (Curtis) Fernald in a South African Estuary. - Estuarine, Coastal and Shelf Science 16: 241–254.

Plus, M. et al. 2009. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. - Continental Shelf Research 29: 1008–1013.

Proença, B. et al. 2019. Intraspecific facilitation explains the spread of the invasive engineer *Spartina anglica* in Atlantic salt marshes. - Journal of Vegetation Science in press.

Rouse, J. W. Jr. et al. 1974. Monitoring vegetation systems in the Great Plains with ERTS. 309–317.

Schlaepfer, M. A. et al. 2011. The potential conservation value of non-native species. - Conserv. Biol. 25: 428–437.

Seabloom, E. W. et al. 2013. Invasive grasses, climate change, and exposure to storm-wave overtopping in coastal dune ecosystems. - Glob Change Biol 19: 824–832.

Silvestri, S. et al. 2002. Salt marsh vegetation radiometry: Data analysis and scaling. - Remote Sensing of Environment 80: 473–482.

Silvestri, S. et al. 2003. Hyperspectral remote sensing of salt marsh vegetation, morphology and soil topography. - Physics and Chemistry of the Earth, Parts A/B/C 28: 15–25.

Simberloff, D. et al. 2013. Impacts of biological invasions: what's what and the way forward. - Trends in Ecology & Evolution 28: 58–66.

Soriano-Sierra, E. J. 1992. Etude Ecologique des Marais Sales du Bassin d'Arcachon: Structure et Evolution de Schorres, Production et Dégradation de leur Végétation et Echanges de Matières Particulaires entre les Schorres et le Bassin. in press.

Strayer, D. L. et al. 2006. Understanding the long-term effects of species invasions. - Trends in Ecology & Evolution 21: 645–651.

Sun, C. et al. 2016. Classification mapping and species identification of salt marshes based on a short-time interval NDVI time-series from HJ-1 optical imagery. - International Journal of Applied Earth Observation and Geoinformation 45: 27–41.

Sun, C. et al. 2017. Saltmarshes response to human activities on a prograding coast revealed by a dual-scale time-series strategy. - Estuaries and Coasts 40: 522–539.

Sun, C. et al. 2018. Classification mapping of salt marsh vegetation by flexible monthly NDVI time-series using Landsat imagery. - Estuarine Coastal and Shelf Science 213: 61–80.

Takasu, T. 2009. RTKLIB: Open source program package for RTK-GPS. - Proceedings of the FOSS4G

Takasu, T. and Yasuda, A. 2009. Development of the low-cost RTK-GPS receiver with an open source program package RTKLIB. - Proceedings of the International Symposium on GPS/GNSS: 4–6.

Thomson, A. G. et al. 2004. Short-term vegetation succession and erosion identified by airborne remote sensing of Westerschelde salt marshes, The Netherlands. - International Journal of Remote Sensing 25: 4151–4176.

Vitousek, P. M. et al. 1997. Human domination of earth's ecosystems. - Science 277: 494–499.

Zak, M. R. and Cabido, M. 2002. Spatial patterns of the Chaco vegetation of central Argentina: Integration of remote sensing and phytosociology. - Applied Vegetation Science 5: 213–226.

Zarnetske, P. L. et al. 2010. Non-target effects of invasive species management : beachgrass, birds, and bulldozers in coastal dunes. - Ecosphere 1: art13.

Zhang, R. S. et al. 2004. Formation of *Spartina alterniflora* salt marshes on the coast of Jiangsu Province, China. - Ecological Engineering 23: 95–105.

Zuo, P. et al. 2012. Distribution of *Spartina* spp. along China's coast. - Ecological Engineering 40: 160–166.

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Conclusions

The remotely sensed long-term assessment of the evolution of the marsh zone in tidal flats of Andernos showed that this is a relatively stable area where the proliferation of the invasive *Spartina anglica* has not displaced the native *Spartina maritima*, which establishment initiated in the 1940s.

Airborne and spaceborne image datasets and field reflectance data highlight:

- The long-term analysis of aerial images (from 1949 to 2016) showed that the high marsh zone of Andernos began to build in the 1940s where the delineation of the *Spartina maritima* meadows that we currently observe dates from 1949. The high marsh zone underwent a strong expansion until the 1980s and no significant changes in the native vegetation meadows occurred after the invasion of *Spartina anglica* up to the present date.
- The spectral signature of the two *Spartina* species at their peak of development and when forming monospecific stands showed that they are distinguishable in particular in the ranges of the Green and Near Infra-Red of the electromagnetic spectrum;
- Supervised pixel classification methods on the Pléiades satellite images was more successful than the unsupervised algorithm Simulated Annealing but the identification of *Spartina anglica* patches at an early stage of development remained difficult despite the fine spatial resolution of the used satellite product. This assessment was particularly affected by the seasonal presence of the transient biological features (algae blooms) and the development of *Zostera noltei* meadows on the tidal flat.

To summarise, the remotely sensed assessment of the monitoring of Andernos salt marshes showed that this area remained relatively stable since the 1980s up to current days, even after the arrival of the invasive *Spartina*. The European native *Spartina maritima* established in the study site in the 1940s and showed a considerable expansion until the 1980s. The arrival of the invasive *Spartina anglica* at this site was reasonably controlled and its presence remained relatively limited. This suggests that the invasive *Spartina* occupied empty niches and does not outcompete the native one which is consistent with the experimental results presented in the following chapters.

The use of a fine spatial resolution satellite product showed limitations in the distinction of small features in the intertidal area, like the recently established *Spartina anglica* patches. This was mostly related to the physical perturbations, characteristic of this environment and especially pronounced during particular times of the year, where the presence of transient biological features strongly interfered with the target features. Further studies exploring coupled methodologies of spectral and textural image analysis on the same type of satellite images could improve the detection of shape specific vegetated features such as *Spartina anglica* patches. Yet, the large scale identification of the total marsh area was successful and applicable to other areas of the Bay.

Contemporary to this study, an assessment of marsh composition and dynamics has been implemented by (Lafon et al. 2017). Their works have shown, for the sector of Andernos, an increase in the schorre surface of 105% between 1950 and 2016, from which 29% occurred

between 2007 and 2016, which is in accordance with the estimations here presented. Additionally, they identified this zone as one of the most extensively colonized by the exotic *Spartina*.
However, the results of the classification of species obtained by these authors with that presented in this chapter show significant differences. Such discrepancy reinforces the need for further attention in the development of vegetation species identification methodologies as well as in the analyses of the results.

Even though, in this work, targeting the invasive *Spartina* was difficult with this spectral based methodology, the results of a field removal experiment, presented in the following section, corroborate and consolidate the analysis of the marsh evolution through the historical aerial images and the hypothesis that *S. maritima* offers biotic resistance to the invasion of *S. anglica.*

CHAPTER 2

Biotic interactions between Spartina anglica and Spartina maritima

When an exotic species is introduced into a new location, in order to succeed, it will necessarily need to cope with both the biotic and abiotic characteristics of the recipient habitat. The intensity of the biotic resistance the local species will offer, according to their life-traits, will play a fundamental role in the new species establishment. Understanding the nature of the interactions between the natives and the exotics, as well as the characteristics of their preferential environmental conditions can be crucial for predicting the evolution of the invasion through time. This knowledge is essential for managing the control of the invasive.

In the previous chapter, through the analysis of historical photographs, we have shown that the arrival of *Spartina anglica* in the Bay of Arcachon was limited in time and space in an area where the native *Spartina maritima* forms well developed, stable meadows in the high marsh zone. Because of this limited expansion and the capacity of the exotic to colonize areas further inside the lagoon, it was suggested by local managers that *Spartina anglica* presented higher tolerance to anoxia niches along a gradient of inundation.

In this chapter, I present complementary and additional work on the comprehension of the exotic *Spartina anglica* spatial occupation along tidal flats in the Bay of Arcachon. The main points addressed in this chapter are the assessment (1) the nature of the interactions between the two *Spartina* species in the Bay of Arcachon, (2) the preferential environmental conditions of the habitat colonized by *Spartina anglica* and (3) the realized niche[1] of the exotic species. In order to address these points, a reciprocal cross transplantation experiment was implemented in the salt marshes of the Bay of Arcachon, at three intertidal levels, both cordgrass species are naturally found.

The results of this work were published in the "**Journal of Vegetation Science**": Proença B, Nez T, Poli A, Ciutat A, Devaux L, de Montaudouin X, Sottolichio A and Michalet R (2019). Intraspecific facilitation explains the spread of the invasive engineer *Spartina anglica* in Atlantic salt marshes. *Journal of Vegetation Science*. doi: 10.1111/jvs.12720. The publication is presented in the next section, followed by a summary of the main findings of this work.

[1] Where a species actualy lives within the *Fundamental niche* that represents all the environmental conditions where a species is able to live.

Publication: Intraspecific facilitation explains the spread of the strong invasive engineer *Spartina anglica* in Atlantic salt marshes.

Research article

Intraspecific facilitation explains the spread of the invasive engineer *Spartina anglica* in Atlantic salt marshes

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Abstract

Questions: Invasiveness depends in part on the ability of exotic species to either exclude native dominants or to fill an empty niche. Comparisons of niches and effects of closely related native and invasive species enable the investigation of this topic. Does *Spartina anglica* invade European salt marshes through competitive exclusion of the native *Spartina maritima* or due to the occurrence of an empty ecological niche in highly anoxic conditions? **Study Site:** The Arcachon Bay (France).

Methods: At three intertidal levels, we quantified competitive response and effect abilities of the two species through a cross-transplantation removal experiment. We also compared the biomass, root/shoot ratio, productivity and environmental conditions (elevation, salinity, redox potential and soil moisture) of salt marsh communities dominated by the exotic *Spartina anglica* or the native *Spartina maritima* at three intertidal levels. **Results:** Both established species showed similar biotic resistance to the invasion of the other species, but the exotic showed important intraspecific facilitation for growth. Species had similar niches and total biomass along a gradient of anoxic conditions, but the exotic had a much higher root/shoot ratio and productivity than the native. Owing to its rhizome density, the exotic showed high ability to increase sediment oxygenation, likely to explain its important intraspecific facilitation.

Conclusions: Our results showed that the invasion success of *S. anglica* cannot be explained by the competitive exclusion of the native or by its ability to fill an empty niche along a gradient of anoxia. Its behaviour as a self-facilitator invasive engineer very likely explains its rapid spread in the Bay and biotic resistance to the colonization of other congeneric species when established in dense patches. Additionally, we suggest that physical disturbance in marsh communities dominated by the native *S. maritima* may disrupt its biotic resistance against the invasion of *S. anglica.*

Keywords: biological invasion, biotic interactions, competitive effect, removal experiment, *Spartina anglica*, *Spartina maritima*

2.1 Introduction

Biological invasions are important threats to diversity and ecosystem services worldwide (Vilà et al. 2011, Vitousek et al. 1997), but at the same time, they are an unprecedented opportunity to test theoretical models of functional strategies and community dynamics under environmental changes (Crooks 2002, Lodge 1993, Shea and Chesson 2002, Tylianakis et al. 2008). One important question in invasion ecology, also crucial in traditional community and functional ecology (Bertness and Callaway 1994, Grime 1974, Lortie et al. 2004, Michalet et al. 2015), is the relative importance of biotic interactions, in particular competition, when compared to other invasion drivers, such as dispersal abilities and environmental conditions (Carboni et al. 2016, Davis et al. 2000, Kennedy et al. 2002, Levine et al. 2003). Several studies have also highlighted the important role of facilitation for the invasion of communities in stressful environmental conditions (Altieri et al. 2010, Bruno et al. 2003, Bulleri et al. 2008, Bulleri et al. 2018, Saccone et al. 2010, Stachowicz and Byrnes 2006).

An assessment of the importance of interactions in plant invasions requires the study of both the resistance of the recipient community and the ability of the invader to outcompete the native species (Levine and D'Antonio 1999, Vilà and Weiner 2004). In a meta-analysis of biotic resistance to exotic plant invasions, Levine et al. (2004) concluded that although biotic resistance significantly reduces the establishment of individual invaders, there was little evidence that species interactions enable communities to resist invasion (but see Saccone et al., 2013). Based on 79 native–invasive plant comparisons, (Daehler 2003) found that the relative performances of invaders and co-occurring natives often depended on the growing conditions. He concluded that there were few "super invaders" but rather that increased resource availability and altered disturbance regimes associated with human activities often differentially increase the performance of invaders over that of natives. This conclusion is consistent with the fluctuating resource availability models of Davis et al. (2000) and experiments by Seabloom et al. (2015). Vilà and Weiner (2004) also reviewed published pairwise experiments between invading and native plant species and found conversely that the effect of invasive species on native species is usually stronger than vice versa. However, they argued that their comparisons might be biased and that a rigorous test of the generality of the hypothesis that invaders are better competitors than natives needs to compare the effects of closely related native and invasive species on each other, in order to control for phylogeny (Lambdon and Hulme 2006).

One excellent system to assess differences in performances between invasive and native congeners is the intertidal salt marsh communities dominated by cordgrass (*Spartina*) species, since both native and invasive *Spartina* species co-occur in several salt marshes worldwide. *Spartina* species are grasses colonizing intertidal mudflats and are known as important ecosystem engineers in several continents due to their ability to stabilize sediments and contribute to salt marsh formation (Bouma et al. 2005, Bruno 2000, Kirwan and Megonigal 2013, Vu et al. 2017) and also for their contrasting abilities to modify ecosystem conditions (Callaway and Josselyn 1992, Seliskar et al. 2002). The physiological characteristics of *Spartina* species allow them to dominate in frequently flooded tidal flats (Pennings et al. 2005), in particular those species that have root systems adapted to soil inundation and low oxygen

levels (Bertness 1991, Castillo et al. 2000). *Spartina* species have been planted in different continents to reclaim estuarine areas and prevent erosion. Several *Spartina* species, in particular *S. alterniflora* (native from the eastern USA) and its derivative, *S. anglica*, have spread beyond their planted area and are now considered as strong invasive species (Strong and Ayres 2013). There is substantial literature concerning *Spartina* invasions, in particular studies focusing on taxon evolution (Ayres et al. 1999, Baumel et al. 2001, Strong and Ayres 2013) and reproductive evolution (Callaway and Josselyn 1992, Crosby et al. 2015, Dethier and Hacker 2005). However, less attention has been given to plant–plant interactions and ecosystem mechanisms that can promote or prevent invasion (Castellanos et al. 1994, Castillo et al. 2000, Hacker et al. 2001, Pennings et al. 2005).

Several comparisons of performances of native vs. invasive *Spartina* species have been made worldwide (e.g. Callaway and Josselyn [1992] in the Bay of San Francisco, USA; Castillo et al. [2000] in the Gulf of Cadiz, Spain; An et al. [2007] in China). These studies showed that there were contrasting differences in growth rate and competitive ability among species and even within species, which might explain their differences in invasiveness and ecosystem engineering effects (Seliskar et al. 2002). For example, *S. anglica* has been shown to have lower growth performance and competitive ability than *S. alterniflora* in coastal China, where the two species were introduced, the former declining since the nineties after the introduction of the latter (Zhi et al. 2007). This result is supported by the observation made by Ayres et al. (2004) who showed that *S. anglica* has not spread in the San Francisco Bay since the seventies, conversely to other species invading the Bay and in particular *S. alterniflora*. However, the recruitment success of *S. anglica* and its effect on native communities has also been primarily explained by environmental and habitat conditions, such as salinity and soil texture (Dethier and Hacker 2005, Hacker and Dethier 2006). These contrasting conclusions highlight the high context dependency of invasion processes (Catford et al. 2009). Notably, during the invasion process, the relative contribution of biotic interactions, compared to tolerance to stress and disturbance, is dependent on both the spatial and temporal variation of the system's local environmental conditions (Wiens 1989).

We addressed these issues in the salt marshes of Arcachon Bay (on the Atlantic coast in the south of France) where invasive *S. anglica* arrived at the end of the 1970s (Le Nindre et al. 2000). Less than 40 years after its arrival, the exotic *Spartina* is now dominating the marshes in some parts of the Bay and is now as abundant as the native *S. maritima* within the whole lagoon. The native *Spartina* is mostly restricted to the near-shore areas, whereas the exotic one occurs both along the coast, in distinct patches located close to the native patches and in scattered, isolated patches further inside the lagoon. These observations suggest that the native species has lower tolerance to anoxic conditions associated with flooding than the invasive (Le Nindre et al. 2004). However, a preliminary survey of vegetation relevés and environmental conditions (Le Nindre et al. 2004) has shown that both species occupy the same elevation range with an optimum at intermediate intertidal level, which suggests that the offshore occurrence of the exotic *Spartina* might be explained by other mechanisms than tolerance to anoxic conditions. Distance to the coast is a complex factor that might also affect exposure to physical disturbances, namely wave energy and current velocity, that are likely to increase with increasing distance from the coast together with variation in local geomorphology (Bouma et

al. 2005). Furthermore, the ability of the exotic to competitively exclude the native in the future is unknown since mixed patches along the coast are very uncommon. Diffuse penetrations of the exotic in patches of the native have been observed but the converse is very rare (R. Michalet, personal observation). The rare mixing between alien and native *Spartina* species has also been reported by Ayres et al. (1999) in the case of *S. alterniflora* replacing *S. foliosa* in the Bay of San Francisco.

Our aim is to assess differences in competitive abilities and tolerance to anoxic conditions between both *Spartina* species in order to explain whether the exotic *Spartina* succeeded to invade by competitive exclusion of the native species or by empty niche colonization. Thus, we conducted a removal experiment to quantify differences in competitive ability (both competitive effect and response ability) among *Spartina* species and measured for the two species environmental variables and productivity along the entire intertidal gradient to quantify differences in tolerance to anoxic conditions.

2.2 Material and methods

2.2.1 Study site and species

Arcachon Bay is a mesotidal lagoon system (tidal range: 0.8–4.6 m), located along the Aquitaine Atlantic coast, in the southwest of France. This study has been carried out in the northern part of the Bay of Arcachon, within the natural reserve of the salt marshes of the municipalities of Arès and Lège (44°45 N, 1°10 W — Figure 2.1a).

Spartina anglica is a hybrid species originating from a cross between *S. alterniflora* (a native from the USA) and *S. maritima*. This crossing occurred in the UK, giving origin to a sterile hybrid that by polyploidy finally gave birth to *S. anglica* (Baumel et al. 2001, Raybould et al. 1991). Both species have contrasting morphologies and biomass allocations, namely *S. maritima* produces several dense and flexible shoots with long and narrow leaves but few roots, whereas *S. anglica* forms rare thick stems with large and stiff leaves but a very dense rhizome system (Figure 2.1d).

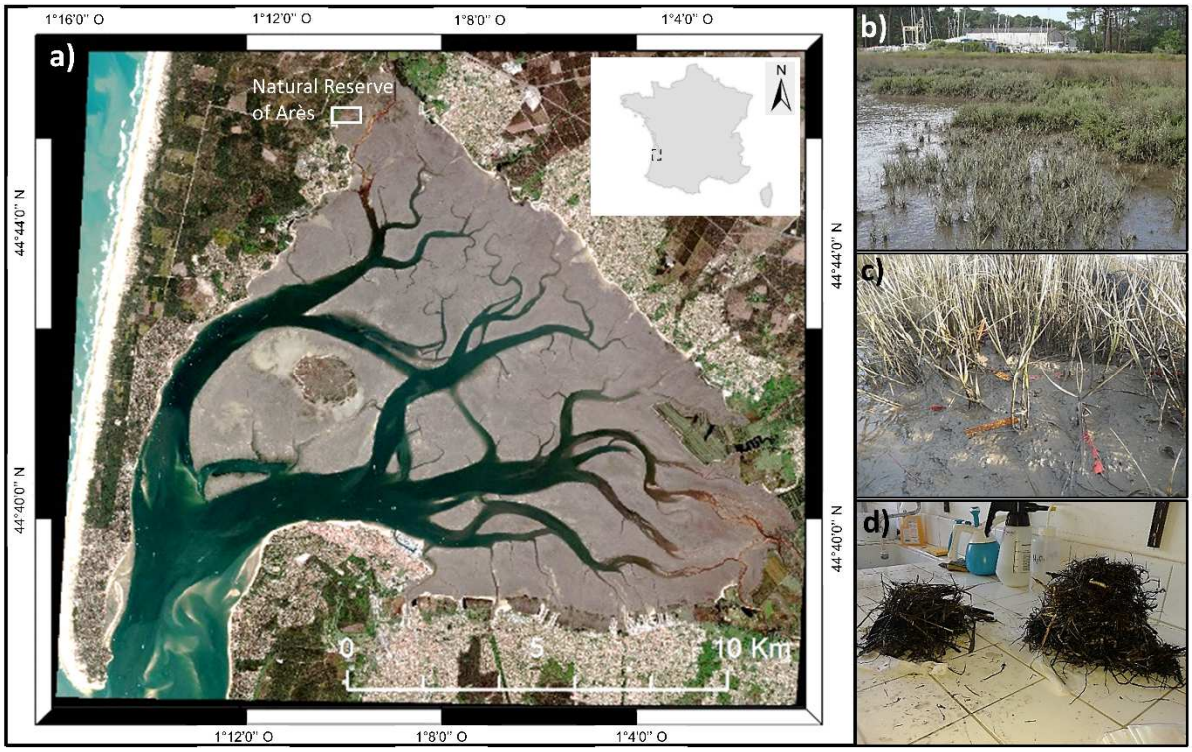

Figure 2.1 *Study site.* ***(a)*** *The Arcachon Bay (40°40 N, 1°10 W), France;* ***(b)*** *Natural reserve of Arès with S. anglica colonizing a low elevation habitat in the front;* ***(c)*** *target Spartina individuals of both species (S. anglica with the red tag and S. maritima with the orange tag) transplanted in a cleared subplot of dominant S. maritima from intermediate elevation;* ***(d)*** *above-(left) and below-ground (right) parts of a S. anglica sample during summer biomass measurements*

2.2.2 Experimental design

For both the removal experiment and the sampling of environmental conditions, biomass and productivity of natural patches made for defining ecological niches of the two species, we selected six replicates for each combination of two main treatments (dominant and elevation,

Figure 2.1c). In order to avoid a circular reasoning in the assessment of the elevation niche of the two species, three intertidal levels were chosen independently for each species, from their lowest to their highest levels of occurrence. This resulted in 36 main plots that were randomly distributed in the marsh since the six host colonies of the two species were organized in a mosaic of small patches (1–5 m large), as shown in Figure 2.2.

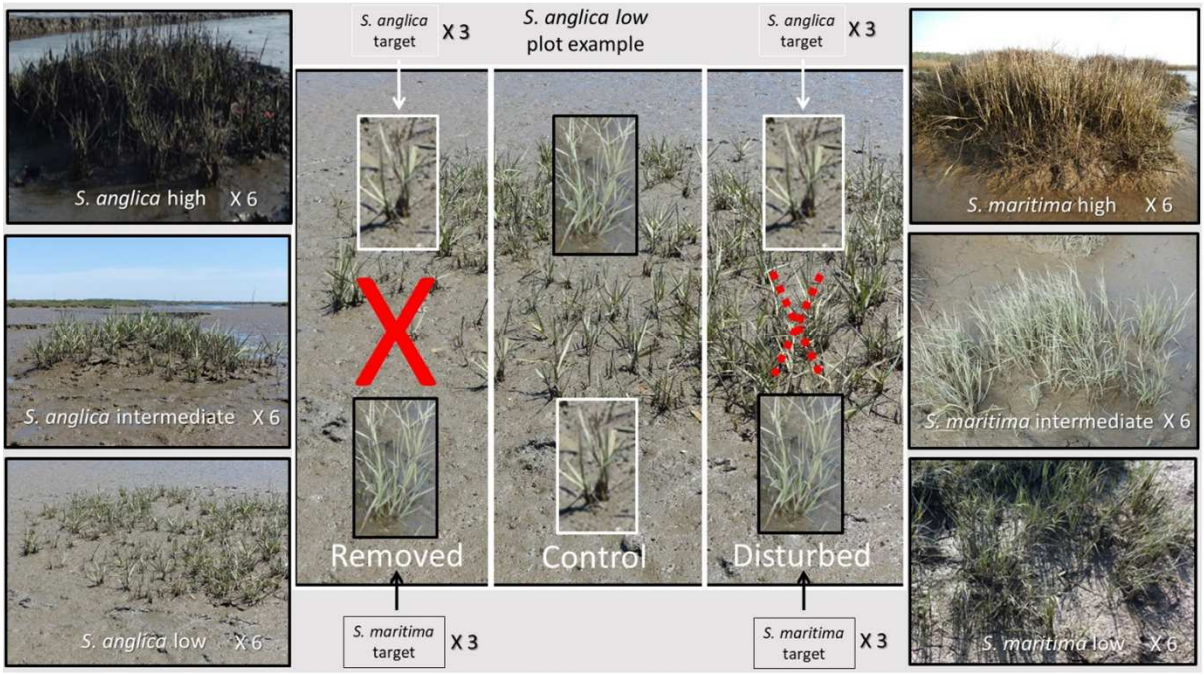

Figure 2.2 *Experimental design of the removal experiment. Images on the left correspond to Spartina anglica dominant plots at the three intertidal levels: low, intermediate and high. Images on the right correspond to Spartina maritima dominant plots at the three same intertidal levels. The image in the centre represents the application of the neighbour sub-treatment applied to all dominant replicas, using the low S. anglica dominant plot as example. In the removed sub-plots, three individuals of S. anglica (white box) and three individuals of S. maritima (black box) were planted and the surrounded neighbours were removed (red cross); in the control sub-plots three individuals of each Spartina species were planted and the neighbouring plants left intact; in the disturbed sub-plots three individuals of each Spartina species were planted while the neighbouring plants were left intact and the soil was manually disturbed (red dotted cross)*

2.2.3 Removal experiment

To investigate the role of plant–plant interactions in the invasion of *S. anglica* in the salt marshes of the Bay of Arcachon, we conducted a one-year-long removal experiment. The experiment was initiated between 13 and 20 November 2014 and ended on 25 October 2015. The experiment consisted of a reciprocal transplantation of *S. anglica* and *S. maritima* individuals into plots, both in the presence and absence of neighbours from the two species to assess both the competitive response and effect of the two species. This was done at the three intertidal levels with six replicates in the 36 main plots. More precisely, we used a split-split-plot design with four factors: host dominant species (*S. anglica* and *S. maritima*), elevation (low, intermediate and high), neighbour (with and without) and target species (*S. anglica* and *S. maritima*). In each of the 36 main plots we randomly selected three 30 cm × 30 cm large

subplots for the neighbour sub-treatment: a control, a removal and a disturbed subplot for controlling the effect of disturbance induced by the removal treatment. We then transplanted three individuals of each *Spartina* species in each subplot (target sub-sub-treatment). In the control subplots, the neighbouring vegetation was left intact, whereas in the removal subplots the vegetation was removed and in the disturbed subplots the soil was only disturbed by hand, as in the removal subplots, but all surrounding vegetation was left in place as in the control subplots. Since initial statistical analyses showed no significant differences in target survival between the control and disturbed subplots, both subplots were then pooled before further statistical analyses and referred to as "with neighbour" subplots. All transplants of approximately similar small sizes were randomly collected in the natural communities close to the experimental plots at intermediate tidal level. They were tagged with coloured rings and transplanted with a minimum distance of 10 cm between transplanted individuals within each subplot. In the removal treatment, the transplanted individuals were planted at least 10 cm from the surrounding local plants to reduce interactions (Figure 2.1c). There were 648 transplants in total (two dominants × three elevations × six treatment replicates × three neighbouring conditions × two target × three measurement replicates).

The height, number of stems and number of leaves of all transplants were measured at the beginning and end of the experiment. We calculated percentage survival per subplot and harvested the living individuals at the end of the experiment for above-ground measurements after drying them at 70°C for 48 h.

2.2.4 Environmental factors and biomass sampling in patches of the two dominants

In order to characterize the abiotic niches of the two species, four environmental variables were measured mid-June 2015 in patches of the two dominants located in each of the 108 subplots, conductivity (σ), redox potential (Eh), volumetric soil water content and elevation (z). For each parameter, three measurements were acquired and averaged per subplot before statistical analyses. Conductivity was measured with a standard conductivity measurement cell (TetraCon 325) and redox potential with an Eh-meter, both probes being assembled in a multi-parameter box (PofiLine Multi 3320 - WTWTM, Weilheim, Germany). Soil humidity was determined with a moisture meter (ML3 ThetaProbe assembled in an HH2 box, Delta-T devices, Cambridge, UK). Elevation was recorded with a RTK Leica GS10 system of centimeter precision.

We sampled the above-and below-ground biomass in the six communities (two dominant × three elevations) in mid-February (before the growing season) and late September (close to the end of the growing season) 2015 in order to calculate above-and below-ground productivity. We used 30 cm × 40 cm quadrats and there were four replicates per combination of treatments. Samples were carefully washed to remove all sediment, separated in above-and below-ground parts and dried at 70°C for 48 h before weighing.

2.2.5 Data treatment

2.2.5.1 Removal experiment

For each subplot, we calculated the survival and mean growth increment (μ) of the surviving transplants during the course of the experiment using initial and final measurements of target growth (*XTi* and *XTf*, respectively)

$$\mu = \frac{(X_{Tf} - X_{Ti})}{X_{Ti}}$$

where *X* corresponds to either height, stem or leaf number.

We also calculated biomass increment with the initial biomass obtained through the relation with leaf number:

$$B_i = 0.0958119 + 0.0694243 * leaf\ number$$

The relationship was obtained measuring the above-ground biomass and number of leaves of 30 additional individuals of each species ($r2 = 0.84$, $p < 0.001$ for *S. anglica* and $r2 = 0.86$, $p < 0.001$ for *S. maritima*).

To quantify the performances of *Spartina* targets growing in the presence or absence of neighbours we used the Relative Interaction Index (RII) according to Armas et al. (2004):

$$RII = \frac{(X_{with\ neighbour} - X_{without\ neighbour})}{(X_{with\ neighbour} + X_{without\ neighbour})}$$

where *X*with neighbour and *X*without neighbour are the values of the target performances measured in the presence and absence of a neighbour. The index is symmetrical around zero (which indicates no significant relationship), varying between 0 and +1 for facilitation and between 0 and – 1 for competition. To avoid redundancy in the results shown, only RII for survival and biomass are presented here and not RII on other growth measurements that provided similar results to biomass.

2.2.5.2 Biomass, productivity and root/shoot ratio of patches of the two dominants

Above-and below-ground production (*P*) and productivity were calculated for the six treatment combinations (two dominants × three elevations) using the biomass measurements made in winter and late summer. Production was expressed in dry weight of organic matter produced per unit area during the growing season ($P = W_{t2} - W_{t1}$) and productivity was quantified as follows:

$$Productivity = \frac{W_{t2} - W_{t1}}{W_{t1} * T}$$

where *Wt*2 is the late-summer biomass, *Wt*1 the winter biomass and *T* the unit time, for which a year was considered. We also quantified the root/shoot ratio in the six communities using summer biomass.

2.2.6 Statistical analysis

The Relative Interaction Index (RII) values on survival and biomass were first analysed using a split-plot ANOVA model with elevation and dominant as main treatments and target as subtreatment. Because elevation had no significant effect on both RIIs neither as simple factor nor in interaction with the other treatments, we re-analysed RII values with a split-plot ANOVA model with dominant as main treatment and target as subtreatment. One-sample *t*-tests were used to analyse the significance of deviations of RII values from zero. Environmental data (elevation, salinity, soil humidity and redox potential) were analysed using a split-plot ANOVA model with elevation and dominant as main treatments and neighbour as subtreatment. Biomass and productivity of patches of the two dominants were analysed with a split-plot ANOVA model with elevation and dominant as main treatments and organ (below-vs. above-ground) as subtreatment. Root/shoot ratio was analysed with a two-way ANOVA model with elevation and dominant as treatments. Environmental, biomass and productivity data were log-transformed before analyses to fulfil ANOVA assumptions. All statistical analyses were done using R (R Development Core Team 2013).

2.3 Results

2.3.1 Removal experiment

We found that both established dominant communities had overall negative effects on the two species (negative RII — Figure 2.3a). This negative effect was slightly higher in the *S. maritima* population ($p < 0.05$ for the dominant effect in Table 2.1), where RIIs of the two target species were significantly negative. In contrast, in the *S. anglica* dominant only the RII of *S. maritima* target was significantly negative. Overall these results show the biotic resistance of both established communities against the other *Spartina* species with a slightly higher resistance of the native dominant.

There was a significant effect of the target treatment on RII for biomass due to overall higher values for *S. anglica* as target than for *S. maritima* as target (Table 2.1, Figure 2.3b). Additionally, there was a significant interaction between the dominant and target treatments, because the RII value of *S. anglica* was much higher in its own populations (with strong and highly significant intraspecific facilitation, see *t*-test in Figure 2.3b) than in the *S. maritima* populations, whereas the RII value of *S. maritima* was significantly negative in the *S. anglica* population and lower than in its own populations. In other words, there was a reversal in competitive effects of the two communities depending on the target species, with the exotic having a stronger positive effect than the native on the exotic target but a slightly more negative effect than the native on the native target.

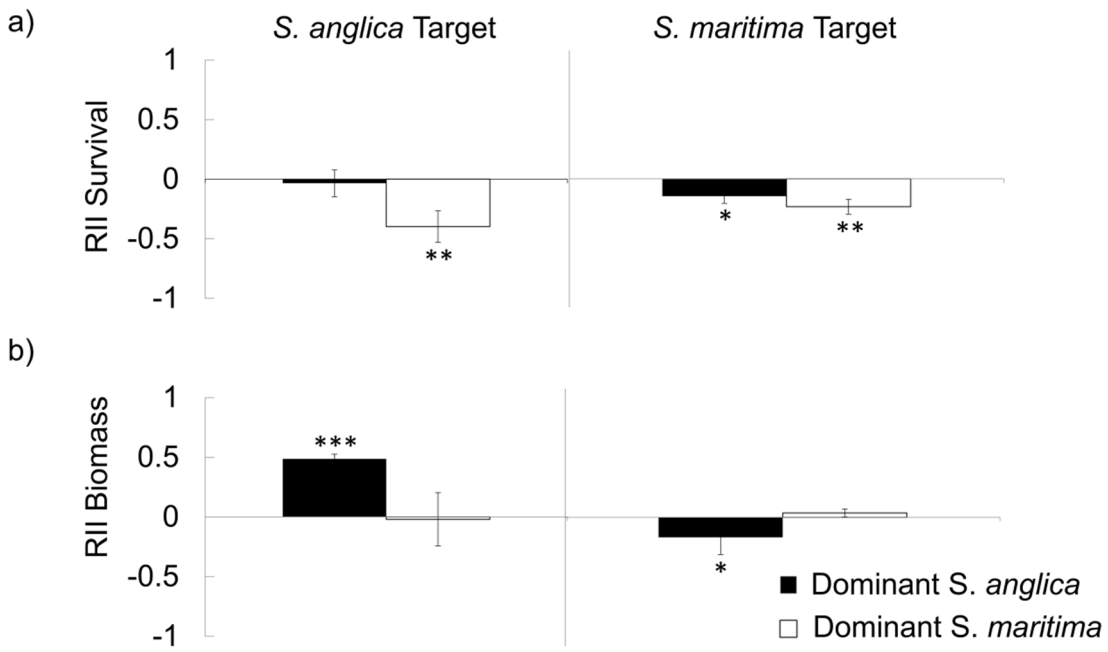

Figure 2.3 *Mean (± SE) Relative Interaction Intensity (RII) index for* ***(a)*** *survival and* ***(b)*** *biomass of S. anglica and S. maritima targets in the two dominants. Positive values correspond to facilitation and negative values to competition. Results of t-tests are indicated above and below bars with asterisks: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$*

Table 2.1 *Results of the split-plot ANOVA on the effects of the elevation, dominant, target treatments and their interactions on RII biomass and RII survival. Significant results are indicated in bold*

		RII survival			**RII biomass**	
Source of variation	**df**	**F**	**p**	**df**	**F**	**p**
Dominant	1	5.44	**0.030**	1	1.73	0.204
Target	1	0.17	0.679	1	6.81	**0.017**
Dominant x Target	1	2.16	0.157	1	8.53	**0.009**
Residuals	20			19		

2.3.2 Environmental measurements

Elevation measurements showed weak differences between the three intertidal levels (low: 1.23 m ± 0.01 m, intermediate: 1.30 m ± 0.02 m, high: 1.47 m ± 0.02 m), but these differences were highly significant ($p < 0.001$ for the elevation effect, data not shown). No significant difference was found between the two *Spartina* species ($p > 0.1$ for the dominant effect, data not shown).

Redox potential strongly increased from low to intermediate and high elevation levels (elevation effect: $p < 0.001$ in Table 2.2, Figure 2.4a) and was overall significantly higher in *S. anglica* than in *S. maritima* communities (Table 2.2). There was also a significant dominant by elevation interaction because Eh was higher in *S. anglica* than in *S. maritima* at intermediate

and high elevations but not at low elevation (Table 2.2 and Figure 2.4a). In particular, at intermediate elevation level the Eh was not significantly different from 0 in the *S. anglica* dominant (*t*-tests, $p > 0.05$, not shown) but still significantly negative in the *S. maritima* dominant (Figure 2.4a). There was a weakly significant dominant effect for conductivity (Table 2.2) with slightly higher conductivity values for *S. maritima* than for *S. anglica* (Figure 2.4b). There was a highly significant elevation effect for soil moisture due to decreasing soil moisture from low to intermediate and high intertidal levels (Table 2.2, data not shown). There was also a highly significant removal effect due to higher soil moisture in the removed than in the control plots (Table 2.2).

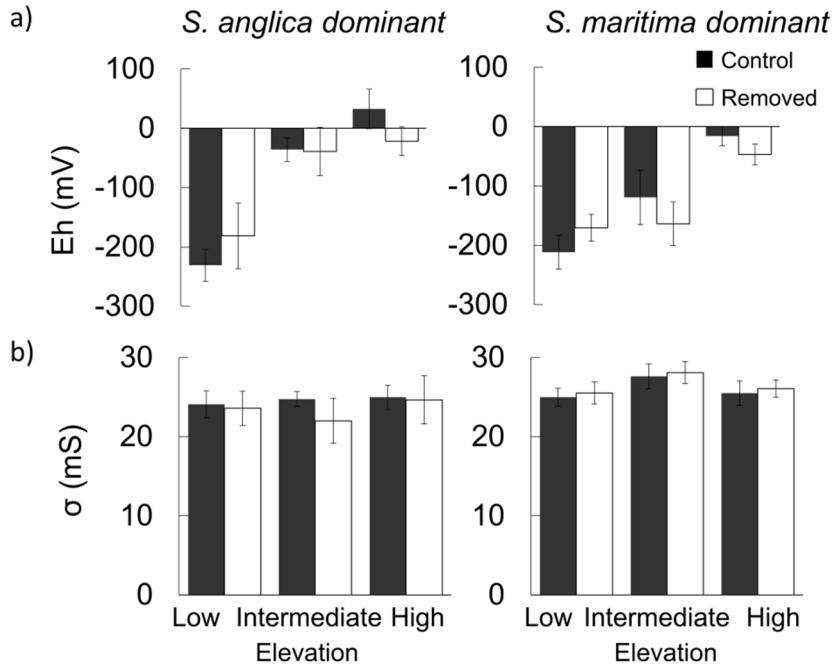

Figure 2.4 *Mean (±SE).* ***(a)*** *Redox potential and* ***(b)*** *conductivity measured below the S. anglica and S. maritima dominants at three elevation levels (low, intermediate and high) in the control (dark bar) and removed (white bars) subplots*

Table 2.2 *Results of the split-plot ANOVAs on the effects of the elevation, dominant, removal treatment and their interactions on redox potential (Eh), conductivity (σ) and soil humidity. Significant results are indicated in bold*

		Redox potential		Conductivity		Humidity	
Source of variation	**df**	**F**	**p**	**F**	**p**	**F**	**p**
Elevation	2	32.38	**<0.001**	0.37	0.692	29.49	**<0.001**
Dominant	1	4.92	**0.030**	4.83	**0.032**	2.30	0.134
Removal	1	0.14	0.710	0.10	0.751	15.51	**<0.001**
E x D	2	3.32	**0.043**	1.12	0.332	0.61	0.548
E x R	2	2	0.144	0.15	0.862	0.13	0.881
D x R	1	0.05	0.820	0.67	0.414	0.98	0.326
E x D x R	2	0.24	0.784	0.14	0.877	1.45	0.242
Residuals	60						

2.3.3 Biomass, root/shoot ratio and productivity of patches of the two dominants

Summer biomass significantly increased with increasing elevation (Figure 2.5, Table 2.3). Indeed, total biomass of both species was 255.5 ± 32.3 g/m2 at low elevation, 1080.7 ± 121.9 g/m2 at intermediate elevation and 1439.9 ± 92.0 g/m2 at high elevation. *Spartina anglica* also had about 30% higher total biomass than *S. maritima* (1068.3 ± 170.3 g/m2 vs. 782.4 ± 149.4 g/m2, $p < 0.01$), but the dominant effect was stronger at intermediate than at low and high elevations (significant elevation by dominant interaction).

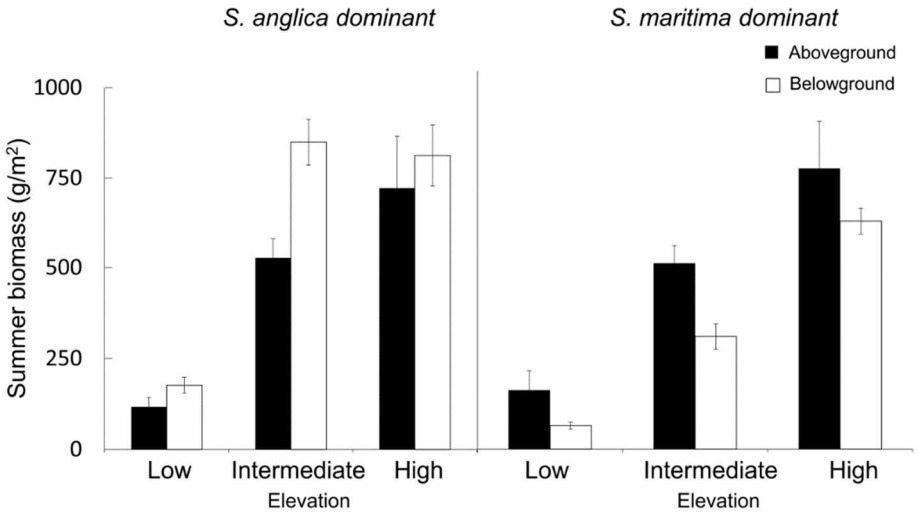

Figure 2.5 *Mean (±SE) above-(dark bars) and below-ground (white bars) summer biomass of S. anglica and S. maritima dominants from the three elevation levels (low, intermediate and high)*

Table 2.3 *Results of the split-plot ANOVAs on the effects of the elevation, dominant, organ treatment and their interactions on summer biomass and productivity of Spartina populations. Significant effects are indicated in bold*

		Summer biomass		**Productivity**	
Source of variation	**df**	**F**	**p**	**F**	**p**
Elevation	2	74.77	**<0.001**	4.99	**0.012**
Dominant	1	12.43	**0.001**	16.98	**<0.001**
Organ	1	0.04	0.847	21.28	**<0.001**
Elevation x Dominant	2	3.70	**0.034**	6.17	**0.005**
Elevation x Organ	2	0.50	0.611	2.24	0.121
Dominant x Organ	1	13.61	**<0.001**	0.33	0.571
Elevation x Dominant x Organ	2	1.86	0.171	2.47	0.099
Residuals	36				

There was a highly significant dominant by organ interaction, because at all elevations the root/shoot ratio was much higher for the exotic than for the native (1.62 ± 0.2 vs. 0.66 ± 0.1, $p < 0.001$ for the dominant effect in the ANOVA on root/shoot ratio, Table 2.4 and Figure 2.6). Additionally, while handling biomass in the lab we observed that most of the below-ground biomass of *S. anglica* was made of thick rhizomes in contrast to *S. maritima*'s below-ground biomass, which was mostly made of fine roots.

We found higher productivity above-than below-ground ($p < 0.001$ for organ effect) and for *S. anglica* than for *S. maritima* ($p < 0.001$ for dominant effect, Table 2.4, Figure 2.6). Productivity was higher for *S. anglica* than for *S. maritima* at intermediate and high elevations but not different at low elevation (significant elevation × dominant interaction, Table 2.4). Finally, this higher productivity for *S. anglica* at intermediate and high elevations was only observed above-but not below-ground (marginally significant three-way interaction, Table 2.4). Additionally, productivity was significantly positive only above-ground and for *S. anglica* at both intermediate and high elevations (see results of *t*-tests in Figure 2.6).

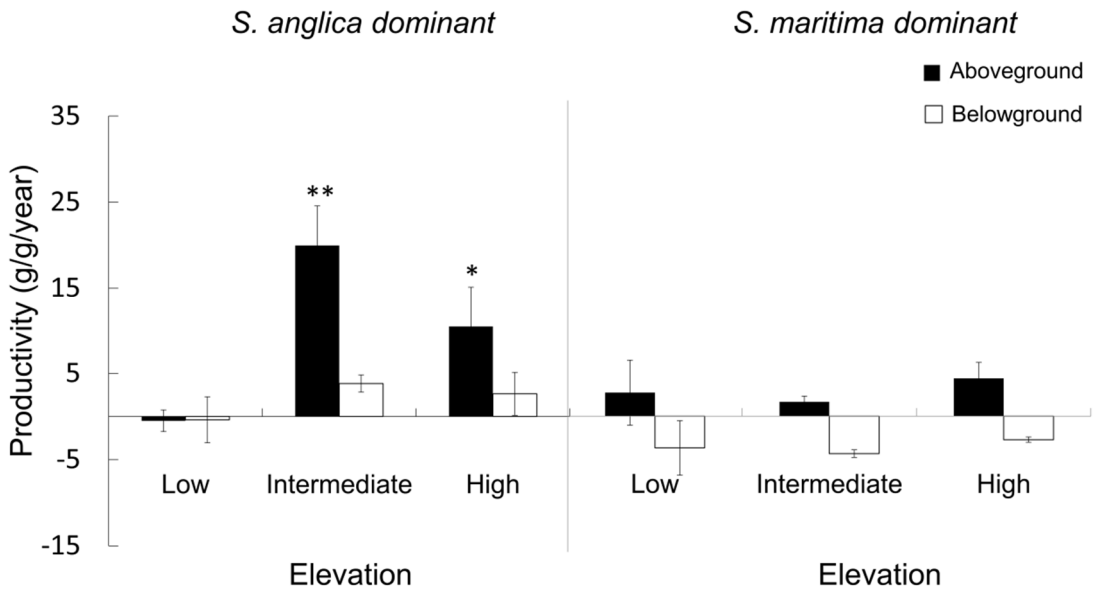

Figure 2.6 Mean (± SE) annual above- (dark bars) and below-ground (white bars) productivity of S. anglica and S. maritima dominants at the three elevation levels (low, intermediate and high). Results of t-tests are indicated above bars with asterisks: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Table 2.4 *Results of the ANOVA on the effects of the elevation, dominant treatment and their interaction on Root/Shoot ratios of Spartina populations. Significant effects are indicated in bold*

		Root/Shoot ratio	
Source of variation	**df**	**F**	**p**
Elevation	2	0.02	0.981
Dominant	1	17.58	**<0.001**
Elevation x Dominant	2	1.30	0.296
Residuals	18		

2.4 Discussion

Our removal experiment showed that the two established *Spartina* dominants exhibited an important biotic resistance against the invasion of the other species, which precludes the competitive exclusion hypothesis as the main mechanism of invasion of *Spartina anglica.* Our environmental and biotic measurements on established patches showed that the two species have similar niches along the intertidal elevation gradient, presenting only small differences in terms of total biomass and soil conductivity. Both species presented the same tolerance to anoxic conditions at the lowest intertidal level, which precludes the empty niche hypothesis along an inundation gradient as the main mechanism of invasion. However, we also found strong differences in root/shoot ratios between the two species. *Spartina anglica* showed higher investment in below-than above-ground organs compared to *S. maritima*. At intermediate and high intertidal levels only *S. anglica* had a significant positive above-ground productivity and

more oxidized soils than *S. maritima*, suggesting higher ecosystem-engineering effects for the exotic. Additionally, our removal experiment showed that the invasive *Spartina* exhibited a high intraspecific facilitation for growth. All together, these results suggest that the invasion success of *S. anglica* is likely to be primarily explained by its higher below-ground investment and ecosystem-engineering effects than those of *S. maritima*, inducing a higher growth rate and self-facilitation in originally similar anoxic conditions.

2.4.1 Interactions between the exotic and the native *Spartina*

Competitive effects are generally more important than competitive responses for explaining species dominance in plant communities (Liancourt et al. 2009). In our system, both *Spartina* species had negative effects on the other species, showing the biotic resistance of the two dominant species when established in dense and mature communities. These results are consistent with natural patterns of invasion in the Arcachon Bay because *S. anglica* and *S. maritima* form distinct patches along the shore and mixed patches are very uncommon. In our removal experiment, we found subtle differences in competitive effects between the two species and their ranking depended on the target performance variable. Considering survival, *S. maritima* showed a higher biotic resistance than *S. anglica* but the reverse was observed for biomass.

However, a main result of the removal experiment was the occurrence of strong differences in competitive response between the two species only for target biomass and within the exotic population. This was explained by the high intraspecific facilitation occurring for the growth of the exotic. Facilitation has been shown to be an important process in invasion ecology in a variety of ecosystems (Altieri et al. 2010, Bruno 2000, Bruno et al. 2003, Rodriguez 2006, Saccone et al. 2010). Most studies have focused on interspecific facilitation and its positive cascading effects on species diversity (e.g. Bruno 2000; Rodriguez, 2006). In contrast, intraspecific facilitation has been rarely assessed in plant communities (but see Fajardo and McIntire 2010). The mechanism behind the intraspecific facilitation of *S. anglica* could be its high rhizome investment and subsequent sediment oxygenation, enhancing differently the growth of the exotic and that of the native. Callaway and Josselyn (1992) argued that the most important factor driving the establishment of *S. alterniflora* at the lower marsh limit in San Francisco Bay (USA) was probably its higher ability, compared to the native *S. foliosa*, to diffuse oxygen throughout the plant due to the existence of continuous gas spaces from the leaves to the roots (Teal and Kanwisher 1966, Maricle and Lee 2002). Bertness (1991) has also shown, for *S. alterniflora* in New England salt marshes, that this species' capacity to oxygenate anoxic soils allows its successful colonization of low marsh levels. In our case, it is very likely that the exotic *Spartina* was more sensitive to this increase in oxygenation level than the native, because of its higher exploitative strategy.

2.4.2 Niche differences

The success of invasive species can be explained by differences with native species in terms of niche occupancy along environmental gradients, i.e. by their ability to fill an empty niche (Saccone et al. 2013). Our results showed that there were no significant differences (at the centimetre precision) in elevation levels between species, consistent with the preliminary observations of Lafon and Michalet (*in* Le Nindre et al. 2004). Additionally, the two species showed the same tolerance to anoxia with similar low population biomass, productivity and potential redox at their lowest intertidal positions. This shows that there are no niche differences along flooding and oxygenation gradients between both species and that this hypothesis cannot explain the higher occurrence of the exotic *Spartina* offshore.

Differences in tolerance of physical disturbance due to wave exposition is, thus, more likely to explain the higher occurrence of the invasive offshore (Bouma et al. 2005). The higher productivity observed at intermediate and high intertidal levels in our study for the exotic than for the native is in line with a higher ruderal syndrome for the former (Grime 1974, MacArthur and Wilson 1967), and, thus, consistent with its likely higher tolerance for physical disturbance. Strong and Ayres (2013) stressed the key role of seed spread by tides in *Spartina* colonization mechanisms but the proximity to a seed source is not the only requirement for a successful invasion (Ayres et al. 1999). Balke et al. (2011) introduced the concept of "window of opportunity" when describing the thresholds seedlings need to overcome in order to successfully anchor and colonize mudflats. According to these authors, due to the harshness of the environmental conditions, vegetative reproduction gains importance over seedling establishment. The substantial amount of rhizomes observed in the below-ground biomass of *S. anglica* also suggests higher colonisation ability for the exotic through rhizome dispersion (Nilsson et al. 2010). However, further experiments should be conducted to test this rhizome-dispersion hypothesis, in particular through transplantation experiments of propagules of both species along a gradient of increasing distance to the shore. To conclude, the empty-niche hypothesis might likely contribute to explain the invasion of *S. anglica* along a gradient of physical disturbance related to the distance from the coast but not along an inundation gradient of tolerance to anoxic stress.

2.4.3 *Spartina anglica*: a case of invasive engineering

Despite their strong ecological similarities at low intertidal level, the two *Spartina* dominant types had contrasting levels of oxygenation in the sediment and of productivity at intermediate and high intertidal levels, suggesting different ecosystem-engineering effects. Seliskar et al. (2002) have shown that different provenances of *S. alterniflora* differentially affected oxygenation level and microbial activity in originally similar abiotic conditions of a salt marsh in which they were transplanted. This result is consistent with previous studies highlighting that macrophytes can modify the oxygenation level of sediments in wetlands (Carpenter and Lodge 1986, Callaway and King 1996). In our study, the higher redox potential measured at intermediate and high intertidal levels below the exotic *Spartina* is likely due to the higher investment of this species in below-ground organs and in particular rhizomes. This higher oxygenation level may also explain the higher above-ground productivity measured in the *S.*

anglica population than in the *S. maritima* population at intermediate and high intertidal levels, likely due to increasing microbial activity in more oxidized sediments and in turn increasing soil nitrogen availability and plant growth (Seliskar et al. 2002).

Invasive engineers have been defined as exotic species that modify their physical environment in such a way that their reproductive output is increased (Cuddington and Hastings 2004). These authors have shown by a modelling approach that invasive species that modify their environment may have significantly faster growth rates into sub-optimal habitats than species that do not. Our results have shown that *S. anglica* behaves as a typical invasive engineer. Like the native, *S. anglica* can recruit in the sub-optimal conditions of the low intertidal level. However, thanks to its higher rhizome investment (Seliskar et al. 2002) the exotic has stronger ecosystem-engineering effects than the native in terms of increasing sediment oxygenation.

In conclusion, in the Bay of Arcachon, the invasion of *S. anglica* cannot be explained by competitive exclusion or differences in niche occupancy in relation to anoxia induced by inundation.

However, a key aspect of the invasion seems to be the ability of *S. anglica* to behave as an invasive engineer (Cuddington and Hastings 2004), through a self-facilitation process involving an amelioration of sediment oxygenation. One missing point in our understanding of the invasion process is the recruitment of the species in the Arcachon Bay, since we did not yet provide evidence for the ecological mechanism explaining its higher occurrence offshore than the native. We argue that this recruitment is very likely due to its higher tolerance to physical disturbance, thanks to its higher growth rate than the native's, but this hypothesis remains to be tested in further experiments. However, we showed that, once established in the Bay, its spread is due to its ability to behave as an invasive engineer.

References

Altieri, A. H. et al. 2010. Facilitation cascade drives positive relationship between native biodiversity and invasion success. - Ecology 91: 1269–1275.

An, S. Q. et al. 2007. *Spartina* invasion in China: implications for invasive species management and future research. - Weed Research 47: 183–191.

Armas, C. et al. 2004. Measuring Plant Interactions: A New Comparative Index. - Ecology 85: 2682–2686.

Ayres, D. R. et al. 1999. Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). - Molecular Ecology 8: 1179–1186.

Ayres, D. R. et al. 2004. Spread of Exotic Cordgrasses and Hybrids (*Spartina* sp.) in the Tidal Marshes of San Francisco Bay, California, USA. - Biological Invasions 6: 221–231.

Balke, T. et al. 2011. Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. - Marine Ecology Progress Series 440: 1–9.

Baumel, A. et al. 2001. Molecular investigations in populations of *Spartina anglica* C.E. Hubbard (Poaceae) invading coastal Brittany (France). - Molecular Ecology 10: 1689–1701.

Bertness, M. D. 1991. Interspecific Interactions among High Marsh Perennials in a New England Salt Marsh. - Ecology 72: 125–137.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. - Trends in Ecology & Evolution 9: 191–193.

Bouma, T. J. et al. 2005. Trade-Offs Related to Ecosystem Engineering: A Case Study on Stiffness of Emerging Macrophytes. - Ecology 86: 2187–2199.

Bruno, J. F. 2000. Facilitation of Cobble Beach Plant Communities through Habitat Modification by *Spartina alterniflora*. - Ecology 81: 1179–1192.

Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. - Trends in Ecology & Evolution 18: 119–125.

Bulleri, F. et al. 2008. Beyond Competition: Incorporating Positive Interactions between Species to Predict Ecosystem Invasibility. - PLOS Biology 6: e162.

Bulleri, F. et al. 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. - PLOS Biology 16: e2006852.

Callaway, J. C. and Josselyn, M. N. 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. - Estuaries 15: 218–226.

Callaway, R. M. and King, L. 1996. Temperature-Driven Variation in Substrate Oxygenation and the Balance of Competition and Facilitation. - Ecology 77: 1189–1195.

Carboni, M. et al. 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. - Ecol Lett 19: 219–229.

Carpenter, S. R. and Lodge, D. M. 1986. Effects of submersed macrophytes on ecosystem processes. - Aquatic Botany 26: 341–370.

Castellanos, E. M. et al. 1994. Nucleation and Facilitation in Saltmarsh Succession : Interactions between *Spartina maritima* and *Arthrocnemum perenne*. - Journal of Ecology 82: 239–248.

Castillo, J. M. et al. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. - Journal of Ecology 88: 801–812.

Catford, J. A. et al. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. - Diversity and Distributions 15: 22–40.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. - Oikos 97: 153–166.

Crosby, S. C. et al. 2015. Flowering and biomass allocation in U.S. Atlantic coast *Spartina alterniflora*. - Am. J. Bot. 102: 669–676.

Cuddington, K. and Hastings, A. 2004. Invasive engineers. - Ecological Modelling 178: 335–347.

Daehler, C. C. 2003. Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. - Annual Review of Ecology, Evolution, and Systematics 34: 183–211.

Davis, M. A. et al. 2000. Fluctuating resources in plant communities : a general theory of invasibility. - Journal of Ecology 88: 528–534.

Dethier, M. N. and Hacker, S. D. 2005. Physical Factors Vs. Biotic Resistance in Controlling the Invasion of an Estuarine Marsh Grass. - Ecological Applications 15: 1273–1283.

Fajardo, A. and McIntire, E. J. B. 2010. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. - Journal of Ecology 99: 642–650.

Grime, J. P. 1974. Vegetation classification by reference to strategies. - Nature in press.

Hacker, S. and Dethier, M. 2006. Community modification by a grass invader has differing impacts for marine habitats. - Oikos 113: 279–286.

Hacker, S. D. et al. 2001. A marine plant (*Spartina anglica*) invades widely varying habitats: potential mechanisms of invasion and control. - Biological Invasions 3: 211–217.

Kennedy, T. A. et al. 2002. Biodiversity as a barrier to ecological invasion. - Nature 417: 636–638.

Kirwan, M. L. and Megonigal, J. P. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. - Nature 504: 53–60.

Lambdon, P. W. and Hulme, P. E. 2006. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. - Journal of Biogeography 33: 1116–1125.

Le Nindre, Y. M. et al. 2000. Terra Symphonie - Aménagement intégré du Bassin d'Arcachon. Etude n°5: Mise au point d'un outil de surveillance et d'aide à la décision en matière d'exhaussement des fonds du Bassin d'Arcachon. Rap. BRGM/RP-50578-FR. in press.

Le Nindre, Y. M. et al. 2004. Etude pour le maintien de l'équilibre bio-sédimentaire des plages du Nord-Est dans le Bassin d'Arcachon. Rapport BRGM/RP-53282-FR 101 p., 60 fig., 15 tabl., 6 ann. in press.

Levine, J. M. and D'Antonio, C. M. 1999. Elton Revisited: A Review of evidence linking diversity and invasibility. - Oikos 87: 15–26.

Levine, J. M. et al. 2003. Mechanisms underlying the impacts of exotic plant invasions. - Proc Biol Sci 270: 775–781.

Levine, J. M. et al. 2004. A meta-analysis of biotic resistance to exotic plant invasions. - Ecology Letters 7: 975–989.

Liancourt, P. et al. 2009. Contrasting community responses to fertilization and the role of the competitive ability of dominant species. - Journal of Vegetation Science 20: 138–147.

Lodge, D. M. 1993. Biological invasions: Lessons for ecology. - Trends in Ecology & Evolution 8: 133–137.

Lortie, C. J. et al. 2004. Rethinking plant community theory. - Oikos 107: 433–438.

MacArthur, R. H. and Wilson, E. O. 1967. The Theory of Island Biogeography. - Princeton University Press.

Maricle, B. R. and Lee, R. W. 2002. Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. anglica*. - Aquatic Botany 74: 109–120.

Michalet, R. et al. 2015. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. - Ecography 38: 335–345.

Nilsson, C. et al. 2010. The role of hydrochory in structuring riparian and wetland vegetation. - Biol Rev Camb Philos Soc 85: 837–858.

Pennings, S. C. et al. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. - Journal of Ecology 93: 159–167.

R Development Core Team 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Raybould, A. F. et al. 1991. The evolution of *Spartina anglica* C. E. Hubbard (Gramineae) : genetic variation and status of the parental species in Britain. - Biological Journal of the Linnean Society 44: 369–380.

Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. - Biol Invasions 8: 927–939.

Saccone, P. et al. 2010. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. - New Phytologist 187: 831–842.

Saccone, P. et al. 2013. Ecological resistance to Acer negundo invasion in a European riparian forest: relative importance of environmental and biotic drivers. - Appl Veg Sci 16: 184–192.

Seabloom, E. W. et al. 2015. Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. - Nature Communications 6: ncomms8710.

Seliskar, D. M. et al. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant : a *Spartina alterniflora* salt-marsh case study. - Journal of Ecology 90: 1–11.

Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. - Trends in Ecology & Evolution 17: 170–176.

Stachowicz, J. J. and Byrnes, J. E. 2006. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. - Mar Ecol Prog Ser 311: 251–262.

Strong, D. and Ayres, D. R. 2013. Ecological and Evolutionary Misadventures of *Spartina*. - Annual Review of Ecology, Evolution, and Systematics 44: 389–410.

Teal, J. M. and Kanwisher, J. 1966. Gas transport in the marsh grass, *Spartina alterniflora*. - J. Exp. Bot. 17: 355–361.

Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. - Ecology Letters 11: 1351–1363.

Vilà, M. and Weiner, J. 2004. Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. - Oikos 105: 229–238.

Vilà, M. et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. - Ecology Letters 14: 702–708.

Vitousek, P. M. et al. 1997. Human Domination of Earth's Ecosystems. - Science 277: 494–499.

Vu, H. D. et al. 2017. Ecosystem engineers drive creek formation in salt marshes. - Ecology 98: 162–174.

Wiens, J. A. 1989. Spatial Scaling in Ecology. - Functional Ecology 3: 385–397.

Zhi, Y. et al. 2007. Inter-specific competition: *Spartina alterniflora* is replacing *Spartina anglica* in coastal China. - Estuarine, Coastal and Shelf Science 74: 437–448.

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Conclusions

The implementation of a cross-transplantation removal experiment in saltmarshes of the Bay of Arcachon allowed a better understanding of the colonization strategies of the invasive cordgrass *Spartina anglica*, and in particular its competitive ability and niche occupancy.

The characterization of the environment (elevation, salinity, soil redox potential and moisture) inhabited by the two *Spartina* species showed that both species preferentially occupy the same niche along a gradient of inundation and anoxia and that they perform better at higher elevations of the intertidal area. The two cordgrass species have shown to be competitive against the invasion of one another and the invasive *Spartina* has additionally shown intra-specific facilitation for growth. The main outcomes of this experiment that support these conclusions are summarized in the following points:

- Both *Spartina anglica* and *Spartina maritima* perform better at higher elevations of the intertidal gradient (intermediate and high) where they achieve higher biomass and productivity.
- *Spartina anglica* favours underground biomass allocation whereas *Spartina maritima* favours aboveground allocation.
- Environmental characteristics do not differ between areas dominated by each of the two cordgrass species. However, soil redox potential indicated that, under the influence of *Spartina anglica*, soils are less anoxic at intermediate and high intertidal levels. This could be a consequence of the fact that biomass allocation of the exotic species was preferentially to roots and rhizomes, thus increasing sediment oxygenation.
- Results of Relative Interaction Indices (RII) on the biotic interaction experiment indicate that the two species reciprocally showed resistance to invasion. This was translated by negative RIIs for both species targets, within the two dominant communities. Additionally, once the survival stage was overcome, *Spartina anglica* showed strong self-facilitation for growth, whereas individuals were still in competition within meadows of the congener *Spartina maritima* dominance.

Overall, these results suggest that the success of the colonization by *Spartina anglica* is probably closely linked to its investment in a developed root system increasing its ecosystem engineering effect relatively to the native *Spartina maritima*, as well as its intraspecific facilitation. Both species are able to colonize the same topographic levels of the intertidal area which leads to the rejection of the hypothesis of empty niche colonization over a gradient of inundation by *Spartina anglica*. However, because the invasive *Spartina* fails to outcompete the native *Spartina* from areas where it is dominant, it successfully spreads into off-shore locations most likely due to a higher tolerance to the disturbance associated to the lower elevation levels. The constraints inherent to these levels are likely overcome by a ruderal strategy translated by the high productivity presented by this species.

CHAPTER 3

Effects of freshwater inputs on Spartina species performances and interactions

Anthropogenic perturbations can alter sediment availability and nutrient loading within wetlands hence affecting marsh development. If, on one hand, sediment deliveries to coastal systems have been experiencing a large decrease, on the other, with the increase in human land use, nutrient inputs have been largely intensified. In the Bay of Arcachon, it was observed that *Spartina* species, in particular the exotic, exhibited a phenotypic plasticity that seemed to be related to the relative distance from freshwater inputs into the Bay. Because resources availability can also affect the strength and sign of biotic interactions, an experiment was designed with the aim of testing how the interaction between *Spartina anglica* and *Spartina maritima* is affected by changes in nutrient supply induced by freshwater inputs.

3.1 Introduction

Land use and transformation, namely through agriculture, forestry and grazing, substantially increased during the last century (Vitousek et al. 1997b). The increased use of land either for agriculture, industry or recreational purposes, leads to an increase in nutrient inputs into coastal zones (Valiela et al. 1978) which can create significant nutrient enrichment influencing coastal ecosystems structure and functioning. An additional outcome from nutrient enrichment is that it can add up to biological invasion and favour the establishment of exotic species. A typical example of the impact of nutrient increase and/or soil properties alteration in coastal environments is the higher frequency of harmful algal blooms due to rapid increases in marine phytoplankton caused by seawater warming and/or enhanced nutrient availability (Hallegraeff 1993).

In wetlands, predicting the response of ecosystems to nutrient loading can be challenging as there are multiple factors influencing the biochemical transformations occurring in the sediment (Sundareshwar et al. 2003). For instance, plant nutrition in salt marshes is influenced by soil flooding and the processes associated with reducing soil redox potential (Eh) conditions, as oxygen supply to the roots is critical for nutrient uptake and ion transport (see Pezeshki and DeLaune 2012 for a review). An important consequence of soil oxygen reduction is that it induces changes in the availability and/or the concentration of the set of nutrients that are essential for plant functioning. On the other hand, plant-mediated belowground sediment oxygenation also affects biogeochemical properties, the composition of the microbial community (Reinhart and Callaway, 2006) and the nutrient dynamics of salt marsh sediments (Koop-Jakobsen et al. 2017), which is an example of the vegetation's role as ecosystem engineer (Vitousek et al. 1997a).

Even though many nutrients are involved in plant growth, the key elements required for aquatic plant production are nitrogen and phosphorus (Bornette and Puijalon 2011). Studies have found nitrogen as the major nutrient limiting macrophytes production in coastal habitats (Vitousek et al. 1997, Sundareshwar et al. 2003). Tyler et al. (2007) have found that N availability strongly enhances the growth of *Spartina alterniflora*, its competitive ability and and its rate of spread, although this species behaves as a successful invader independently of the N concentration. Indeed, macrophyte growth has been observed to positively respond to nitrogen addition, but not to that of phosphorus (Sundareshwar et al. 2003). However,

Sundareshwar et al. (2003) experiment showed that the greatest response in macrophytes production happened with the addition of both nutrients.

Plant morphology and growth strategies adapt to the local environment (Díaz et al. 2016). In the case of *Spartina*, differences in morphology within the same population have already been observed and related to the presence of freshwater inputs (DeLaune et al. 1979). Notably, these authors have reported, a decreasing profile of plant height within *Spartina alterniflora* meadows bordering streams where meadows alongside the streams where denser and presented taller *Spartina* individuals than inland from the streams. Variable environmental conditions have also been reported to result in a high degree of morphological variation for *Spartina anglica* that was related to phenotypic plasticity rather than genetic characteristics (Thompson et al. 1991, Ainouche et al. 2004).

Nutrient availability can modulate species interactions (Grime 1974, Davis et al. 2000). Studies comparing the performances of different native invasive marsh species have been conducted in order to understand the influence of environmental factors in interactions (Seliskar et al. 2002, Duarte et al. 2015). In salt marsh species, along with other abiotic factors, competition for nitrogen has been found to be of major importance (Pennings and Bertness 2001). Notably, Levine et al. (1998) have suggested that if access to nutrient regulates competitive dominance among marsh species, then different vegetation zonation patterns should be found in marshes presenting different levels of nutrient inputs.

In the Bay of Arcachon, our observations of a gradient in the phenotypic form of the dominant *Spartina* species, *Spartina maritima* and *Spartina anglica*, with increasing distance from freshwater inputs into the Bay lead to the hypothesis that nutrient load variations can affect not only the cordgrasses plasticity but also their competitive abilities, creating an eventual competitive shift that can open an important window of opportunity to the exotic colonization of high marsh zones, previously dominated by the native *S. maritima*. In order to test this hypothesis, namely the influence of environmental soil conditions for the performance of the two *Spartina* species, a reciprocal removal experiment was performed within different freshwater inputs in the Eastern part of the Bay of Arcachon along with the characterization of the edaphic conditions along the streams and inland from them.

3.2 Material and methods

3.2.1 Riverine inputs in the Bay of Arcachon

The water masses in the Bay of Arcachon are mainly influenced by tidal entrance of oceanic waters. However, two main sources of freshwater into the lagoon can be considered, The Leyre river, at the southeast, and the Porge Canal at the north ends. Overall, freshwater inputs into the lagoon represent less than 1% of the tidal prism (Plus et al. 2009). However, a salinity dilution induced by the Leyre has been registered on the eastern – southeastern section of the Bay (Bouchet et al. 1997). Several small streams of continental water discharge can be found along the eastern side of the Bay but they are of small dimensions with surfaces not exceeding 30 Km^2 (Canton 2009). Even though this influence is low at the scale of the Bay, it gains importance at local scale where it might affect the plant species dominance.

3.2.2 Experimental design

A removal experiment was implemented, between the 17 March 2017 and the 11 May 2017, on freshwater streams running into on marshes on the eastern side of the Bay of Arcachon. We considered two distances from the streams, in both the native and exotic *Spartina* patches within eight sites. The experiment was implemented with a split-plot design. The height sites were randomly chosen for the presence of a freshwater input into the Bay and the dominance of the *Spartina* species, with four sites dominated by *Spartina maritima* and four sites by *Spartina anglica* (Dominant species as main treatment – Figure 3.1a). Within each site, two distances from the source of freshwater were considered, one close, on the border of the freshwater input, and one far, at approximately 10 m from it (sub-treatment). At each distance, two replicates of each experimental treatment were implemented. The experiment consisted in two plots of 30 x 30 cm, one with neighbours, where the plants of the local *Spartina* population were left intact (control treatment) and, one without neighbours where the individuals of the local population were removed by hand (removed treatment). In each plot, six plant individuals were transplanted, three from the native *Spartina maritima* and three from the exotic *Spartina anglica* (transplant species treatment – second sub-sub-treatment). The height and leaf number of all transplanted individuals was registered at the moment of the transplant (T_i) and again at the end of the experiment (T_f). In total, 384 transplants were used (2 Dominants x 4 Dominant replicates x 2 Distances x 2 Removal treatments x 2 Removal treatment replicates x 2 Transplant species x 3 transplant replicates – Figure 3.1b). Within each plot environmental measurements were performed the 12 April 2017, using a multi-parameter probe that measured pH, redox potential (Eh) and conductivity.

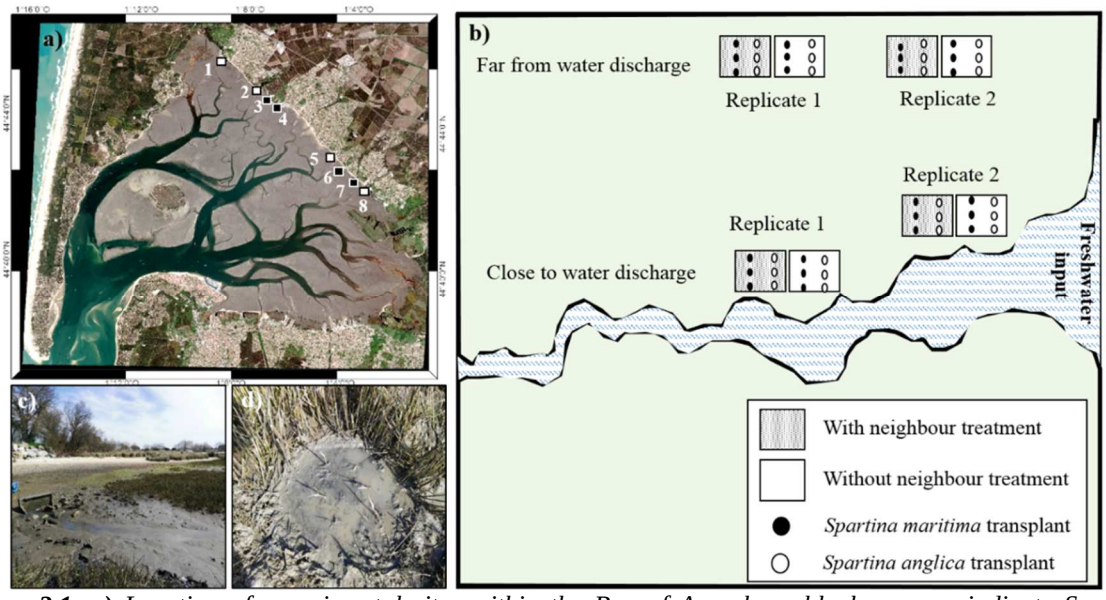

Figure 3.1. a) *Location of experimental sites within the Bay of Arcachon; black squares indicate Spartina maritima dominated sites and white squares indicate Spartina anglica dominated sites; Numbers label site names as follows: 1 – Arès, 2 – St. Brice, 3 – Andernos, Quinconces beach, 4 – Andernos, oyster farm, 5 – Taussat, oyster farm, 6 – Taussat, 7 – Cassy harbour north, 8 – Cassy harbour south.* ***b)*** *Schematic representation of the design experiment within one site.* ***c)*** *Photograph of freshwater input at Andernos, Quinconces beach (site 3) and d) Photograph of removal plot with transplanted Spartina individuals.*

3.2.2.1 Interaction data processing

Survival percentages were estimated based on the number of transplant individuals found alive at the end of the experiment. Individuals that were not found were considered as dead.

For survivor transplants, in order to understand how both biotic interactions and environmental conditions affected growth, the height or leaf increment rate (μ) was estimated as follows:

$$\mu = (X_{Tf} - X_{Ti}) / X_{Ti}$$

where X corresponds to the height of transplanted individuals or their leaf number, respectively at the initial (T_i) and final (T_f).

In order to quantify the performance of both *Spartina* species' transplants growing in the presence and absence of neighbours, the Relative Interaction Index (RII) was estimated according to Armas et al. (2004):

$$RII = \frac{(X_{with\ neighbour} - X_{without\ neighbour})}{(X_{with\ neighbour} + X_{without\ neighbour})}$$

where $X_{with\ neighbour}$ corresponds to the performance of individuals growing in the presence of neighbours and $X_{without\ neighbour}$ corresponds to the performance of individuals growing in the absence of neighbours. This index comprises values between -1 and 1 where negative values indicate competition, positive values indicate facilitation and 0 corresponds to no significant interactions.

3.2.3 Sediment and water sampling

Water and sediment samples were collected for the 8 sites between the 14 and the 17 March 2017.

Sediment cores were collected with a 30 cm long and 6 cm diameter PVC tube. Three replicates were performed per distance from the water input within each site.

3.2.3.1 Treatment of sediment and water samples and estimation of nutriment concentration profiles

Sediment samples were prepared by cutting the sediment cores at different depths, namely, from 0 – 2 cm, 2 – 7 cm, 10 – 15 cm and 15 – 20 cm. In the laboratory, the interstitial water from each sample was recovered through centrifugation and it was sub-sampled for subsequent analysis of iron, phosphate and nitrate and ammonium concentration applying the respective methods according to the target nutrient. To ensure that only dissolved nutriment content was analysed, all water samples (both interstitial sediment water and from the freshwater source) were filtered at 2 μm. Samples for nitrate and nitrites analysis were frozen and samples for iron and phosphate analysis were acidified with chloride acid (HCL) in order to prevent precipitation from iron oxides. Colour analyses was then performed for iron (Stookey 1970), phosphate (Murphy and Riley 1962), nitrate (Schnetger and Lehners 2014) and nitrite (Strickland and Parsons 1972) samples. Ammonium samples were analysed through conductivity flow injection analysis following Hall and Aller (1992).

Nutrient concentration profiles were then obtained by the estimation of the cumulated concentration of all considered levels. Concentrations for the level between 7 – 10 cm, that were not considered for logistic reasons, were estimated through averaging concentrations from 2 -7 cm and 10 – 15 cm levels. Samples corresponding to 15 – 20 cm depth were not considered as they presented much higher porosity than the above layers and sediment composition was mainly sandy. Because of the relatively surficial considered depths, in order to obtain significant results nutrient concentrations were brought to $mol.m^{-2}$.

3.2.4 Plant trait measurements

At the end of the experiment, measurements of plant morphological traits were performed within the two *Spartina* communities, following Cornelissen et al. (2003). Plant vegetative and reproductive height were measured in situ at the two considered distances from the stream for 5 individuals (replicates) randomly picked within a 30 x 30 cm quadrat. Additionally, five plant individuals were sampled and taken to the lab, where they were scanned to determine the Specific Leaf Area (SLA). They were also weighted before and after being dried for 48h at 70°C. The Leaf Dry Mass Content (LDMC) was estimated with the fresh and dry weights through the relation

$$LDMC = \text{Leaf dry mass} / \text{Leaf fresh mass}$$

which is given in $g.g^{-1}$.

3.2.5 Statistical analysis

Survival, height and leaf increment rate data were analysed with a 4-way ANOVA considering dominant community (*S. maritima* and *S. anglica*), distance from the stream (close and distant), neighbours (presence and absence) and target species (*S. maritima* and *S. anglica*) as crossed factors. For RII analysis, a 3-way ANOVA was implemented, considering dominant species, distance from the stream and target species as crossed factors. The environmental parameters Eh and conductivity were analysed with a 3-way ANOVA with dominant, distance from the stream and neighbours as crossed factors. Nutrient cumulated concentrations were analysed with a 2-way ANOVA considering dominant species and distance to the stream as independent factors. Plant height, SLA and LDMC were analysed with a two-way ANOVA considering dominant species and distance to the stream as independent factors. The ANOVA analyses were considered with a split -plot design considering the dominant community as the main treatment and distance from the stream, removal and target species as sub-treatments.

Simple Student tests were performed on RII values in order to determine significant differences from zero value. All statistical tests were performed with R software (R Development Core Team 2013).

3.3 Results

3.3.1 Environmental and nutrient characterization

For soil oxygenation, there was a significant interaction between the dominant community and the relative distance to the stream (p = 0.04, Table 3.1) because only within *S. maritima* communities Eh values were more negative further from the freshwater stream (Figure 3.2a). For conductivity, we found a tendency for a significant dominant effect (p = 0.08, Table 3.1) because values tended to be higher within *S. anglica* than within *S. maritima* communities (Figure 3.2b). Finally, for pH, there was also a tendency for significant dominant X removal X distance interaction because at close distance to the stream pH increased in the removed plots for *S. maritima* but decreased for *S. anglica* while there were no differences due to the removal treatment effect in both communities further away from the stream (Figure 3.2c, Table 3.1).

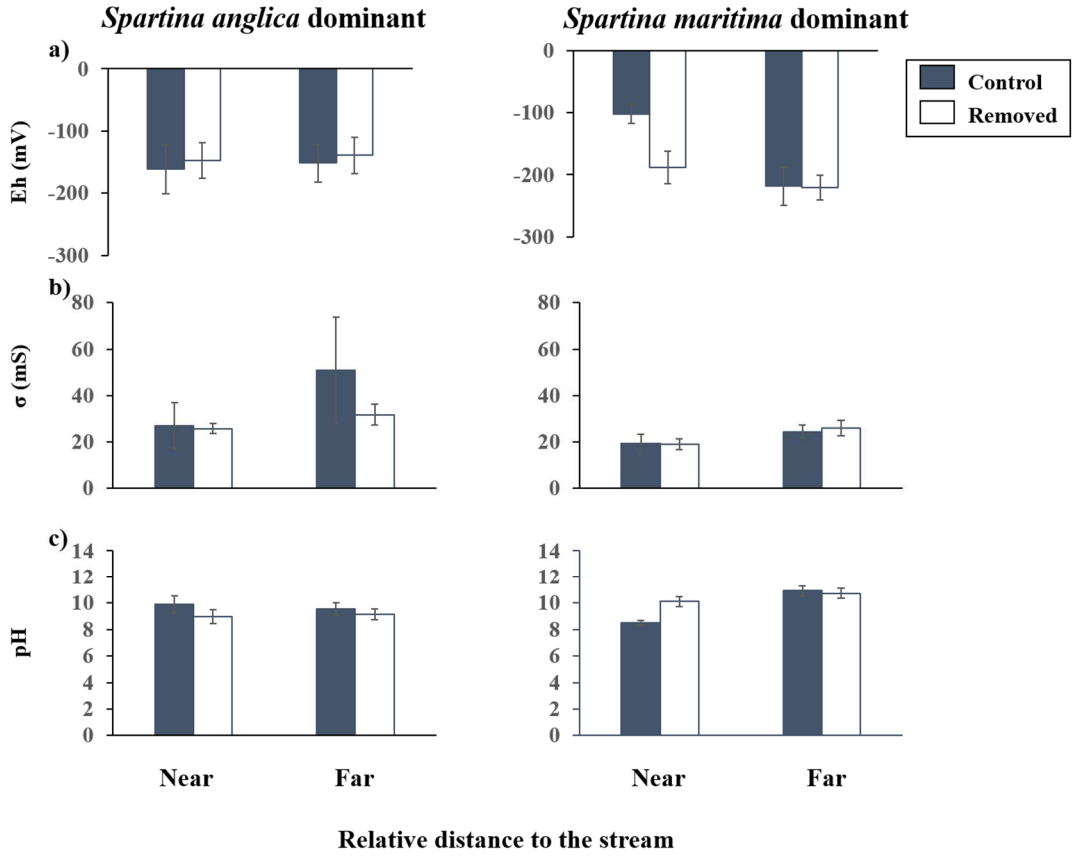

Figure 3.2. *Means (± SE, N = 64) of* ***a)*** *redox potential,* ***b)*** *conductivity and* ***c)*** *pH in the control (dark bars) and removed (white bars) subplots of S. anglica and S. maritima dominants at the two distances from the freshwater stream (near and far).*

***Table 3.1**. Results of the ANOVA on the effects of dominant, distance to the stream and removal treatment and their interactions redox potential (Eh), conductivity (σ) and pH. Significant effects are indicated in bold.*

	Redox potential			Conductivity			pH		
Source of variation	df	F	p	df	F	p	df	F	p
Dominant	1	2.63	0.11	1	3.21	0.08	1	4.52	**0.04**
Distance	1	2.68	0.11	1	2.57	0.11	1	5.38	**0.02**
Removal	1	0.61	0.44	1	0.54	0.46	1	0.005	0.94
Dom. x Dist.	1	4.41	**0.04**	1	0.43	0.51	1	6.55	**0.01**
Dom. x Rem.	1	2.08	0.15	1	0.69	0.41	1	4.78	**0.03**
Dist. x Rem.	1	1.07	0.30	1	0.37	0.54	1	1.08	0.30
Dom. x Rem. x Dist.	1	1.14	0.29	1	0.57	0.45	1	3.39	0.07
Residuals	56			56			56		

For nitrates, although the statistic tests were not significant, we found a tendency for distance and dominant effects, with higher nitrates concentration away from the stream and in *S. maritima* than *S. anglica* dominants, respectively (Figure 3.3 and Table 3.2). In contrast, for ammonium, there was a highly significant distance effect, due to lower values further away than closer to the stream. For phosphates, there was a significant dominant by distance interaction, due to higher values close to the stream within *S. anglica* community only (Figure 3.3 and Table 3.2). For iron, there was a highly significant dominant effect, due to higher values within *S. maritima* than within *S. anglica* communities (Figure 3.3 and Table 3.2).

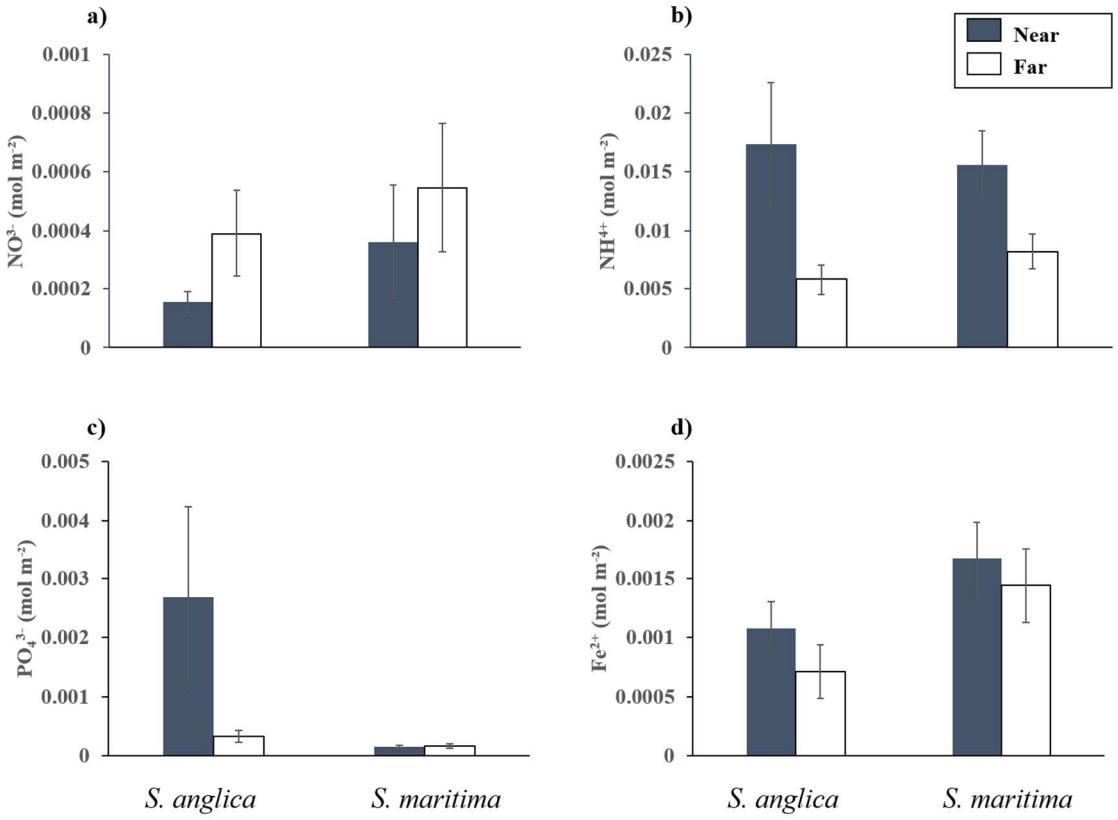

Figure 3.3. *Cumulated concentrations (± SE mol m-2) of* ***a)*** *Nitrate (NO 3-),* ***b)*** *ammonium (NH4+),* ***c)*** *phosphate (PO43-) and* ***d)*** *iron (Fe2+) in soil sediments within the two dominant species (S. anglica and S. maritima) at the two relative distances from the freshwater stream, near (dark bars) and far (white bars).*

Table 3.2. *Results of the ANOVA on the effects of dominant, distance to the stream and depth of soil sample and their interactions on nutrient concentrations nitrate Nitrate (NO 3-), ammonium (NH4+), phosphate (PO43-) and iron (Fe2+). Significant results are indicated in bold.*

	Nitrate			Ammonium			Phosphate			Iron		
Source of variation	df	F	p	df	F	p	df	F	p	df	F	p
Dominant	1	2.79	0.1	1	0.003	0.96	1	8.21	**0.005**	1	10.86	**0.001**
Distance	1	3.71	0.06	1	18.5	**< 0.001**	1	6.15	**0.01**	1	2.14	0.14
Depth	3	1.22	0.30	3	4.73	**0.003**	3	1.66	0.18	3	9.68	**< 0.001**
Dom. x Dist.	1	0.05	0.82	1	1.45	0.23	1	6.26	**0.01**	1	0.11	0.74
Dom. x Depth	3	0.18	0.91	3	0.16	0.92	3	1.28	0.28	3	2.48	0.06
Dist. x Depth	3	0.22	0.88	3	1.57	0.2	3	0.92	0.43	3	1.81	0.15
Dom. x Dist. x Depth	3	0.66	0.58	3	0.44	0.72	3	0.91	0.43	3	0.07	0.98
Residuals	176			175			176			176		

3.3.2 Plant traits

For height, there was a highly significant distance effect because both species were 20% taller close to the stream than away from it (Figure 3.4, Table 3.3).

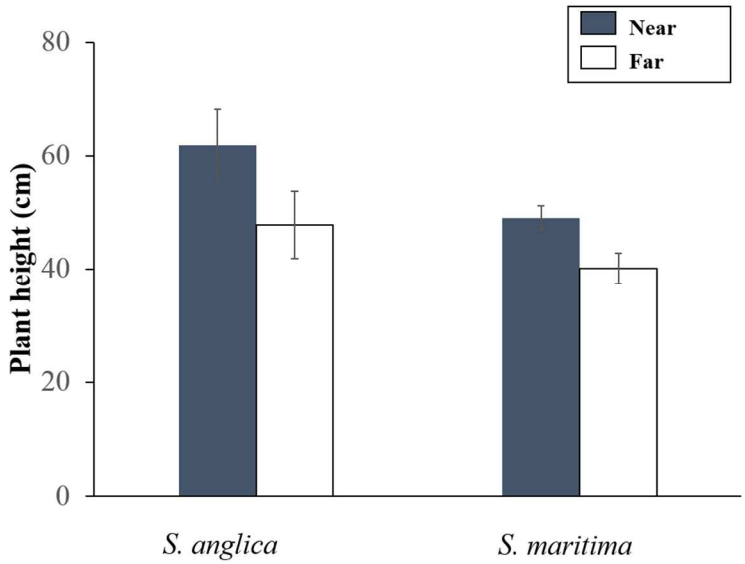

Figure 3.4. *Mean plant height (± SE) for Spartina anglica and Spartina maritima dominated communities at the two relative distances from the freshwater stream, near (dark bars) and far (white bars).*

For SLA, there was a highly significant dominant by distance interaction (p = 0.001, Table 3.3), because, closer from the stream, there was a much higher increase (36 %) in SLA in the *S. anglica* community than in the *S. maritima* community (Figure 3.5a). Finally, there was no significant treatment effects for Leaf Dry Mass Content (LDMC – Figure 3.5b).

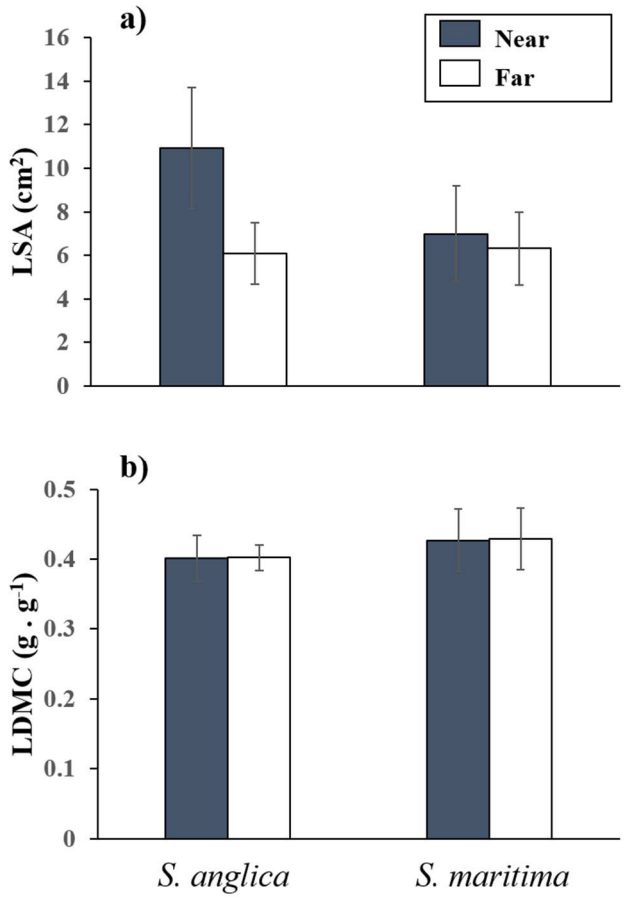

Figure 3.5. a) *Specific leaf area (LSA) and* ***b)*** *Leaf Dry Mass Content (LDMC) for Spartina anglica and Spartina maritima at the two relative distances from the freshwater stream, near (dark bars) and far (white bars).*

Table 3.3. *Results for ANOVA on the effects of dominant and distance to the stream and their interaction on Plant height, Specific Leaf Area (SLA) and Leaf Dry Mass Content (LDMC). Significant results are indicated in bold.*

	Plant height			SLA			LDMC		
Source of variation	df	F	p	df	F	p	df	F	p
Dominant	1	43.20	< **0.001**	1	9	**0.003**	1	0.12	0.72
Distance	1	55	< **0.001**	1	19.92	< **0.001**	1	0.80	0.37
Dom. x Dist.	1	2.67	0.10	1	11.27	**0.001**	1	0.69	0.41
Residuals	116			116			116		

3.3.3 Removal experiment

For survival (Figure 3.6), there was a significant Dominant x Treatment x Distance interaction, because in the *S. maritima* community there was an increase in the negative effect of neighbours when getting further from the stream, whereas there was an opposite tendency in the *S. anglica* community (p = 0.03, Table 3.4).

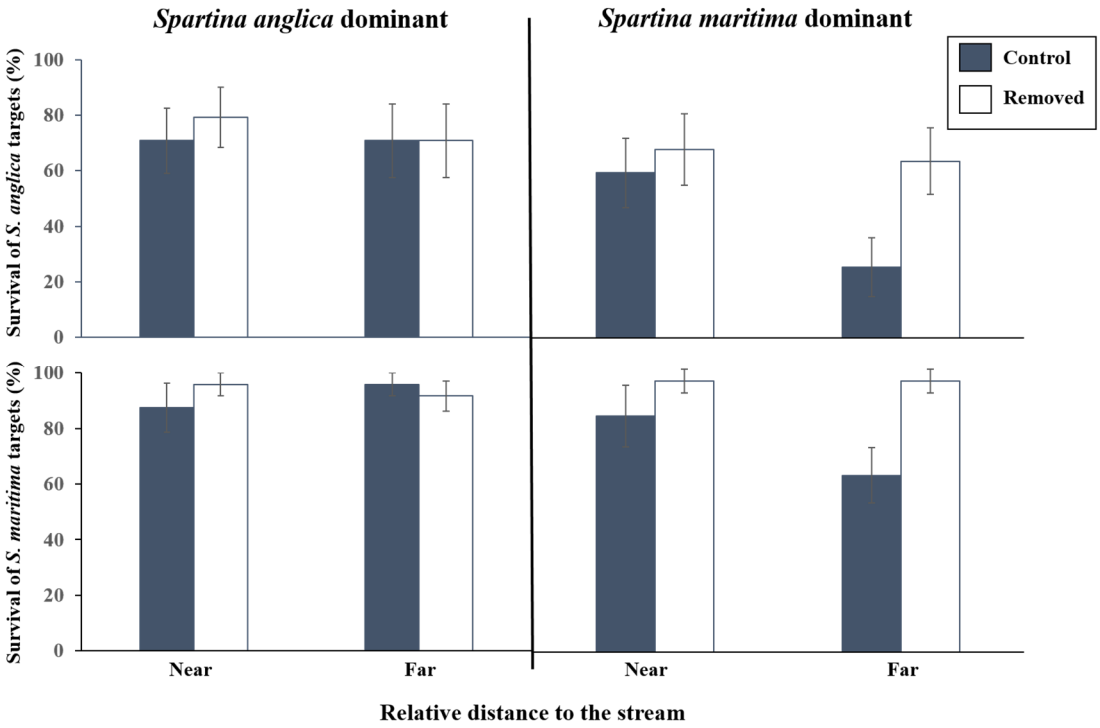

Figure 3.6. *Mean survival (± SE) of the two target species, Spartina anglica and Spartina maritima, within the two dominant communities at different distances from the freshwater stream (near and far), both in the presence (control – black bars) and absence of neighbours (removed – white bars).*

For growth, there was a significant distance effect (p = 0.02, Table 3.4), because growth rate was higher for transplants close to the stream (Figure 3.7). There was also a significant Dominant by Treatment interaction because of higher growth rates in the presence of neighbours in the *S. anglica* community and the opposite for *S. maritima* communities (p = 0.04, Table 3.4).

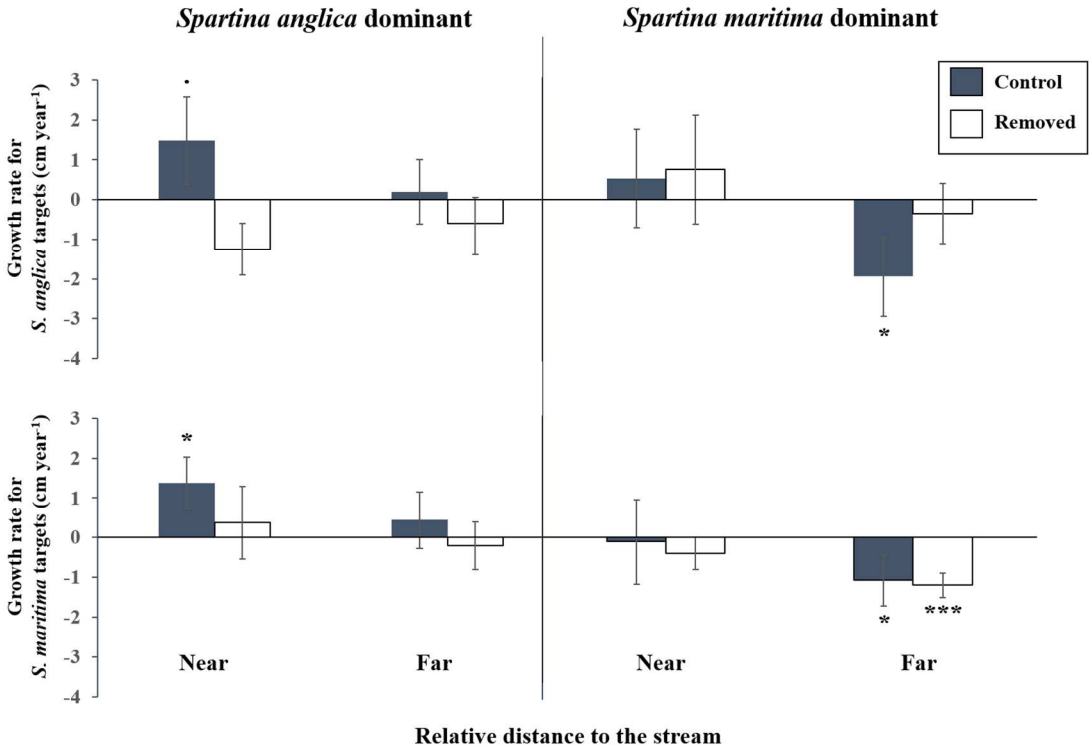

Figure 3.7. *Mean growth rate (± SE) of the two target species, Spartina anglica and Spartina maritima, within the two dominant communities at the two distances from the freshwater stream (near and far), both in the presence (control – black bars) and absence of neighbours (removed – white bars). Results of t-tests are indicated above and below respective bars with asterisks: ., p < 0.1; *, p < 0.05; **, p< 0.01; ***, p< 0.001*

Table 3.4. *Results of the split-plot ANOVA on the effects of dominant, distance to the stream, removal treatment and target and their interactions on transplant survival and growth rate. Significant effects are indicated in bold.*

	Survival			Growth rate		
Source of variation	df	F	p	df	F	p
Dominant	1	14.54	**0.00016**	1	5.68	**0.02**
Distance	1	4.13	**0.043**	1	5.63	**0.02**
Removal	1	7.82	**0.0054**	1	3.25	0.07
Target	1	37.21	**< 0.0001**	1	0.08	0.79
Rem. x Dist.	1	0.58	0.45	1	1.25	0.26
Dom. x Rem.	1	4.13	**0.043**	1	4.42	**0.04**
Rem. x Target	1	0.06	0.8	1	0.13	0.72
Dom. x Rem. x Dist.	2	3.65	**0.03**	2	1.09	0.34
Dom. x Rem. x Dist. x Target	6	0.46	0.83	6	0.78	0.58
Residuals	368			276		

Results for RII survival were consistent with those of Figure 3.6, with a significant Dominant by Distance interaction, due to an increase in competition only in the *S. maritima* community when getting further away from the stream (p = 0.01, Table 3.5, Figure 3.8).

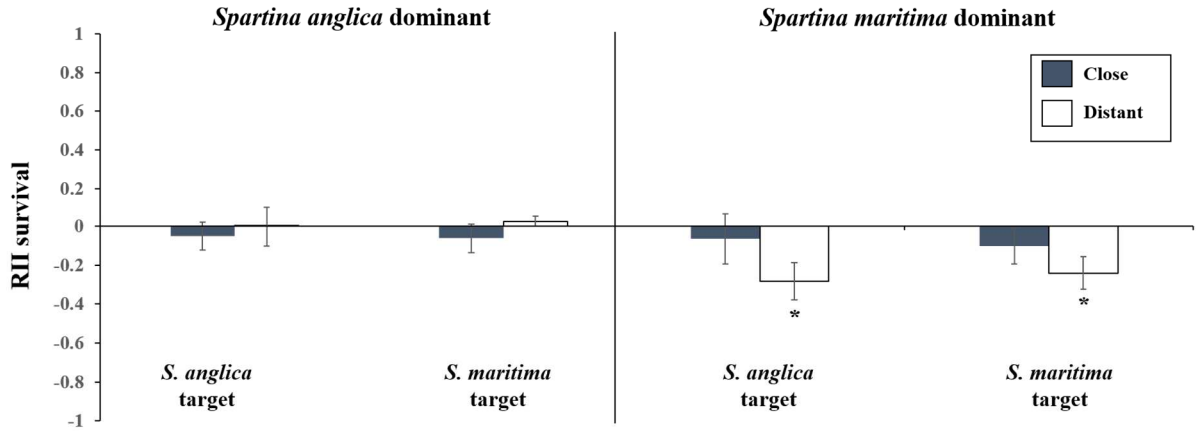

Figure 3.8. *Mean (± SE) Relative Interaction Index (RII) for target species survival both in Spartina anglica and Spartina maritima dominance at two distances form the freshwater stream, close (black bars) and distant (white bars). Positive values correspond to facilitation and negative values to competition. Results of t-tests are indicated below the respective bars with asterisks: *, $p < 0.05$.*

Table3. 5. *Results of the split-plot ANOVA on the effects of dominant, distance to the stream and target and their interactions on RII survival. Significant effects are indicated in bold.*

	RII Survival		
Source of variation	df	F	p
Dominant	1	8.26	**0.006**
Distance	1	2.17	0.14
Target	1	0.55	0.46
Dom. x Dist.	1	3.30	**0.01**
Dom. x Target.	1	0.41	0.53
Dist. x Target	1	1.21	0.27
Dom. x Dist. X Target	1	0.69	0.41
Residuals	56		

3.4 Discussion

We showed that the proximity to freshwater discharges ameliorates plant growth conditions in salt marshes. A general increase in ammonium and phosphate concentrations was found, close to freshwater input, particularly for *Spartina anglica* communities. Both species grew taller closer to the streams. However, only *S. anglica* showed higher growth rates closer to the freshwater streams, translated by higher values of SLA. The proximity to freshwater inputs induced a decrease in the competitive behaviour of *S. maritima* considering target plant survival, whereas for *S. anglica* facilitated plant growth for both species. Overall, nutrient loads into the Bay, through freshwater discharges seem to decrease the competitive resistance of the native *Spartina* and to ameliorate the conditions for *Spartina anglica* that lead to a self-facilitating behaviour for this species and, consequently, increasing its invasion success. This self-facilitation for growth had already been observed in the previous assessment of niche occupation by the two *Spartina* species (**Chapter 2**), where the exotic *Spartina* presented high intraspecific facilitation for growth that was linked to its investment in a well-developed root system inducing subsequent sediment oxygenation.

3.4.1 Environmental and nutrient characterization

Previous studies have shown that the small freshwater streams running into the Bay of Arcachon are a source of nutrients (Rimmelin et al. 1998, Canton 2009). For plant absorption, independently of loading, the most essential nutrients are nitrates and phosphates, under their mineral form. Ammonium is also important as its biological degradation (nitrification) can be fast and, hence, increase nitrates availability for plant assimilation.

With this experiment, it was shown that phosphorus availability was higher closer to the freshwater inputs, particularly within *S. anglica* communities. Indeed, phosphorus is a particularly dynamic element that undergoes rapid recycling (Canton 2009). This element is easily absorbed by metallic oxides, namely iron and aluminium (Anschutz et al. 1998) and within highly anoxic sediments, during organic matter degradation, metallic oxides work as oxidisers instead of oxygen (Froelich et al. 1979). The fact that *S. maritima* communities presented very low concentrations of phosphates can be related to the high iron concentrations within this community, meaning that the above mentioned absorption processes are probably happening, keeping phosphorus concentrations very low.

Concerning ammonium availability, higher and alike concentrations were also found within closer distance from the streams, independently of *Spartina* dominance which indicates that freshwater inputs are a likely a source of this element into the system. Conversely, nitrate concentrations showed both a dependency on the distance to the streams, being lower closer to the freshwater inputs and in the *Spartina* community, higher within *S. maritima* communities. The higher nitrate concentrations found within *S. maritima* communities suggest that this nutrient is not being absorbed by the native species. Additionally, before being absorbed by the plants, nitrates go through a bacterial denitrification process and mudflats in general are a favourable environment for such process. Therefore, the general high biological activity within the mudflat, that is additionally certainly dependent on the plant communities, is a likely

explanation of these variations in nitrate concentration within the sediments underneath the two *Spartina* species.

However, the role of freshwater discharges and the performance of macrophytes is not always directly related (Adams et al. 2009) as other indirect effects can interfere with nutrient availability, like salinity or sediment redox potential. For example, it has been shown for *Spartina patens*, that abiotic stresses, such as increased salinity, negatively affected nutrient uptake and plant growth (Merino et al. 2010). Higher salt marsh production in the presence of freshwater inputs is related not only to increased nutrient availability, but also to salinity dilution by freshwater (Adams et al. 2009). However, Matzke and Elsey-Quirk (2018) found that, despite large plant response to added nutrients, soil properties were unaffected. Here, conductivity measurements showed lower values in the proximity of the water discharge, which certainly contributes to better nutrient uptake by both species which can improve plant growth, and, in particular, that of the exotic *Spartina*.

3.4.2 Removal experiment

Studies on salt marsh vegetation have reported phenotypic variations linked to the proximity of nutrient sources that translated into higher plants and more dense meadows (Matzke and Elsey-Quirk 2018). Additionally, nutrient availability is likely to affect species performance through their competitive strategies. Nutrient enrichment has previously been demonstrated to positively affect plant aboveground biomass and productivity (Valiela et al. 1976, Sundareshwar et al. 2003, Więski and Pennings 2014, Matzke and Elsey-Quirk 2018). The removal experiment presented in this chapter has shown that both the exotic and the native *Spartina* benefited from the proximity to the freshwater source as transplants on plots close to the stream presented better performances. We have observed distinct results for community dominance between the two species. The effect of the exotic *Spartina*'s community on target survival was overal neutral. However, for growth there was an overall facilitative behaviour of *Spartina anglica* for both conspecific and congeneric plants. Additionally, with the inproximity to the stream, the intraspecific facilitation of *S. anglica* was increased. Conversely, within *S. maritima* communities, there was mostly competition because both target survival and growth were negatively affected by the dominant species.

On the contrary, within *S. maritima* communities, *S. anglica* transplants experienced stronger competition for survival, particularly with increasing distance from the freshwater source which corroborates previous findings, suggesting that the native species provides biotic resistance against the invasion of *S. anglica*. Within the two communities, results on both survival and growth rate showed contrasting competitive effects and responses, for both species. For instance, *S. maritima* community presented a strong competitive effect at increasing distance from the stream while *Spartina anglica* community exhibited a facilitator behaviour, independently of the distance to the freshwater stream. These results are consistent with the findings presented in the previous chapter (Proença et al. 2019). However, in contrast with the former study, where *S. anglica* only presented a self-facilitating behaviour, here, the exotic species community facilitated also the native species. In Proença et al. (2019), this facilitating behaviour was related to the higher rhizome density presented by the exotic *Spartina* which resulted in higher soil redox potential, indicating more aerated substrates within

S. anglica communities. However, in this experiment, redox potential measurements are not completely consistent with the previous ones as soils were found to be more anoxic within *S. anglica* than *S. maritima*. Such difference could be related to the fact that environmental measurements of the present experiment were performed in May whereas for the experiment previously presented in **Chapter 2** they were performed in mid-June. Indeed, May still corresponds to an early stage of seasonal development of the invasive *Spartina* whereas the native one is already developed.

Overall, transplant survival and growth rates were positive in the proximity of the streams which is probably a result of an environmental amelioration related to nutrient availability and lower salinity. In contrast the survival and growth rates of the exotic *Spartina* were negatively affected by the increase in distance from the stream. This effect was particularly stronger in the presence of neighbours. Such result suggests that the position further away from the riverine discharge corresponds to a more stressful environment where competition between individuals becomes more important. Indeed, competitive interactions among plant species vary along resource gradients and observations are sometimes conflicting (Davis et al. 2000). According to Grime's theory (1974), competition decreases with increasing levels of disturbance and stress. However, the results here presented have shown that for *S. maritima* communities competition increased further away from the freshwater streams, independently of the target species. As it was mentioned above, the positions further from the stream presented more stressful conditions being characterized by more saline soils and, particularly within *Spartina maritima* communities, phosphorus availability is low indicating it as a limitation resource. Within *Spartina anglica* communities on the contrary, a general tendency for facilitation was found. We can also consider (Tilman 1982) model that proposes that competition is related to resource allocation trade-offs and, in that case, competition intensity might still be high within unproductive and stressful environments but it will concern root-competition in nutrient poor environments and competition for light in nutrient rich ones. *Spartina anglica* presented higher SLA than *Spartina maritima*, indicating a more exploitative strategy than *S. maritima*. Even though *Spartina anglica* presents a rapid growth that is typical from ruderal plants, previous results (**Chapter 2**) have shown that this species also favours the allocation to roots and rhizomes, which contradicts Tilman's theory of the trade-offs that indicates fast growing plants as poorly attributed in roots. Such capacity to combine two different strategies is probably related to *Spartina anglica* success in colonize harsh environments that present strong physical perturbations and cope with frequent inundation and highly anoxic soils.

Additionally, previous studies have demonstrated that the importance of positive interactions increases in harsh environments, like salt marshes, (Bertness and Hacker 1994, Bertness and Callaway 1994). In accordance with this, it has been shown that the exotic *Spartina* exhibits intraspecific facilitation. However, Michalet (2006) found facilitating behaviours in medium-stress environments that decreased in extremely stressed conditions and, according to Maestre and Cortina (2004), when stress levels become extreme, biotic interactions might even switch back to competition. Mudflats are usually poor nutrient systems that present low oxygen diffusion conditions that characterize them as stressful environments. This could explain the low performance of *S. anglica* within the native *Spartina* communities, since the latter presents high competitive abilities. Alternatively, the low performance of the

invasive species could be related to a premature ending of the experiment, at a time where this species was not at the peak of its seasonal development. In order to confirm this, further experiments should be performed lasting to the end of the summer season and thus considering the full development of the exotic species.

3.5 Conclusions

Freshwater streams are not only a source of nutrients but also they favour soil oxygenation induced by the water flow. Both species presented better performances (higher survival and growth rates) in the proximity of freshwater streams, where environmental conditions were characterized by lower salinities, higher nutrient concentrations and higher redox potential. It was shown that competition is stronger within the native *Spartina* communities and at further distances from the freshwater streams. For both species, competition decreased with decreasing distance from the streams. Additionally, for *S. anglica*, away from the freshwater inputs, interactions even shifted back to facilitation.

In summary, we can conclude that nutrient inputs allied to soil oxygenation through the freshwater inputs induce a decrease in the biotic resistance of *Spartina maritima*. Such conditions can provide an opportunity for the invasion of the exotic species that, has a strong self-facilitative behaviour. This self-facilitation presented by *S. anglica* becomes even more important as it presents higher growth plasticity than the native *Spartina*, within more favourable environmental conditions.

References

Adams, J. B. et al. 2009. The distribution of estuarine macrophytes in relation to freshwater. - Botanica Marina 35: 215–226.

Ainouche, M. L. et al. 2004. *Spartina anglica* C. E. Hubbard: a natural model system for analysing early evolutionary changes that affect allopolyploid genomes. - Biological Journal of the Linnean Society 82: 475–484.

Anschutz, P. et al. 1998. Burial efficiency of phosphorus and the geochemistry of iron in continental margin sediments. - Limnology and Oceanography 43: 53–64.

Armas, C. et al. 2004. Measuring plant interactions: a new comparative index. - Ecology 85: 2682–2686.

Bertness, M. D. and Hacker, S. D. 1994. Physical stress and positive associations among marsh plants. - The American Naturalist 144: 363–372.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. - Trends in Ecology & Evolution 9: 191–193.

Bornette, G. and Puijalon, S. 2011. Response of aquatic plants to abiotic factors: a review. - Aquat Sci 73: 1–14.

Bouchet, J.-M. et al. 1997. Etude Intégrée du Bassin d'Arcachon - Synthèse.

Canton, M. 2009. Dynamique des éléments biogènes dans le continuum fluvio-estuarien de la zone hydrologique d'influence du Bassin d'Arcachon.

Cornelissen, J. H. C. et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. - Australian Journal of Botany 51: 335.

Davis, M. A. et al. 2000. Fluctuating resources in plant communities: a general theory of invasibility. - Journal of Ecology 88: 528–534.

DeLaune, R. D. et al. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. - Estuarine and Coastal Marine Science 8: 477–487.

Díaz, S. et al. 2016. The global spectrum of plant form and function. - Nature 529: 167–171.

Duarte, B. et al. 2015. A tale of two spartinas: Climatic, photobiological and isotopic insights on the fitness of non-indigenous versus native species. - Estuarine, Coastal and Shelf Science 167: 178–190.

Froelich, P. N. et al. 1979. Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. - Geochimica et Cosmochimica Acta 43: 1075–1090.

Grime, J. P. 1974. Vegetation classification by reference to strategies. - Nature 250: 26–31.

Hall, P. 0 J. and Aller, R. C. 1992. Rapid, small-volume, flow injection analysis for SCO2, and NH4+ in marine and freshwaters. - Limnology and Oceanography 37: 1113–1119.

Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase*. - Phycologia 32: 79–99.

Koop-Jakobsen, K. et al. 2017. Survey of sediment oxygenation in rhizospheres of the saltmarsh grass - *Spartina anglica*. - Science of The Total Environment 589: 191–199.

Levine, J. M. et al. 1998. Nutrients, competition and plant zonation in a New England salt marsh. - Journal of Ecology 86: 285–292.

Maestre, F. T. and Cortina, J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. - Proc Biol Sci 271: S331–S333.

Maestre, F. T. et al. 2003. Positive, Negative, and Net Effects in Grass–Shrub Interactions in Mediterranean Semiarid Grasslands. - Ecology 84: 3186–3197.

Matzke, S. and Elsey-Quirk, T. 2018. *Spartina patens* Productivity and Soil Organic Matter Response to Sedimentation and Nutrient Enrichment. - Wetlands 38: 1233–1244.

Merino, J. H. et al. 2010. Implication of nutrient and salinity interaction on the productivity of *Spartina patens*. - Wetlands Ecol Manage 18: 111–117.

Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? - New Phytologist 169: 3–6.

Murphy, J. and Riley, J. P. 1962. A modified single solution method for the determination of phosphate in natural waters. - Analytica Chimica Acta 27: 31–36.

Pennings, S. C. and Bertness, M. D. 2001. Salt Marsh Communities. - *In:* Marine Community Ecology. Bertness MD, Gaines SD,Hay M. in press.

Pezeshki, S. R. and DeLaune, R. D. 2012. Soil Oxidation-Reduction in Wetlands and Its Impact on Plant Functioning. - Biology (Basel) 1: 196–221.

Plus, M. et al. 2009. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. - Continental Shelf Research 29: 1008–1013.

Proença, B. et al. 2019. Intraspecific facilitation explains the spread of the invasive engineer *Spartina anglica* in Atlantic salt marshes. - Journal of Vegetation Science in press.

R Development Core Team 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Reinhart, K. O. and Callaway, R. M. 2006. Soil biota and invasive plants. - New Phytol. 170: 445–457.

Rimmelin, P. et al. 1998. Study of Annual and Seasonal Dissolved Inorganic Nitrogen Inputs into the Arcachon Lagoon, Atlantic Coast (France). - Estuarine, Coastal and Shelf Science 47: 649–659.

Schnetger, B. and Lehners, C. 2014. Determination of nitrate plus nitrite in small volume marine water samples using vanadium(III)chloride as a reduction agent. - Marine Chemistry 160: 91–98.

Seliskar, D. M. et al. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant : a *Spartina alterniflora* salt-marsh case study. - Journal of Ecology 90: 1–11.

Stookey, L. L. 1970. Ferrozine-a new spectrophotometric reagent for iron. - Anal. Chem. 42: 779–781.

Strickland, J. D. H. and Parsons, T. R. 1972. A practical handbook of seawater analysis. - Fisheries Research Board of Canada Bulletin 167: 1–31.

Sundareshwar, P. V. et al. 2003. Phosphorus Limitation of Coastal Ecosystem Processes. - Science 299: 563–565.

Thompson, J. D. et al. 1991. Population Variation in *Spartina anglica* C. E. Hubbard. III. Response to Substrate Variation in a Glasshouse Experiment. - The New Phytologist 117: 141–152.

Tilman, D. 1982. Resource Competition and Community Structure. - Princeton University Press.

Tyler, A. C. et al. 2007. Nitrogen inputs promote the spread of an invasive marsh grass. - Ecol Appl 17: 1886–1898.

Valiela, I. et al. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass - download. - Limnology and Oceanography 21: 245–252.

Valiela, I. et al. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: Tidal exchanges and inputs by precipitation and groundwater 1. - Limnol. Oceanogr. 23: 798–812.

Vitousek, P. M. et al. 1997a. Introduced species: A significant component of human-caused global change. - New Zealand Journal of Ecology 21: 116.

Vitousek, P. M. et al. 1997b. Human Domination of Earth's Ecosystems. - Science 277: 494–499.

Więski, K. and Pennings, S. C. 2014. Climate Drivers of *Spartina alterniflora* Saltmarsh Production in Georgia, USA. - Ecosystems 17: 473–484.

CHAPTER 4

Spatial and temporal interactions between Spartina anglica and Zostera noltei

Ecosystem engineers are living species that contribute to the shaping of the environment they inhabit by interacting with the incident physical forces they are subjected to. In the long-term, such modifications can propagate from a local scale and evolve into changes in the landscape morphology affecting physical habitats on a larger extent. *Spartina* sp. are known for their ecosystem engineering ability, mostly related to sediment-trapping by their aerial biomass. Because of such effect *Spartina species* tend to change intertidal mudflat, a marine environment, into a terrestrial one.

We have seen in **Chapter 2** that the European native *Spartina maritima* is a competitive species that offers resistance to the invasion of *Spartina anglica*. Because the exotic species has the capacity to colonize towards the inner Bay, which is an area originally mainly occupied by the seagrass *Zostera noltei*, the question that arises is: how can the seagrass be affected by the arrival of this stronger ecosystem engineer? In order to assess the extent of the impact of tidal flat colonization by *S. anglica* over *Z. noltei*, an experimentation was implemented in the Bay of Arcachon. Individual *Spartina anglica* tussocks were randomly selected on the mudflats within Lanton community, on the eastern side of the Bay. *Spartina* vegetation within half of the tussock was left intact and on the other half its aerial parts were cut. A transect of *Z. noltei* transplants was performed over each one of the two previously described treatments, as well as control transect on sounding mudflat, out of *Spartina* influence.

The aim of this work was to understand the extent of the effect of habitat alteration by the colonization of mudflats by *Spartina anglica* for *Zostera noltei*. In particular, I seek answering the two following questions: (1) Does *S. anglica* affect *Z. noltei* through short- (mainly effects on resources) or long-term processes (ecosystem engineering legacy effects)? and (2) Does the influence of *S. anglica* on *Z. noltei* extend to larger spatial scales than the immediate neighbour level?

The results of this work were published in "**Marine Ecology Progress Series**": Proença B, Romuald M, Auby I, Ganthy F, Sottolichio A and Michalet R (2019). Disentangling ecosystem engineering from short-term biotic effects of a strong invader on a native foundation species. doi.org/10.3354/meps12999
The publication is presented in the following section and the main conclusions are subsequently summarised.

Publication: Disentangling ecosystem engineering from short-term biotic effects of a strong invader on a native foundation species

Research article

Disentangling ecosystem engineering from short-term biotic effects of a strong invader on a native foundation species

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Abstract: Ecosystem engineering effects of dominant species on habitats and consequently on other species are likely to propagate through time at longer distance than the close neighbourhood. Such effects are important to disentangle from short-term biotic effects, especially in biological invasions, as engineering can explain changes in invasion rates over the course of the invasion. We assessed the contribution and spatial dynamics of ecosystem engineering effects of a strong invader, the cordgrass *Spartina anglica*, on *Zostera noltei*, a foundation seagrass species of muddy intertidal systems in Europe. *Z. noltei* transplants were grown at different positions along transects crossing intact *S. anglica* patches, cut patches and nearby bare sediment on tidal flats in the Bay of Arcachon (France), in order to separate ecosystem engineering effects from short-term biotic effects and evaluate their likely spatial propagation. Bed altimetry, sediment redox potential and granulometry were measured in all treatments. Within *Spartina* patches, we found strong negative ecosystem engineering effects of the cordgrass on the seagrass associated with increased sediment elevation and relative fine sediment content. Up to 2 m outside the patch, we found significant negative ecosystem engineering effects and positive short-term biotic effects, but they were weak and counterbalanced each other. We conclude that *S. anglica* can transform a marine muddy intertidal habitat into a drier and more oxidized terrestrial habitat, no longer suitable for the seagrass. Although these effects may propagate at several metres from a patch, they appeared to be too weak to likely affect the seagrass at the scale of a whole bay.

Key words: Biological invasion, competition, ecosystem engineer, *Spartina anglica*, *Zostera noltei*

4.1 Introduction

Biological invasion is a highly dynamic process, both in time and space (Pyšek and Hulme 2005, Mitchell et al. 2006, Theoharides and Dukes 2007). The impact of an invasive species may vary over the course of the invasion, with invasion rates changing through different ecological and evolutionary processes that may increase or attenuate the impact of invaders on the resident community (Strayer et al. 2006). Indeed, species' evolution is an important driver of invasion accelerations, as shown for several plant species after hybridization and polyploidy events (Baumel et al. 2001, Treier et al. 2009, Ainouche et al. 2009, te Beest et al. 2012). For example, the cordgrass *Spartina anglica* became a strong invader in European salt marshes after hybridization in the UK between the North American species *S. alterniflora* and the native *S. maritima*, followed by a polyploidy evolution (Baumel et al. 2001, Strong and Ayres 2013). In contrast, a decrease in invasion success may arise from plant−soil feedback processes (Dostál et al. 2013) or decrease in allelopathic compounds of the invader through time (Lankau et al. 2009).

Changes in invasion rates related to population and community dynamics can be fast, in contrast to ecosystem-driven invasion changes that might need a much longer time to occur, in particular when soil weathering processes are involved (Vilà et al. 2011, Strayer 2012). In coastal systems, several species strongly enhance their invasion rate due to their high ecosystem engineering abilities (Crooks 2002, Zarnetske et al. 2012). Ecosystem engineers contribute to shaping the space they colonize by interacting with incident physical forces like wind in sand dune systems (Seabloom et al. 2013) and currents and waves in marine systems (Bouma et al. 2005, 2007, Paul and Gillis 2015) and, hence, inducing long-term changes in landscape morphology and physical habitats (Balke et al. 2012). One important challenge in biological invasion studies is to disentangle short-term biotic processes, mainly related to the effects of vegetation on resources, from ecosystem engineering processes, associated with soil or sediment modification, in order to improve our understanding of the temporal and spatial dynamics of biological invasions and their effects on biological diversity, ecosystem functioning and ecosystem services. This is particularly the case for cordgrass invasion in salt marshes, which involves both evolutionary and ecosystem changes (Baumel et al. 2001, Bouma et al. 2005, Ainouche et al. 2012, Strong and Ayres 2013).

Disentangling ecosystem engineering from short-term biotic effects is feasible using specific methodologies, as already applied in terrestrial systems (Michalet 2006, Schöb et al. 2012, Noumi et al. 2015, 2016, Michalet et al. 2015b, 2017), but not yet tested in coastal systems. This method can only be used in stressed and/or highly disturbed systems where vegetation cover is not continuous, with patches of vegetation alternating with patches of bare ground. The short-term biotic effects of a living neighbour on resources (light, water and nutrients), disturbance and microclimate are quantified by comparing the performance of a plant individual growing within the canopy of the living neighbour to that of an individual growing in an area where neighbours have been removed. The ecosystem-engineering effects of the neighbours are quantified by comparing the performance of a third individual growing in naturally open patches to that of the second individual growing in removed vegetation. This quantifies the legacy effects over several generations of the neighbours on soil characteristics, and in particular positive effects on nutrients and water retention, but also interference effects

due to litter accumulation (Michalet et al. 2017). Finally, the comparison of the performance of the first and third individuals quantifies the sum of the short-term biotic and ecosystem engineering effects of the neighbour, i.e. its net effects on the target plant. This method has proven efficient in separating these 2 effects but can only be used in communities where within-habitat environmental heterogeneity is due to ecosystem engineering effects. Indeed, the results can be confounded by pre-existing environmental heterogeneity, as likely occurs in many mountainous systems at the metrescale (see Steinbauer et al. 2016). In contrast, such confounding effects are less likely to occur at this scale in muddy intertidal systems where within-habitat environmental heterogeneity is low and thus mostly exists when induced by ecosystem engineering effects (Bouma 2009).

One interesting aspect of the ecosystem engineering effects on landscape dynamics and biological invasions compared to short-term biotic effects is their likely extension to larger spatial scales than the closest neighbours (Rietkerk and van de Koppel 2008, Vu et al. 2017). One example are the dune-forming species in coastal systems, where their sand-trapping effects can have landscape consequences on dune height and morphology and, ultimately, control storm-wave overtopping, as shown by Zarnetske et al. (2012) and Seabloom et al. (2013) along the North American Pacific coast (Oregon, USA). Similarly, Bouma et al. (2005) suggested that the invasive *S. anglica* may negatively affect *Zostera noltei* in Dutch tidal flats through sediment trapping, likely to affect neighbouring habitats at several metres beyond their canopy. These species' effects at large scales are important to consider in biological invasions since they may explain changes in invasion rates in natural landscapes. However, their assessment needs specific methodologies that, to our knowledge, have never been applied nor implemented.

In coastal intertidal systems, saltmarshes and mudflats are vulnerable habitats characterized by a high susceptibility to biological invasions (Hacker et al. 2001). The importance of natural and anthropogenic physical disturbances facilitates the colonization by invasive species, as shown in riparian systems (Planty-Tabacchi et al. 1996, Saccone et al. 2010a, b). Studies in intertidal coastal systems have highlighted the importance of interactions between plants or other sessile organisms in enhancing native diversity or favouring biological invasions (Bertness and Ewanchuk 2002, Bruno et al. 2003, Altieri et al. 2010). Natural ecosystem vulnerability is even higher when invaders are also strong ecosystem engineers (Vitousek 1990, Crooks 2002).

Here we assessed the responses of the native foundation species of intertidal mudflats, *Z. noltei*, to the ecosystem engineering and short-term biotic effects of the strong invasive ecosystem engineer of European salt marshes, *S. anglica*. There is a current important concern about the global decline of *Zostera* beds (Orth et al. 2006, Waycott et al. 2009), due to the crucial role of *Zostera* species as foundation species of coastal intertidal systems (Duarte 2002). Several reports of decaying *Zostera* beds have been documented, e.g. in the Wadden Sea, Netherlands (Den Hartog and Polderman 1975), in the Bay of Arcachon, France (Plus et al. 2010), in the Mira estuary, Portugal (Branco et al. 2017), and in the Chesapeake Bay, USA (Lefcheck et al. 2017). Although the influence of anthropogenic factors in this decline has been suggested (Orth et al. 2006, Waycott et al. 2009), the exact causes are still not fully understood. In France (Boudouresque et al. 2009), and in particular in the Bay of Arcachon (Plus et al. 2010), it has been hypothesized that the decline could be related to a combination of factors,

which includes extreme temperature events (Massa et al. 2009) and decrease in light availability due to increasing sediment content in the water column (van der Heide et al. 2010, Suykerbuyk et al. 2016a, Lefcheck et al. 2017). Recently, Cognat et al. (2018) showed that the performance of *Z. noltei* in the Bay of Arcachon was primarily controlled by the hydrodynamics and secondarily by light availability. Although some experimental studies have investigated interactions between *Zostera* species (Bando 2006, Gribben et al. 2009), to our knowledge, no studies have directly assessed the interactions between seagrasses and marsh species using removal procedures.

In the Bay of Arcachon, the decline of *Z. noltei* meadows was first reported in the early 2000s, and its dynamics have been documented during the last 20 yr (Auby and Labourg 1996, Plus et al. 2010). Specifically, Plus et al. (2010) calculated a 33% decline in meadows between 1989 and 2007. Interestingly, this decline occurred approximately 10−15 yr after the introduction and expansion peak of *S. anglica* (Le Nindre et al. 2004). Considering the high sensitivity of *Z. noltei* to light conditions, the decrease in light availability associated with sediment dynamics (Suykerbuyk et al. 2016a, b) and the well-known role of *S. anglica* as an ecosystem engineer through sediment trapping (Bouma et al. 2005, 2007), it can be hypothesized that the contingency of the recent dynamics of the 2 species in the Bay of Arcachon could be explained by causal relationships. The ecosystem engineering effect of *S. anglica* may be sufficiently strong to modify the environment in a negative way for the seagrass beds. As suggested by Bouma et al. (2005), the stiff stems of the cordgrass may affect waves and currents, promoting accretion and bed elevation to levels offering too much drought stress for the seagrass. However, and in order to ultimately consider the contribution of the cordgrass to the decline of the seagrass, we first need to assess if the cordgrass can negatively affect the seagrass through ecosystem engineering effects and at least at longer distances than the patch scale. Thus, we aimed to answer 2 main questions:

(1) Does *S. anglica* affect *Z. noltei* through either ecosystem engineering or short-term biotic processes?

(2) Do *S. anglica* effects on *Z. noltei* extend to larger spatial scales than the immediate neighbour level?

4.2 Materials and methods

4.2.1 Study site and species

Our experiment was conducted in the eastern part of the Bay of Arcachon, a mesotidal lagoon system (tidal range: 0.8−4.6 m), located along the Aquitaine Atlantic coast, in south-western France (44° 43' N, 1° 04'W; Figure 4.1a). The introduction of *Spartina anglica* in this lagoon dates from the mid-1980s (Laporte-Cru and Werno 1989). The origin of this invasive species began with the hybridization between *S. alterniflora* (native to the USA) and *S. maritima*, another cordgrass species native to Europe. This event occurred in the UK and first produced a sterile hybrid and then gave rise to the fertile new species *S. anglica* through polyploidy evolution (Raybould et al. 1991a, Baumel et al. 2001). *S. anglica* forms diffuse thick stems with large and stiff leaves and a very dense rhizome system. This species occurs not only close to the land, like the native *S. maritima*, but also in small patches throughout the tidal flat. *Z. noltei* is an intertidal seagrass species that presents a high sensitivity to physical disturbances. While the decline of *Z. noltei* meadows was first noticed in the Wadden Sea in the 1960s, it was not until the 2000s that this species' meadows started to be affected in the Bay of Arcachon (Plus et al. 2010).

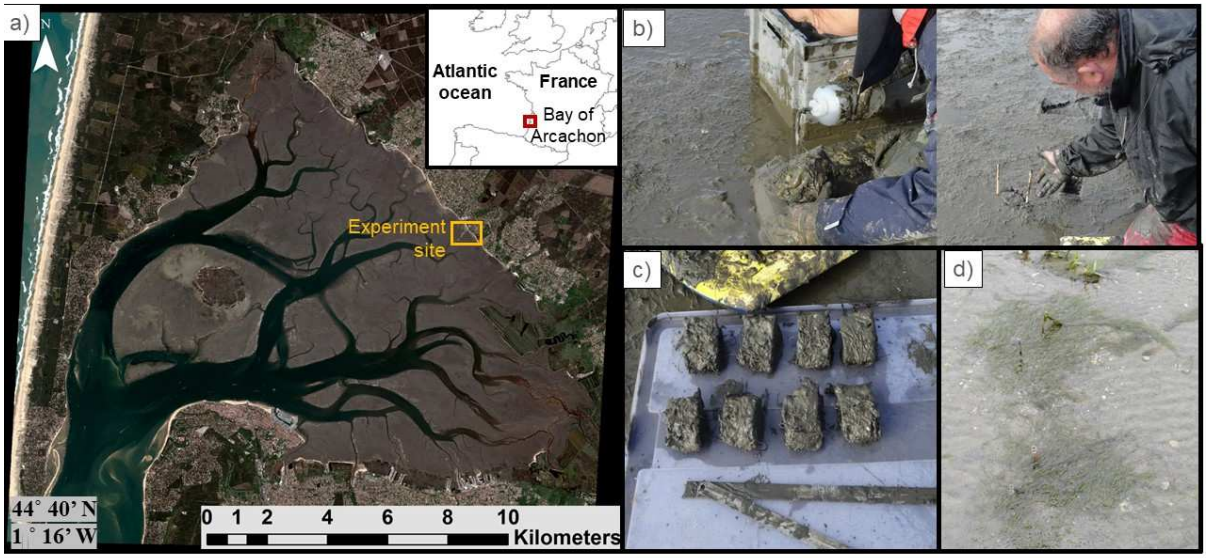

Figure 4.1. (a) *Study site.* ***(b)*** *Counting of Zostera noltei individuals in a transplant plot (left) and placement of transplant plot in transect, with the wooden sticks delimiting 2 diagonal extremes of the transplant plot at the initial time (ti) (right).* ***(c)*** *Transplant plots to be placed in a transect. The plots shown are representative of the development stage of the Z. noltei individuals at the beginning of the experiment.* ***(d)*** *Two positions within a transect, outside the Spartina patch at the final time (tf)*

4.2.2 Experimental design

In order to assess the ecosystem engineering and short-term biotic effects of *S. anglica* on the performance of *Z. noltei*, and the spatial extent of these effects, between 21 January (*ti)* and 20 May 2016 (*tf),* we conducted a field experiment in which we transplanted *Z. noltei* in 3 conditions of *S. anglica* influence (without *Spartina*, within intact *Spartina* and within cut *Spartina)* and at different distances from the influence of *Spartina* (Figure 4.2). We first randomly selected as treatment replicates 4 patches of *S. anglica* of approximately 40−50 m2. We considered isolated, elliptical *S. anglica* tussocks, and within each tussock, we delineated 2 parallel transects to the length of the tussock for the transect treatment, with at least 5 m between transects within a single patch. All transects were oriented in the direction of the predominant wave incidence, i.e. perpendicular to the shore. We randomly selected half of the patch to apply the cut *Spartina* treatment (SAC) and used scissors to remove all aboveground parts of *S. anglica* (the only plant species present in the patch) within a distance of 2 m from each side of the transect. The cut vegetation was removed from the site, and removal was conducted twice during the experiment due to the regrowth of *S. anglica*. The vegetation was left intact in the other transect for the intact *Spartina* treatment (SA). For each replicate, we also delineated in the bare sediment nearby a third transect at a minimum of 10 m away from the patch, for the control treatment. In each of the 3 × 4 transects, for the position treatment, we selected 8 positions along the transect where we transplanted *Z. noltei*: 2 on the offshore side of the patch, at 1 and 0.5 m from the limit of the *S. anglica* patch, 3 inside the patch (1 at the centre and the 2 others at 0.5 m from the offshore and onshore edges of the *S. anglica* patch) and 3 on the onshore side of the *S. anglica* patch at 0.5, 1 and 5 m away from the patch. We collected all *Z. noltei* transplants in the vicinity of the patches using a metal box (12.5 × 8.5 × 8 cm) inserted within the muddy sediment. Each transplanted plot included 6 to 12 *Z. noltei* individuals (Figure 4.1b−d). All transplanted plots were inserted at the 8 positions of the 12 transects, for a total of 96 transplanted plots. The transects had varying lengths across replicates, but the distances between positions within replicates were kept constant to allow a comparison between the cut, intact and control transects. Each transplanted plot was delimited with wooden sticks located on the corners of the transplant surface to enable their identification during site inspections (Figure 4.1b). Non-transplanted *Z. noltei* performance transects were also designed in order to control for the effects of transplantation. No significant effects associated with transplanting methodology were found.

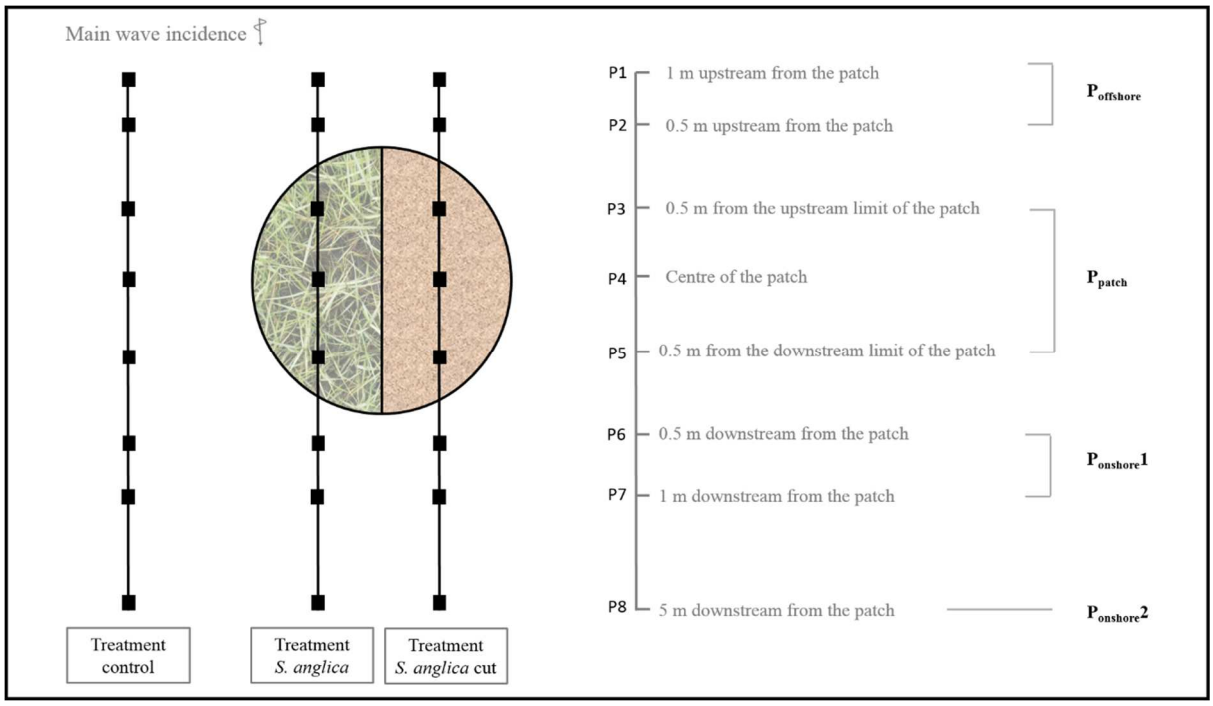

Figure 4.2. *Experimental design. Black squares represent the positions of the Zostera noltei transplants along transects for each treatment. Control treatments were located on the mudflat in the direct vicinity of Spartina patches (approximately 10 m). The S. anglica treatment corresponds to transects crossing the intact half of Spartina patches, and the S. anglica cut treatment corresponds to transects crossing the cut half of Spartina patches where aerial vegetation was cut. Positions showing no significant performance differences were pooled and reduced to 4 main positions: offshore ($P_{offshore}$), inside patch (P_{patch}) and first and second positions onshore ($P_{onshore1}$ and $P_{onshore2}$)*

4.2.3 Monitoring of *Zostera noltei* performance and environmental measurements

Shoot density *(D)* and the length of the longest leaf *(L)* of *Z. noltei* were measured at *ti* and *tf* for all transplanted plots. We then calculated *Z. noltei* growth rates (μ) between the initial (*ti)* and final times (*tf)* of the experiment using Eq. (1), where *X* corresponds to *D* or *L*:

$$\mu = (X_{tf} - X_{ti}) / X_{ti} \qquad (1)$$

At each transect position and for all transects, elevation measurements were made at the centimetre precision with a RTK Leica GS10 system, and surface sediment samples were collected in order to perform grain size analysis. Redox potential was measured with an Eh-meter probe assembled in a multi-parameter box (PofiLine Multi 3320). The analysis of the sediment of overall samples revealed that the sediment was mainly composed of sand and silt, with a very low percentage of clay (<5%). To simplify the analysis of sediment characterisation, silt and clay percentages were merged into 1 category, in order to provide a quantification of fine (cohesive) vs. sandy (granular non-cohesive) sediment content.

4.2.4 Plant-plant interaction indices

To investigate the effects of *Spartina anglica* on *Zostera noltei* performances in the transplanted plots we used the Relative Interaction Index of Armas et al. (2004):

$$RII = (X_{\text{with neighbour}} - X_{\text{without neighbour}}) / (X_{\text{with neighbour}} + X_{\text{without neighbour}}) \quad (2)$$

where X corresponds to the performances (*D* or *L*) of *Z. noltei* in the transplanted plots.
This index varies between -1 and 1. Negative values indicate a negative effect (competition), positive values a positive effect (facilitation) and zero value corresponds to no significant interaction.

Three RIIs were calculated in order to separate the ecosystem engineering and short-term biotic effects of *S. anglica* on *Z. noltei*, following Michalet et al. (2015, 2017). The short-term biotic effects were assessed using the RII of vegetation (RII_{veg}), which quantifies the relative difference in performance between *Z. noltei* transplants growing in intact *Spartina* transects vs. in cut *Spartina* transects (actual effect of living *S. anglica* individuals on *Z. noltei*, through changes in resources, disturbance, space and microclimate), whereas the ecosystem engineering effects were assessed using RII_{soil}, which quantifies the relative difference in performance of *Z. noltei* transplants growing in cut *Spartina* transects vs. control transects (long-term effects of *S. anglica* on *Z. noltei*, through legacy effects on environmental conditions within the sediment, i.e. changes in sediment elevation, texture, nutrient content). Finally, $RII_{Spartina}$ quantifies the total effects of *S. anglica* on *Z. noltei* performance, i.e. the sum of the 2 previous effects, through the estimation of the relative difference in performance of *Z. noltei* transplants growing in intact *Spartina* transects vs. control transects. The descriptions of the variables considered in each RII are summarized in Table 4.1.

Table 4.1. *Neighbouring treatments used for calculating the 3 relative interaction indices (RIIs) for vegetation, soil and net Spartina effects on Zostera noltei performance. SA: intact Spartina anglica treatment; SAC: cut S. anglica treatment; control: bare sediment treatment*

	With neighbour	*Without neighbour*
$\boldsymbol{RII_{vegetation}}$	Abundance of *Z. noltei* in **SA**	Abundance of *Z. noltei* in **SAC**
$\boldsymbol{RII_{soil}}$	Abundance of *Z. noltei* in **SAC**	Abundance of *Z. noltei* in **control**
$\boldsymbol{RII_{Spartina}}$	Abundance of *Z. noltei* in **SA**	Abundance of *Z. noltei* in **control**

4.2.5 Statistical analysis

We analysed the effects of transect (SA, SAC and control), position treatments and their interaction on the logarithm of final abundance of *Z. noltei* with a split-plot ANCOVA, with transect as the main effect and position as the sub-effect. We also used a split-plot ANCOVA to analyse the effects of the method (to quantify short-term biotic and ecosystem engineering effects of *S. anglica)*, position treatments and their interaction on RII final abundance of *Z. noltei*, with method as the main effect and position as the sub-effect. In both split-plot ANCOVAs, we used both a linear and quadratic term of the position effect in order to eventually detect non-linear relationships. The best model was chosen by application of a stepwise method using Akaike's information criterion (Akaike 1973). We also used 1-way ANOVA to assess the effects of the transect or method effects at each position along transects. To simplify the representation of the results, we pooled the 2 upstream positions into 1 upstream point ($P_{offshore}$), the 3 positions within the patch into 1 patch position (P_{patch}) and the 2 first downstream positions into a first downstream point ($P_{onshore1}$). We used 1-sample *t*-tests to assess significant deviations of RII means from 0 values. For environmental data (altimetry, redox potential and relative fine sediment content), we used a 3-way ANCOVA to test effects of Transect, Position and Position^2 and their interactions. We also used 1-way ANOVAs to assess the effect of the transect treatment at each position. For all analyses, we also conducted post hoc Tukey HSD tests when necessary. Data normality was verified through a Shapiro-Wilk test, for which we obtained $W = 0.916$ ($p < 0.001$) on final *Z. noltei* abundance and $W = 0.934$ ($p < 0.001$) on RII. Because data met the normality criterium (values of *W* close to 1), no transformations were applied. All statistical analyses were performed with R version 3.3.2 (R Development Core Team 2013).

4.3 Results

There was a highly significant transect effect in the ANCOVA on *Zostera noltei* abundance ($F_{2,87} = 12.96$, $p < 0.001$, Table 4.2), because, over all positions along the transects, the abundance of *Z. noltei* was higher in the control transects (without *Spartina*) than in the cut-*Spartina* transects, with intermediate values for the intact-*Spartina* transects (Figure 4.3, Tukey, intact-*Spartina* (A), cut-*Spartina* (A), control (B)). We also found a highly significant effect of the position^2 treatment ($F_{1,87} = 19.55$, $p < 0.001$, Table 4.2) because, overall transects, *Z. noltei* abundance was much lower at the P_{patch} position than at the other three positions (Figure 4.3, Tukey, $p < 0.05$). However, there was a significant treatment X position^2 interaction, because this quadratic position effect was only observed for the cut-*Spartina* and intact-*Spartina* transects ($F_{2,87} = 5.42$, $p = 0.006$, Table 4.2). Indeed, at the P_{patch} position Z. *noltei* abundance was close to 0 in both the SA and SAC transects vs. 24 (± 3.15) individuals on average in the control transects. In contrast, at the $P_{onshore1}$ position Z. *noltei* abundance was 50% lower (16.6 ± 6.35 individuals) in the cut-*Spartina* than in the intact-*Spartina* transects (32 ± 5.7 individuals) and there were no significant differences among treatments at the other two positions.

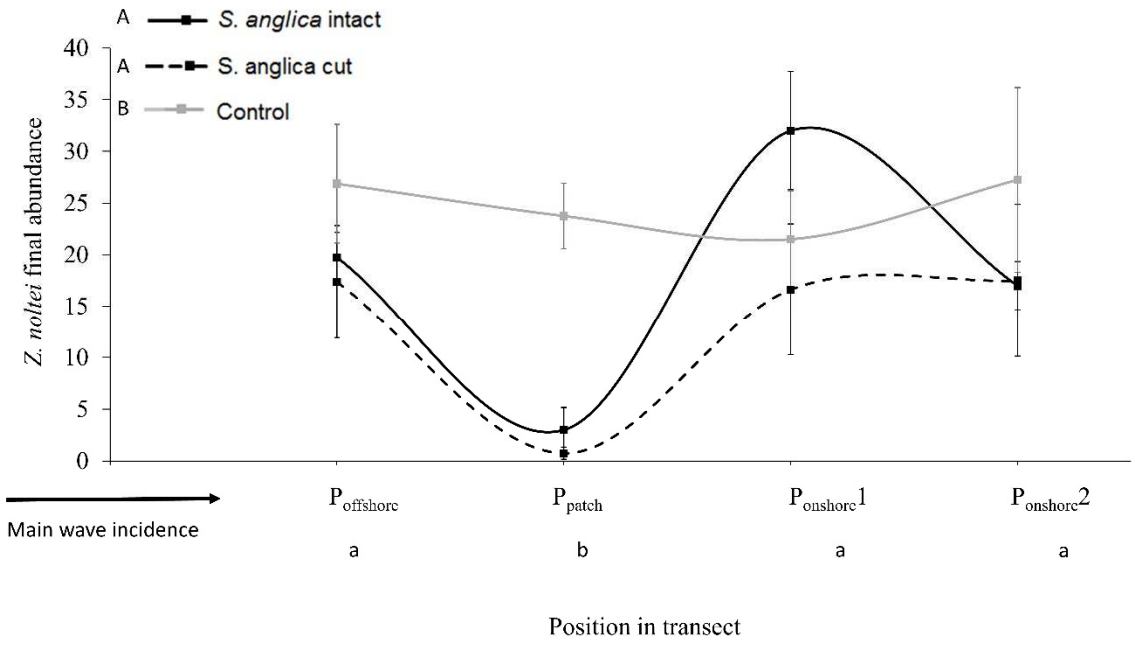

Figure 4.3. *Mean (± SE) Zostera noltei final number of individuals per transplant plot at four positions along intact-Spartina transect (SA) – solid black line, along cut-Spartina transect (SAC) – dashed black line and along control transect (bare sediment) – grey solid line. Positions along transect: within 1 m on the offshore side of the patch ($P_{offshore}$), inside the patch (P_{patch}), within 1 m on the onshore side of the patch ($P_{onshore1}$) and 5 m away from the patch ($P_{onshore2}$). Upper-case letters are the results of the Tukey test for the transect effect and lower-case letters are the results of the Tukey test for the position effect (with significance at $p < 0.05$).*

We observed a highly significant Method effect ($F_{2,87}$ = 23.59, p < 0.001, Table 4.2) in the ANCOVA on RII abundance, because over all positions, both RII_{soil} and $RII_{Spartina}$ values were globally negative, whereas RII_{veg} values were slightly positive (Figure 4.4). There was also a significant Position^2 effect ($F_{1,87}$ = 11.46, p = 0.001, Table 4.2), because RII abundance values were lower (and negative) at the P_{patch} position than at the other 3 positions. Even though the interaction Method × Position^2 was not significant, we observed a tendency for very negative RII values at the P_{patch} position that were only observed for RII_{soil} and $RII_{Spartina}$, but not for RII_{veg}. In addition, at the $P_{onshore1}$ position, only RII_{soil} was still significantly negative, whereas $RII_{Spartina}$ was null and RII_{veg} was significantly positive. Overall, these results show that *S. anglica* had dominant negative soil effects and that, although these effects were by far the strongest within the *Spartina* patch, they slightly extended at least up to 5 m downstream from the *Spartina* patch (position $P_{onshore2}$) and even up to 1 m upstream (significant sample *t*-tests at all positions along transects for RII_{soil}).

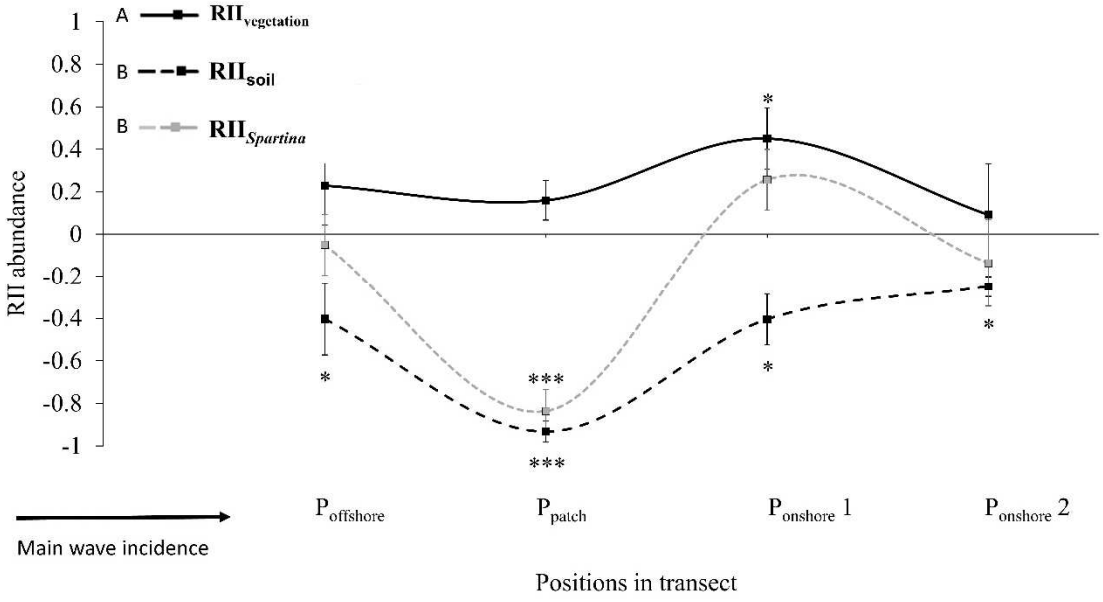

Figure 4.4. *Mean (± SE) Relative Interaction Intensity (RII) index for final Zostera noltei abundance per transplant plot at four positions along transects. See Table 4.2 for the ecological significance of the three RII indices, RII_{canopy} (solid black line), RII_{soil} (black dashed line) and $RII_{Spartina}$ (grey dashed line). Positions along transect: within 1 m on the offshore side of the patch ($P_{offshore}$), inside the patch (P_{patch}), within 1 m on the onshore side of the patch ($P_{onshore1}$) and 5 m away from the patch ($P_{onshore2}$). Asterisks show the results of the T-tests: * < 0.05, ** < 0.01 and *** < 0.001. Upper-case letters indicate the results of the Tukey test for the method effect (with significance at $p < 0.05$).*

Table 4.2. *Results of the mixed linear models on the effects of the transect (or method), position (and position^2) and their interactions on the logarithm of final abundance of Zostera noltei (left) and Relative Interaction Index (right). Significant results are indicated in bold. P-value significance thresholds: *, p < 0.05; **, p < 0.01; ***, p < 0.001.*

		Log(final abundance+1)				**RII**	
Effects	*df*	F	P	Variable	*df*	F	p
transect	2	12.96	**< 0.001**	**method**	2	23.59	**< 0.001**
Position	1	1.31	0.256	**position**	1	4.14	**0.045**
position^2	1	19.55	**< 0.001**	**position^2**	1	11.46	**0.001**
transect x pos.	2	0.77	0.466	**method x pos.**	2	0.59	0.557
transect x pos.^{2}	2	5.42	**0.006**	**method x pos.^{2}**	2	2.73	0.071
Residuals	87				87		

There was a significant Transect effect ($F_{2,103}$ = 4.42, p = 0.014) in the ANCOVA conducted on elevation, because, over all positions, elevation was lower in the control transects than in both intact *Spartina* and cut *Spartina* transects (Figure 4.5a). We also found a significant Position^2 effect ($F_{1,103}$ = 8.17, p = 0.005); across all transects, elevation was higher at the level of the *Spartina* patches (positions 3 to 5) than at all other positions. Finally, there was a significant Transect × Position^2 interaction ($F_{2,103}$ = 3.95, p = 0.022), because the higher elevations observed at the levels of the *Spartina* patches occurred only in the SA and SAC transects but not in the control transects, and in particular at P4, the position at the centre of the patch (see results of the 1-way ANOVA at P4; p < 0.001).

For redox potential, we found a tendency for overall higher values in the intact *Spartina* than in the cut *Spartina* transects on the offshore side of the patch and in the *Spartina* patch, whereas the opposite was observed on the onshore side of the patch. In particular, at position 4 (centre of the patch), redox potential was significantly lower in the cut *Spartina* transects than in the other 2 transect types (1-way ANOVA $F_{2,11}$ = 7.71, p = 0.008; Figure 4.5b). There was a significant position effect ($F_{1,103}$ = 10.81, p < 0.01) in the ANCOVA conducted on relative fine sediment content; over all transects, points from the level of the *Spartina* patches and upstream of the patches had lower fine sediment content than points downstream of the patches, in particular position 2 vs. position 5, respectively (Figure 4.5b, Tukey, p < 0.01). These differences in relative fine sediment content across positions were mostly found for the SA and SAC transects but not for the control transects, and in particular for position P5 (1-way ANOVA at P5: $F_{2,11}$ = 10.61, p = 0.003).

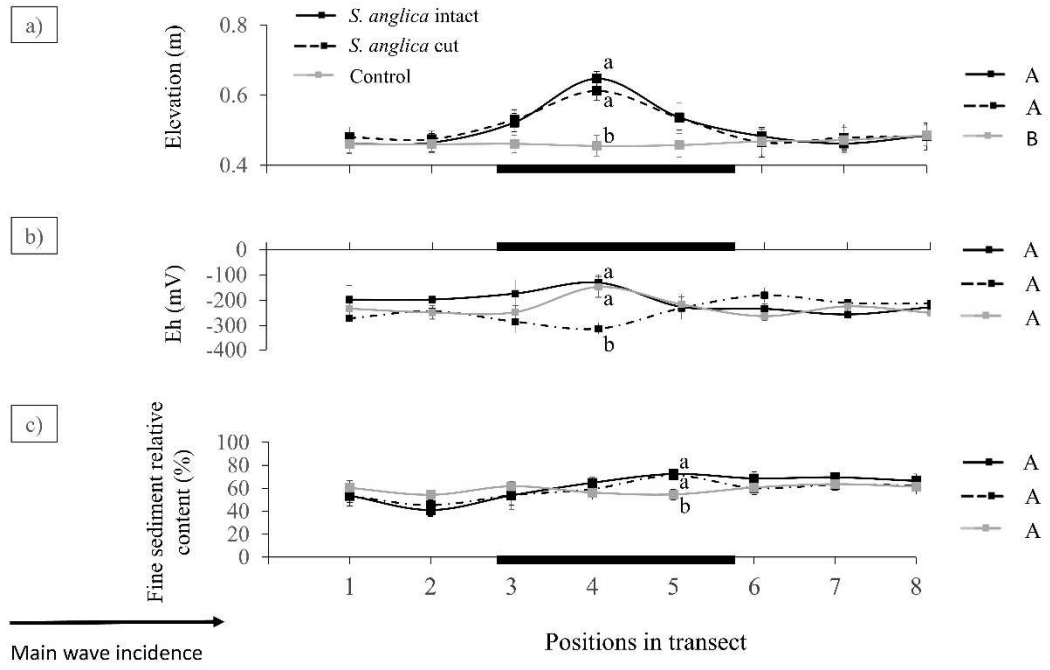

Figure 4.5. *Mean (± SE) (a) elevation of transect positions, (b) soil redox potential (Eh) and (c) relative fine sediment content, for the 3 transect types: intact Spartina (SA), cut Spartina (SAC) and control transects (bare sediment). For transect positions see Figure.4. 2. The thick black line between P3 and P5 shows the position of the Spartina patch within the transect. Uppercase letters indicate the results of the Tukey test for the Transect treatment (with significance at p < 0.05). Lowercase letters indicate the results of the Tukey test for the particular positions where the Transect treatment is significant, namely P4 for altimetry and Eh and P5 for fine sediment content*

Table 4.3. *Results of the ANOVA on the effects of the transect, position (and position^2) treatments and their interactions on altimetry, redox potential (Eh) and relative fine sediment content. Significant results are indicated in bold. P-value significance thresholds: *, p < 0.05; **, p < 0.01; ***, p < 0.001.*

	Altimetry			**Eh**			**Relative fine sediment content**		
Effects	*df*	F	p	*df*	F	p	*df*	F	p
transect	2	4.42	**0.014**	2	2.16	0.121	2	0.36	0.670
position	1	0.01	0.916	1	0.11	0.737	1	10.81	**0.001**
position^2	1	8.17	**0.005**	1	1.62	0.206	1	1.05	0.309
transect x pos.	2	0.40	0.670	2	2.96	0.056	2	2.66	0.074
transect x pos.^{2}	2	3.95	**0.022**	2	0.34	0.713	2	1.23	0.297
Residuals	103			103			103		

4.4 Discussion

At short distances (i.e. within *Spartina* patches), we found dominant negative ecosystem engineering effects of *S. anglica* on *Zostera noltei* that were correlated with 2 long-term environmental modifications, an increase in elevation and in relative fine sediment content. This was also correlated to an increase in sediment oxygenation, but not to any positive shortterm effect for the seagrass. At long distances, effects on *Z. noltei* were much weaker, but negative ecosystem engineering effects on environmental conditions were still significant up to 2 m downstream from the *Spartina* patch, while weak significant positive shortterm biotic effects were observed up to 1 m downstream from the *Spartina* patch. These results provide evidence that a strong invader of salt marshes can negatively affect an important foundation seagrass species of intertidal mud flats, mostly through ecosystem engineering effects occurring at short distances.

4.4.1 The short-distance effects of *Spartina anglica* on environmental conditions and *Z. noltei*

The role of *Spartina* species as ecosystem engineers of muddy intertidal systems has been widely documented (Crooks 2002, Bouma et al. 2005, Strong and Ayres 2013). In tidal flats, they interact with the hydrodynamic forces in a way that promotes significant bed level elevation, commonly forming dome-shaped tussocks or small islands, and ultimately salt marshes (Balke et al. 2012). The specific ability of *S. anglica* to trap sediment and to behave as an ecosystem engineer that expands its habitat by enhancing sediment accretion has been widely acknowledged (Castellanos et al. 1994, Sánchez et al. 2001, Bouma et al. 2005). Bouma et al. (2005) showed that *S. anglica* was able to modify its physical environment by reducing hydrodynamic energy from waves with its stiff stems, at the cost of relatively large drag forces. In our study, we showed, through differential GPS (dGPS) elevation measurements in the tidal

flat, that *Spartina* meadows were associated with significant higher bed levels than surrounding *Z. noltei* habitats. Contrasting elevations were associated with higher relative fine sediment content for the *Spartina* patches, since both habitat modifications were induced by the higher sediment-trapping ability of *S. anglica* as compared to *Z. noltei* (Bouma et al. 2005). These parallel changes in habitat conditions and random distribution of *Spartina* patches on the tidal flats (B. Proença pers. obs.) strongly suggest that differences in elevation between *S. anglica* and *Z. noltei* habitats cannot be due to pre-existing environmental heterogeneity that could have confounded our results, as likely to occur in terrestrial habitats where within-habitat environmental heterogeneity is much higher than in muddy intertidal systems (Steinbauer et al. 2016). Additionally, our measurements of annual sediment deposition below *Spartina* canopies in the Arcachon Bay show that the observed differences in elevation between *Spartina* patches and adjacent bare tidal flats are achieved at time scales on the order of decades (B. Proença unpubl. data).

Given the low performance of *Z. noltei* transplants within the cordgrass patches, the sediment-trapping activity of *S. anglica* can gradually transform this marine habitat into a system that can no longer be inhabited by *Z. noltei*, as already suggested by Bouma (2009). Several studies have shown the sensitivity of seagrasses to desiccation stress (van der Heide et al. 2010, Kim et al. 2016, Suykerbuyk et al. 2016b) and, even though *Z. noltei* possesses physiological adaptations to reduce tissue water loss and keep appropriate photosynthesis levels during emersion periods (Larkum et al. 2006, Folmer et al. 2016), desiccation stress might still limit its colonization of higher intertidal levels (van der Heide et al. 2010, Folmer et al. 2016). Additionally, at higher exposed bed levels, *Z. noltei* is submitted to a wider range of temperature changes, another relevant factor for seagrass performance (Marba et al. 1996).

Using a specific methodology that was already applied in terrestrial systems, we were able to disentangle ecosystem engineering legacy from short-term biotic effects and to demonstrate that only the former could explain the competitive exclusion of *Z. noltei* by *S. anglica*, thus supporting this assumption of previous authors. At short distances (within *Spartina* patches), we showed that *S. anglica* had no significant short-term biotic effects for *Z. noltei*. *S. anglica* had a significant short-term biotic effect on habitat conditions, in particular by strongly enhancing sediment oxygenation. Although higher sediment oxygenation due to the effects of ecosystem engineers positively affects many salt marsh species (Callaway and King 1996, Hacker and Bertness 1999), it did not positively affect *Z. noltei*, likely because this is an aquatic species adapted to anoxia but not to drought. Additionally, a likely benefit of increased oxygenation might have been outweighed by the cost of drought. It should be noted that the competitive exclusion of *Z. noltei* due to drought stress induced by *S. anglica* could not be considered as an example of resource competition related to the high ability of *S. anglica* to take up water, but it is a consequence of a long-term ecosystem engineering effect of the invasive. Thus, this is rather an example of interference effect on water sediment content due to legacy effects of ecosystem engineers on habitat conditions, as already shown in terrestrial alpine systems where the accumulation of hydrophobic litter through time may induce water stress for other species (Michalet et al. 2017).

4.4.2 The long-distance effects of *Spartina anglica* on environmental conditions and *Zostera noltei*

Although much weaker than within *Spartina* patches, negative ecosystem engineering effects were still present outside the patch, because RII_{soil} values were significantly negative at all points along the transects. Downstream of the patch, this was correlated with a tendency for higher relative fine sediment content for intact *Spartina* transects than for the control transects, whereas it was the opposite upstream of the patch, where relative fine sediment content of the control transects tended to be higher than those of the other 2 transect types (significant interaction between the Transect and Position treatments). This suggests that the negative ecosystem engineering effects on *Z. noltei* occurring downstream of the patch were still due to the sediment-trapping effect of *S. anglica.* This shows that these effects may negatively affect seagrass beds located several metres from the invasive species, as suggested by Bouma (2009). In contrast, the negative ecosystem engineering effects occurring on the offshore side of the *Spartina* patches were likely due to increased wave energy and, thus, physical disturbance for the seagrass at the front of the patch. Ganthy et al. (2013) also showed for *Z. noltei* beds that an increase in wave action during energetic winter events favours superficial fine sediment erosion, thus inducing a coarser sediment texture. In contrast, they found higher fine sediment content under lower energy incidence.

Remarkably, we found positive short-term biotic effects of *S. anglica* on *Z. noltei* at a distance of 1 m downstream of the patch. This shows that the canopy of the cordgrass facilitated the seagrass, just downstream of the *Spartina* patch, likely through a reduction in hydrodynamic energy by the stiff stems of the cordgrass (Bouma et al. 2005). Again, considering sediment properties as a proxy for the hydrodynamic conditions, our sediment measurements along the transects are consistent with an effective energy reduction by the *Spartina* vegetation and a protective effect downstream of the *Spartina* patches. In our experiment, for *Z. noltei* growing at positions receiving the shelter effect of *S. anglica*, both the reduction of incident energy and the associated more stable sediment conditions likely decreased physical disturbance, thus slightly ameliorating the habitat for a suitable development of the seagrass (Suykerbuyk et al. 2016a, b, Folmer et al. 2016). However, a minimum level of wave and current action is required for the seagrass since the physical remobilization of the leaves, especially in dense meadows, can decrease self-shading and increase nutrient uptake (Paul and Gillis 2015).

However, all of these subtle negative or positive legacy or short-term effects observed outside of the *Spartina* patches, up to a distance of 2 m from the patches, counterbalanced each other since all net effects measured outside the patch were not significant. Thus, although further experiments including longer transects with more replicates and located in varying conditions of hydrodynamics are certainly needed, our results strongly suggest that the long-distance effects of *S. anglica* are too weak to potentially contribute to the decline of *Z. noltei* in Arcachon Bay. Indeed, the decline of the seagrass has been shown to occur throughout the Bay, even in tidal flat areas where *S. anglica* has never been observed.

4.5 Conclusion

Using a specific methodology to disentangle ecosystem engineering effects from short-term biotic effects at different distances from *Spartina anglica*, we showed that the invasive cordgrass had strong negative ecosystem engineering effects on *Zostera noltei* likely through sediment trapping and sediment accretion occurring mostly at short distances (within *Spartina* patches). *S. anglica* also increased sediment oxygenation, a short-term positive effect on environmental conditions for a terrestrial plant, but that did not affect *Z. noltei*, an aquatic species strongly adapted to anoxia. We also found significant negative ecosystem engineering effects and positive short-term biotic effects of the cordgrass on the seagrass at a distance up to 2 m from the *Spartina* patches, likely due its ability to alter wave energy with its stiff stems. However, these effects were much weaker than the short-distance effects and neutralized each other outside the *Spartina* patches, which allows us to conclude that the cordgrass weakly contributed to the regional decline of the seagrass documented throughout Arcachon Bay. However, this does not preclude that in the long term, the coalescence of all *Spartina* patches on a tidal flat might transform this low intertidal habitat in a continuous salt marsh from which *Z. noltei* will be excluded. To complement this study and assess the role of the inter-annual variability in abiotic conditions, it would be appropriate to perform further experiments including measurements of nutrient and light availability for the *Zostera* transplants. Our results are crucial for stakeholders strongly involved in the control of invasives, in particular through mechanical removal of the plants. Although these actions include a root removal of the invasive species, they are very unlikely to limit long-term invasion due to the legacy effects on sediment elevation and oxygenation, which will remain in the absence of sediment removal. Indeed, the new cordgrass recruits will find in these strongly modified habitats more suitable environmental conditions than before the invasion, thus increasing the probability of further invasion.

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References

Ainouche, M. L. et al. 2009. Hybridization, polyploidy and invasion : lessons from *Spartina* (Poaceae). - Biol Invasions 11: 1159.

Ainouche, M. et al. 2012. Polyploid evolution in *Spartina*: dealing with highly redundant hybrid genomes. - In: Polyploidy and Genome Evolution. Soltis PS, Soltis DE. Springer, pp. 255–244.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. - Proceedings of the Second International Symposium on Information theory: 267–281.

Altieri, A. H. et al. 2010. Facilitation cascade drives positive relationship between native biodiversity and invasion success. - Ecology 91: 1269–1275.

Armas, C. et al. 2004. Measuring plant interactions: a new comparative index. - Ecology 85: 2682–2686.

Auby, I. and Labourg, P.-J. 1996. Seasonal dynamics of *Zostera noltii* hornem. In the Bay of Arcachon (France). - Journal of Sea Research 35: 269–277.

Balke, T. et al. 2012. Conditional outcome of ecosystem engineering: A case study on tussocks of the salt marsh pioneer *Spartina anglica*. - Geomorphology 153–154: 232–238.

Bando, K. J. 2006. The roles of competition and disturbance in a marine invasion. - Biol Invasions 8: 755–763.

Baumel, A. et al. 2001. Molecular investigations in populations of *Spartina anglica* C.E. Hubbard (Poaceae) invading coastal Brittany (France). - Molecular Ecology 10: 1689–1701.

Bertness, M. D. and Ewanchuk, P. J. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. - Oecologia 132: 392–401.

Boudouresque, C. F. et al. 2009. Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress : a critical review. - Botanica Marina 52: 395–418.

Bouma, T. 2009. Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. - Helgol Mar Res: 3–18.

Bouma, T. J. et al. 2005. Trade-Offs Related to Ecosystem Engineering : A Case Study on Stiffness of Emerging Macrophytes. - Ecology 86: 2187–2199.

Bouma, T. J. et al. 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures : Combining field, flume and modelling experiments. - Continental Shelf Research 27: 1020–1045.

Branco, J. et al. 2017. Natural recovery of *Zostera noltii* seagrass beds and benthic nematode assemblage responses to physical disturbance caused by traditional harvesting activities. - Journal of Experimental Marine Biology and Ecology in press.

Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. - Trends in Ecology & Evolution 18: 119–125.

Callaway, R. M. and King, L. 1996. Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. - Ecology 77: 1189–1195.

Castellanos, E. M. et al. 1994. Nucleation and Facilitation in Saltmarsh Succession : Interactions between *Spartina maritima* and *Arthrocnemum perenne*. - Journal of Ecology 82: 239–248.

Cognat, M. et al. 2018. Environmental factors controlling biomass development of seagrass meadows of *Zostera noltei* after a drastic decline (Arcachon Bay, France). - Journal of Sea Research 140: 87–104.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. - Oikos 97: 153–166.

Den Hartog, C. and Polderman, P. J. G. 1975. Changes in the seagrass populations of the Dutch Waddenzee. - Aquatic Botany 1: 141–147.

Dostál, P. et al. 2013. The impact of an invasive plant changes over time. - Ecology Letters 16: 1277–1284.

Duarte, C. M. 2002. The future of seagrass meadows. - Environmental Conservation 29: 192–206.

Folmer, E. O. et al. 2016. Consensus forecasting of intertidal seagrass habitat in the Wadden Sea. - J Appl Ecol 53: 1800–1813.

Ganthy, F. et al. 2013. Seasonal modification of tidal flat sediment dynamics by seagrass meadows of *Zostera noltii* (Bassin d'Arcachon, France). - Journal of Marine Systems 109–110: S233–S240.

Gribben, P. E. et al. 2009. Behavioural interactions between ecosystem engineers control community species richness. - Ecol. Lett. 12: 1127–1136.

Hacker, S. D. and Bertness, M. D. 1999. Experimental evidence for factors maintaining plant species diversity in a new england salt marsh. - Ecology 80: 2064–2073.

Hacker, S. D. et al. 2001. A marine plant (*spartina anglica*) invades widely varying habitats : potential mechanisms of invasion and control. - Biological Invasions 3: 211–217.

Kim, J.-H. et al. 2016. Growth dynamics of the seagrass *Zostera japonica* at its upper and lower distributional limits in the intertidal zone. - Estuarine, Coastal and Shelf Science 175: 1–9.

Lankau, R. A. et al. 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. - PNAS 106: 15362–15367.

Laporte-Cru, J. and Werno, J. 1989. *Spartina* X Townsendii groves dans le Bassin d'Arcachon. - Bulletins de la Société Linnéenne de Bordeaux 17: 7–12.

Larkum, A. W. D. et al. 2006. Photosynthesis and metabolism in seagrasses at the cellular level. - In: Seagrasses: Biology, Ecology and Conservation. Springer, in press.

Le Nindre, Y. M. et al. 2004. Etude pour le maintien de l'équilibre bio-sédimentaire des plages du Nord-Est dans le Bassin d'Arcachon. Rapport BRGM/RP-53282-FR 101 p., 60 fig., 15 tabl., 6 ann. in press.

Lefcheck, J. S. et al. 2017. Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. - Glob Change Biol 23: 3474–3483.

Marba, N. et al. 1996. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. - Marine Ecology Progress Series 133: 203–215.

Massa, S. I. et al. 2009. Temperature tolerance and survival of intertidal populations of the seagrass *Zostera noltii* (Hornemann) in Southern Europe (Ria Formosa, Portugal). - Hydrobiologia 619: 195–201.

Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? - New Phytologist 169: 3–6.

Michalet, R. et al. 2015. Disentangling direct and indirect effects of a legume shrub on its understorey community. - Oikos 124: 1251–1262.

Michalet, R. et al. 2017. Direct litter interference and indirect soil competitive effects of two contrasting phenotypes of a spiny legume shrub drive the forb composition of a Mediterranean community. - Oikos 126: 1090–1100.

Mitchell, C. E. et al. 2006. Biotic interactions and plant invasions. - Ecology Letters 9: 726–740.

Noumi, Z. et al. 2015. Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study (R Ohlemuller, Ed.). - Applied Vegetation Science 18: 391–401.

Noumi, Z. et al. 2016. The relative contribution of short-term versus long-term effects in shrub-understory species interactions under arid conditions. - Oecologia 180: 529–542.

Orth, R. J. et al. 2006. A Global Crisis for Seagrass Ecosystems. - BioScience 56: 987–996.

Paul, M. and Gillis, L. G. 2015. Let it flow: how does an underlying current affect wave propagation over a natural seagrass meadow? - Mar Ecol Prog Ser 523: 57–70.

Planty-Tabacchi, A.-M. et al. 1996. Invasibility of Species-Rich Communities in Riparian Zones. - Conservation Biology 10: 598–607.

Plus, M. et al. 2010. Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). - Estuarine, Coastal and Shelf Science 87: 357–366.

Pyšek, P. and Hulme, P. E. 2005. Spatio-temporal dynamics of plant invasions: Linking pattern to process. - Ecoscience 12: 302–315.

R Development Core Team 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Raybould, A. F. et al. 1991. The evolution of *Spartina anglica* C.E. Hubbard (Gramineae): origin and genetic variability. - Biological Journal of the Linnean Society 43: 111–126.

Rietkerk, M. and van de Koppel, J. 2008. Regular pattern formation in real ecosystems. - Trends in Ecology & Evolution 23: 169–175.

Saccone, P. et al. 2010a. *Acer negundo* invasion along a successional gradient : early direct facilitation by native pioneers and late indirect facilitation by conspecifics. - New Phytologist 187: 831–842.

Saccone, P. et al. 2010b. Challenging growth–survival trade-off : a key for *Acer negundo* invasion in European floodplains ? - Canadian Journal of Forest Research. - Canadian Journal Forest Research 40: 1879–1886.

Sánchez, J. M. et al. 2001. Primary colonisation of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain : vegetation structure and sediment accretion. - Aquatic Botany 69: 15–25.

Schöb, C. et al. 2012. Foundation species influence trait-based community assembly. - New Phytologist 196: 824–834.

Seabloom, E. W. et al. 2013. Invasive grasses, climate change, and exposure to storm-wave overtopping in coastal dune ecosystems. - Glob Change Biol 19: 824–832.

Steinbauer, M. J. et al. 2016. How to differentiate facilitation and environmentally driven co-existence (M Palmer, Ed.). - Journal of Vegetation Science 27: 1071–1079.

Strayer, D. L. 2012. Eight questions about invasions and ecosystem functioning (H Hillebrand, Ed.). - Ecology Letters 15: 1199–1210.

Strayer, D. L. et al. 2006. Understanding the long-term effects of species invasions. - Trends in Ecology & Evolution 21: 645–651.

Strong, D. and Ayres, D. R. 2013. Ecological and evolutionary misadventures of *Spartina*. - Annual Review of Ecology, Evolution, and Systematics 44: 389–410.

Suykerbuyk, W. et al. 2016a. Surviving in Changing Seascapes : Sediment Dynamics as Bottleneck for Long-Term Seagrass Presence. - Ecosystems 19: 296–310.

Suykerbuyk, W. et al. 2016b. Unpredictability in seagrass restoration : analysing the role of positive feedback and environmental stress on *Zostera noltii* transplants. - J Appl Ecol 53: 774–784.

te Beest, M. et al. 2012. The more the better? The role of polyploidy in facilitating plant invasions. - Ann. Bot. 109: 19–45.

Theoharides, K. A. and Dukes, J. S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. - New Phytol. 176: 256–273.

Treier, U. A. et al. 2009. Shift in cytotype frequency and niche space in the invasive plant *Centaurea maculosa*. - Ecology 90: 1366–1377.

van der Heide, T. et al. 2010. Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. - Ecology 91: 362–369.

Vilà, M. et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. - Ecology Letters 14: 702–708.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. - In: Ecosystem Management. Springer, New York, NY, pp. 183–191.

Vu, H. D. et al. 2017. Ecosystem engineers drive creek formation in salt marshes. - Ecology 98: 162–174.

Waycott, M. et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. - PNAS 106: 12377–12381.

Zarnetske, P. L. et al. 2012. Biophysical feedback mediates effects of invasive grasses on coastal dune shape. - Ecology 93: 1439–1450.

Conclusions

In this chapter, I assessed to what extent the invasive cordgrass *Spartina anglica* can affect, temporaly and spatially, the performance of the seagrass *Zostera noltei*. The application of two treatments, *S. anglica* intact and *S. anglica* cut, allowed to distinguish the influence of the living cordgrass vegetation (short-term biotic effects) from its effect through soil modification (long-term ecosystem engineering effects), respectively, on the seagrass. Spatial effects were considered through different distance positons of transplants from the *Spartina* patches.
From this experiment, two main conclusions are highlighted:

- Strong, short-distance negative effects of *S. anglica* over *Z. noltei* performance. This is related to the cordgrass strong ecosystem engineering capacity to modify the soil and promote elevation of the tidal flat level. Such modification likely induces important drought stress, a factor found in the literature to be limiting for the seagrass colonization of higher levels of the tidal flat.

- At a distance up to 2 m from the *S. anglica* patch, we found significant negative long-term effects and positive short-term effects of the cordgrass on *Z. noltei*. However, effects counterbalanced and cancelled each other leading to a null net influence on *Z. noltei'*s performance. These positive short-term biotic effects are likely related to the interactions between the cordgrass and the local hydrodynamics, translated by an attenuation of wave energy.

In conclusion, this study shows the presence of strong long-term effects that are important to consider in the global comprehension of the dynamics of *Spartina anglica*'s invasion and in eventual control measures. Nevertheless, the results on the spatial influence of the cordgrass do not highlight any particular ability that could explain the global decline of the *Zostera* on the short-term. Still, the long-term coalescence of the *Spartina* patches could contribute to the seagrass's decline through the transformation of a transitional marine environment into a more terrestrial one, no longer suitable for *Zostera noltei*.

CHAPTER 5

Ecosystem-engineering impacts of Spartina anglica and Spartina maritima o tidal flat sedimentation

Cordgrasses in general are known for their ability to influence sediment motion through their interaction with the hydrodynamic forces. On one hand, the physical conditions of the environment determine the success of the intertidal vegetation settlement. On the other hand, the intertidal vegetation itself will contribute to the shaping of the environment and the magnitude of its impact is dependent on the physical characteristics of each plant species. In systems that are substantially shaped by such interactions between the plants and the physical environment, like in coastal wetlands, a biological invasion can induce important changes to the system. These changes can occur at different levels and affect both the local biodiversity and the resilience the resilience of the system to the natural physical forces it is subjected to. In this sense, it is not only important to understand the conditions and tolerances that favour the installation of exotic species but also to assess the impacts on the wetland stability resulting from an eventual vegetation species replacement.

We have seen in the previous chapter that the most substantial effect of the exotic cordgrass on the seagrass *Zostera noltei* was its strong capacity to change bed level elevation. Therefore, in this chapter, I assess the ecosystem-engineering ability of both *Spartina anglica* and *Spartina maritima* in order to understand the outcoming physical impacts on the environment happening in the sequence of the exotic *Spartina*'s invasion. Field measurements of wind waves and associated sedimentation and erosion levels were performed within patches of the two *Spartina* species for a period of nearly two years.

The work presented in this chapter was prepared for submission to a peer review journal. The version to be submitted is presented in the following section and the main conclusions are subsequently summarised.

Publication: Comparing the impacts of a native and an exotic *Spartina* species on tidal flat sedimentation

Research article

Comparing the impacts of a native and an exotic *Spartina* species on tidal flat sedimentation

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Abstract. Field measurements of bed elevation variation and related wave events were performed within meadows of two *Spartina* species, *Spartina anglica* (exotic species) and *Spartina maritima* (native species), in tidal flats of the Bay of Arcachon (SW France) in order to explore species dependency of sediment dynamics within vegetation. The collected time series data allowed to infer on the sediment behaviour patterns from short-term (wave to tidal events) to long-term (seasonal to year). A good correlation was found between the bed level variation and the incident wave forcing, with erosion occurring during storm events and accretion occurring during low energy periods. Such behaviour was observed within the two species but the magnitude of bed level variation was significantly higher within the native *S. maritima* than the exotic *S. anglica*. This difference in the magnitude of sediment deposition in the order of the centimetre, was explained by the opposite allocation of biomass between the two species, with the native favouring aboveground biomass and the exotic one underground biomass. The tidal regime was also found to affect sedimentation and erosion patterns within the study site, where sediment delivery was found to occur during spring tides and, conversely, sediment mobilization was observed during neap tides. On the long-term, the balance between the short-term (wave and tidal) processes showed a dominance of the episodic storm wave events over the tidal forcing and, a general sediment deficit on the site, as suggested by an overall bed level decrease registered within the patches of the two species. Understanding the different species ability to attenuate hydrodynamic energy, influence bed sediment stabilization and their potential to build marsh from the mudflat pioneer stage is of great importance for coastal management in the context of global change and, in particular, biological invasion.

Keywords: mesotidal lagoon; ecosystem engineering; field experiment, acoustic altimetry, sedimentation/erosion patterns; *Spartina*

5.1 Introduction

The two-way interaction between aquatic vegetation and the environment it inhabits plays a major role in the evolution of coastal areas (D'Alpaos et al., 2007; Kirwan and Murray, 2007; Temmerman et al., 2007; Murray et al., 2008; Bouma et al., 2013; Fagherazzi et al., 2013). The resultant biologically mediated modifications of the physical environment are commonly known as ecosystem engineering (Jones et al., 1994; 1997; Crooks, 2002; Bouma et al., 2005). In particular, the bio-geomorphic feedback between the hydrodynamic forces and the aquatic organisms is a complex process. The resulting erosion and accretion patterns at the scale of an ecosystem depend on local, short-term, sediment dynamics around or within patches of vegetated structures, where their species dependency is still poorly understood (Tinoco and Coco 2018). The comprehension of the underlying physics governing the formation and evolution of these landscapes is crucial (Coco et al. 2013), as growing attention is given to ecosystem-based coastal defence solutions where the environment is favourable (Borsje et al., 2011; Temmerman et al., 2013, Ondiviela et al., 2014), like in the case of tidal wetlands.

Given the valuable ecosystem functioning and services provided by tidal marshes (Barbier et al. 2011), considerable attention has been given to the understanding of the feedback loop between plants, hydrodynamics and sediment motion both in current-driven flows and wave-driven ones (Bouma et al., 2005; 2007; Neumeier and Amos, 2006; Nepf, 2012; Ganthy et al., 2015; Maza et al., 2015, Weitzman et al., 2015; Losada et al., 2016, Nowacki et al., 2017). Indeed, an organisms efficiency to sediment trapping and stabilization by alteration of incident physical forcing is closely related to its traits, which are species (Horstman et al., 2013) and season dependent (Neumeier, 2007; Chen et al., 2016). In particular, in the case of aquatic vegetation, the plant traits action can then be separated in aboveground and belowground effects.

The aboveground effects directly concern the vegetation's aerial biomass and are dependent on specific traits, such as height, density and stiffness (Temmerman et al., 2005; Nepf, 2012; Bouma et al., 2007; 2013; Chen et al., 2018) and surface of occupation (Bernik et al. 2018). More specifically, vegetation aerial biomass contributes to the reduction of the hydrodynamic energy (Peralta et al., 2008; Bouma et al., 2005; 2013), leading to a decrease of bottom shear stresses (Bouma, 2009; Nepf, 2012; Green and Coco, 2014). For example, Chen et al., (2018) observed that *Spartina alterniflora* pioneer patches on the bare mudflats show considerable flow reduction ability, even better than homogenous *Spartina* cover with high biomass density, but they failed to confirm the same pattern for other types of vegetation. Such result supports the strong species dependency of the response of abiotic forces. By slowing water velocities, plant shoot will consequently tend to favour terrigenous sediment deposition (Balke et al., 2012; Fagherazzi, 2012; Kirwan and Megonigal, 2013) and, specific marsh grass morphologies can further affect inorganic sediment accretion (Friedrichs and Perry 2001).

Furthermore, mechanical reinforcement of soil stability can be largely enhanced by plant root systems (Coops et al., 1996; Schwarz et al., 2010). For instance, the erosion-reducing potential of species presenting root systems with different properties (diameter and length) has been shown by Vannoppen, (2016) with a field experiment in Belgium river dikes. They investigated the depth of action of five communities of plant root systems, each of them showing different properties on soil resistance to erosion and found an overall rapid decrease of both root density

and soil cohesion with depth. Erosion tests conducted in tidal flats colonized by the seagrass *Zostera noltei* (Ganthy et al., 2011) also showed an increase in bed sediment stabilisation related to an increase in the critical shear stress for bed erosion, due to seasonally more developed root systems.

In the Bay of Arcachon (Southwest Atlantic coast of France), salt marshes are dominated by two cordgrass species, *Spartina maritima*, a European native species, and *Spartina anglica*, a species that was introduced in the Bay in the 1980s (Baumel et al., 2001). The two species present significant differences in terms of traits, biomass allocation and seasonal development (Proença et al. 2019). Given the numerous functioning values provided by salt marshes and considering the growing global change pressure they are facing, a deep knowledge of the underlying processes of marsh adaptation capacity through tidal flat colonization is needed (Bouma et al. 2016). The evolution of tidal flats into salt marsh entails an evolution of its functioning, both physically (hydrodynamics and morphology) and biologically. The processes underlying the interactions between vegetation and the incident hydrodynamic forces have been widely assessed both with field and laboratory studies. However, they mostly consider well-developed marsh vegetation and less attention has been given to marsh vegetation at the pioneer stage. Hence, for management purposes, it is important to understand the underlying processes of the transition between the pioneer mudflat stage and marsh development. With this study, we aim at comparing the relative impact of the two cordgrass species present in the Bay of Arcachon on sedimentation during the tidal flat colonisation stage.

5.2 Material and methods

5.2.1 Study area

The Bay of Arcachon is a mesotidal coastal lagoon, semi-enclosed from the ocean by the Cap Ferret sandspit, located in the Bay of Biscay (south west Atlantic coast of France – Figure 5.1). The Bay has an equilateral triangular shape of 20 km long sides. Its mean depth is of 4.6 m (Plus et al. 2009) and 75% of the total surface corresponds to intertidal mudflats (Allard et al. 2009).

The Cap Ferret sandspit and the presence of sand banks and shoals at the inlet strongly limit the entrance of oceanic swell and thus, circulation inside the bay is mainly driven by tidal currents and locally-generated wind waves (Parisot et al. 2008). Tides are predominantly semi-diurnal and tidal amplitude in the lagoon ranges from 0.8 m at neap tides to 4.5 m at spring tides (Cayocca 2001). The general circulation in the Bay is ebb-dominated (Plus et al. 2009), which means that the lagoon mostly exports sediment (Cayocca 2001). The strength of the tidal currents significantly decreases throughout the lagoon, where highest values can reach more than 2 m/s at the entrance passes (Plus et al., 2009; Salles et al., 2015), decreasing to values between 0.1 and 0.5 m/s on the intertidal zone (Plus et al., 2009; Ganthy et al., 2013). The waves are wind dominated and thus, closely related the wind conditions (Parisot et al. 2008). Strongest winds come mostly from W-NW sector. Because of this wind dependency, wave heights inside the Bay are limited by the fetch, which, on its hand, depends on wind direction and is strongly affected by the presence of an island in the middle of the Bay, “l’Ile aux oiseaux”. Wave and wind measurements by Parisot et al. (2008) inside the lagoon showed a good correlation between wind intensity and wind wave formation. More precisely, they found

that winds higher than 10 $m.s^{-1}$ generated waves higher than 10 cm and strongest wind events could generate waves higher than 20 cm that could reach up to 50 cm. They also verified a non-linear relationship between the increase of significant wave height and water depth and typical wave periods between 1 and 4 seconds.

Many small streams discharge into the lagoon. However, the main riverine input mostly comes from two rivers: the Eyre, in the SE, and the Porge canal, on the northern limit, contributing with 73 and 24% of the total annual discharge, respectively (Plus et al., 2009; 2010). This riverine discharge (and inherent sediment input) is negligible, as it is significantly lower (400 times) than the volume of incoming seawater, and the overall sediment budget in the Bay is negative (Allard et al. 2009). At the mouth of the lagoon the sediment is mainly composed of coarse-grain sand (Blanchet et al. 2005). At the inner tidal flats sediment is mostly muddy, which shows the sheltered character of the internal section of the Bay.

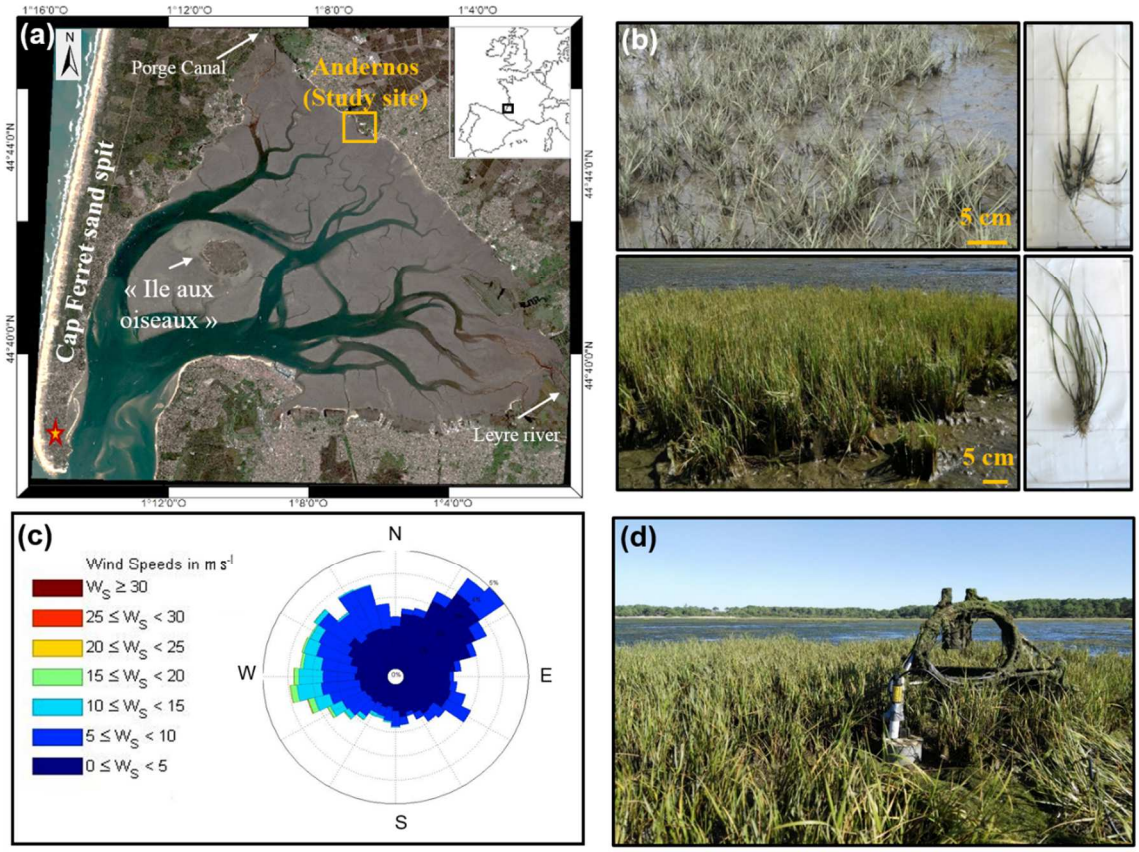

Figure 1.1: (a) *Location of the study site of Andernos (yellow box) within the Bay of Arcachon. Red/yellow star indicates the location of the Cap Ferret's meteorological station.* ***(b)*** *Characterization of Spartina anglica meadow (top left) and individual plant (top right) and Spartina maritima meadow (bottom left) and individual plant (bottom right).* ***(c)*** *Wind rose for wind records at the meteorological station of Cap Ferret indicated in (a) during the period of the field experiment.* ***(d)*** *ALTUS device mounted on a structured installed within Spartina maritima vegetation patch.*

5.2.2 Vegetation in the Bay of Arcachon

Mudflats in the Bay of Arcachon are extensively colonized by *Zostera noltei*. These seagrass meadows occupy more than 40% of the intertidal surface and it has been demonstrated that they damp tidal currents (Kombiadou et al. 2014) and play a major role on tidal flat sediment stabilization (Ganthy et al., 2011, 2013). However, this species presence in the Bay is

reportedly declining since the middle of the 2000s (Plus et al. 2010). Since seagrass beds have important ecological values (Barbier et al. 2011), importance is currently given to the study of the factors contributing to its decline in the Bay (Cognat et al. 2018).

Salt marshes in the Bay of Arcachon were initially dominated by the cordgrass species *Spartina maritima*, a native European species. In the 1980s, there was the introduction of the exotic species *Spartina anglica*, which is considered as a strong invader in several countries (Baumel et al., 2001; Strong and Ayres, 2013,). Both *Spartina* species present the same range of occupation along the intertidal profile (Proença et al., 2019). They typically form extensive meadows along the coast but, they can also extend towards the inner Bay in isolated clonal patches, especially the exotic *Spartina*, where it co-occurs with seagrass *Zostera noltei*. Even though the two cordgrass species are very similar, they present significant differences in terms of biomass allocation, where the native species favours aerial biomass and the exotic one, on the contrary, presents a more developed root and rhizome system (Proença et al., 2019).

5.2.3 Sampling and analysis

Field work was conducted on the tidal flat at Andernos (44.74° N, 1.12° W), located in the north eastern part of the Bay of Arcachon (Figure 5.1a), during a total period of 14 months, between the 28th of November 2016 and the 3rd of February 2018.

The choice of the sampling zone was determined by the presence of patches of *S. anglica* and *S. maritima* located nearby, at the same topographic level and exposed to the same hydrodynamic conditions. The patches of the two *Spartina* species presented roughly the same characteristics, with a diameter of 2.5 m and plant height between 10 and 20 cm (variable with the season). They were placed approximately 20 m apart and located at about 250 m from the shoreline. At the centre of the two selected patches (one of each species) we positioned an ALTUS probe (Bassoullet et al. 2000), consisting of an acoustic altimeter coupled to a pressure sensor to perform continuous measurements of the bed level variation and associated wave events under the influence of each *Spartina* species (Figure 5.1b and 5.1d). We followed the protocol proposed by Ganthy et al. (2013) for the use of ALTUS systems within vegetation. Plants growing under the range of the ALTUS sensor were cut at the beginning of the experiment and the need of plant trimming was monitored at every site inspection.

ALTUS devices are submergible acoustic altimeters with 0.2 mm resolution and 5 mm precision (Jestin et al. 1998). Both water depth and sediment bed level data were acquired in bursts of 260 seconds, every 15 minutes at a frequency of 2 Hz, during immersion periods. Sediment bed level measurements are performed through the emission and reception of a 1 MHz acoustic wave. The sensor can record up to 4 beams (B1 to B4). Each one of these beams is based on a different threshold of the returned acoustic energy, which is a proxy of the degree of the bed level's density. This allows the detection of an eventually layered sediment bed. More precisely, in the case of a bed composed of more fluid sediment over consolidated one, the beam with lowest return signal should detect the water/sediment interface and the remaining beams progressively detect the deeper layers up to the consolidated bottom. In absence of bed layering, all beams should provide an equivalent distance to the bottom. Because altimetry measurements can be affected by the presence of particles in the water column that can diffuse the beams return signal and originate spikes of anomalous data, here we consider the altimetry based on the maximum echo obtained through the calculation of the standard deviation over

the despiked burst, following the standard-deviation method described by Cea et al. (2007), initially applied to velocity measurements using Acoustic Doppler velocimeters (ADV).

Water depth measurements by the ALTUS pressure sensor are provided at a resolution of 20 mm. Skewness of water elevation (γ) was computed for each semi-diurnal tide according to Nidzieko and Ralston (2012), following Eq. (1):

$$\gamma = \frac{\mu_3}{\mu_2^{3/2}} \quad (1)$$

where the m-th moment about zero is defined by Eq. (2):

$$\mu_m = \frac{1}{N-1}\sum_{1=1}^{N}(n_i)^m \quad (2)$$

where N is the number of samples n_i and, in particular for water level asymmetry, n is given by the variation of the water level over time following Eq. (3):

$$n = \frac{\partial h}{\partial t} \quad (3)$$

The skewness of water elevation was used as a proxy for tidal horizontal asymmetry in order to estimate the asymmetry of tidal currents at the study site, where $\gamma > 0$ indicates ebb-dominance (ebb currents stronger than flood currents) and $\gamma < 0$ indicates flood dominance (flood currents stronger than ebb currents).

Wave height and period were extracted from the high-frequency water depth measurements through spectral analysis. Maximum wave orbital velocities (Ub) were then calculated through linear wave theory. Subsequent bottom shear stress estimations were based on the wave induced friction factor (f_w) from Eq. (4), according to Soulsby (1997):

$$\tau_w = \frac{1}{2} \cdot \rho_{water} \cdot f_w \cdot {U_b}^2 \quad (4)$$

where ρ_{water} is the water density (kg m^{-3}) and f_w is estimated according to Soulsby (1993), as function of the quotient between half the fluid particle excursion at the bottom and the bed roughness length (Z_0), expressed by Eq. (5):

$$f_w = 1.39 \cdot (A/Z_0)^{0.52} \quad (5)$$

and assuming the typical value of Z_0 for muddy sediments of 0.2 mm. Even though sediment from the two stations presented slight differences in sediment composition, these differences were small and the same Z_0 was considered for both. Nevertheless, we do not exclude the possibility that further attention should be given to variations in the influence of the Z_0 value in the bed sediment dynamics within the two species of vegetation. However, given the magnitude of differences we observed in the sediment dynamics patterns within the two vegetation species, even with the assumption of the same bed roughness length for both stations; such analysis goes beyond the scope of the present study.

The total wave energy over each tidal cycle was estimated from Eq. (6):

$$E_{wave} = \sum_{t-12}^{t}\frac{1}{8} \cdot 9.81 \cdot \rho_{water} \cdot H_{wave}(t)^2 \quad (6)$$

Considering that waves in the Bay are mainly wind generated, wind measurements (direction and intensity – Figure 5.1c) available at the meteorological station of Lège-Cap Ferret (Figure 5.1a) were used and directly correlated to wave direction. Atmospheric pressure data was also obtained to apply atmospheric and non-hydrostatic corrections to water depth measurements.

Surficial sediment samples were collected within the two meadows of *Spartina* in winter and summer to perform grain size analysis, water content and density determination.

Finally, since the two species may differently impact the state of bed sediments regarding erosion processes, we estimated the critical bottom shear stress for erosion (τ_{ce}) from time-series of measured bed level and wave-induced bottom shear stress (τ_w) on each of the species. We first selected, as much as possible, wave events during which the bed experienced erosion for both species. Ten events matching this criterion were found, with durations ranging from one single tidal cycle up to five consecutive tides. For each selected we applied the Partheniades erosion law given by Eq. (7):

$$E(t) = E_0.\left(\frac{\tau_w(t)}{\tau_{ce}} - 1\right) \quad \text{for } \tau_w > \tau_{ce}, \text{ and } E(t) = 0 \text{ for } \tau_w <= \tau_{ce} \qquad (7)$$

where E_0 is the erosion rate (kg m^{-2} s^{-1}). Based on the recent work of Mengual et al. (2017), we determined E_0 values depending on winter value of sand fraction measured within both species, giving 4.06x10^{-5} and 3.1x10^{-5} kg m^{-2} s^{-1} for *S. anglica* and *S. maritima*, respectively. For each wave event and species, 1000 values of τ_{ce} were alternatively tested (ranging from 0.001 to 4.000 N m^{-2}) and the value providing the best theoretical bed level evolution compared with data was retained. From the Partheniades relationship (Partheniades 1965) we could then estimate the theoretical bed evolution for each selected wave event following Eq. (8):

$$Hbed_{theoretical}(t) = Hbed_{theoretical}(t-1) - dh(t) \qquad (8)$$

where *dh* (m) corresponds to the eroded thickness between time *t-1* and *t* according to Eq. (9):

$$dh(t) = dt.\frac{E(t)}{\rho_{dry}} \qquad (9)$$

where *dt* is the time step between measurements *t-1* and t (seconds), ρ_{dry} is the dry density of bed sediment (kg m^{-3}), and *E(t)* is the instantaneous erosion sediment flux, previously obtained through Eq. (7).

5.3 Results

We collected time-series data of water elevation and bed variation under the influence of a native and an exotic *Spartina* species in the pioneer zone of the tidal flats in the Bay of Arcachon for over one year. In this section, we first present the short-term events, responsible for most relevant changes in bed level within the two *Spartina* species and determinant for the long-term trends, following presented. We then compare the differences in bed variation between the two species.

5.3.1 Seasonal to event patterns of sediment dynamics within *Spartina anglica* and *Spartina maritima*

Seasonal registered wave, sediment and vegetation characteristics for both stations are summarised in Table 5.1.

The hydrodynamic measurements showed significant differences between wave conditions during Autumn/Winter and Spring/Summer. Whereas during the low energy seasons wave heights were on average around 5 cm and did not exceed 20 cm, during the high energy seasons, wave heights varied between 5 cm and up to 65 cm, during periods of strong winds (Figure 5.2b). Even though wave heights within the two species of vegetation were of the same order of magnitude, with differences under 5 cm, they translated into significant differences in terms of impact on the bottom (Figure 5.2d). Notably, for the same wave events, wave bottom shear stress (τ_w) was consistently higher by 4 to 30 % within *Spartina anglica* than *Spartina maritima*

stands (Figure 5.2c). In terms of plant specific characteristics, significant differences were mostly found in terms of patch density, where *S. maritima* density was twice higher than *Spartina anglica* during summer and their difference tripled in winter time. This is likely a central factor explaining the differences observed within the hydrodynamics within the two *Spartina* species.

Table 5.1. *Summary data for the two Spartina species stations. ρ dry = sediments dry density; ρ bulk = sediments bulk density D50 = Sediment mean particle size; Hm0 = mean spectral wave height (m); Hmax = maximum wave height (m); Tp = wave peak period (s);* ***τ****w = Bed shear stress (N m-2); h = water depth.*

Parameters		*Spartina anglica*		*Spartina maritima*	
		Autumn/Winter	Spring/Summer	Autumn/Winter	Spring/Summer
Plant properties	Patch density (n° individuals m^{-2} ± SE)	39 (± 8)	63 (± 13)	124 (± 16)	130 (± 24)
	Plant height (cm)	15	15	20	20
	Water content (%)	188 (± 60)	216 (± 23)	224 (± 20)	218 (± 15)
Sediment properties	ρ dry (Kg m^{-3})	505 (± 152)	391 (± 34)	380 (± 29)	384 (± 9)
	ρ bulk (Kg m^{-3})	1363 (± 90)	1229 (± 19)	1226 (± 25)	1220 (± 14)
	Porosity (-)	0.86 (± 0.06)	0.84 (± 0.02)	0.85 (± 0.02)	0.84 (± 0.01)
	D50 (µm)	23.1 (± 7.5)	28.5 (± 3.1)	18.3 (± 1.9)	28.7 (± 3.18)
	Fine sed. fraction (mud and silt %)	81.3 (± 11)	73.6 (± 4.7)	87.5 (± 1.9)	74.7 (± 4.4)
	Sand fraction (%)	18.7 (± 11)	26.4 (± 4.7)	12.5 (± 1.9)	25.3 (± 4.4)
	Hm0 (min, max)	< 0.05, 0.65	< 0.05, 0.34	< 0.05, 0.63	< 0.05, 0.29
Hydrodynamics	Hmax (min, max)	0.06, 0.85	0.06, 0.38	0.05, 0.86	0.06, 0.33
	Tp (min, max)	1, 9	1, 9	1, 9	1, 9
	T_w (min, max)	0.09, 16.42	0.1, 5.29	0.11, 15.12	0.16, 0.5
	Hm0/h	0.02, 0.27	0.02, 0.36	0.03, 0.47	0.08, 0.27

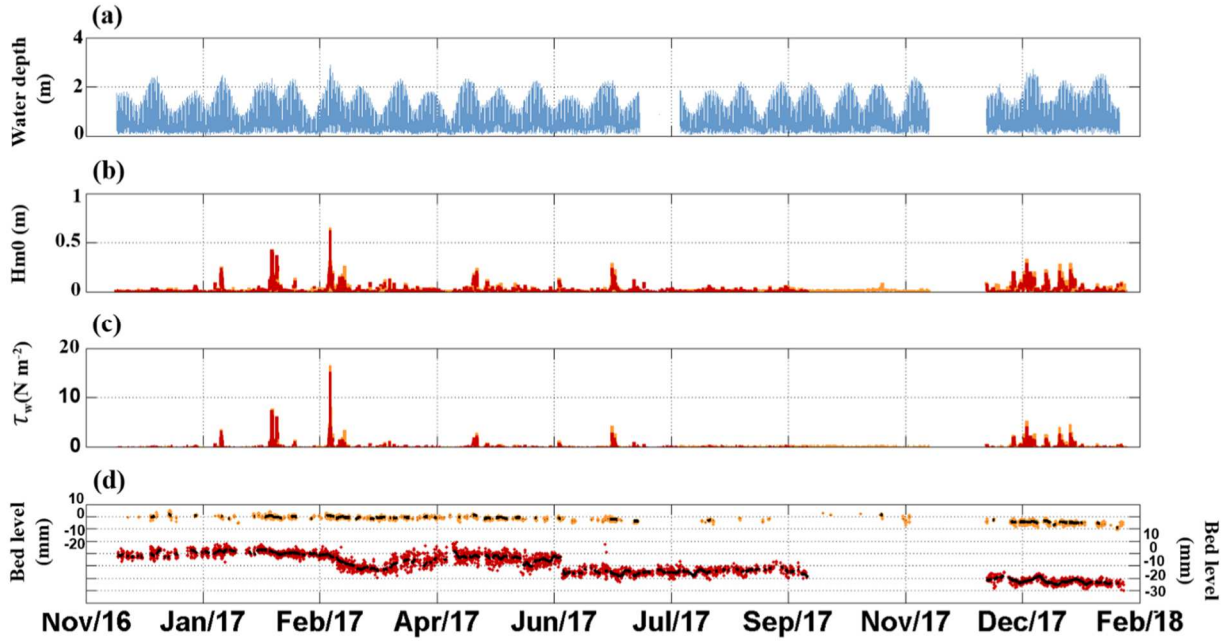

Figure 5.2: *Time-series records of* ***(a)*** *water level,* ***(b)*** *spectral wave height for Spartina anglica station (yellow) and Spartina maritima (red) station,* ***(c)*** *wave bottom shear stress for S. anglica station (yellow) and S. maritima (red) station and* ***(d)*** *bed level variation within S. anglica (yellow – left axis) and S. maritima (red – right axis) and tide average bed level variation for both species (black line), for the entire survey period, between November 28, 2016 and February 3, 2018.*

The comparison between the critical wave bed shear stress between the two *Spartina* species (Figure 5.3) showed that in any case, higher values (up to 3 times) of wave bed shear stress are required for sediment mobilisation within the exotic *S. anglica* which is consistent with the lower bed level variability verified within the stands of this species.

However, the analysis of wave action over the bed, both through its energy and wave bed shear stress did not reveal a clear tendency in terms of bed level response within the two *Spartina* species (data not shown).

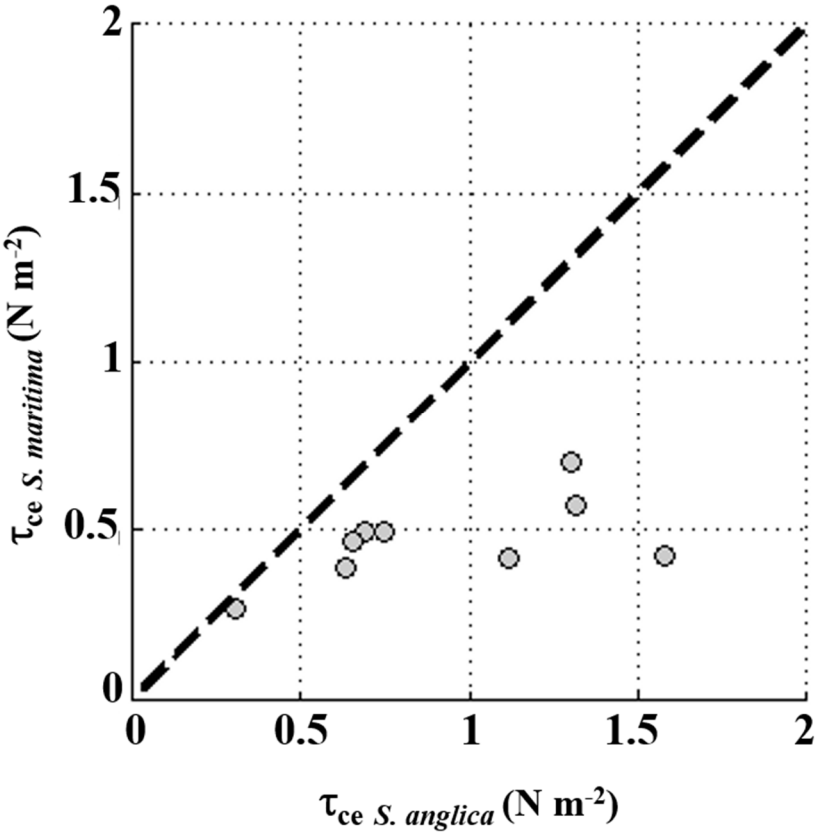

Figure 5.3: *Critical wave shear stress (τ_{ce} – N m^{-2}) within Spartina anglica versus Spartina maritima ($p < 0.002$ with significance threshold at $p = 0.05$). The black dashed line represents the line of equality $y = x$.*

Sediment characteristics within the meadows of the two *Spartina* species were similar for the Spring/Summer period. Overall, both species presented a sediment characterized by medium silt and, during the low energy season, mean sediment grain size was of 28 µm for the two species. Still under low energy conditions, both fine sediment and sand fractions presented close values, around 74% and 25%, respectively. However, differences between the two species increased during the high energy season (Autumn/Winter). Precisely, sediment in *S. maritima* showed higher percentage of fine sediments (6 %) and, conversely, sand percentage was lower of 6 % than in the exotic *Spartina*. This translated in a slightly higher D50 (23.1 µm against 18.3 µm) for the exotic species. Dry sediment density ($\rho_{dry)}$ was also significantly different for the two species within this season, when sediment under the influence of *S. anglica* presented a ρ_{dry} of 505 Kg m^{-3} whereas within *S. maritima* ρ_{dry} was of 384 Kg m^{-3} (Table 5.1). Considering the seasonal sediment budget, presented in Figure 5.4, we observed that the sediment trapping capacity of the two species in the tidal flat during the survey period was strongly counterbalanced by the erosive processes as both species presented overall negative sediment budget, except for the Spring/Summer season within *Spartina anglica*, that presented an accretion of 2.5 mm. Comparing the two Autumn/Winter seasons, we verified a strong inversion in the sediment budget in the behaviour of the bed level between the two species

explaining the contrasting net budget observed during the two winter periods in Figure 5.5. During Autumn/Winter 2016/2017, characterized by two spaced but stronger wave episodes, *Spartina maritima* presented a higher erosive behaviour. During the second Autumn/Winter (2017/2018), wave events did not reach the same magnitudes as the previous one and the wave induced bottom shear stresses were more frequently above 1 N m^{-2}, comparing to the previous year. With this continuous action of waves, it was the bottom under the influence of *S. anglica* that presented higher sediment loss. However, the total budget indicates an erosion twice higher within *S. maritima* than *S. anglica* (Figure 5.4).

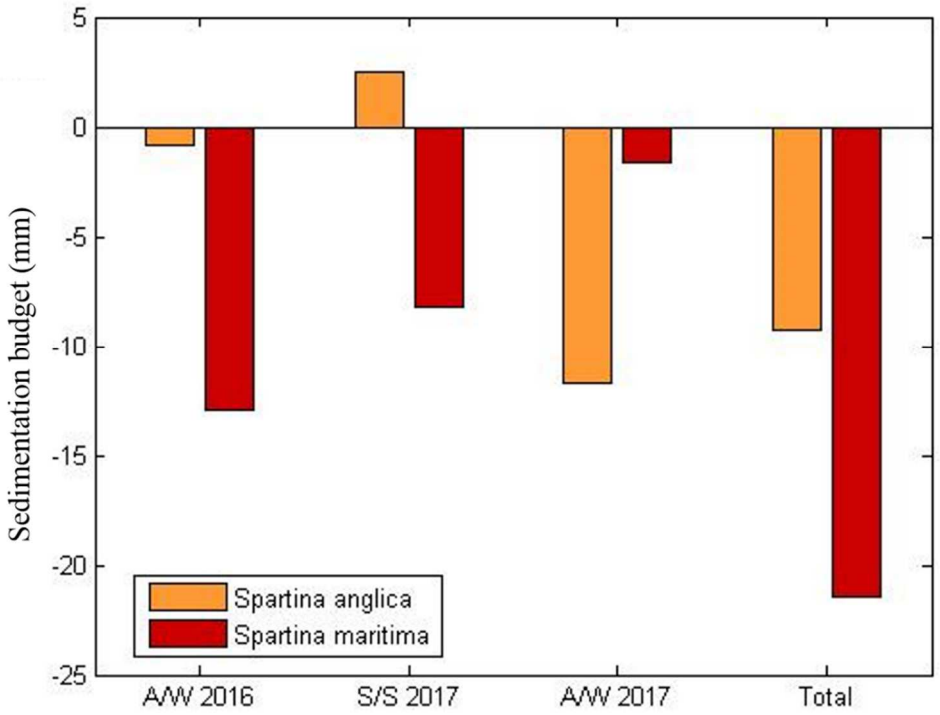

Figure 5.4: *Sedimentation budget (mm) per season (A/W – Autumn/Winter and S/S – Spring/Summer) estimated from the difference in the bed level at the beginning and at the end of each season and total budget estimated from the difference in bed level between the beginning and the end of the survey. Negative values indicate erosion and positive values indicate accretion.*

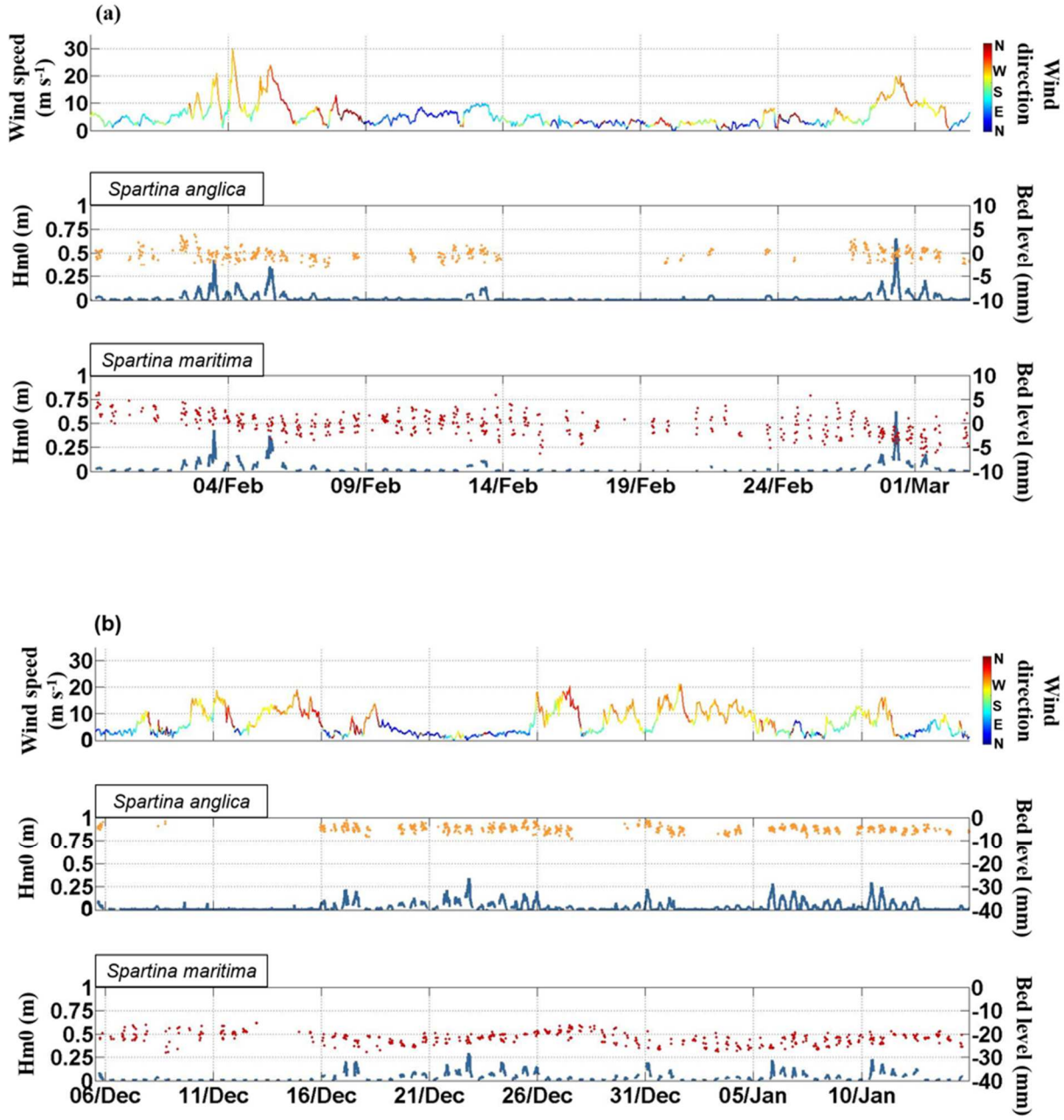

Figure 5.5: *Zoom on winter storm events from* ***(a)*** *Autumn/Winter 2016 and* ***(b)*** *Autumn/Winter 2017. Top graphics consider wind conditions measured at Cap Ferret's meteorological station with wind speed (line representation) and wind direction (colour representation). Central graphics represent measured mean wave height (blue line) and bed level variation (yellow dots) under the influence of Spartina anglica. Bottom graphics represent measured mean wave height (blue line) and bed level variation (red dots) under the influence of Spartina maritima.*

The evolution of the consolidation state of surficial sediment within the two *Spartina* species presented both seasonal and event related patterns (Figure 5.6). Notably, between mid-March and Mid-June, during the low energy season, the thickness of the non-consolidated bed (soft mud layer) tended to be higher than during more energetic periods, in particular within *S. maritima*, where it ranged from under 5 mm up to around 1 cm, whereas within *S. anglica* the variation was always under 5 mm. During storm events, in particular the one of the 28th February 2017, within *S. maritima*, we observed a strong erosion, with a decrease of the

consolidated bed of more than 1 cm. However, this did not produce an effective erosion of this order of magnitude as it was accompanied by a liquefaction of the upper layer of the bed, translated into an increase the soft mud layer thickness. The same behaviour was found for *S. anglica* with variations of lower magnitude.

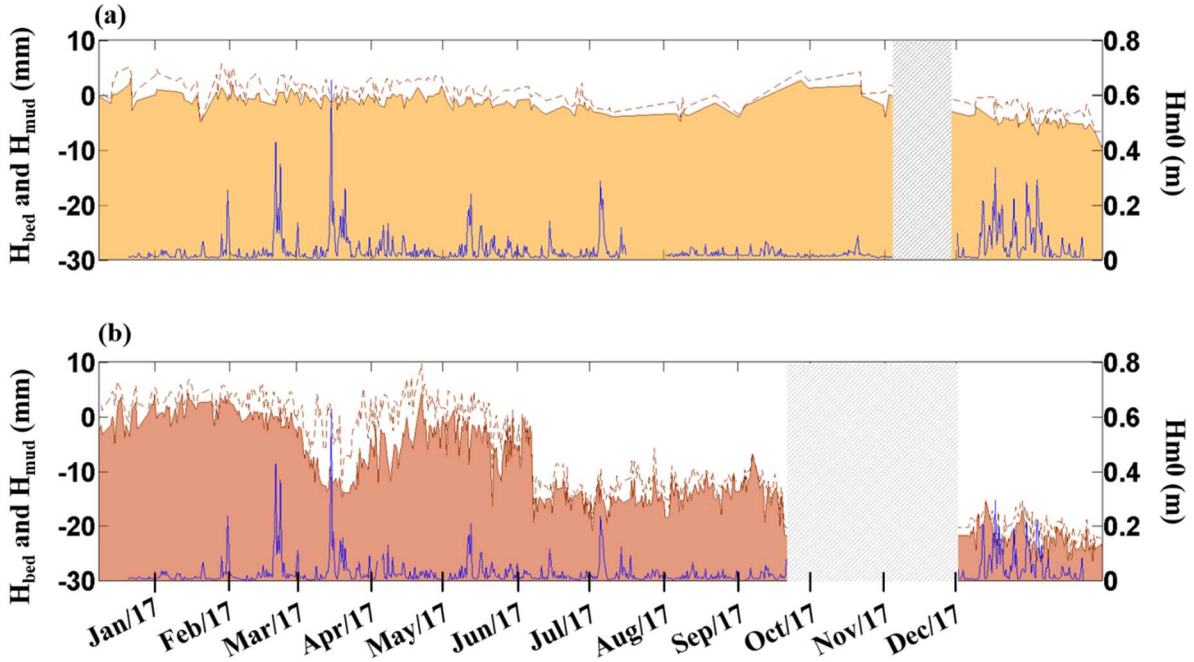

Figure 5.6: *Consolidated bed level (solid surface) and soft mud level (dashed line) and corresponding mean wave height (blue line) within the vegetation patches of* ***(a)*** *Spartina anglica and* ***(b)*** *Spartina maritima. Dashed grey box indicates "no data" period.*

5.3.2 Tide-induced variations in sediment dynamics

As expressed by the long-term time-series of bed level change under the action of both *Spartina* species, tide-induced bed level dynamics showed the same behaviour (well correlated accretion and erosion episodes) but with variations within *S. maritima* twice higher that within *S. anglica* (Figure 5.7).

The tidal asymmetry (γ) was found to increase with tidal range (Figure 5.8). The scatterplot indicates that the tide is ebb dominant for neap tides, while it becomes flood dominant for spring tides, above a tidal range of approximately 1.2m. The linear increase in flood dominance with tidal range, can favour sediment import into the study site for spring tides conditions. More precisely, during spring tides, when currents are stronger, more sediment is likely to be eroded from channels and tidal flats and because flood currents are stronger (flood dominance), sediment transport occurs mostly towards the inner Bay where it settles with lower probability of being re-suspended in ebb due to weaker currents. Conversely, during neap tides, when ebb currents exceed flood currents, sediment is more likely to be re-suspended and mobilized from the site.

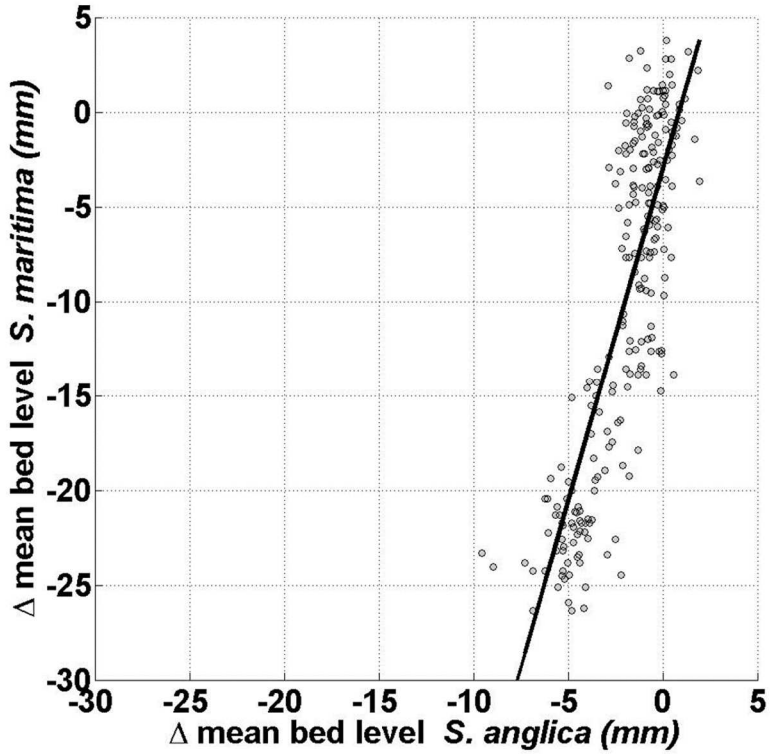

Figure 5.7. *Bed level variation (in mm) within Spartina maritima versus variations within Spartina anglica vegetation. Bed levels variations are tidally averaged values. Negative values indicate erosion and positive values indicate accretion. Black line corresponds to linear regression expressed by the equation* $y = 3.51x - 3$ ($R^2 = 0.83$, $n = 235$, $p < 0.001$, *with significance threshold at* $p = 0.05$).

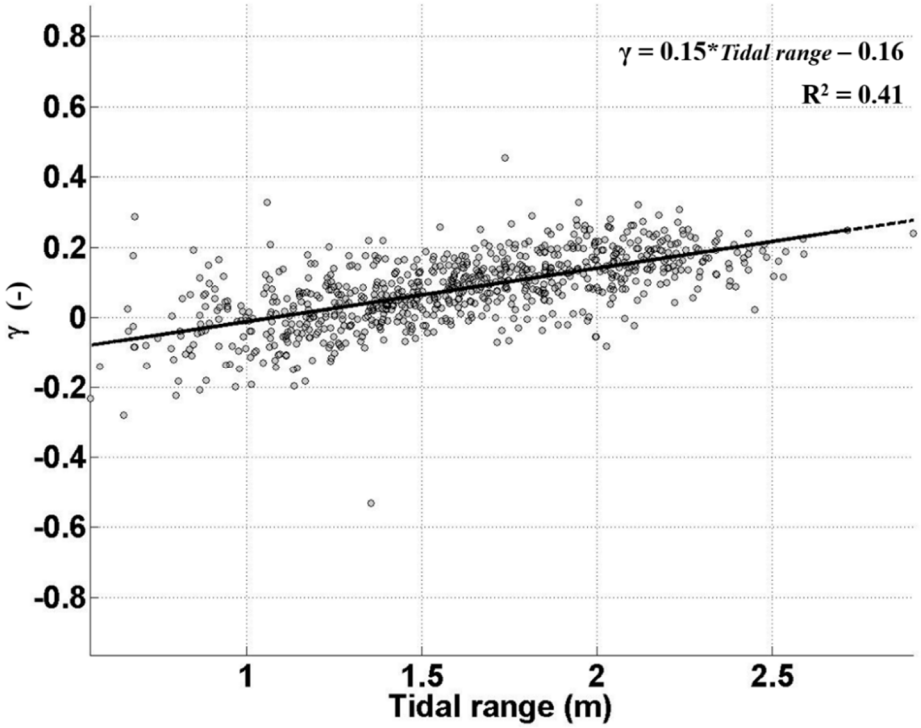

Figure 5.8. *Tidal asymmetry index (γ) as a function of tidal range (m) at the study site. Black line corresponds to linear regression expressed by the equation* $y = 0.15x - 0.16$ ($R^2 = 0.41$, $n = 778$, $p < 0.001$ *with significance threshold at* $p = 0.05$). *Values of* $\gamma > 0$ *correspond to flood dominance and values of* $\gamma < 0$ *correspond to ebb dominance.*

The sediment trapping efficiency of the two species can be verified by the estimation of the sedimentation rate at the two sites. The relationship between sedimentation rate and tidal range variation (Figure 5.9) showed strong correlation for the exotic *Spartina* (R^2 = 0.8, p < 0.001) and no correlation for the native *Spartina* (R^2 = 0.08, p < 0.001), significant in both cases. Within *Spartina anglica*, a clear trend for accretion was verified (sedimentation rate > 0) in the transition from spring to neap tides (tidal range variation < 0). This is consistent with the previously indicated higher sediment availability during spring tides, that can settle with decreasing tidal currents as we move towards a neap tide regime. In the transition from neap to spring tides, a tendency for erosion was found instead, mostly related to the increase in tidal current velocities that will then re-suspend sediment that previously settled. Sediment variation within *Spartina maritima* influence showed a lower direct response to this tidal regime.

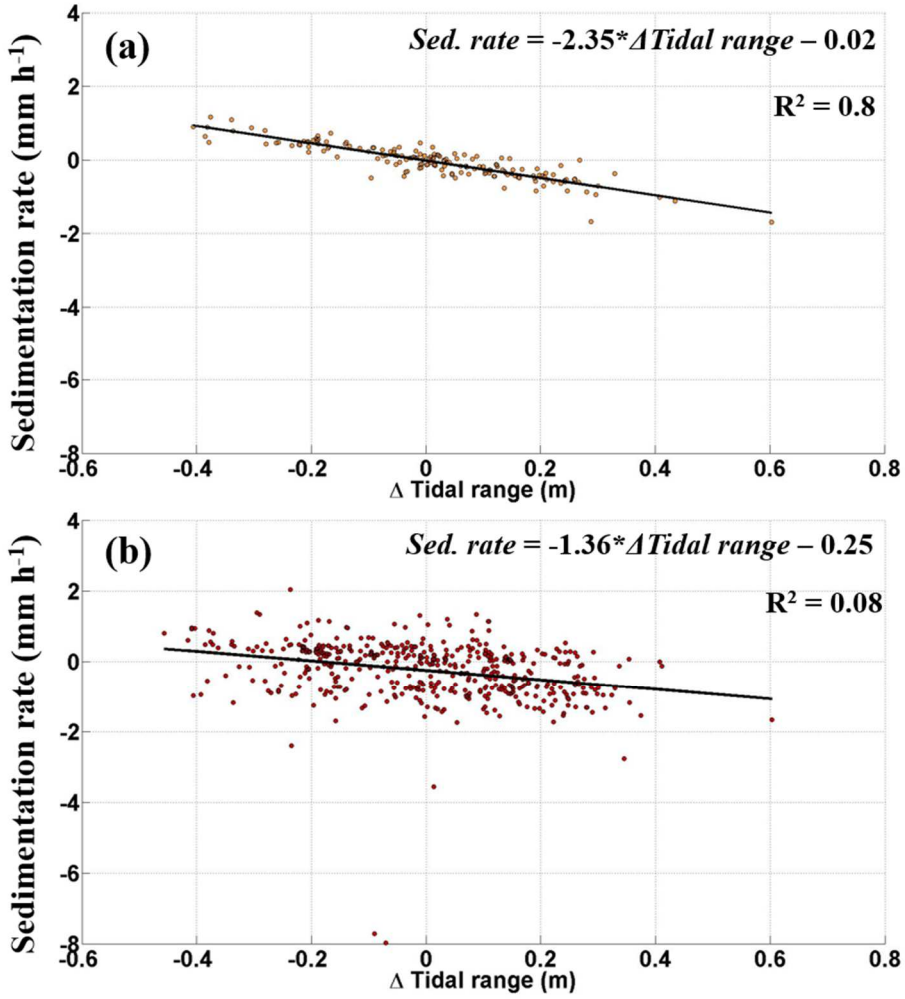

Figure 5.9. *Sedimentation rate (mm h^{-1}) as function of tidal range variation within* ***(a)*** *Spartina anglica and* ***(b)*** *Spartina maritima. Black lines correspond to linear regression expressed by the equations y = -2.35x-0.02 (R^2 = 0.8, n = 168, p < 0.001) for S. anglica and y = -1.36x-0.25 (R^2 = 0.08, n = 472, p < 0.001) for S. maritima (with significance threshold at p = 0.05).*

5.3.3 Annual bed level evolution under *Spartina* species influence

The hydrodynamic measurements for the whole time series (Figure 5.2a – 5.2c) showed that the two considered winters presented overall different energetic conditions. Notably, the Autumn/Winter 2016/2017 was marked by strong episodic storm events where wave heights and wave bed shear stress reached around 0.85 m and 16 N m^{-2}, respectively, whereas Autumn/Winter 2017/2018 was characterized by longer and lower magnitude wave events where wave heights and wave bed shear stresses did not go over 0.4 m and 5 N m^{-2}, respectively.

The observations of the long-term time series (whole period of survey) revealed a general stronger tendency for sediment stability under the influence of the exotic *S. anglica* than the native *S. maritima*, both under calm and energetic hydrodynamic conditions (Figure 5.2d). The bed level within the exotic *Spartina* patch experienced little change, presenting variations within an amplitude of 5 mm. On the other hand, inside the patch of the native *S. maritima*, the amplitude of bed level change was considerably larger, not only on a regular basis, with variations going up to ± 1 cm, but also in response to particular wave events, like the storm from the 4th February 2017 (Figure 5.2b-5.2c), presenting a net total decrease in bed level of 2.4 cm. Although, it is to note, that the abrupt decrease in the bed level within *S. maritima* registered in June is not associated to any meaningful physical event but most likely to a field survey where vegetation under the sensor was trimmed hence possibly releasing soft sediment deposits. However, average bed level evolution within the two *Spartina* species was strongly correlated (R = 0.83 – Figure 5.7) which indicates that the same processes govern sediment patterns within both species of vegetation, i.e., that erosion and accretion occurred simultaneously for both species as response to the hydrodynamic forcing.

5.4 Discussion

To assess the differences in the ecosystem-engineering ability of two *Spartina* species, a native and an exotic, field measurements of waves and associated bed level variation were performed in the tidal flats of the Bay of Arcachon. The bed level variation is an important parameter for the understanding of the extent of the interactions between the vegetation, hydrodynamics and the resultant sediment motion (Willemsen et al. 2018). The importance of bed level variation is due to the fact that it integrates a series of physical and biological processes that determine marsh formation. With the present study, we observed strong differences in bed level dynamics between *Spartina anglica* and *Spartina maritima*, where, overall, sediment influenced by the exotic *Spartina* had a higher temporal stability than those influenced by the native species.

5.4.1 Sediment dynamics under the influence of waves

In tidal flats, waves are considered as a primary driver for sediment dynamics (Hu et al., 2015, Belliard et al., 2019) and the two considered *Spartina* species presented distinct magnitudes of response to energetic wave events. However, in both cases, a time shift was verified between the highest wave action and the starting time of erosion. Indeed, the first impact of wave action, rather than immediate sediment mobilization, is the liquefaction of the sediment bed, i.e., the oscillatory pressure generated by the incident waves on a consolidated bed level induce a fluidization of the surficial bed sediments that then become erodible and available for

mobilization at the subsequent wave incidences (Forsberg et al. 2018). Such process is consistent with our measurements of surficial mud layer thickness that showed, for the two species, an increase in the non-consolidated bed thickness at the arrival of energetic wave events, in particular for the native *S. maritima*. This higher fluidization within the native *Spartina* translated in higher erosion rate than within *Spartina anglica*. The sediment colonized by the native *Spartina* presented lower critical bottom shear stresses, which can be explained by less consolidated sediments. This may be due to the high sediment trapping capacity and consequent high bed level variability. In this case, a less dense root system can also contribute to a lower impact on sediment bed resistance to erosion.

The higher resistance to erosion of sediments underneath the exotic *Spartina,* demonstrated by the higher critical wave shear stresses within its meadow, supports an increased bed consolidation within this species, probably related to its voluminous root system. Alternatively, the erosion differences found for the two species could be explained by the canopy density related turbulence. It has been experimentally shown by Tinoco and Coco (2018) that higher plant density requires higher critical wave orbital velocity for sediment resuspension but denser arrays of vegetation also increase turbulent kinetic energy levels. Consequently, it is turbulence and not wave orbital velocity the main driver for sediment resuspension because they found a decrease in wave orbital velocity in increased vegetation and they still had high suspended sediment concentrations. Indeed, our meadows did show a substantial difference in terms of canopy density, but further hydrodynamic measurements should be performed in order to verify the experimental findings of Tinoco and Coco (2018).

Nevertheless, erosion events were always correlated to the occurrence of storms and they were more significant for the sediment bed under the action of *Spartina maritima* than within *Spartina anglica*.

5.4.2 Tidally driven sediment dynamics

The duration of the tidal inundation is directly linked with sedimentation rates in tidal flats (Kirwan et al. 2010). Therefore, the tidal forcing action, which is the dominant forcing during summertime, when periods characterized by large waves are scarce, represents an important factor in the sediment trapping capacity of a particular species. The relationship between the sedimentation rate and tidal range variation within the two species of *Spartina* showed a much higher variability with tidal action within the native *S. maritima* than the exotic *S. anglica*. Due to its denser canopy, the native *Spartina maritima* showed a stronger ability capacity for sediment trapping. However, freshly deposited sediments are more easily eroded than consolidated muddier sediments and increased permeability and water content reduces soil strength and resistance to erosion (Escapa et al. 2008). Because *S. maritima* exhibits a strong ability for sediment trapping, new sediment is continuously depositing without time get consolidated and is easily washed away as has been verified by Ganthy et al. (2011) within *Zostera noltei* meadows during low energy summer season. On the other hand, the exotic *Spartina,* at the pioneer stage, presented sparse aerial surface coverage, which indicates that its action on flow deceleration and subsequent capacity for sediment trapping is probably limited, inducing less sediment motion variation. This suggests that at the earlier stage of development, the ecosystem-engineering ability of *Spartina anglica* to vertically increase soil elevation is mostly related to its high resistance to erosion and the organic contributions of vegetation

(Nyman et al. 2006) rather than by accumulation of inorganic sediment. Overall, tidally driven sediment dynamics mostly induced accretion at the site but it was of very low magnitude and, on the short-term, more significant within the native *Spartina* canopy. Considering the combination between tides and episodic storm events, essential for the long-term dynamics, we verified that, on one hand storms induce erosion and on the other hand tidal dominance during fair weather induces accretion. The weighing of these two processes indicates a stronger predominance of storm-induced erosion which, along with sediment supply deficiency within the inner zone of the Bay, leads to a general trend to bed erosion at the study site.

5.4.3 Long-term differences in bed level variation between *Spartina anglica* and *Spartina maritima*

The seasonal continuous monitoring of bed level evolution under the action of two species of *Spartina* reveals a species dependent influence on soil stabilization in the tidal flats. As demonstrated by Bouma et al., (2013), species' traits impact the intensity and scale of the interactions between organisms and their environment. Biomass measurements of the two *Spartina* species in the Bay of Arcachon (Proença et al. 2019) have shown that, on the lower intertidal levels, the exotic *Spartina, S. anglica*, presents twice higher belowground allocation than aboveground whereas the native one, *S. maritima* favours aboveground biomass to the detriment of roots and rhizomes. The long-term variations in bed evolution we have registered within the two types of vegetation are consistent with this biomass distribution for the two *Spartina* species. The soil under the influence of the invasive *Spartina* presented significant stability, even during the action of energetic hydrodynamic events. This capacity of voluminous root systems to increase soil resistance (Schwarz et al., 2010; Balke et al., 2012; Fagherazzi et al., 2013) to erodibility has particularly been shown by the works of Vannoppen, (2016). These authors verified an inter-specific effectiveness in reducing soil erosion rates and that resistance to erosion was positively correlated to root biomass density.

Strong ecosystem engineers in tidal flats, such as *Spartina* species, are most commonly known to enhance bed elevation (Thompson 1991). This is valid for homogenous well-developed marshes. However, for isolated clone *Spartina* patches in the pioneer zone it is not always the case and the topographic evolution (expansion or shrinking) of the tussock strongly depends on the large-scale net-sediment dynamics, sediment grain size and other prevailing abiotic conditions that can change in time (Balke et al. 2012). Indeed, the size of clone is considered as a major conditioning accretion (Castellanos et al. 1994) and Sánchez et al. (2001) have found an increase in accretion rates with increasing patch diameter for *Spartina maritima* population. In our study we found a general tendency for sediment loss within the patches of the two species of *Spartina*. Considering that rivers are a major player in intertidal morphodynamics providing sediment for saltmarsh expansion (Fagherazzi et al. 2013), this can possibly be due to the low mineral sediment availability in the Bay of Arcachon. In fact, salt marshes maintain their elevation by deposition of mineral sediment and production of organic matter, but vertical and horizontal marsh growth is only possible if there is enough sediment available in the water column (Friedrichs and Perry, 2001; Kirwan et al., 2010; Fagherazzi et al., 2013; Lauzon et al., 2018). In this process, the tidal inundation is an important factor and it can be considerably affected by changes in Sea Level Rise. The channel network at the entrance of the Bay has

been giving signs that the lagoon is currently adapting to Sea Level Rise (Nahon et al., 2019). However, further studies should be performed to address the role of the saltmarshes in the Bay to this adaptation.

5.5 Conclusions

The understanding of vegetation related short-term tidal flat sediment dynamics is essential to the knowledge of the species' dependent long-term cyclic processes of marsh development, which is crucial in a context of global change.

The monitoring of bed level variation under the influence of the invasive *Spartina anglica* showed weak erosion both on the event scale (response to storms) and on the long-term in opposition to *Spartina maritima* that presented much higher vulnerability for sediment loss during high energy events. However, the exotic species also showed a limited ability in promoting accretion on the pioneer zone of the mudflat comparing to the native one. The joint action of these two effects seems to lead to a more effective bed stabilization and protection against erosion from the exotic *Spartina anglica*, pointing out this species as a better ecosystem engineer on the mudflat's pioneer zone.

We have shown that closely related species can present different influences on sedimentation/erosion patterns which should be taken into account within management actions. Additionally, in a context where marshes are globally being threatened by human action, it is important to understand the different species' adaptation mechanisms to the environment they colonize as well as the repercussions these biologically induced changes can have on a global scale and with an interdisciplinary perspective in order to achieve a balanced evaluation of eventual management actions that should be taken.

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References

Allard, J. et al. 2009. A synthesis of morphological evolutions and Holocene stratigraphy of a wave-dominated estuary : The Arcachon lagoon, SW France. - Continental Shelf Research 29: 957–969.

Balke, T. et al. 2012. Conditional outcome of ecosystem engineering: A case study on tussocks of the salt marsh pioneer *Spartina anglica*. - Geomorphology 153–154: 232–238.

Barbier, E. B. et al. 2011. The value of estuarine and coastal ecosystem services. - Ecological Monographs 81: 169–193.

Bassoullet, P. et al. 2000. Sediment transport over an intertidal mudflat: field investigations and estimation of fluxes within the ``Baie de Marenngres-Oleron'' (France). - Continental Shelf Research 20: 1635–1653.

Baumel, A. et al. 2001. Molecular investigations in populations of *Spartina anglica* C.E. Hubbard (Poaceae) invading coastal Brittany (France). - Molecular Ecology 10: 1689–1701.

Belliard, J.-P. et al. 2019. High-resolution bed level changes in relation to tidal and wave forcing on a narrow fringing macrotidal flat : Bridging intra-tidal, daily and seasonal sediment dynamics. - Marine Geology in press.

Bernik, B. M. et al. 2018. Clonal vegetation patterns mediate shoreline erosion. - Geophysical Research Letters 45: 6476–6484.

Blanchet, H. et al. 2005. Structuring factors and recent changes in subtidal macrozoobenthic communities of a coastal lagoon, Arcachon Bay (France). - Estuarine, Coastal and Shelf Science 64: 561–576.

Borsje, B. W. et al. 2011. How ecological engineering can serve in coastal protection. - Ecological Engineering 37: 113–122.

Bouma, T. 2009. Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. - Helgol Mar Res: 3–18.

Bouma, T. J. et al. 2005. Trade-Offs Related to Ecosystem Engineering : A Case Study on Stiffness of Emerging Macrophytes. - Ecology 86: 2187–2199.

Bouma, T. J. et al. 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures : Combining field, flume and modelling experiments. - Continental Shelf Research 27: 1020–1045.

Bouma, T. J. et al. 2013. Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks : A flume study on three intertidal plant species. - Geomorphology 180–181: 57–65.

Bouma, T. J. et al. 2016. Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics : Lateral Salt Marsh Dynamics. - Limnology and Oceanography 61: 2261–2275.

Castellanos, E. M. et al. 1994. Nucleation and facilitation in saltmarsh succession: Interactions between *Spartina maritima* and *Arthrocnemum perenne*. - Journal of Ecology 82: 239–248.

Cayocca, F. 2001. Long-term morphological modeling of a tidal inlet: the Arcachon Basin, France. - Coastal Engineering 42: 115–142.

Cea, L. et al. 2007. Velocity measurements on highly turbulent free surface flow using ADV. - Exp Fluids 42: 333–348.

Chen, Y. et al. 2016. A comparison of biohydrodynamic interaction within mangrove and saltmarsh boundaries. - Earth Surface Processes and Landforms 41: 1967–1979.

Chen, Y. et al. 2018. Comparison of Flow and Energy Reduction by Representative Intertidal Plants, Southeast China. - Proceedings of the Twenty-eighth (2018) International Ocean and Polar Engineering Conference

Coco, G. et al. 2013. Morphodynamics of tidal networks: Advances and challenges. - Marine Geology 346: 1–16.

Cognat, M. et al. 2018. Environmental factors controlling biomass development of seagrass meadows of *Zostera noltei* after a drastic decline (Arcachon Bay, France). - Journal of Sea Research 140: 87–104.

Coops, H. et al. 1996. Interactions between waves, bank erosion and emergent vegetation: an experimental study in a wave tank. - Aquatic Botany 53: 187–198.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. - Oikos 97: 153–166.

D'Alpaos, A. et al. 2007. Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. - Journal of Geophysical Research in press.

Escapa, M. et al. 2008. Sediment dynamics modulated by burrowing crab activities in contrasting SW Atlantic intertidal habitats. - Estuarine, Coastal and Shelf Science 80: 365–373.

Fagherazzi, S. 2012. Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. - Reviews of Geophysics in press.

Fagherazzi, S. et al. 2013. Marsh Collapse Does Not Require Sea Level Rise. - Oceanography 26: 70–77.

Forsberg, P. L. et al. 2018. The effect of successive storm events and seagrass coverage on sediment suspension in a coastal lagoon. - Estuarine, Coastal and Shelf Science 212: 329–340.

Friedrichs, C. T. and Perry, J. E. 2001. Tidal salt marsh morphodynamics: A synthesis. - Journal of Coastal Research SI 27: 7–37.

Ganthy, F. et al. 2011. The Stability of Vegetated Tidal Flats in a Coastal Lagoon Through Quasi In-Situ Measurements of Sediment Erodibility. - Journal of Coastal Research: 1500–1504.

Ganthy, F. et al. 2013. Seasonal modification of tidal flat sediment dynamics by seagrass meadows of *Zostera noltii* (Bassin d'Arcachon, France). - Journal of Marine Systems 109–110: S233–S240.

Ganthy, F. et al. 2015. Effects of short flexible seagrass *Zostera noltei* on flow, erosion and deposition processes determined using flume experiments (D Mohrig, Ed.). - Sedimentology 62: 997–1023.

Green, M. O. and Coco, G. 2014. Review of wave-driven sediment resuspension and transport in estuaries - Green - 2014 - Reviews of Geophysics - Wiley Online Library. - Reviews of Geophysics 52: 77–117.

Horstman, E. M. et al. 2013. Flow routing in mangrove forests: A field study in Trang province, Thailand. - Continental Shelf Research 71: 52–67.

Hu, Z. et al. 2015. Predicting long-term and short-term tidal flat morphodynamics using a dynamic equilibrium theory: Modeling Tidal Flat Dynamic Equilibrium. - Journal of Geophysical Research: Earth Surface 120: 1803–1823.

Jestin, H. et al. 1998. Development of ALTUS, a high frequency acoustic submersible recording altimeter to accurately monitor bed elevation and quantify deposition or erosion of sediments. - OCEANS '98 Conference Proceedings

Jones, C. G. et al. 1994. Organisms as Ecosystem Engineers. - In: Ecosystem Management. Springer New York, pp. 130–147.

Jones, C. G. et al. 1997. Positive and negative effects of organisms as physical ecosystem engineers. - Ecology 78: 1946–1957.

Kirwan, M. L. and Murray, A. B. 2007. A coupled geomorphic and ecological model of tidal marsh evolution. - PNAS 104: 6118–6122.

Kirwan, M. L. and Megonigal, J. P. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. - Nature 504: 53–60.

Kirwan, M. L. et al. 2010. Limits on the adaptability of coastal marshes to rising sea level. - Geophysical Research Letters 37: n/a-n/a.

Kombiadou, K. et al. 2014. Modelling the effects of *Zostera noltei* meadows on sediment dynamics: application to the Arcachon lagoon. - Ocean Dynamics 64: 1499–1516.

Lauzon, R. et al. 2018. Effects of marsh edge erosion in coupled barrier island-marsh systems and geometric constraints on marsh evolution. - Journal of Geophysical Research: Earth Surface in press.

Losada, I. J. et al. 2016. A new formulation for vegetation-induced damping under combined waves and currents. - Coastal Engineering 107: 1–13.

Maza, M. et al. 2015. Large-scale 3-D experiments of wave and current interaction with real vegetation. Part 2: Experimental analysis. - Coastal Engineering 106: 73–86.

Mengual, B. et al. 2017. Modelling Fine Sediment Dynamics: Towards a Common Erosion Law for Fine Sand, Mud and Mixtures. - Water 9: 564.

Murray, A. B. et al. 2008. Biomorphodynamics: Physical-biological feedbacks that shape landscapes. - Water Resources Research in press.

Nepf, H. M. 2012. Flow and transport in regions with aquatic vegetation. - Annu. Rev. Fluid Mech. 44: 123–142.

Neumeier, U. 2007. Velocity and turbulence variations at the edge of saltmarshes. - Continental Shelf Research 27: 1046–1059.

Neumeier, U. and Amos, C. L. 2006. The influence of vegetation on turbulence and flow velocities in European salt-marshes. - Sedimentology 53: 259–277.

Nidzieko, N. J. and Ralston, D. K. 2012. Tidal asymmetry and velocity skew over tidal flats and shallow channels within a macrotidal river delta. - Journal of Geophysical Research: Oceans in press.

Nowacki, D. J. et al. 2017. Spectral wave dissipation by submerged aquatic vegetation in a back-barrier estuary. - Limnol. Oceanogr. 62: 736–753.

Nyman, J. A. et al. 2006. Marsh vertical accretion via vegetative growth. - Estuarine, Coastal and Shelf Science 69: 370–380.

Ondiviela, B. et al. 2014. The role of seagrasses in coastal protection in a changing climate. - Coastal Engineering 87: 158–168.

Parisot, J.-P. et al. 2008. Modélisation des agitations dans le Bassin d'Arcachon.: 435–444.

Partheniades, E. 1965. Erosion and deposition of cohesive soils. - Journal of Hydraulics Division (ASCE) 91: 105–139.

Peralta, G. et al. 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. - Marine Ecology Progress Series 368: 103–115.

Plus, M. et al. 2009. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. - Continental Shelf Research 29: 1008–1013.

Plus, M. et al. 2010. Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). - Estuarine, Coastal and Shelf Science 87: 357–366.

Proença, B. et al. 2019. Intraspecific facilitation explains the spread of the invasive engineer *Spartina anglica* in Atlantic salt marshes. - Journal of Vegetation Science in press.

Salles, P. et al. 2015. Wind-driven modifications to the residual circulation in an ebb-tidal delta: Arcachon Lagoon, Southwestern France - Salles - 2015 - Journal of Geophysical

Research: Oceans - Wiley Online Library. - Journal of Geophysical Research 120: 728–740.

Sánchez, J. M. et al. 2001. Primary colonisation of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain: vegetation structure and sediment accretion. - Aquatic Botany 69: 15–25.

Schwarz, M. et al. 2010. Quantifying lateral root reinforcement in steep slopes – from a bundle of roots to tree stands. - Earth Surface Processes and Landforms 35: 354–367.

Soulsby, R. L. 1993. Modelling of coastal processes.: 111–118.

Soulsby, R. L. 1997. Dynamics of marine sands. - Thomas Telford.

Strong, D. and Ayres, D. R. 2013. Ecological and Evolutionary Misadventures of *Spartina*. - Annual Review of Ecology, Evolution, and Systematics 44: 389–410.

Temmerman, S. et al. 2005. Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh: vegetation impact on flow routing. - Journal of Geophysical Research: Earth Surface 110: n/a-n/a.

Temmerman, S. et al. 2007. Vegetation causes channel erosion in a tidal landscape. - Geology 35: 631–634.

Temmerman, S. et al. 2013. Ecosystem-based coastal defence in the face of global change. - Nature 504: 79–83.

Thompson, J. D. 1991. The biology of an invasive plant: What makes *Spartina anglica* so successful? - BioScience 41: 393–401.

Tinoco, R. O. and Coco, G. 2018. Turbulence as the main driver of resuspension in oscillatory flow through vegetation. - Journal of Geophysical Research: Earth Surface in press.

Vannoppen, W. 2016. Root properties of vegetation communities and their impact on the erosion resistance of river dikes. - Earth Surface Processes and Landforms

Weitzman, J. S. et al. 2015. The attenuation of current- and wave-driven flow within submerged multispecific vegetative canopies. - Limnology and Oceanography 60: 1855–1874.

Willemsen, P. W. J. M. et al. 2018. Quantifying bed level change at the transition of tidal flat and salt marsh: can we understand the lateral location of the marsh edge? - Journal of Geophysical Research: Earth Surface in press.

Conclusions

Field measurements of wave events and the associated bed level variations under the influence of *Spartina anglica* and *Spartina maritima* showed that the two species present contrasting sedimentation/erosion patterns. Notably the observations highlighted that:

- The sediment under the influence of the exotic *S. anglica* presented an overall more stable behaviour than under the influence of the native *S. maritima*;

- *S. maritima* presented a higher sediment trapping capacity that was related to its dense aerial biomass;

- *S. anglica* presented a higher soil consolidation capacity that was related to its dense underground biomass.

The combination of the biomass measurements presented in **Chapter 2** and the observations sediment patterns here presented allowed an integrative understanding of the capacity of the two cordgrass species to build marsh within the pioneer zone. Overall, even when the aerial biomass of *S. anglica* is reduced to a minimum, in winter time, during more energetic wave events, soil stabilisation tends to be higher under the influence of the exotic *Spartina* influence. Such results can be of great relevance to face erosion in a scenario of climate change and increased storm events.

Synthesis and perspectives

Synthesis and general conclusions

The present thesis aimed at improving the understanding of the impacts of *Spartina anglica* invasion in the Bay of Arcachon, both on the physical environment and on the native plant communities. *Spartina anglica* is considered as a strong invasive species in salt marshes throughout the world. However, salt marshes worldwide are facing major threats, mostly concerning direct and indirect human actions and there is a global concern to adopt preservation strategies as such systems sustain several ecological functions of importance. In this sense, the evaluation of the impacts of a biological invasion and its temporal evolution becomes crucial to correctly assess the needs for intervention. In the Bay of Arcachon, contemporary changes to the arrival of *Spartina anglica* were noticed in the Bay, such as the decline of *Zostera noltei* beds and intensive colonization of some coastline areas of the Bay, that brought concerns to local human communities and management entities.

The analysis of aerial photographs from 1949 to 2016 (**Chapter 1**) showed that even the European native *Spartina* has a relatively recent presence in the Bay, dating from the years 1940/50s in the study site of Andernos, at the north eastern part of the Bay. Even though the exotic *Spartina* has had a recent important development in some areas of the Bay (that were not considered in this study), the invasive species did not replace the native one where it was well installed and formed well-developed meadows. Instead, remote sensing inspection of salt marsh evolution primarily colonized by the native *Spartina* has demonstrated that, *Spartina anglica* occupies empty niches along the intertidal gradient. Previous cartography works on the *Spartina* sp. occupation in the Bay had already been performed (Le Nindre et al. 2004 - BRGM reports). These studies showed a considerable distance of expansion of the exotic *Spartina* towards the inner Bay. Because of this success in colonizing interior zones of the mudflat, local managers suggested that this species colonized the tidal flat along a gradient of anoxia due to higher tolerance to inundation than the native *Spartina*. However, the environmental and biomass measurements here presented have shown that the two *Spartina* species occur at the same intertidal levels (**Chapter 2**). Even though both the exotic and the native *Spartina* showed preferential occupation for higher levels of the intertidal profile, they were both found at the lower tidal levels, excluding the hypothesis previously suggested by local managers that the invasive *Spartina* has higher tolerance to anoxia. Thus, its success to colonize inner zones of the Bay may only be explained by a better resistance to perturbation, as suggested by its high investment in rhizome and growth, as compared to native *Spartina*. However, this new hypothesis remains to be directly tested. The exotic *Spartina* did not reveal to be capable of outcompeting the native *Spartina* in stable undisturbed communities. In contrast, its performance was clearly improved within the presence of neighbours of its own species. This intra-specific facilitation is likely due to its particularly voluminous root system that certainly contributed to its ability to cope with the constraints of the lower tidal levels, for instance the amelioration of soil oxygenation.

Even if the exotic *Spartina* faces a strong biotic resistance from the native one, making its colonization more difficult in places where the latter one is well-installed, several places around the Bay's coastline are currently dominated by exotic *Spartina*. Additionally, it has been observed that *Spartina* species presented phenotypic plasticity that seemed to be linked with anthropogenic perturbations on nutrient loads into the Bay. An experiment was then

conducted in order to understand how these perturbations can affect the strength and sign of the interactions between the two *Spartina* species that might have influenced *Spartina* dominance in some zones of the Bay (**Chapter 3**). It was observed that both the native and the exotic *Spartina* were favoured by the freshwater inputs into the Bay that induced an amelioration in environmental conditions, namely through increased nutrient contribution (particularly ammonium and phosphates) and soil redox potential and a decrease in sediment salinity. In accordance with the previous results, the native *S. maritima* showed again to be resistant to the invasion of the exotic species at long distance from the source of perturbation (the freshwater streams). However, close to the freshwater inputs the competitive ability of the native *Spartina* experienced a decrease related to the environmental ameliorations which can likely provide a window of opportunity to the exotic *Spartina*. *Spartina anglica* on its hand, presented a consistent absence of competition within its communities which is likely the key of its success. Additionally, this species seems to be able to combine two different strategies that represent a great asset in the colonization of salt marshes. On one hand, it favours the allocation to roots that contribute to a better soil oxygenation and likely nutrient absorption and, on the other hand, it also presents high productivity and rapid growth which is an advantageous ability in fertilized environments.

The fact that *Spartina anglica* successfully extends towards the inner zones of the Bay, which are typically occupied by *Zostera noltei,* does not seem, at short-term level to represent a threat to the seagrass species. Indeed, the presence of the exotic *Spartina* on the inner Bay is restricted to scattered isolated patches and probably limited the hydrodynamic disturbances. The most negative effect of mudflat colonization by the cordgrass is related to its long-term ecosystem engineering ability to increase the mudflat level (**Chapter 4**). However, this transition from mudflat to marsh zone is slow (**Chapter 5**) and the capacity of the exotic *Spartina* to promote accretion seems to be on one hand dependent on the morphology of the cordgrass species and, on the other hand, limited by the availability of inorganic sediment. There is extensive literature showing the capacity of submerged aquatic vegetation to attenuate the hydrodynamic forcing and consequently favour the sedimentation of suspended sediments. In this study such behaviour was observed for the native *Spartina* which presented a higher sediment trapping ability than *S. anglica* but also a much reduced ability to maintain trapped sediment. Conversely, the exotic *Spartina* showed a particularly increased capacity to promote soil stabilisation, probably due to its high root investment, and consequently, bed level variations within this species were reduced comparing to the native one. Coming back the consequences of mudflat colonization by the exotic cordgrass to *Zostera noltei*, it is a fact that the *Spartina* is able to settle in the pioneer mudflat, occupying zones that could eventually be suitable for the seagrass. However, the presence of *S. anglica* in such zones is limited probably due to the fact that these are highly disturbed zones and its extent of colonization cannot be related to the recent decline of the seagrass. Additionally, the exotic *Spartina* species particularly favours soil consolidation.

Either way, in the Bay of Arcachon, the presence of the exotic *Spartina anglica* does not seem to currently represent a significant threat to the native species *Spartina maritima* and *Zostera noltei.* The exotic *Spartina* has gained territory in places that have been previously disturbed and that present perturbations to which the native *Spartina* is less tolerant to. However, given the pervasiveness of human activities existing in the Bay, on the long-term

and at large scale the widespread presence of the exotic in the Bay can represent a threat for the native species. Indeed, simple physical disturbances on the native *Spartina* communities, likely occurring during eliminations of the exotic by stakeholders, or nutrient loads by the freshwater streams may certainly disrupt its biotic resistance. Additionally, long-term bottom elevation and fusion of *Spartina* of the exotic *Spartina* patches on the inner areas of the Bay may contribute to damage seagrass meadows.

On the other hand, in a context of global change, where Sea Level Rise and storm frequency are set to increase, several studies worldwide have indicated that intertidal vegetation plays a major role in hydrodynamic energy attenuation and shoreline protection. In this sense, the exotic *Spartina*, with its strong capacity for soil stabilization and resistance to disturbance, seems to be a suitable ally in coastal protection and weighted considerations should be done one whether it is preferable to have a marsh dominated by an exotic species or no marsh at all.

Perspectives and future lines of investigation

The present thesis contributed to the understanding of *Spartina anglica*'s colonization mechanisms in the Bay of Arcachon and its interactions with native species with an interdisciplinary perspective. In addition to the enlightening of the colonization processes by the exotic species, several other questions were also raised providing further directions of investigation that would be interesting to pursue with in order to achieve a better comprehension of the subject.

- **Remote sensing approach**

The use of satellite images presented a great potential in the assessment of marsh evolution and species identification. Despite the good results achieved with supervised classification methods depending on the vegetation's seasonal development, the biological perturbations of the intertidal environments can still represent a constraint to the accuracy of species distinction especially when the target features are of small dimensions as it is the case of small cordgrass patches at the early stage of colonization.

Even though one of the objectives of using remotely sensed images is to limit field works on access difficult environments, ground truth knowledge revealed to be essential and necessary on a regular basis. Precisely, due to the variability of spectral signatures, each biological feature can have, related to its phenology, interference from itinerant biological deposits and response to particular meteorological conditions. Prior to the application of an operational remote sensing based methodology it is crucial to acquire a robust data base of the different spectral signatures of the vegetation species present on site. Another point to consider is that, even though nadir images are preferable, the actual taken image can present small angle variations going up to 30°. In this sense, field reflectance measurements, should also be performed considering a range of angles in order to achieve the possible accordance between field and satellite data. Additionally, it could be useful to explore upscaling analysis of field reflectance data which has been previously shown to improve the agreement between hyperspectral ground truth data and satellite data increasing species spectral distinction in salt marshes. Finally, because intertidal vegetation tends to form monospecific patches sometimes with particular shapes, it would be relevant to perform a combined spatial and spectral analysis of satellite images, first through exploitation of the full spatial resolution of Pléiades products for the detection of patch patterns and then the application of the pixel classifications algorithms on the detected patches.

- **Experimental and field measurement approaches**

The different manipulative experiments performed within this study provided relevant information on the two *Spartina* species niche occupation. It was shown that the two *Spartina* species occupy the same levels along the intertidal topographic profile. However, due to higher tolerance to disturbances, the exotic *Spartina* has a more abundant presence towards the inner Bay. In order to verify this higher tolerance to disturbance from *Spartina anglica*, further experiments should be performed, notably through the transplantation of propagules from both *Spartina* species along profiles of increasing distance to the coast. Another question that still

remains is whether this zones where *S. anglica* thrives to colonize correspond in general to previously elevated levels or if they were originally mudflat pioneer low levels that were subsequently increased by the ecosystem engineering ability of the cordgrass. One way to assess this question could be to perform dGPS measurements of newly colonized mudflat zones all over the Bay. Complementary and to reduce fastidious point measurements on a difficult environment as the mudflats, it would be interesting to acquire terrestrial scan (LIDAR) data which provides topography of large surfaces at a few centimetres resolutions.

The nutrient characterization within the two *Spartina* communities have shown interesting differences namely in the availability of nitrates and phosphates. In order to better understand these differences, it would be convenient to proceed with analysis of the microbiotic communities associated to both *Spartina* species and integrated these results in the understanding of nutrient absorption by the two species.

Even though the assessment of the consequences of the exotic cordgrass mudflat colonization have presented a clear long-term and short-distance effects based on the strong ecosystem engineering capacity of *S. anglica*, short-term and long-distance effects could be better explored as interesting tendencies were found. Notably, it would be opportune to reproduce the experiment presented in **Chapter 4** considering more replicates and transects of *Z. noltei* transplants over the cordgrass patches considering longer distances.

Finally, the altimetry measurements within the two *Spartina* species have shown very distinct behaviours for the two species. To further understand the relationship between the exotic *Spartina*'s root system and its ability for sediment stabilisation it would be necessary to perform laboratory erodimetry experiments. Additionally, to be able to extrapolate the current results to the scale of the Bay it wold be necessary to perform more measurements following the protocol presented in the **Chapter 5** considering more replicates and *Spartina* meadows at the high marsh levels.

Résumé étendu

L'arrivée d'une nouvelle espèce dans un écosystème est source de préoccupations quant aux possibles menaces sur la biodiversité locale. Toutefois, cela représente aussi une excellente opportunité de comprendre la capacité d'un système à s'adapter aux changements (Crooks 2002). Dans un contexte de changements globaux, la compréhension des dynamiques temporelle et spatiale des invasions biologiques est essentielle pour en évaluer les impacts (Strayer et al. 2006), notamment, l'acclimatation de la nouvelle espèce et l'adaptation de l'environnement d'accueil.

Une difficulté majeure lors d'invasions biologiques est de comprendre les mécanismes d'adaptation aux changements de la part des différentes espèces. La complexité augmente lorsque le résultat de l'invasion est à la fois contrôlé par des interactions biotiques (à travers de la compétition pour les ressources et pour l'espace, entre espèces invasives et populations natives) et influencé par les modifications de l'environnement physico-chimique induites par les espèces exotiques (Vitousek 1990, Vitousek et al. 1997). Les organismes qui présentent une telle capacité à changer leur environnement sont qualifiés d'ingénieurs d'écosystèmes (Jones et al. 1994, Jones et al. 1997, Crooks 2002). D'une façon générale, l'ingénierie d'écosystèmes consiste en la création, destruction ou modification des habitats par des organismes vivants, par des moyens directs ou indirects (Crooks 2002).

Les environnements côtiers sont très dynamiques et fortement façonnés par des processus physiques. Pour cette raison, ils représentent d'excellents sites pour l'étude de l'ingénierie d'écosystèmes (Murray et al. 2008). Ces systèmes sont caractérisés par des patrons de distribution de la végétation résultant d'un compromis entre les habilités compétitives des plantes et leur tolérance au stress (Grime 1977). Dans le cas des zones intertidales, où la croissance des plantes est fortement conditionnée par le stress physique (Belliard et al. 2017), l'ingénierie d'écosystèmes et les interactions positives représentent un facteur clé dans le succès de la colonisation (Bertness et Callaway 1994, Bruno et al. 2003). De nombreuses études ont montré que la végétation a tendance à développer des associations positives qui lui permettent de surmonter les contraintes liées aux inondations fréquentes, aux sols fortement salins et à l'anoxie (Bertness et Hacker 1994, Bruno 2000, Dethier et Hacker 2005, Pennings et al. 2005).

Les prés salés sont des environnements très productifs, offrant de nombreux bénéfices (Constanza et al. 2008, Barbier et al. 2011). Notamment, ils contribuent à la purification de l'eau et à la séquestration du carbone atmosphérique (Mitch et Grosselink 2007). Ce sont également des zones de nidification et jouent un rôle dans la protection côtière, à travers l'atténuation des vagues (Möller et al. 1999, Mendez et Losada 2004, Bouma et al 2005,

Temmerman et al. 2013) et la stabilisation des sédiments (Castellanos et al. 1994, French et al. 1995).

Les processus locaux d'interaction entre les plantes et les flux incidents (eau ou air) se propagent à large échelle et peuvent être déterminants pour l'évolution du paysage dans les environnements côtiers (D'Alpaos et al. 2007, Kirwan et Murray 2017, Temmerman et al. 2007). Ils affectent ainsi la croissance des organismes et leur survie à une plus large échelle. Ces interactions sont à l'origine de la bio-géomorphodynamique (Corenblit et al 2008, Murray et al. 2008, Coco et al 2013). La bio-geomorphodynamique s'appuie sur des approches pluri- et interdisciplinaires, qui répondent aujourd'hui au besoin de comprendre la réponse de ces écosystèmes, aux perturbations extérieures. Du fait des menaces globales sur la biodiversité et sur la santé des systèmes côtiers, ce besoin se trouve aujourd'hui de plus en plus préssant.

La présente thèse répond à ce besoin et vise à la compréhension des mécanismes de colonisation de la Spartine anglaise dans le Bassin d'Arcachon, ainsi que ses interactions avec les environnements biotique et abiotique. Notamment, trois questions majeures sont abordées :

(1) Quels sont les principaux mécanismes d'invasion de la Spartine anglaise et quelle est sa niche d'occupation préférentielle ?
(2) Quels sont les impacts de la colonisation de la Spartine anglaise dans les prés salés auparavant dominés par la Spartine maritime ?
(3) Dans quelle mesure la colonisation des zones intertidales du Bassin par la Spartine anglaise peut affecter les herbiers de Zostère naine ?

Pour répondre à ces questions, différentes méthodes sont utilisées, qui composent une approche interdisciplinaire.

Le chapitre 1 traite de de l'évolution spatio-temporelle des prés salés dans le secteur nord este du Bassin (commune d'Andernos). Pour cela, deux méthodologies de télédétection sont utilisées. Une série d'images aériennes, acquises entre 1949 et 2016, a permis d'éstimer la dynamique à long-terme. Ensuite, des images stellite à haute résolution spatiale ont éte utilisées pour tester le potentiel d'identification de l'espèce exotique lors d'un état peu avancé de l'invasion. Les résultats ont montré que, sur la zone d'Andernos, les prés salés occupent une surface relativement stable depuis les années 1980, même après l'arrivée de la Spartine anglaise. L'espèce native européenne, la Spartine maritime, s'est établie sur ce site dès les années 1940 et les herbiers de cette espèce présentent une importante expansion jusqu'aux années 1980. L'arrivée de la Spartine anglaise sur ce site s'est faite de façon modérée, sa

présence restant relativement restreinte aux zones dépourvues de Spartine maritime. Ce résultat suggère que la Spartine anglaise n'est pas suffisamment compétitive pour remplacer la Spartine maritime et vient surtout s'installer dans des niches vides.

Le chapitre 2 porte sur les interactions biotiques entre les deux espèces de Spartine. L'approche expérimentale mise en place vise à élucider trois points majeurs : (i) la nature des interactions entre Spartine maritime (native) et Spartine anglaise (exotique) ; (ii) la caractérisation des niches préférentielement colonisées par chacune des deux espèces et (iii) l'identification des niches effectivement occupées par l'espèce native et l'espèce exotique. Une expérience de transplantation réciproque a d'abord éte conduite à différents niveaux topographiques, auxquels se trouvent naturellement les deux espèces de Spartine. Cette expérience s'est accompagnée de mesures de paramètres environnementaux et d'échantillonages de biomasse. Les résultats de biomasse et les estimations de productivité ont montré que les deux espèces de Spartine ont une meilleure performance aux niveaux les plus hauts de la zone intertidale. Ces résultats ont aussi mis en évidence des allocations de biomasse opposées entre les deux espèces. Notamment, l'espèce native favorise la production de parties aériennes, alors que l'espèce exotique a un système racinaire plus développé. En ce qui concerne les paramètres environnementaux, la principale différence entre l'habitat des deux espèces est l'oxygénation des sols. Les sites colonisés par la Spartine anglaise (principalement aux niveaux topographiques intermédiaires et élevés) ont présenté des sols moins anoxiques, c'est-à-dire plus oxygénés. Ce résultat pourrait être lié à la forte allocation en biomasse souterraine par cette espèce. Le calcul d'indices d'interaction a montré ensuite que les deux espèces sont réciproquement résistantes à l'invasion. De plus, la Spartine anglaise présente également une forte auto-facilitation pour la croissance des individus au sein de ces herbiers. Ces résultats suggèrent que le succès de la colonisation de la Spartine anglaise est probablement lié à son système racinaire bien développé, qui améliore l'oxygénation du sol, ainsi qu'à son auto-facilitation intra-spécifique, qui favorise sa croissance.

Le chapitre 3 présente les résultats d'une expérience visant à déterminer l'impact des apports en eau douce sur les performances de la Spartine maritime et de la Spartine anglaise. En effet, dans le Bassin d'Arcachon, il semblerait que la plasticité phénotipique des Spartines (en particulier celle de l'espèce exotique) varie en fonction de leur proximité avec les apports en eau douce. Les résultats de l'expérience montrent que pour les deux espèces de Spartine, le taux de survie et la croissance des plantes soient plus élevés à proximité des apports, soit là où les conditions environemmentales sont caractérisées par une plus faible salinité et par des concentrations en nutriments et des potentiels redox plus élevés. En général, une plus forte

compétition est observée au sein des communautés de Spartine maritime, en particulier à plus grande distance des apports en eau douce. A proximité des affluents, la compétition diminue pour les deux espèces de Spartine et, pour l'espèce exotique, le signal des interactions s'inverse, indiquant un comportement facilitatif. Ces résultats permettent de conclure que l'augmentation de la disponibilité en nutriments, allié à l'amélioration de l'oxygénation des sols induits par la présence des apports en eau douce mènent à une décroissance de la résistance biotique de la Spartine maritime. Ainsi, cela peut créer une opportunité à l'invasion de la Spartine anglaise qui présente une forte capacité de facilitation.

Le chapitre 4 présente une expérience de transplantation de Zostères le long de patchs de Spartine. En effet, en colonisant le Bassin d'Arcachon, la Spartine anglaise vient cohabiter avec les herbiers de Zostères naines. Cela pose la question des conséquences de cette cohabitation pour la Zostère, dont l'importance pour le bon équilibre du Bassin est reconnue. Le dispositif expérimental a été défini de sorte à répondre à deux questions principales : « Quelles sont les effets à court terme (effets sur les ressources) et à long terme (effets d'ingénieur d'écosystèmes) de la Spartine sur la Zostère ? » et « Est-ce que l'influence de la Spartine sur la Zostère s'étend au-delà du voisinage proche des patchs de Spartine ? ». Les résultats montrent qu'au sein des patchs, la Spartine anglaise exerce un fort impact négatif sur la performance de la Zostère naine. Cet impact est sûrement lié à la forte capacité d'ingénieur d'écosystèmes de la Spartine, qui favorise la surélévation du sol et augmente ainsi le stress hydrique au sein des patchs de Spartine. Les résultats quant à l'influence spatiale de la Spartine sur la Zostère n'ont pas mis en évidence des facteurs indiquant une influence de l'espèce exotique sur le déclin des herbiers de Zostère.

Enfin, dans le chapitre 5, les capacités d'ingénieur d'écosystèmes de chacune des deux Spartines sont évaluées. Pour cela, des mesures simultanées des vagues et des variations altimétriques du fond ont été réalisées au sein des deux espèces concernées, pendant une période de presque deux ans. Ces mesures montrent qu'au sein des patchs de Spartine anglaise, le fond est relativement stable. Au contraire, au sein des patchs de Spartine maritime, les variations interannuelles et verticales du fond sont plus marquées. Il est ainsi fait l'hypothèse que le plus grand développement du système racinaire de l'espèce exotique favorise la stabilité des sédiments, alors que l'espèce native, grâce à son importante biomasse aérienne, capte plus largement les sédiments en suspension. Ceux-ci sont ensuite facilement mobilisables lors des événements de tempête, du fait d'une moindre capacité de fixation. Ces résultats devront permettre de déterminer dans quelle mesure les Spartines pourraient modifier l'environnement physique qu'elles colonisent.

Ainsi, la présence de Spartine anglaise (exotique) dans le Bassin d'Arcachon ne semble pas représenter, à court terme, une menace significative pour les espèces natives, que sont la Spartine maritime et la Zostère naine. Aussi, l'espèce exotique a proliféré essentiellement sur des sites préalablement perturbés, perturbations auxquelles la Spartine maritime (native) serait moins tolérante, ce qui aurait induit indirectement sa disparition. Etant donné l'importance des activités humaines sur le Bassin, la prolifération de l'espèce exotique est à priori favorisée et pourraient éventuellement remplacer la Spartine native. Notamment, les interventions locales de « combat » (i.e. campagnes d'arrachage de la Spartine exotique), ainsi que les décharges d'eaux usagées perturbent davantage la résistance biotique des herbiers voisins de Spartine maritime et fournissent une opportunité à la Spartine anglaise de l'y remplacer.

Enfin, la végétation intertidale est reconnue pour son rôle d'atténuateur de l'énergie hydrodynamique et de protection côtière. En ce sens, dans le contexte actuel de changements globaux (i.e. augmentation du niveau de la mer et de la fréquence des évènements de tempête), la Spartine anglaise, grâce à sa plus forte capacité de stabilisation des sols et sa plus forte résistance aux perturbations, devrait représenter un important allié pour la préservation des contours du Bassin d'Arcachon.

Bibliography

Adam, E. et al. 2010. Multispectral and hyperspectral remote sensing for identification and mapping of wetland vegetation: a review. - Wetlands Ecol Manage 18: 281–296.

Adams, J. B. et al. 2009. The distribution of estuarine macrophytes in relation to freshwater. - Botanica Marina 35: 215–226.

Ainouche, M. L. et al. 2004. *Spartina anglica* C. E. Hubbard: a natural model system for analysing early evolutionary changes that affect allopolyploid genomes. - Biological Journal of the Linnean Society 82: 475–484.

Ainouche, M. L. et al. 2009. Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). - Biol Invasions 11: 1159.

Ainouche, M. et al. 2012. Polyploid evolution in *Spartina*: dealing with highly redundant hybrid genomes. - In: Polyploidy and Genome Evolution. Soltis PS, Soltis DE. Springer, pp. 255–244.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. - Proceedings of the Second International Symposium on Information theory: 267–281.

Akula, R. et al. 2012. An efficient PAN sharpening technique by merging two hybrid approaches. - Procedia Engineering 30: 535–541.

Alekseenko, E. et al. 2017. The effect of wind induced bottom shear stress and salinity on *Zostera noltii* replanting in a Mediterranean coastal lagoon. - Estuarine, Coastal and Shelf Science 187: 293–305.

Allard, J. et al. 2009. A synthesis of morphological evolutions and Holocene stratigraphy of a wave-dominated estuary: The Arcachon lagoon, SW France. - Continental Shelf Research 29: 957–969.

Altieri, A. H. et al. 2010. Facilitation cascade drives positive relationship between native biodiversity and invasion success. - Ecology 91: 1269–1275.

An, S. Q. et al. 2007. Spartina invasion in China: implications for invasive species management and future research. - Weed Research 47: 183–191.

Anschutz, P. et al. 1998. Burial efficiency of phosphorus and the geochemistry of iron in continental margin sediments. - Limnology and Oceanography 43: 53–64.

Armas, C. et al. 2004. Measuring plant interactions: a new comparative index. - Ecology 85: 2682–2686.

Auby, I. 1993. Evolution de la richesse biologique du Bassin d'Arcachon. Contrat IFREMER/SSA n° 91 5 527019. https://archimer.ifremer.fr/doc/00040/15144/

Auby, I. and Labourg, P.-J. 1996. Seasonal dynamics of *Zostera noltii* hornem. In the Bay of Arcachon (France). - Journal of Sea Research 35: 269–277.

Ayres, D. R. et al. 1999. Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). - Molecular Ecology 8: 1179–1186.

Ayres, D. R. et al. 2004. Spread of exotic cordgrasses and hybrids (*Spartina* sp.) In the tidal marshes of San Francisco Bay, California, USA. - Biological Invasions 6: 221–231.

Balke, T. et al. 2011. Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. - Marine Ecology Progress Series 440: 1–9.

Balke, T. et al. 2012. Conditional outcome of ecosystem engineering: A case study on tussocks of the salt marsh pioneer *Spartina anglica*. - Geomorphology 153–154: 232–238.

Bando, K. J. 2006. The roles of competition and disturbance in a marine invasion. - Biol Invasions 8: 755–763.

Barbier, E. B. et al. 2011. The value of estuarine and coastal ecosystem services. - Ecological Monographs 81: 169–193.

Barillé, L. et al. 2010. Increase in seagrass distribution at Bourgneuf Bay (France) detected by spatial remote sensing. - Aquatic Botany 92: 185–194.

Bassoullet, P. et al. 2000. Sediment transport over an intertidal mudflat: field investigations and estimation of fluxes within the "Baie de Marenngres-Oleron" (France). - Continental Shelf Research 20: 1635–1653.

Baumel, A. et al. 2001. Molecular investigations in populations of *Spartina anglica* C.E. Hubbard (Poaceae) invading coastal Brittany (France). - Molecular Ecology 10: 1689–1701.

Belliard, J.-P. et al. 2017. Ecogeomorphic relations between marsh surface elevation and vegetation properties in a temperate multi-species salt marsh. - Earth Surf. Process. Landforms 42: 855–865.

Belliard, J.-P. et al. 2019. High-resolution bed level changes in relation to tidal and wave forcing on a narrow fringing macrotidal flat: Bridging intra-tidal, daily and seasonal sediment dynamics. - Marine Geology in press.

Belluco, E. et al. 2006. Mapping salt-marsh vegetation by multispectral and hyperspectral remote sensing. - Remote Sensing of Environment 105: 54–67.

Bernard, G. et al. 2007. Long term changes in *Zostera* meadows in the Berre lagoon (Provence, Mediterranean Sea). - Estuarine, Coastal and Shelf Science 73: 617–629.

Bernik, B. M. et al. 2018. Clonal vegetation patterns mediate shoreline erosion. - Geophysical Research Letters 45: 6476–6484.

Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England Salt Marsh. - Ecology 72: 125–137.

Bertness, M. D. and Hacker, S. D. 1994. Physical stress and positive associations among marsh plants. - The American Naturalist 144: 363–372.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. - Trends in Ecology & Evolution 9: 191–193.

Bertness, M. D. and Ewanchuk, P. J. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. - Oecologia 132: 392–401.

Bertsimas, D. and Tsitsiklis, J. 1993. Simulated Annealing. - Statist. Sci. 8: 10–15.

Blanchet, H. et al. 2005. Structuring factors and recent changes in subtidal macrozoobenthic communities of a coastal lagoon, Arcachon Bay (France). - Estuarine, Coastal and Shelf Science 64: 561–576.

Bornette, G. and Puijalon, S. 2011. Response of aquatic plants to abiotic factors: a review. - Aquat Sci 73: 1–14.

Borsje, B. W. et al. 2011. How ecological engineering can serve in coastal protection. - Ecological Engineering 37: 113–122.

Bouchet, J.-M. et al. 1997. Etude Intégréé du Bassin d'Arcachon - Synthèse.

Boudouresque, C. F. et al. 2009. Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. - Botanica Marina 52: 395–418.

Bouma, T. 2009. Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. - Helgol Mar Res: 3–18.

Bouma, T. J. et al. 2005. Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. - Ecology 86: 2187–2199.

Bouma, T. J. et al. 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. - Continental Shelf Research 27: 1020–1045.

Bouma, T. J. et al. 2013. Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. - Geomorphology 180–181: 57–65.

Bouma, T. J. et al. 2016. Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics: Lateral salt marsh dynamics. - Limnology and Oceanography 61: 2261–2275.

Branco, J. et al. 2017. Natural recovery of *Zostera noltii* seagrass beds and benthic nematode assemblage responses to physical disturbance caused by traditional harvesting activities. - Journal of Experimental Marine Biology and Ecology in press.

Breiman, L. 2001. Random Forests. - Machine Learning 45: 5–32.

Brown, A. H. D. and Marshall, D. R. 1981. Evolutionary changes accompanying colonization in plants. - In: Colonization, succession and stability. Schuder GCE, Reveal JL. Blackwell Scientific Publications, pp. 351–363.

Bru, D. et al. 2017. Atmospheric correction of multi-spectral littoral images using a PHOTONS/AERONET-based regional aerosol model. - Remote Sensing 9: 814.

Bruno, J. F. 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. - Ecology 81: 1179–1192.

Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. - Trends in Ecology & Evolution 18: 119–125.

Bulleri, F. et al. 2008. Beyond competition: incorporating positive interactions between species to predict ecosystem invasibility. - PLOS Biology 6: e162.

Bulleri, F. et al. 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. - PLOS Biology 16: e2006852.

Bustamante, J. et al. 2016. Hyperspectral sensors as a management tool to prevent the invasion of the exotic cordgrass *Spartina densiflora* in the Doñana wetlands. - Remote Sensing 8: 1001.

Cabaço, S. et al. 2008. The impact of sediment burial and erosion on seagrasses: A review. - Estuarine, Coastal and Shelf Science 79: 354–366.

Callaway, J. C. and Josselyn, M. N. 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. - Estuaries 15: 218–226.

Callaway, R. M. and King, L. 1996. Temperature-Driven Variation in Substrate Oxygenation and the Balance of Competition and Facilitation. - Ecology 77: 1189–1195.

Canton, M. 2009. Dynamique des éléments biogènes dans le continuum fluvio-estuarien de la zone hydrologique d'influence du Bassin d'Arcachon.

Carboni, M. et al. 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. - Ecol Lett 19: 219–229.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America.

Carpenter, S. R. and Lodge, D. M. 1986. Effects of submersed macrophytes on ecosystem processes. - Aquatic Botany 26: 341–370.

Carter, G. A. et al. 2009. Remote sensing and mapping of Tamarisk along the colorado river, usa: a comparative use of summer-acquired hyperion, Thematic Mapper and QuickBird Data. - Remote Sensing 1: 318–329.

Castel, J. et al. 1996. Eutrophication gradients in coastal lagoons as exemplified by the Bassin d'Arcachon and the Etang du Prévost. - Hydrobiologia 329: ix–xxviii.

Castellanos, E. M. et al. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. - Journal of Ecology 82: 239–248.

Castillo, J. M. et al. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. - Journal of Ecology 88: 801–812.

Catford, J. A. et al. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. - Diversity and Distributions 15: 22–40.

Cayocca, F. 2001. Long-term morphological modeling of a tidal inlet: the Arcachon Basin, France. - Coastal Engineering 42: 115–142.

Cea, L. et al. 2007. Velocity measurements on highly turbulent free surface flow using ADV. - Exp Fluids 42: 333–348.

Chapman, V. J. 1964. Coastal vegetation. - Pergamon Press; Macmillan.

Chen, Y. et al. 2016. A comparison of biohydrodynamic interaction within mangrove and saltmarsh boundaries. - Earth Surface Processes and Landforms 41: 1967–1979.

Chen, Y. et al. 2018. Comparison of flow and energy reduction by representative intertidal plants, Southeast China. - Proceedings of the Twenty-eighth (2018) International Ocean and Polar Engineering Conference

Christiansen, T. et al. 2000. Flow and sediment transport on a tidal salt marsh surface. - Estuarine, Coastal and Shelf Science 50: 315–331.

Chung, C.-H. 1993. Thirty years of ecological engineering with Spartina plantations in China. - Ecological Engineering 2: 261–289.

Clint Slatton, K. et al. 2008. Modeling temporal variations in multipolarized radar scattering from intertidal coastal wetlands. - ISPRS Journal of Photogrammetry and Remote Sensing 63: 559–577.

Coco, G. et al. 2013. Morphodynamics of tidal networks: Advances and challenges. - Marine Geology 346: 1–16.

Cognat, M. et al. 2018. Environmental factors controlling biomass development of seagrass meadows of *Zostera noltei* after a drastic decline (Arcachon Bay, France). - Journal of Sea Research 140: 87–104.

Coops, H. et al. 1996. Interactions between waves, bank erosion and emergent vegetation: an experimental study in a wave tank. - Aquatic Botany 53: 187–198.

Corenblit, D. et al. 2008. Reciprocal adjustments between landforms and living organisms: Extended geomorphic evolutionary insights. - CATENA 73: 261–273.

Cornelissen, J. H. C. et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. - Australian Journal of Botany 51: 335.

Correll, M. D. et al. 2018. Fine-scale mapping of coastal plant communities in the Northeastern USA. - Wetlands: 1–12.

Costanza, R. et al. 2008. The value of coastal wetlands for hurricane protection. - AMBIO: A Journal of the Human Environment 37: 241–248.

Cottet, M. et al. 2007. *Spartina anglica* eradication experiment and in situ monitoring assess structuring strength of habitat complexity on marine macrofauna at high tidal level. - Estuarine, Coastal and Shelf Science 71: 629–640.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. - Oikos 97: 153–166.

Crosby, S. C. et al. 2015. Flowering and biomass allocation in U.S. Atlantic coast *Spartina alterniflora*. - Am. J. Bot. 102: 669–676.

Cuddington, K. and Hastings, A. 2004. Invasive engineers. - Ecological Modelling 178: 335–347.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. - Annual Review of Ecology, Evolution, and Systematics 34: 183–211.

D'Alpaos, A. et al. 2007. Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. - Journal of Geophysical Research in press.

Davis, M. A. 2003. Biotic globalization: does competition from introduced species threaten biodiversity? - BioScience 53: 481.

Davis, M. A. et al. 2000. Fluctuating resources in plant communities: a general theory of invasibility. - Journal of Ecology 88: 528–534.

DeLaune, R. D. et al. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. - Estuarine and Coastal Marine Science 8: 477–487.

Den Hartog, C. and Polderman, P. J. G. 1975. Changes in the seagrass populations of the Dutch Waddenzee. - Aquatic Botany 1: 141–147.

Dethier, M. N. and Hacker, S. D. 2005. Physical factors vs. Biotic resistance in controlling the invasion of an estuarine marsh grass. - Ecological Applications 15: 1273–1283.

Díaz, S. et al. 2016. The global spectrum of plant form and function. - Nature 529: 167–171.

Dostál, P. et al. 2013. The impact of an invasive plant changes over time. - Ecology Letters 16: 1277–1284.

Duarte, C. 1989. Temporal biomass variability and production/biomass relationships of seagrass communities. - Marine Ecology Progress Series 51: 269–276.

Duarte, C. M. 2002. The future of seagrass meadows. - Environmental Conservation 29: 192–206.

Duarte, B. et al. 2015. A tale of two spartinas: Climatic, photobiological and isotopic insights on the fitness of non-indigenous versus native species. - Estuarine, Coastal and Shelf Science 167: 178–190.

Duggin, M. J. and Philipson, W. R. 1982. Field measurement of reflectance: some major considerations. - Applied Optics 21: 2833–2840.

Early, R. et al. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. - Nat Commun 7: 12485.

Erftemeijer, P. L. A. and Robin Lewis, R. R. 2006. Environmental impacts of dredging on seagrasses: A review. - Marine Pollution Bulletin 52: 1553–1572.

Escapa, M. et al. 2008. Sediment dynamics modulated by burrowing crab activities in contrasting SW Atlantic intertidal habitats. - Estuarine, Coastal and Shelf Science 80: 365–373.

Fagherazzi, S. 2012. Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. - Reviews of Geophysics in press.

Fagherazzi, S. et al. 2013. Marsh collapse does not require sea level rise. - Oceanography 26: 70–77.

Fajardo, A. and McIntire, E. J. B. 2010. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. - Journal of Ecology 99: 642–650.

Folmer, E. O. et al. 2016. Consensus forecasting of intertidal seagrass habitat in the Wadden Sea. - J Appl Ecol 53: 1800–1813.

Forsberg, P. L. et al. 2018. The effect of successive storm events and seagrass coverage on sediment suspension in a coastal lagoon. - Estuarine, Coastal and Shelf Science 212: 329–340.

Frappart, F. et al. 2016. High rate GNSS measurements for detecting non-hydrostatic surface wave. Application to tidal bore in the Garonne River. - European Journal of Remote Sensing 49: 917–932.

French, J. R. et al. 1995. Geostatistical Analysis of Sediment Deposition in Two Small Tidal Wetlands, Norfolk, U.K. - Journal of Coastal Research 11: 308–321.

Friedrichs, C. T. and Perry, J. E. 2001. Tidal salt marsh morphodynamics: A synthesis. - Journal of Coastal Research SI 27: 7–37.

Friedrichs, M. et al. 2000. Skimming flow induced over a simulated polychaete tube lawn at low population densities. - Marine Ecology Progress Series 192: 219–228.

Froelich, P. N. et al. 1979. Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. - Geochimica et Cosmochimica Acta 43: 1075–1090.

Ganthy, F. et al. 2011. The stability of vegetated tidal flats in a coastal lagoon through quasi in-situ measurements of sediment erodibility. - Journal of Coastal Research: 1500–1504.

Ganthy, F. et al. 2013. Seasonal modification of tidal flat sediment dynamics by seagrass meadows of *Zostera noltii* (Bassin d'Arcachon, France). - Journal of Marine Systems 109–110: S233–S240.

Ganthy, F. et al. 2015. Effects of short flexible seagrass *Zostera noltei* on flow, erosion and deposition processes determined using flume experiments (D Mohrig, Ed.). - Sedimentology 62: 997–1023.

Garzelli, A. et al. 2004. Pan-sharpening of multispectral images: a critical review and comparison. - IGARSS 2004. 2004 IEEE International Geoscience and Remote Sensing Symposium 1: 84.

Green, M. O. and Coco, G. 2014. Review of wave-driven sediment resuspension and transport in estuaries - Green - 2014 - Reviews of Geophysics - Wiley Online Library. - Reviews of Geophysics 52: 77–117.

Gribben, P. E. et al. 2009. Behavioural interactions between ecosystem engineers control community species richness. - Ecol. Lett. 12: 1127–1136.

Grime, J. P. 1974a. Vegetation classification by reference to strategies. - Nature in press.

Grime, J. P. 1974b. Vegetation classification by reference to strategies. - Nature 250: 26–31.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. - The American Naturalist 111: 1169–1194.

Hacker, S. D. and Bertness, M. D. 1999. Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. - Ecology 80: 2064–2073.

Hacker, S. and Dethier, M. 2006. Community modification by a grass invader has differing impacts for marine habitats. - Oikos 113: 279–286.

Hacker, S. D. et al. 2001. A marine plant (*Spartina anglica*) invades widely varying habitats: potential mechanisms of invasion and control. - Biological Invasions 3: 211–217.

Hall, P. 0 J. and Aller, R. C. 1992. Rapid, small-volume, flow injection analysis for SCO2, and NH4+ in marine and freshwaters. - Limnology and Oceanography 37: 1113–1119.

Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase*. - Phycologia 32: 79–99.

Hill, V. J. et al. 2014. Evaluating light availability, seagrass biomass, and productivity using hyperspectral airborne remote sensing in Saint Joseph's Bay, Florida. - Estuaries and Coasts 37: 1467–1489.

Horstman, E. M. et al. 2013. Flow routing in mangrove forests: A field study in Trang province, Thailand. - Continental Shelf Research 71: 52–67.

Hu, Z. et al. 2015. Predicting long-term and short-term tidal flat morphodynamics using a dynamic equilibrium theory: Modeling Tidal Flat Dynamic Equilibrium. - Journal of Geophysical Research: Earth Surface 120: 1803–1823.

Hubbard, J. C. E. and Partridge, T. R. 1981. Tidal immersion and the growth of Spartina anglica marshes in the Waihopai River Estuary, New Zealand. - New Zealand Journal of Botany 19: 115–121.

Hutchinson, C. F. 1986. Land remote sensing technology and methodology. - Climatic Change 9: 149–166.

Inglada, J. and Christophe, E. 2009. The Orfeo Toolbox remote sensing image processing software. - 2009 IEEE International Geoscience and Remote Sensing Symposium 4: IV-733-IV–736.

Jestin, H. et al. 1998. Development of ALTUS, a high frequency acoustic submersible recording altimeter to accurately monitor bed elevation and quantify deposition or erosion of sediments. - OCEANS ’98 Conference Proceedings

Jones, C. G. et al. 1994. Organisms as ecosystem engineers. - In: Ecosystem Management. Springer New York, pp. 130–147.

Jones, C. G. et al. 1997. Positive and negative effects of organisms as physical ecosystem engineers. - Ecology 78: 1946–1957.

Kennedy, T. A. et al. 2002. Biodiversity as a barrier to ecological invasion. - Nature 417: 636–638.

Kim, J.-H. et al. 2016. Growth dynamics of the seagrass *Zostera japonica* at its upper and lower distributional limits in the intertidal zone. - Estuarine, Coastal and Shelf Science 175: 1–9.

Kirwan, M. L. and Murray, A. B. 2007. A coupled geomorphic and ecological model of tidal marsh evolution. - PNAS 104: 6118–6122.

Kirwan, M. L. and Megonigal, J. P. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. - Nature 504: 53–60.

Kirwan, M. L. et al. 2010. Limits on the adaptability of coastal marshes to rising sea level. - Geophysical Research Letters 37: n/a-n/a.

Kirwan, M. L. et al. 2016. Overestimation of marsh vulnerability to sea level rise. - Nature Climate Change 6: 253–260.

Klemas, V. 2011. Remote sensing of wetlands: case studies comparing practical techniques. - Journal of Coastal Research: 418–427.

Kombiadou, K. et al. 2014. Modelling the effects of *Zostera noltei* meadows on sediment dynamics: application to the Arcachon lagoon. - Ocean Dynamics 64: 1499–1516.

Koop-Jakobsen, K. et al. 2017. Survey of sediment oxygenation in rhizospheres of the saltmarsh grass - *Spartina anglica*. - Science of The Total Environment 589: 191–199.

Labourg, P. J. et al. 1995. Evolution récente de la végétation intertidale du Delta de l'Eyre.

Lafon, V. et al. 2017. Suivi des populations de spartines sur le Bassin d'Arcachon. Carthographie des différentes espèces - Elaboration d'un guide des bonnes pratiques de gestion.: 106. https://www.siba-bassin-arcachon.fr/sites/default/files/2018-09/2017-10-23_SIBA_carto_spartine_rapportfinal_V4_LIVREE_0.pdf

Lai, W.-L. et al. 2012. Radial oxygen loss, photosynthesis, and nutrient removal of 35 wetland plants. - Ecological Engineering 39: 24–30.

Lambdon, P. W. and Hulme, P. E. 2006. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. - Journal of Biogeography 33: 1116–1125.

Lankau, R. A. et al. 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. - PNAS 106: 15362–15367.

Laporte-Cru, J. and Werno, J. 1989. *Spartina* X Townsendii groves dans le Bassin d'Arcachon. - Bulletins de la Société Linnéenne de Bordeaux 17: 7–12.

Larkum, A. W. D. et al. 2006. Photosynthesis and metabolism in seagrasses at the cellular level. - In: Seagrasses: Biology, Ecology and Conservation. Springer, in press.

Lauzon, R. et al. 2018. Effects of marsh edge erosion in coupled barrier island-marsh systems and geometric constraints on marsh evolution. - Journal of Geophysical Research: Earth Surface in press.

Le Nindre, Y. M. et al. 2000. Terra Symphonie - Aménagement intégré du Bassin d'Arcachon. Etude n°5: Mise au point d'un outil de surveillance et d'aide à la décision en matière d'exhaussement des fonds du Bassin d'Arcachon. Rap. BRGM/RP-50578-FR. in press.

Le Nindre, Y. M. et al. 2004. Etude pour le maintien de l'équilibre bio-sédimentaire des plages du Nord-Est dans le Bassin d'Arcachon. Rapport BRGM/RP-53282-FR 101 p., 60 fig., 15 tabl., 6 ann. in press.

Lee, W. G. and Partridge, T. R. 1983. Rates of spread of *Spartina anglica* and sediment accretion in the New River Estuary, Invercargill, New Zealand. - New Zealand Journal of Botany 21: 231–236.

Lefcheck, J. S. et al. 2017. Multiple stressors threaten the imperiled coastal foundation species eelgrass (Zostera marina) in Chesapeake Bay, USA. - Glob Change Biol 23: 3474–3483.

Levine, J. M. and D'Antonio, C. M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. - Oikos 87: 15–26.

Levine, J. M. et al. 1998. Nutrients, competition and plant zonation in a New England salt marsh. - Journal of Ecology 86: 285–292.

Levine, J. M. et al. 2003. Mechanisms underlying the impacts of exotic plant invasions. - Proc Biol Sci 270: 775–781.

Levine, J. M. et al. 2004. A meta-analysis of biotic resistance to exotic plant invasions. - Ecology Letters 7: 975–989.

Li, J. et al. 2010. Invading cord grass vegetation changes analyzed from Landsat-TM imageries: a case study from the Wanggang area, Jiangsu coast, eastern China. - Acta Oceanol. Sin. 29: 26–37.

Liancourt, P. et al. 2009. Contrasting community responses to fertilization and the role of the competitive ability of dominant species. - Journal of Vegetation Science 20: 138–147.

Lodge, D. M. 1993. Biological invasions: Lessons for ecology. - Trends in Ecology & Evolution 8: 133–137.

Lortie, C. J. et al. 2004. Rethinking plant community theory. - Oikos 107: 433–438.

Losada, I. J. et al. 2016. A new formulation for vegetation-induced damping under combined waves and currents. - Coastal Engineering 107: 1–13.

MacArthur, R. H. and Wilson, E. O. 1967. The Theory of Island Biogeography. - Princeton University Press.

Maestre, F. T. and Cortina, J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. - Proc Biol Sci 271: S331–S333.

Maestre, F. T. et al. 2003. Positive, Negative, and Net Effects in Grass–Shrub Interactions in Mediterranean Semiarid Grasslands. - Ecology 84: 3186–3197.

Mahall, B. E. and Park, R. B. 1976. The ecotone between *Spartina foliosa* trin. and *Salicornia virginica* l. In salt marshes of Northern San Francisco Bay: III. Soil Aeration and Tidal Immersion. - Journal of Ecology 64: 811–819.

Marani, M. et al. 2004. Tidal landforms, patterns of halophytic vegetation and the fate of the lagoon of Venice. - Journal of Marine Systems 51: 191–210.

Marba, N. and Duarte, C. M. 1995. Coupling of Seagrass (Cymodocea Nodosa) Patch Dynamics to Subaqueous dune Migration. - Journal of Ecology 83: 381–389.

Marba, N. et al. 1996. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. - Marine Ecology Progress Series 133: 203–215.

Maricle, B. R. and Lee, R. W. 2002. Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. anglica*. - Aquatic Botany 74: 109–120.

Massa, S. I. et al. 2009. Temperature tolerance and survival of intertidal populations of the seagrass *Zostera noltii* (Hornemann) in Southern Europe (Ria Formosa, Portugal). - Hydrobiologia 619: 195–201.

Matzke, S. and Elsey-Quirk, T. 2018. *Spartina patens* productivity and soil organic matter response to sedimentation and nutrient enrichment. - Wetlands 38: 1233–1244.

Maza, M. et al. 2015. Large-scale 3-D experiments of wave and current interaction with real vegetation. Part 2: Experimental analysis. - Coastal Engineering 106: 73–86.

Mendez, F. J. and Losada, I. J. 2004. An empirical model to estimate the propagation of random breaking and nonbreaking waves over vegetation fields. - Coastal Engineering 51: 103–118.

Mengual, B. et al. 2017. Modelling Fine Sediment Dynamics: Towards a Common Erosion Law for Fine Sand, Mud and Mixtures. - Water 9: 564.

Merino, J. H. et al. 2010. Implication of nutrient and salinity interaction on the productivity of *Spartina patens*. - Wetlands Ecol Manage 18: 111–117.

Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? - New Phytologist 169: 3–6.

Michalet, R. et al. 2015a. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. - Ecography 38: 335–345.

Michalet, R. et al. 2015b. Disentangling direct and indirect effects of a legume shrub on its understorey community. - Oikos 124: 1251–1262.

Michalet, R. et al. 2017. Direct litter interference and indirect soil competitive effects of two contrasting phenotypes of a spiny legume shrub drive the forb composition of an oromediterranean community. - Oikos 126: 1090–1100.

Mitchell, C. E. et al. 2006. Biotic interactions and plant invasions. - Ecology Letters 9: 726–740.

Mitsch, W. J. and Gosselink, J. J. 2007. Wetlands. - Hoboken N.J. : John Wiley & Sons.

Möller, I. 2006. Quantifying saltmarsh vegetation and its effect on wave height dissipation: Results from a UK East coast saltmarsh. - Estuarine, Coastal and Shelf Science 69: 337–351.

Möller, I. et al. 1999. Wave transformation over salt marshes: a field and numerical modelling study from North Norfolk, England. - Estuarine, Coastal and Shelf Science 49: 411–426.

Möller, I. et al. 2014. Addendum: Wave attenuation over coastal salt marshes under storm surge conditions. - Nature Geosci 7: 848–848.

Mouw, C. B. et al. 2015. Aquatic color radiometry remote sensing of coastal and inland waters: Challenges and recommendations for future satellite missions. - Remote Sensing of Environment 160: 15–30.

Murphy, J. and Riley, J. P. 1962. A modified single solution method for the determination of phosphate in natural waters. - Analytica Chimica Acta 27: 31–36.

Murray, A. B. et al. 2008. Biomorphodynamics: Physical-biological feedbacks that shape landscapes. - Water Resources Research in press.

Nepf, H. M. 2012. Flow and transport in regions with aquatic vegetation. - Annu. Rev. Fluid Mech. 44: 123–142.

Neumeier, U. 2007. Velocity and turbulence variations at the edge of saltmarshes. - Continental Shelf Research 27: 1046–1059.

Neumeier, U. and Amos, C. L. 2006. The influence of vegetation on turbulence and flow velocities in European salt-marshes. - Sedimentology 53: 259–277.

Nidzieko, N. J. and Ralston, D. K. 2012. Tidal asymmetry and velocity skew over tidal flats and shallow channels within a macrotidal river delta. - Journal of Geophysical Research: Oceans in press.

Nilsson, C. et al. 2010. The role of hydrochory in structuring riparian and wetland vegetation. - Biol Rev Camb Philos Soc 85: 837–858.

Noumi, Z. et al. 2015. Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study (R Ohlemuller, Ed.). - Applied Vegetation Science 18: 391–401.

Noumi, Z. et al. 2016. The relative contribution of short-term versus long-term effects in shrub-understory species interactions under arid conditions. - Oecologia 180: 529–542.

Nowacki, D. J. et al. 2017. Spectral wave dissipation by submerged aquatic vegetation in a back-barrier estuary. - Limnol. Oceanogr. 62: 736–753.

Nyman, J. A. et al. 2006. Marsh vertical accretion via vegetative growth. - Estuarine, Coastal and Shelf Science 69: 370–380.

Oenema, O. and DeLaune, R. D. 1988. Accretion rates in salt marshes in the Eastern Scheldt, South-west Netherlands. - Estuarine, Coastal and Shelf Science 26: 379–394.

Ondiviela, B. et al. 2014. The role of seagrasses in coastal protection in a changing climate. - Coastal Engineering 87: 158–168.

Orth, R. et al. 2000. A review of issues in seagrass seed dormancy and germination: implications for conservation and restoration. - Marine Ecology Progress Series: 277–288.

Orth, R. J. et al. 2006. A Global Crisis for Seagrass Ecosystems. - BioScience 56: 987–996.

Ouyang, Z.-T. et al. 2013. Spectral discrimination of the invasive plant *Spartina alterniflora* at multiple phenological stages in a saltmarsh wetland. - PLoS One in press.

Pandit, M. K. et al. 2006. Polyploidy in invasive plant species of Singapore. - Botanical Journal of the Linnean Society 151: 395–403.

Parisot, J.-P. et al. 2008. Modélisation des agitations dans le Bassin d'Arcachon.: 435–444.

Partheniades, E. 1965. Erosion and deposition of cohesive soils. - Journal of Hydraulics Division (ASCE) 91: 105–139.

Paul, M. and Gillis, L. G. 2015. Let it flow: how does an underlying current affect wave propagation over a natural seagrass meadow? - Mar Ecol Prog Ser 523: 57–70.

Pennings, S. C. and Callaway, R. M. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. - Ecology 73: 681–690.

Pennings, S. C. and Bertness, M. D. 2001. Salt Marsh Communities. - In: Marine Community Ecology. Bertness MD, Gaines SD,Hay M. in press.

Pennings, S. C. et al. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. - Journal of Ecology 93: 159–167.

Peralta, G. et al. 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. - Marine Ecology Progress Series 368: 103–115.

Pezeshki, S. R. and DeLaune, R. D. 2012. Soil oxidation-reduction in wetlands and its impact on plant functioning. - Biology (Basel) 1: 196–221.

Pierce, S. M. 1983. Estimation of the non-seasonal production of *Spartina maritima* (Curtis) Fernald in a South African Estuary. - Estuarine, Coastal and Shelf Science 16: 241–254.

Planty-Tabacchi, A.-M. et al. 1996. Invasibility of Species-Rich Communities in Riparian Zones. - Conservation Biology 10: 598–607.

Plus, M. et al. 2009. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. - Continental Shelf Research 29: 1008–1013.

Plus, M. et al. 2010. Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). - Estuarine, Coastal and Shelf Science 87: 357–366.

Proença, B. et al. 2019. Intraspecific facilitation explains the spread of the invasive engineer *Spartina anglica* in Atlantic salt marshes. - Journal of Vegetation Science in press.

Pyšek, P. and Hulme, P. E. 2005. Spatio-temporal dynamics of plant invasions: Linking pattern to process. - Ecoscience 12: 302–315.

Quan, W. et al. 2011. Comparison of Nekton Use for Cordgrass *Spartina alterniflora* and *Bulrush Scirpus* mariqueter Marshes in the Yangtze River Estuary, China. - Estuaries and Coasts 34: 405–416.

Quan, W. et al. 2016. Does invasion of *Spartina alterniflora* alter microhabitats and benthic communities of salt marshes in Yangtze River estuary? - Ecological Engineering 88: 153–164.

R Development Core Team 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Raybould, A. F. et al. 1991a. The evolution of *Spartina anglica* C.E. Hubbard (Gramineae): origin and genetic variability. - Biological Journal of the Linnean Society 43: 111–126.

Raybould, A. F. et al. 1991b. The evolution of *Spartina anglica* C. E. Hubbard (Gramineae): genetic variation and status of the parental species in Britain. - Biological Journal of the Linnean Society 44: 369–380.

Rietkerk, M. and van de Koppel, J. 2008. Regular pattern formation in real ecosystems. - Trends in Ecology & Evolution 23: 169–175.

Rimmelin, P. et al. 1998. Study of annual and seasonal dissolved inorganic nitrogen inputs into the Arcachon Lagoon, Atlantic Coast (France). - Estuarine, Coastal and Shelf Science 47: 649–659.

Roberts, P. D. and Pullin, A. S. 2006. The effectiveness of management options used for the control of *Spartina* species. CEE review 06-001 (SR22) Collaboration for Environmental Evidence: www.environmentalevidence.org/SR22.html.

Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. - Biol Invasions 8: 927–939.

Rooijen, A. A. van et al. 2016. Modeling the effect of wave-vegetation interaction on wave setup. - Journal of Geophysical Research: Oceans 121: 4341–4359.

Rouse, J. W. Jr. et al. 1974. Monitoring vegetation systems in the Great Plains with ERTS.: 309–317.

Saccone, P. et al. 2010a. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. - New Phytologist 187: 831–842.

Saccone, P. et al. 2010b. Challenging growth–survival trade-off: a key for *Acer negundo* invasion in European floodplains? - Canadian Journal of Forest Research. - Canadian Journal Forest Research 40: 1879–1886.

Saccone, P. et al. 2013. Ecological resistance to *Acer negundo* invasion in a European riparian forest: relative importance of environmental and biotic drivers. - Appl Veg Sci 16: 184–192.

Salles, P. et al. 2015. Wind-driven modifications to the residual circulation in an ebb-tidal delta: Arcachon Lagoon, Southwestern France - Journal of Geophysical Research: Oceans - Wiley Online Library. - Journal of Geophysical Research 120: 728–740.

Sánchez, J. M. et al. 2001. Primary colonisation of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain: vegetation structure and sediment accretion. - Aquatic Botany 69: 15–25.

Schlaepfer, M. A. et al. 2011. The potential conservation value of non-native species. - Conserv. Biol. 25: 428–437.

Schnetger, B. and Lehners, C. 2014. Determination of nitrate plus nitrite in small volume marine water samples using vanadium (III) chloride as a reduction agent. - Marine Chemistry 160: 91–98.

Schöb, C. et al. 2012. Foundation species influence trait-based community assembly. - New Phytologist 196: 824–834.

Schwarz, M. et al. 2010. Quantifying lateral root reinforcement in steep slopes – from a bundle of roots to tree stands. - Earth Surface Processes and Landforms 35: 354–367.

Seabloom, E. W. et al. 2013. Invasive grasses, climate change, and exposure to storm-wave overtopping in coastal dune ecosystems. - Glob Change Biol 19: 824–832.

Seabloom, E. W. et al. 2015. Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. - Nature Communications 6: ncomms8710.

Seddon, S. et al. 2000. Large-scale seagrass dieback in northern Spencer Gulf, South Australia. - Aquatic Botany 66: 297–310.

Seliskar, D. M. et al. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant: a *Spartina alterniflora* salt-marsh case study. - Journal of Ecology 90: 1–11.

Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. - Trends in Ecology & Evolution 17: 170–176.

Sheehan, M. R. and Ellison, J. C. 2014. Intertidal morphology change following *Spartina anglica* introduction, Tamar Estuary, Tasmania. - Estuarine, Coastal and Shelf Science 149: 24–37.

Short, F. T. and Wyllie-Echeverria, S. 1996. Natural and human-induced disturbance of seagrasses. - Environmental Conservation 23: 17–27.

Silvestri, S. et al. 2002. Salt marsh vegetation radiometry: Data analysis and scaling. - Remote Sensing of Environment 80: 473–482.

Silvestri, S. et al. 2003. Hyperspectral remote sensing of salt marsh vegetation, morphology and soil topography. - Physics and Chemistry of the Earth, Parts A/B/C 28: 15–25.

Simberloff, D. et al. 2013. Impacts of biological invasions: what's what and the way forward. - Trends in Ecology & Evolution 28: 58–66.

Singer, A. et al. 2017. Modelling benthic macrofauna and seagrass distribution patterns in a North Sea tidal basin in response to 2050 climatic and environmental scenarios. - Estuarine, Coastal and Shelf Science 188: 99–108.

Soriano-Sierra, E. J. 1992. Etude Ecologique des Marais Sales du Bassin d'Arcachon: Structure et Evolution de Schorres, Production et Dégradation de leur Végétation et Echanges de Matières Particulaires entre les Schorres et le Bassin. in press.

Soulsby, R. L. 1993. Modelling of coastal processes.: 111–118.

Soulsby, R. L. 1997. Dynamics of marine sands. - Thomas Telford.

Stachowicz, J. J. and Byrnes, J. E. 2006. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. - Mar Ecol Prog Ser 311: 251–262.

Steinbauer, M. J. et al. 2016. How to differentiate facilitation and environmentally driven co-existence (M Palmer, Ed.). - Journal of Vegetation Science 27: 1071–1079.

Stookey, L. L. 1970. Ferrozine - a new spectrophotometric reagent for iron. - Anal. Chem. 42: 779–781.

Strayer, D. L. 2012. Eight questions about invasions and ecosystem functioning (H Hillebrand, Ed.). - Ecology Letters 15: 1199–1210.

Strayer, D. L. et al. 2006. Understanding the long-term effects of species invasions. - Trends in Ecology & Evolution 21: 645–651.

Strickland, J. D. H. and Parsons, T. R. 1972. A practical handbook of seawater analysis. - Fisheries Research Board of Canada Bulletin 167: 1–31.

Strong, D. and Ayres, D. R. 2013. Ecological and Evolutionary Misadventures of *Spartina*. - Annual Review of Ecology, Evolution, and Systematics 44: 389–410.

Sun, Z. et al. 2015. China's coastal wetlands: conservation history, implementation efforts, existing issues and strategies for future improvement. - Environ Int 79: 25–41.

Sun, C. et al. 2016. Classification mapping and species identification of salt marshes based on a short-time interval NDVI time-series from HJ-1 optical imagery. - International Journal of Applied Earth Observation and Geoinformation 45: 27–41.

Sun, C. et al. 2017. Saltmarshes response to human activities on a prograding coast revealed by a dual-scale time-series strategy. - Estuaries and Coasts 40: 522–539.

Sun, C. et al. 2018. Classification mapping of salt marsh vegetation by flexible monthly NDVI time-series using Landsat imagery. - Estuarine Coastal and Shelf Science 213: 61–80.

Sundareshwar, P. V. et al. 2003. Phosphorus limitation of coastal ecosystem processes. - Science 299: 563–565.

Suykerbuyk, W. et al. 2016a. Surviving in changing seascapes: sediment dynamics as bottleneck for long-term seagrass presence. - Ecosystems 19: 296–310.

Suykerbuyk, W. et al. 2016b. Unpredictability in seagrass restoration: analysing the role of positive feedback and environmental stress on *Zostera noltii* transplants. - J Appl Ecol 53: 774–784.

Takasu, T. 2009. RTKLIB: Open source program package for RTK-GPS. - Proceedings of the FOSS4G

Takasu, T. and Yasuda, A. 2009. Development of the low-cost RTK-GPS receiver with an open source program package RTKLIB. - Proceedings of the International Symposium on GPS/GNSS: 4–6.

te Beest, M. et al. 2012. The more the better? The role of polyploidy in facilitating plant invasions. - Ann. Bot. 109: 19–45.

Teal, J. M. and Kanwisher, J. 1966. Gas transport in the marsh grass, *Spartina alterniflora*. - J. Exp. Bot. 17: 355–361.

Temmerman, S. et al. 2005. Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh: vegetation impact on flow routing. - Journal of Geophysical Research: Earth Surface 110: n/a-n/a.

Temmerman, S. et al. 2007. Vegetation causes channel erosion in a tidal landscape. - Geology 35: 631–634.

Temmerman, S. et al. 2012. Impact of vegetation die-off on spatial flow patterns over a tidal marsh. - Geophysical Research Letters in press.

Temmerman, S. et al. 2013. Ecosystem-based coastal defence in the face of global change. - Nature 504: 79–83.

Theoharides, K. A. and Dukes, J. S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. - New Phytol. 176: 256–273.

Thompson, J. D. 1991. The Biology of an Invasive Plant: What makes *Spartina anglica* so successful? - BioScience 41: 393–401.

Thompson, J. D. et al. 1991. Population Variation in *Spartina anglica* C. E. Hubbard. III. Response to Substrate Variation in a Glasshouse Experiment. - The New Phytologist 117: 141–152.

Thomson, A. G. et al. 2004. Short-term vegetation succession and erosion identified by airborne remote sensing of Westerschelde salt marshes, The Netherlands. - International Journal of Remote Sensing 25: 4151–4176.

Tilman, D. 1982. Resource Competition and Community Structure. - Princeton University Press.

Tinoco, R. O. and Coco, G. 2014. Observations of the effect of emergent vegetation on sediment resuspension under unidirectional currents and waves. - Earth Surface Dynamics 2: 83–96.

Tinoco, R. O. and Coco, G. 2016. A laboratory study on sediment resuspension within arrays of rigid cylinders. - Advances in Water Resources 92: 1–9.

Tinoco, R. O. and Coco, G. 2018. Turbulence as the main driver of resuspension in oscillatory flow through vegetation. - Journal of Geophysical Research: Earth Surface in press.

Treier, U. A. et al. 2009. Shift in cytotype frequency and niche space in the invasive plant *Centaurea maculosa*. - Ecology 90: 1366–1377.

Tyler, A. C. et al. 2007. Nitrogen inputs promote the spread of an invasive marsh grass. - Ecol Appl 17: 1886–1898.

Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. - Ecology Letters 11: 1351–1363.

Valiela, I. et al. 1976. Production and dynamics of experimentally enriched salt marsh vegetation : Belowground biomass - download. - Limnology and Oceanography 21: 245–252.

Valiela, I. et al. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: Tidal exchanges and inputs by precipitation and groundwater 1. - Limnol. Oceanogr. 23: 798–812.

Valle, M. et al. 2013. Comparing the performance of species distribution models of *Zostera marina*: Implications for conservation. - Journal of Sea Research 83: 56–64.

van der Heide, T. et al. 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. - Ecosystems 10: 1311–1322.

van der Heide, T. et al. 2008. Toxicity of reduced nitrogen in eelgrass (*Zostera marina*) is highly dependent on shoot density and pH. - Oecologia 158: 411–419.

van der Heide, T. et al. 2010. Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. - Ecology 91: 362–369.

Vannoppen, W. 2016. Root properties of vegetation communities and their impact on the erosion resistance of river dikes. - Earth Surface Processes and Landforms

Vermaat, J. E. and Verhagen, F. C. A. 1996. Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. - Aquatic Botany 52: 259–281.

Vilà, M. and Weiner, J. 2004. Are invasive plant species better competitors than native plant species?: evidence from pair-wise experiments. - Oikos 105: 229–238.

Vilà, M. et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. - Ecology Letters 14: 702–708.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. - In: Ecosystem Management. Springer, New York, NY, pp. 183–191.

Vitousek, P. M. et al. 1997a. Introduced species: A significant component of human-caused global change. - New Zealand Journal of Ecology 21: 116.

Vitousek, P. M. et al. 1997b. Human Domination of Earth's Ecosystems. - Science 277: 494–499.

Vu, H. D. et al. 2017. Ecosystem engineers drive creek formation in salt marshes. - Ecology 98: 162–174.

Warner, R. F. 2012. Environmental impacts of hydroelectric power and other anthropogenic developments on the hydromorphology and ecology of the Durance channel and the Etang de Berre, southeast France. - J. Environ. Manage. 104: 35–50.

Waycott, M. et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. - PNAS 106: 12377–12381.

Weitzman, J. S. et al. 2015. The attenuation of current- and wave-driven flow within submerged multispecific vegetative canopies. - Limnology and Oceanography 60: 1855–1874.

Wiens, J. A. 1989. Spatial Scaling in Ecology. - Functional Ecology 3: 385–397.

Więski, K. and Pennings, S. C. 2014. Climate Drivers of *Spartina alterniflora* Saltmarsh Production in Georgia, USA. - Ecosystems 17: 473–484.

Willemsen, P. W. J. M. et al. 2018. Quantifying bed level change at the transition of tidal flat and salt marsh: can we understand the lateral location of the marsh edge? - Journal of Geophysical Research: Earth Surface in press.

Yang, J. Q. et al. 2016. The onset of sediment transport in vegetated channels predicted by turbulent kinetic energy. - Geophysical Research Letters 43: 11,261-11,268.

Zak, M. R. and Cabido, M. 2002. Spatial patterns of the Chaco vegetation of central Argentina: Integration of remote sensing and phytosociology. - Applied Vegetation Science 5: 213–226.

Zarnetske, P. L. et al. 2010. Non-target effects of invasive species management: beachgrass, birds, and bulldozers in coastal dunes. - Ecosphere 1: art13.

Zarnetske, P. L. et al. 2012. Biophysical feedback mediates effects of invasive grasses on coastal dune shape. - Ecology 93: 1439–1450.

Zhang, R. S. et al. 2004. Formation of *Spartina alterniflora* salt marshes on the coast of Jiangsu Province, China. - Ecological Engineering 23: 95–105.

Zhi, Y. et al. 2007. Inter-specific competition: *Spartina alterniflora* is replacing *Spartina anglica* in coastal China. - Estuarine, Coastal and Shelf Science 74: 437–448.

Zuo, P. et al. 2012. Distribution of *Spartina* spp. along China's coast. - Ecological Engineering 40: 160–166.