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*

1. INTRODUCTION

Biological invasion is a highly dynamic process, both in time and space (Pyšek & Hulme 2005, Mitchell et al. 2006, Theoharides & 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, Ainouche et al. 2009, Treier 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 & 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 & 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 & 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, Michalet et al. 2015, 2017, Noumi et al. 2015, 2016), 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 metre-scale (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 et al. 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 & 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 & 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 & Polderman 1975), in the Bay of Arcachon, France (Plus et al. 2010), in the Mira estuary, Portugal (Branco et al. 2018), 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 & 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?

2. MATERIALS AND METHODS

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 southwestern France (44° 43′ N, 1° 04′ W; Fig. 1a). The introduction of *Spartina an-*

Fig. 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 (t_i) (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 (t_f)
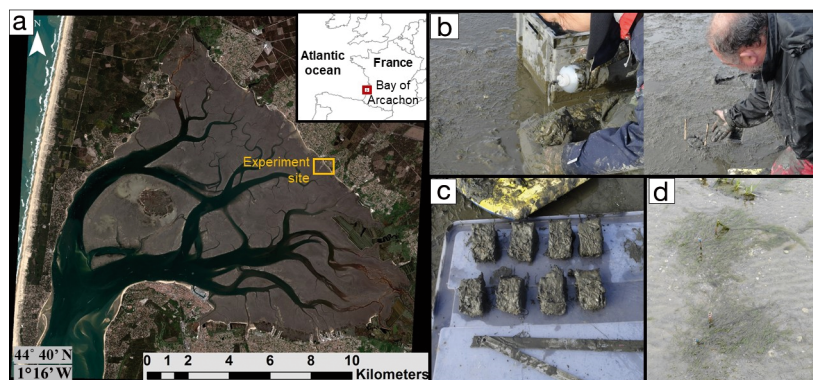
glica in this lagoon dates from the mid-1980s (Laporte-Cru & Werno 1989). The origin of this invasive species began with the hybridization between *S. alterniflora* (native to the USA) and *S. maritima*, another cordgrass species native to Europe. This event occurred in the UK and first produced a sterile hybrid and then gave rise to the fertile new species *S. anglica* through polyploidy evolution (Raybould et al. 1991, 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).

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 (t_i) and 20 May 2016 (t_f), 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* (Fig. 2). We first randomly selected as treatment replicates 4 patches of *S. anglica* of approximately 40–50 m^2. 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
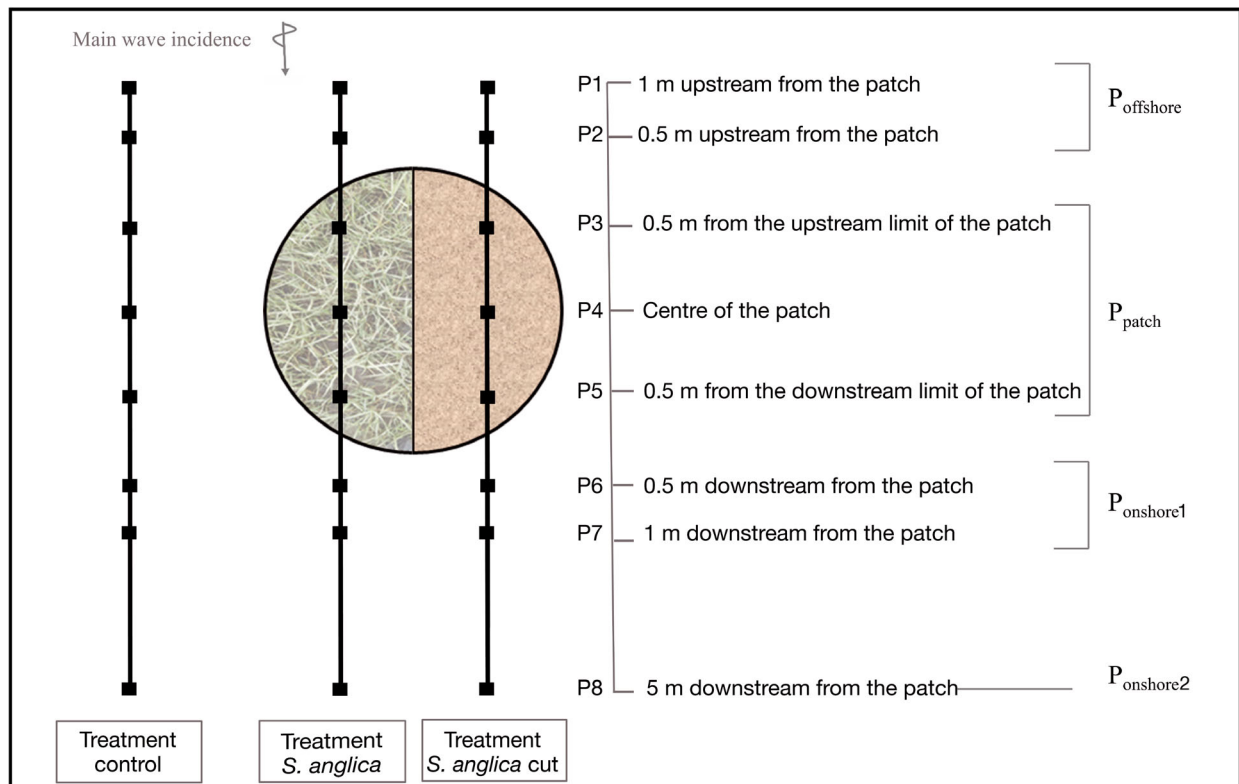

Fig. 2. Experimental design. Black squares represent the positions of the *Zostera noltei* transplants along transects for each treatment. Control treatments were located on the mudflat in the direct vicinity of *Spartina* patches (approximately 10 m). The *S. anglica* treatment corresponds to transects 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 $P_{onshore2}$)

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 (Fig. 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 (Fig. 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.

2.3. Monitoring *Z. noltei* performance and environmental measurements

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

$$\mu = (X_{t_f} - X_{t_i})/X_{t_i} \tag{1}$$

At each transect position and for all transects, elevation measurements were made at the centimetre precision with a RTK Leica GS10 system, and sur-face 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.

2.4. Plant–plant interaction indices

To investigate the effects of *S. anglica* on *Z. noltei* performance in the transplanted plots, we used the relative interaction index (RII) of Armas et al. (2004):

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

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 0 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$_{\text{veg}}$), 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$_{\text{soil}}$, 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 1.

Table 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
$RII_{vegetation}$	Abundance of *Z. noltei* in SA	Abundance of *Z. noltei* in SAC
RII_{soil}	Abundance of *Z. noltei* in SAC	Abundance of *Z. noltei* in control
$RII_{Spartina}$	Abundance of *Z. noltei* in SA	Abundance of *Z. noltei* in control

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).

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 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 (Fig. 3). We also found a highly significant effect of the Position[2] treatment ($F_{1,87} = 19.55$, p < 0.001, Table 2); across all transects, *Z. noltei* abundance was much lower at the P_{patch} position than at the other 3 positions (Fig. 3, Tukey, p < 0.05). However, there was a significant Treatment × 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 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 (±SE) 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

Table 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* and the relative interaction index (RII). Significant results at p < 0.05 are indicated in **bold**

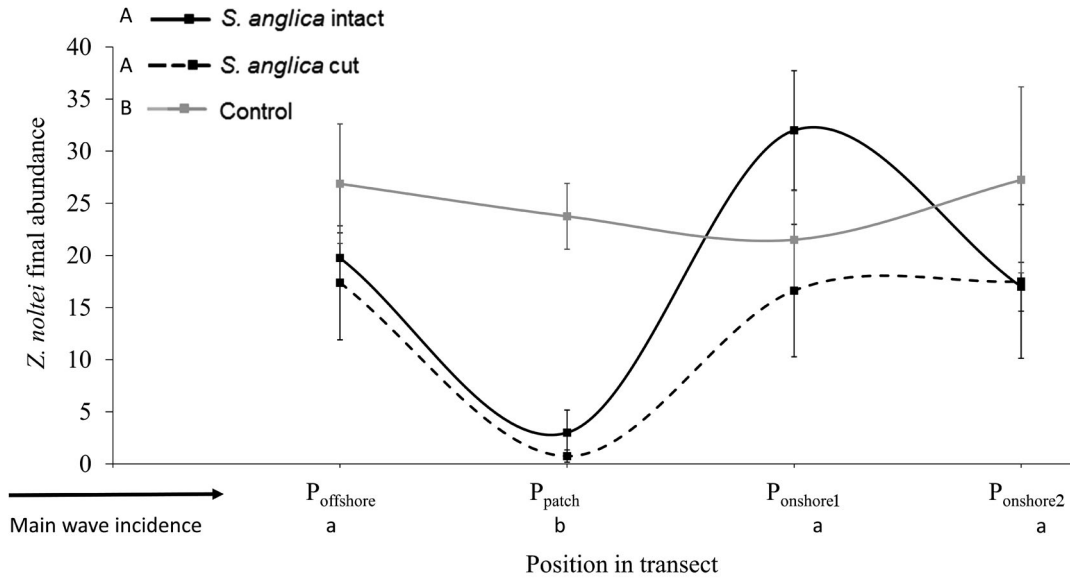| Effects	Log(final abundance+1)			Variable		RII	
	df	*F*	p		df	*F*	p
Transect	2	12.96	**<0.001**	Method	2	23.59	**<0.001**
Position	1	1.31	0.256	Position	1	4.14	**0.045**
Position[2]	1	19.55	**<0.001**	Position[2]	1	11.46	**0.001**
Transect × Position	2	0.77	0.466	Method × Position	2	0.59	0.557
Transect × Position[2]	2	5.42	**0.006**	Method × Position[2]	2	2.73	0.071
Residuals	87				87		

Fig. 3. Mean (± SE) *Zostera noltei* final number of individuals per transplant plot at 4 positions along the intact *Spartina* transect (SA; solid black line), along the cut *Spartina* transect (SAC; dashed black line) and along the control transect (bare sediment; grey solid line). Positions along transect as described in Fig. 2. Uppercase letters in the key and lowercase letters under the *x*-axis show the results of the Tukey tests for the transect effect and for the position effect, respectively (with significance at p < 0.05)

Spartina transects (32 ± 5.7 individuals), and there were no significant differences among treatments at the other 2 positions.

We observed a highly significant Method effect ($F_{2,87}$ = 23.59, p < 0.001, Table 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 (Fig. 4). There was also a significant Position^2 effect ($F_{1,87}$ = 11.46, p = 0.001, Table 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}).

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 (Fig. 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; Fig. 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 (Fig. 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,
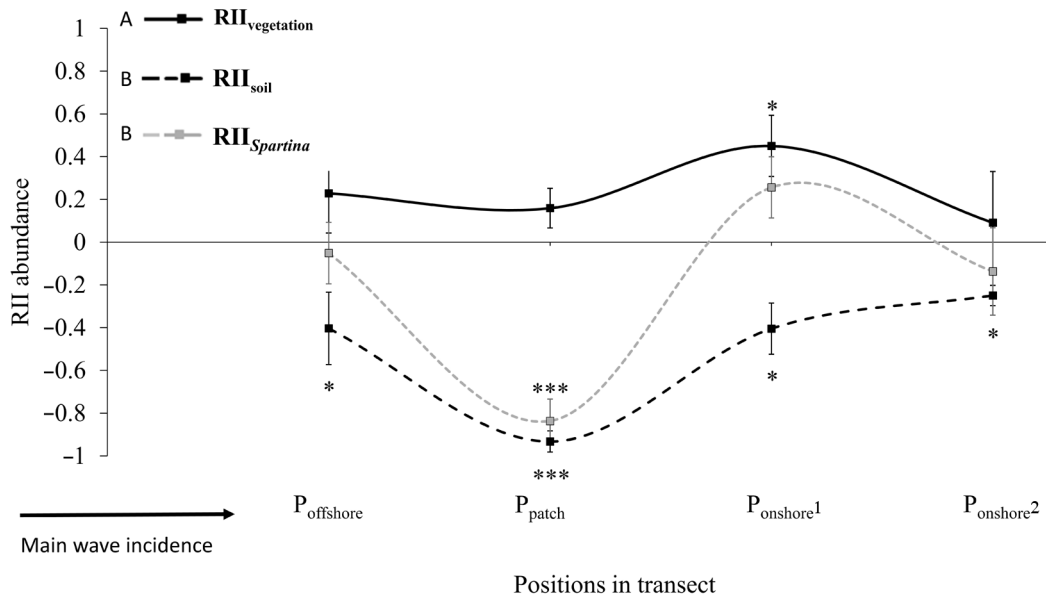
Fig. 4. Mean (± SE) relative interaction intensity (RII) index for final *Zostera noltei* abundance per transplant plot at 4 positions along transects. See Table 2 for the ecological significance of the 3 RII indices, RII_{canopy} (solid black line), RII_{soil} (black dashed line) and $RII_{Spartina}$ (grey dashed line). Positions along transect as described in Fig. 2. Asterisks show the results of the *t*-tests: *p < 0.05, **p < 0.01, ***p < 0.001. Uppercase letters in the key indicate the results of the Tukey test for the method effect (with significance at p < 0.05)
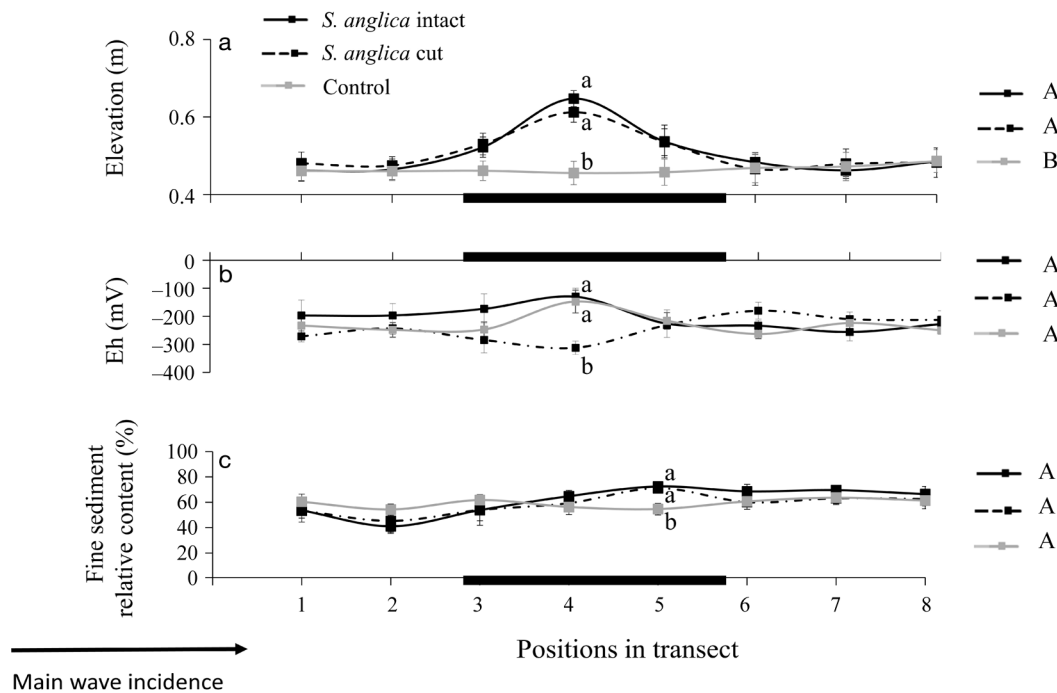

Fig. 5. Mean (± SE) (a) elevation of transect positions, (b) soil redox potential (Eh) and (c) relative fine sediment content, for the 3 transect types: intact *Spartina* (SA), cut *Spartina* (SAC) and control transects (bare sediment). For transect positions see Fig. 2. The thick black line between 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

and in particular for position P5 (1-way ANOVA at P5: $F_{2,11}$ = 10.61, p = 0.003).

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 short-term 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 short-term 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.

4.1. Short-distance effects of *S. 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 & 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 et al. (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

Table 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 at p < 0.05 are indicated in **bold**

Effects	Altimetry			Eh			Fine sediment		
	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 × Position	2	0.40	0.670	2	2.96	0.056	2	2.66	0.074
Transect × Position[2]	2	3.95	**0.022**	2	0.34	0.713	2	1.23	0.297
Residuals	103			103			103		

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 (Marbà 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 & King 1996, Hacker & 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).

4.2. Long-distance effects of *S. anglica* on environmental conditions and *Z. 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 et al. (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 (Folmer et al. 2016, Suykerbuyk et al. 2016a,b). 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 & 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.

5. CONCLUSION

Using a specific methodology to disentangle ecosystem engineering effects from short-term biotic effects at different distances from S*partina 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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