Coastal restoration success via emergent trait-mimicry is context dependent

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ABSTRACT

Coastal ecosystems provide vital ecosystem functions and services, but have been rapidly degrading due to human impacts. Restoration is increasingly considered key to reversing these losses, but is often unsuccessful. Recent work on seagrasses and salt marsh cordgrasses highlights that restoration yields can be greatly enhanced by temporarily mimicking key emergent traits. These traits are not expressed by individual seedlings or small clones, but emerge in clumped individuals or large clones to locally suppress environmental stress, causing establishment thresholds where such density-dependent self-facilitation is important for persistence. It remains unclear, however, to what extent the efficacy of restoration via emergent trait-based mimicry depends on the intensity of stressors. We test this in a restoration experiment with the temperate seagrass *Zostera marina* at four sites (Finland, Sweden, UK, USA) with contrasting hydrodynamic regimes, where we simulated dense roots mats or vegetation canopies with biodegradable structural mimics. Results show that by mimicking sediment-stabilizing root mats, seagrass transplant survival, growth and expansion was strongly enhanced in hydrodynamically exposed environments. However, these positive effects decreased and turned negative under benign conditions, while mimics insufficiently mitigated physical stress in extremely exposed environments, illustrating upper and lower limits of the application. Furthermore, we found that aboveground structures, designed to mimic stiff rather than flexible vegetation canopies, underperformed compared to belowground mimics. Our findings emphasize the importance of understanding the conditions at the restoration site, species-specific growth requirements, and self-facilitating traits that organisms may express when applying emergent trait-mimicry as a tool to improve restoration success.

1. Introduction

Coastal ecosystems make up less than 4% of the Earth's surface, but are of great social, economic and ecological importance. Combined, seagrass meadows, salt marshes, mangroves, coastal dunes, coral and bivalve reefs generate a global annual value of over 6 trillion US$ by providing vital ecosystem services (Costanza et al., 1997). These include flood protection, water purification, nutrient cycling, carbon storage,

tourism enhancement, fisheries enhancement, and biodiversity provisioning (Costanza et al., 1997; Barbier et al., 2008; Barbier et al., 2011; Bayraktarov et al., 2016; Menéndez et al., 2020). Over the last century, however, these ecosystems, and their associated services and values, have been rapidly degrading. Although hundreds of millions of dollars are invested annually to protect threatened coastal ecosystems, their global decline continues due to combined anthropogenic impacts (Silliman et al., 2015). A major challenge is that local pressures, such as eutrophication and infrastructure development, are amplified by climate change related stressors such as increased storms, drought, heat waves, and ocean acidification (Orth et al., 2006; Gedan et al., 2009; Silliman et al., 2015; Bayraktarov et al., 2016). As a result, coastal dunes are under pressure as 70% of the world's sandy beaches are eroding, while 42% of salt marshes, 35% of mangroves, 29% of seagrass, 85% of oyster reefs, and 19% of coral reefs worldwide are now lost or degraded (Feagin et al., 2005; Reid et al., 2005; Wilkinson, 2008; Gedan et al., 2009; Waycott et al., 2009; Beck et al., 2011).

Agreements at the national, regional and global level have set goals and targets to restore degraded ecosystems. For example, the EU Biodiversity Strategy for 2030 aims to strengthen the protection of marine ecosystems and to restore them to achieve "good environmental status" (Commission, 2011). Furthermore, the UN Decade on Ecosystem Restoration 2021–2030 aims to halt the degradation of ecosystems, and restore them to achieve global goals (Waltham et al., 2020). Thus, restoration is increasingly considered as a vital tool by governments, industry, and nature conservation organizations to halt and reverse the losses of these ecosystems and their services (Silliman et al., 2015; Bayraktarov et al., 2016; Temmink et al., 2020; Valdez et al., 2020). However, current efforts to rebuild coastal ecosystems are often small-scale, ineffective (<50% success) and over 10 times more expensive compared to most terrestrial ecosystems (Zedler, 2000; Wolters et al., 2005; Orth et al., 2006; de Groot et al., 2013; Bayraktarov et al., 2016; van Katwijk et al., 2016).

Over the last decades, evidence has been mounting that positive interactions play an essential role in the functioning and stability of coastal ecosystems by reducing physical stress in these harsh environments (Bertness and Callaway, 1994; Bruno and Kennedy, 2000; He et al., 2013; Meysick et al., 2019; Bekkby et al., 2020; Gagnon et al., 2020; Meysick et al., 2020). Such interactions can be interspecific, such as mutualistic interactions between ribbed mussels and cordgrass (Angelini et al., 2016; Derksen-Hooijberg et al., 2018), and lucinid bivalves and seagrasses (van der Heide et al., 2012a, 2012b; de Fouw et al., 2016; Chin et al., 2020). Interactions can also be intraspecific, such as the facilitation of seagrasses by other plants (Gustafsson and Boström, 2011), cockles by mussel beds on intertidal mudflats (Donadi et al., 2013) and forbs by cordgrasses on cobble beaches (van de Koppel et al., 2006). Moreover, intraspecific facilitation often also occurs, and is generated via positive (i.e., self-reinforcing) feedbacks, in which habitat quality improves with the density and/or patch-size of the habitat-modifying species. These mechanisms increase in importance as environmental conditions become harsher (Bouma et al., 2009; Maxwell et al., 2017). Clear examples are reef-forming bivalves such as mussels whose aggregations provide stable settlement substrate for conspecific recruits, while minimizing losses from waves and predation (van der Heide et al., 2014; de Paoli et al., 2015; de Paoli et al., 2017). Similarly, clonal seagrass and cordgrass establishment hinges on creating sufficiently large and dense patches to stabilize the soil with their root mats and attenuate hydrodynamic energy with their canopy (Bouma et al., 2005; van der Heide et al., 2007; Silliman et al., 2015; Maxwell et al., 2017; van Belzen et al., 2017).

Recent work in multiple coastal ecosystems demonstrated that harnessing intra- and interspecific positive feedbacks can greatly increase restoration yields, because strong feedbacks can create critical density and patch-size dependent establishment thresholds in harsh systems (Maxwell et al., 2017). Under natural conditions, establishment may occur during a Window of Opportunity – a sufficiently long period of

exceptionally calm conditions during which isolated individuals or small clones can settle and grow (Balke et al., 2011). However, as such Windows are relatively rare, natural reestablishment may often take decades or longer (Balke et al., 2011). In such systems, reconstruction of positive feedbacks via restoration actions may accelerate ecosystem recovery. Indeed, recent work in multiple coastal ecosystems demonstrated that harnessing intra- and interspecific positive feedbacks can greatly increase restoration yields, particularly in harsh conditions such as wave-exposed areas with unstable sediments or sheltered sites with anoxic soils. For instance, co-transplantation of ribbed mussels with cordgrass transplants was demonstrated to increase restoration yields by 50% (Derksen-Hooijberg et al., 2018). Moreover, whereas earlier work showed that increasing planting density can increase success (Teas, 1977; Bos and van Katwijk, 2007), Silliman et al. (2015) demonstrated that yields can be doubled simply by planting in clumps rather than applying plantation-style dispersed designs, while keeping overall density unchanged. In addition, de Paoli et al. (2017) achieved similar results by transplanting intertidal blue mussels in clumped instead of dispersed designs.

Simple clumping techniques can increase coastal restoration success (Shaver and Silliman, 2017; Renzi et al., 2019). Yet, facilitation-harnessing approaches could gain further efficacy when facilitation-generating organism traits can be engineered (Schotanus et al., 2020) or mimicked with mass-produced artificial structures that allow cost reductions and limit impacts on often vulnerable donor populations (Temmink et al., 2020). Indeed, this recent work highlights that restoration yields can be greatly enhanced by mimicking key emergent traits, i.e., traits not expressed by individuals or small clones, but that emerge in clumped individuals or large clones as they locally suppress physical stress (Temmink et al., 2020). Specifically, Temmink et al. (2020) demonstrate that simulating dense roots mats with biodegradable mimics facilitate seagrass establishment, while mimics of aboveground plant structures most facilitate cordgrass establishment in salt marshes, emphasizing that self-facilitating emergent traits can be strongly species-specific. Moreover, follow-up work focusing on restoration of mussel and oyster reefs reveal that mimicry of reef structures and settlement cues can similarly enhance bivalve reef restoration by facilitating natural recruitment by stimulating settlement and reducing predation pressure (Fivash et al., 2021a, 2021b; Temmink et al., 2021a).

Recent studies applying trait-based mimicry highlight that this approach has the potential to allow upscaling, and simultaneously reduce or eliminate the need for harvesting large amounts of donor material. This could particularly be helpful for seagrass restoration where restoration is typically required at large spatial scale to be successful (van Katwijk et al., 2016). Although these emergent trait-based mimicry approaches proved effective for seagrasses in hydrodynamically exposed environments, it remains unclear how their efficiency depends on the intensity of abiotic stressors that should be mitigated by feedbacks generated from emergent traits. Yet, it is clearly important to understand such potential context dependency as it determines when and where this novel approach could be applied. In seagrasses, nine distinct positive feedback mechanisms driving self-facilitation were identified (Maxwell et al., 2017). However, whether consideration of each specific feedback is important or not for conservation or restoration purposes depends on the local environmental setting. For instance, sediment stabilization by a seagrass root mat is likely more important in hydrodynamically exposed environments compared to sheltered ones. By contrast, alleviation of sulfide toxicity by radial oxygen losses via the seagrass roots or mutualistic interactions with sulfide-consuming lucinid bivalves is most useful in organic matter-rich, anoxic sediments (van der Heide et al., 2012a, 2012b; Maxwell et al., 2017).

In this study, we investigate how transplantation success of the temperate seagrass *Zostera marina* using trait-mimicry is affected by hydrodynamic intensity in a restoration experiment at four sites (Finland, Sweden, UK, USA). Specifically, we transplanted seagrass ramets into (1) aboveground biodegradable establishment structures that

attenuate hydrodynamic energy as observed in large patches of dense vegetation canopies (Bouma et al., 2005; Temmerman et al., 2007; Bouma et al., 2009), (2) belowground establishment structures that stabilize the soil similar to dense vegetation root mats (Christianen et al., 2013), and (3) unmanipulated bare control plots. During our experiments, we monitored sediment movement as a proxy of hydrodynamic exposure, and followed seagrass transplant survival, shoot density, and lateral expansion as indicators of restoration success.

2. Methods

2.1. Study sites

The experiment was carried out over 14–15 months in 2017–2018 (covering 2 growing seasons and a winter season) using perennially growing *Z. marina* at shallow subtidal sites (Fig. 1, Fig. A1 and Table 1). To compare the generality of our findings we selected three sites in Western Europe (Skagerrak Sea, Sweden; Baltic Sea, Finland; Celtic Sea, United Kingdom) and one along the Pacific US coast (Puget Sound, Washington). Sites differed from each other in terms of tidal range and fetch length, yielding a gradient of relatively mild (Finland) to most intense (United Kingdom) hydrodynamic exposure regime. At all four sites, seagrass was historically present. Furthermore, seagrass meadows are also still present in the direct vicinity of the transplant sites (i.e., within the same bay), indicating that water quality was sufficient to support seagrass growth.

2.2. Experimental setup and monitoring

At each site, we established 12 plots, spaced >2 m apart, in unvegetated, sandy areas where seagrass had previously been mapped but had disappeared or is still present close by. We randomly assigned one of three treatments to each plot in a randomized block design: aboveground establishment structure, belowground establishment structure, or control (n = 4 replicate blocks per site). Aboveground structures were placed on top of the sediment with the aim of attenuating hydrodynamic energy and accreting sediment. Belowground structures were dug into the sediment, so that the top of the structure was flush with the sediment surface to increase sediment stabilization without modifying flow velocities and shear stress (Fig. 1c).

Establishment structures consisted of BESE elements (BESE Ecosystem Restoration Products, Culemborg, The Netherlands) composed of biodegradable potato-waste-derived Solanyl C1104M (Rodenburg Biopolymers, Oosterhout, the Netherlands). This Solanyl biopolymer blend is officially certified as biodegradable (see Appendix A5), and gradually degrades in field conditions over the course of 5 to 10 years, depending on the local environmental setting (Nitsch et al., 2021). Single sheets (91 × 45.5 × 2.0 cm; 0.44 kg, surface:volume ratio 80 m^2/m^3) can be stacked and connected to form a modular complex 3D-structure (Fig. 1b,d).

In this study, we combined 3 sheets to form a 6-cm high, open 3D honeycomb-shaped matrix that allows rhizomal expansion of the seagrasses through the structure (Fig. 1). Next, half a circle with a diameter of 10 cm was removed from the middle of a long side of the 3-layer stack using a disk grinder. Combining two of these resulting modules yielded a 6-cm high 91 × 91 cm establishment structure with a 10-cm circle in the middle. Each unit was secured with six L-shaped steel rebar pins (90 cm long). Control plots were marked on the corners with rebar pins.

Seagrass transplants were obtained from nearby donor sites. Seagrass shoots with intact rhizomal apical meristems, were selected and planted by hand in the center circle of each experimental plot with basal leaf/rhizome meristem pointing outwards. Three rhizome fragments (length = 6–10 cm), each holding 3–4 shoots were planted per plot, resulting in 2.9 ± 0.2 (mean ± SEM) shoots per plot for Sweden, 6.5 ± 1 shoots for Finland, 1.8 ± 0.1 shoots for United Kingdom and 10.3 ± 0.4 shoots for USA at the start of the experiment. Seagrass shoots with rhizome were anchored using u-shaped metal pins (20 cm length) and cable ties. The experiments started in the early growing season of 2017 (May/June) and ran between 13 and 14 months (Table 1). To assess restoration yields, we measured survival and shoot number at the end of the experiment. In addition, maximum expansion distance was measured using the straight-line distance from the mid-point of the plot to the newest shoot at the end of the most distant rhizome.

As a general and relative indication of sediment stability, we carried out sediment movement measurements in the growing season over the course of one month at all sites, apart from the UK where the experiment was quickly destroyed (see Results). Sediment movement was measured by placing a sediment-burial pin in the center of each plot in September
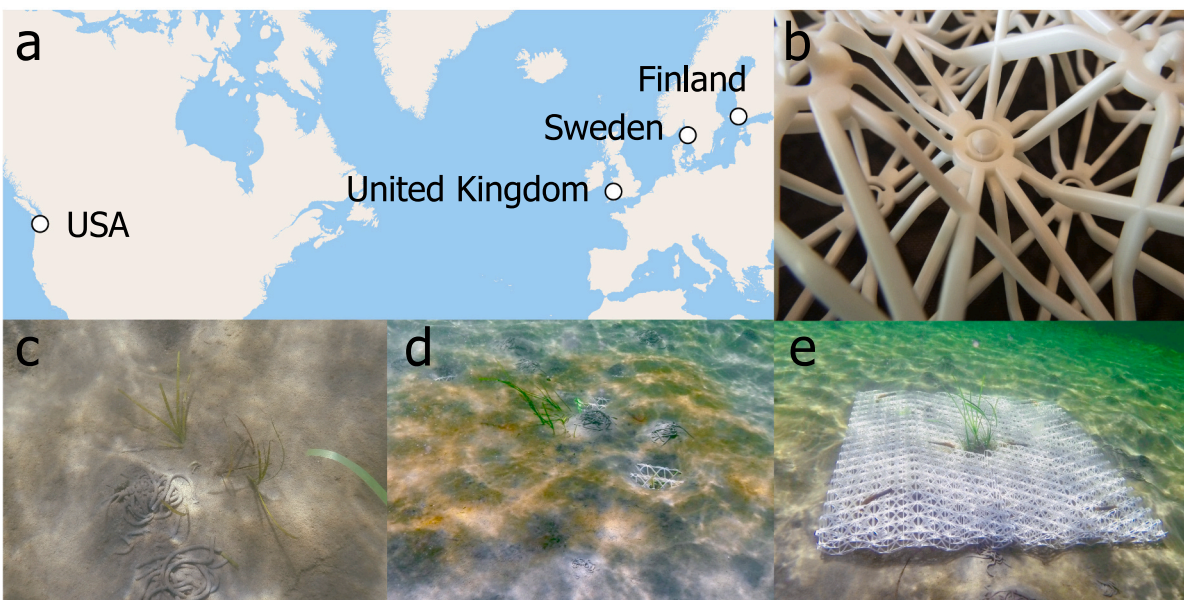

Fig. 1. Map highlighting the locations of the field sites (a), a close-up of the open 3D honeycomb biodegradable structure, and the experimental treatments: control (c), belowground (d), and aboveground (e) establishment structures with seagrass transplants in Sweden after setup. (c–e) photos from Temmink et al., 2020. Map source: Natural Earth. See Fig. A1 for an indicative overview of each experimental site.

Table 1
Coordinates and general environmental characteristics of our four experimental sites.

Site (country)	Latitude (degrees)	Longitude (degrees)	Experimental period (months: period)	Sediment type	Average depth (m)	Tidal range (m)	Maximum fetch length direction	Range highest fetch (km)	Wind speed (m/s)[a]	Significant wave height (m)
Archipelago Sea (Finland)	59.919726	21.796689	13: June 2017 – July 2018	Fine sand	2.0	0	Northeast to Southeast	1.5–4	15.3[b]	0.32–0.43[f]
Gullmarsfjord (Sweden)	58.335320	11.542482	14: June 2017 – September 2018	Medium sand, little clay and silt	1.3	0.2	Northeast to Southeast	2–4	11.3[c]	0.26–0.36[f]
Puget Sound (USA)	47.222461	–122.810239	14: May 2017 – Jul 2018	Fine sand, very little gravel, silt and clay	3.6	4.3	South to Southwest	6–10	9.8[d]	0.38–0.49[f]
Longoar Bay (United Kingdom)	51.712468	−5.114020	NA: destroyed by storms between 16/09–21/10/2017	Sand with pebbles	6.5	7.8	Southwest to West	6 to >100	18.4[e]	0.8–3.2[f]

[a] The average of the top 5% strongest winds from the direction of the highest fetch length measured during the experimental period at local weather stations.
[b] Station Kristineberg.
[c] Station Fagerholm, Parainen.
[d] Station Longbranch.
[e] Station Waterston (2017 data).
[f] Calculated with https://planetcalc.com/.

2017 in Sweden, and in July 2017 in both Finland and the USA (Temmink et al., 2020). Specifically, 50-cm long stainless pins were driven 20 cm into the ground, after which a flat stainless-steel disc (washer) was placed around the pin on top of the sediment surface. Next, we measured the distance between the upper tip of the pin and the sediment level. Over the course of the following month, the disc moved downward each time the sediment became unstable. As a proxy of sediment mobility, we therefore measured the distance between the sediment surface level and the position of the disc after one month.

2.3. Statistical analyses

Transplant survival and shoot number were analyzed using General Linear Models (GLM) with binomial and Poisson distributions, respectively. Maximum lateral expansion and sediment movement were analyzed using Gaussian GLMs. Each of the variables was analyzed for treatment effects (i.e., above and belowground establishment structures and control) and site effects and potential interactions. Random effects (i.e., block effects) were not included in the models, as they proved not significant. We performed planned pairwise comparisons to explore differences between sites and treatments. Assessments were first carried out with Benjamini-Hochberg's False Discovery Rate (FDR) correction of the significance level. As this method did not detect any differences in some occasions where the overarching model did, we also ran the more liberal Fisher's Least Significant Difference (LSD; i.e., no correction of the significance level) to highlight weaker differences.

Finally, to obtain a more in-depth understanding of the relation between sediment mobility and restoration yields, we performed nonlinear regression analyses (exponential decay function) on sediment movement data versus shoot number and lateral expansion, respectively. As aboveground structures not only affect sediment mobility, but also flow conditions, and because this treatment demonstrated poor overall performance, we conducted the regression analyses twice per variable – once with all data and once without the aboveground treatment. All analyses were performed with R version 3.6.0 (R Core Team, 2019). All data are depicted as means ± SEM.

3. Results

Whereas the experiments in Finland, Sweden and the US lasted throughout the entire experimental period (14–15 months), storm-driven waves combined with the extreme tidal amplitude (Table 1) destroyed the UK experiment within the first months, leaving no further data to collect. Further transplant survival analyses of the three remaining sites revealed that presence of the transplants at the end of the experiment significantly depended on both site and treatment (Fig. 2A; Table A1). When comparing control treatments between sites, LSD-based comparisons found a significant 4 times higher survival at the Finnish site (100 ± 0%) compared to the Swedish and USA sites (25 ± 25% for both). However, this was not detected by FDR-based comparisons (Fig. A2a). Moreover, this survival difference disappeared when transplants were protected by either above- or belowground structures. According to LSD-based comparisons, belowground structures yielded significantly higher survival at the Swedish site (100%) compared to controls, while in the USA belowground treatments (100%) outperformed both control and aboveground structures (25 ± 25% for both). These differences, however, were not detectable with FDR-based corrections of the significance levels.

Shoot counts and maximum lateral expansion showed highly similar responses (Fig. 2b,c), with the facilitating effect of belowground structures being strongly site dependent, while aboveground structures had consistent negative effects relative to controls. As a consequence of these interactive responses, both main effects (i.e., treatment and site) as well as their interaction was significant for both shoot counts and lateral expansion (Table S1). Both with LSD and FDR-based planned comparisons of control treatments between sites demonstrate that shoot count was significantly higher at the Finnish site (63.8 ± 19.4), compared to the US (11.5 ± 11.5) and Swedish (0.5 ± 0.5) sites. Lateral expansion, however, only differed between Finland (66.0 ± 13.9 cm,) and Sweden (4.5 ± 4.5 cm) in the LSD comparisons. These differences, however, were alleviated when the transplants were planted into either below- or aboveground structures.

The positive effect of belowground structures on both shoot count and expansion was highly significant at the Swedish site (30.3 ± 4.5 and 29.8 ± 7.2 cm, respectively). By contrast, shoot counts in Finland were almost 2 times higher in controls compared to belowground structures (34.5 ± 9.3 and 42.8 ± 7.6 cm, respectively), while we detected no effects on lateral expansion. Similar to Sweden, belowground structures at the USA site significantly outperformed controls by >5 and >7 times for shoot count and lateral expansion (59.5 ± 33.6, and 33.5 ± 7.3 cm, respectively). However, the latter effect was not detectable when applying FDR-based analyses (Fig. A2c). By contrast, aboveground treatments performed significantly better than controls, but worse than belowground in Sweden and the USA, while this treatment was the worst performer in Finland. Of treatments with structures, belowground structures performed consistently better than aboveground structures
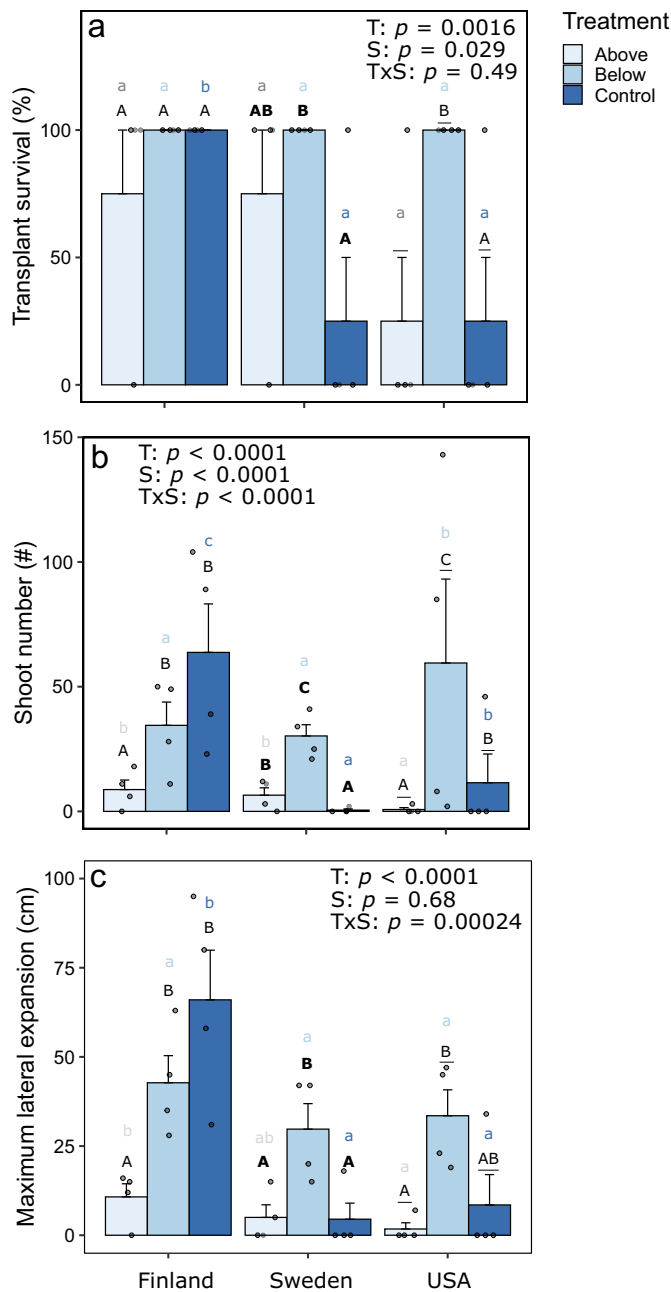
Fig. 2. Transplant survival (a), shoot number (b), and maximum lateral expansion of the seagrass transplants after 14 months, depending on site and treatment (control, belowground and aboveground structures). Data are presented as mean values + SEM (n = 4), exact p values are shown for overall treatment effects when p > 0.0001. Significant planned contrasts following the LSD procedure are indicated by different letters (see Fig. A2 for multiple comparisons based on FDR). Black letters indicate comparisons between treatments for a site (S) and colored letters depict comparisons between sites for a treatment (T). Results of the statistical analyses are presented in Supplementary Table A1.

for all sites. Specifically, aboveground structures performed ~4 (Sweden and Finland) to almost 80 times (USA) worse than belowground structures for shoot count, and 4, 6, and 19 times worse for lateral expansion in Finland, Sweden and in the USA, respectively.

Apart from the highly exposed UK site that did not yield any data (see Table 1), sediment movement data revealed that Sweden was the site with the most unstable sediments. Sweden was followed by the USA and Finland, respectively, as indicated by a strong main site effect, and

significant differences in all planned comparisons between the control treatments (Fig. 3; Table A1). Disc burial depth in the Swedish control plots (13.5 ± 1.6 cm) was 3 times deeper compared to the USA plots (4.5 ± 1.0 cm), while the discs in Finnish control plots were only barely covered (0.3 ± 0.3 cm). Furthermore, we found no significant main treatment effect, but did detect a strong Site × Treatment interaction, indicating that potential treatment effects depended on site. Indeed, we found that at the Swedish site, disc burial depth in belowground treatments was reduced by >80% (2.8 ± 0.3 cm) compared to controls, while aboveground structures reduced burial depth by just over 40% (7.8 ± 1.0 cm). By contrast, burial depth at the Finnish site was not significantly affected by the treatments. At the USA site, LSD-based comparisons revealed a significant 62% burial reduction in belowground treatments (1.8 ± 0.8 cm) compared to controls, but this difference was not detectable when using FDR-based corrections of the significance level (Fig. A3).

To further explore the relation between sediment mobility and restoration success, we performed nonlinear regression on disc burial depth versus shoot count and maximum lateral expansion. The first analyses, performed on the overall dataset, revealed relatively weak but significant correlations between burial depth versus shoot count (R^2 = 0.15, p = 0.02) and lateral expansion (R^2 = 0.20, p = 0.008), respectively (Fig. 4). In the next step, as factors other than sediment mobility appear to interact with the results in the aboveground structures, we exclude this treatment from our regression analyses. As a consequence, correlations strength between burial depth versus shoot count (R^2 = 0.30, p = 0.01) and lateral expansion (R^2 = 0.40, p = 0.002) doubled, suggesting that belowground structures increase transplant yields by reducing sediment mobility.

4. Discussion

Here, we provide proof of principle and support previous findings (Temmink et al., 2020) that mimicry of emergent traits can enhance seagrass restoration success by mitigating physical stress from hydrodynamics and high sediment mobility. However, our results also clearly
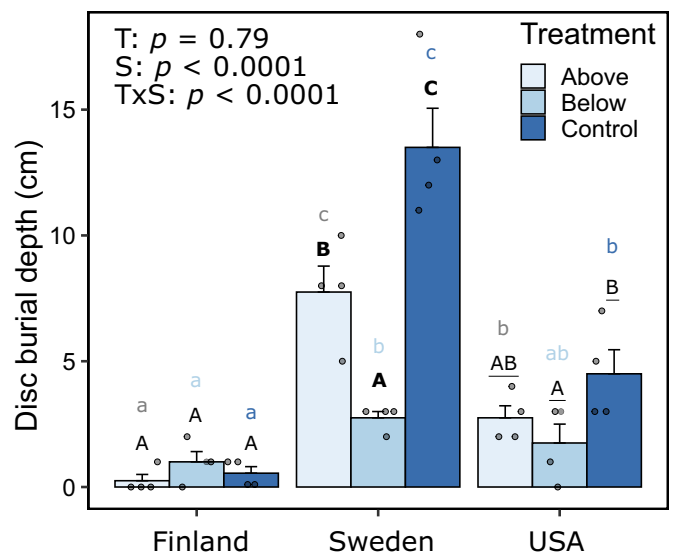

Fig. 3. Disc burial depth depending on site and treatment (control, belowground or aboveground establishment structures). Data are presented as mean values + SEM (n = 4), exact p values are shown for overall treatment effects when p > 0.0001. Significant planned contrasts following the LSD procedure are indicated by different letters (see Fig. A2 for multiple comparisons based on FDR). Black letters indicate comparisons between treatments (T) for a site (S) and colored letters depict comparisons between locations for a treatment (T). Results of the statistical analyses are presented in Supplementary Table A1.
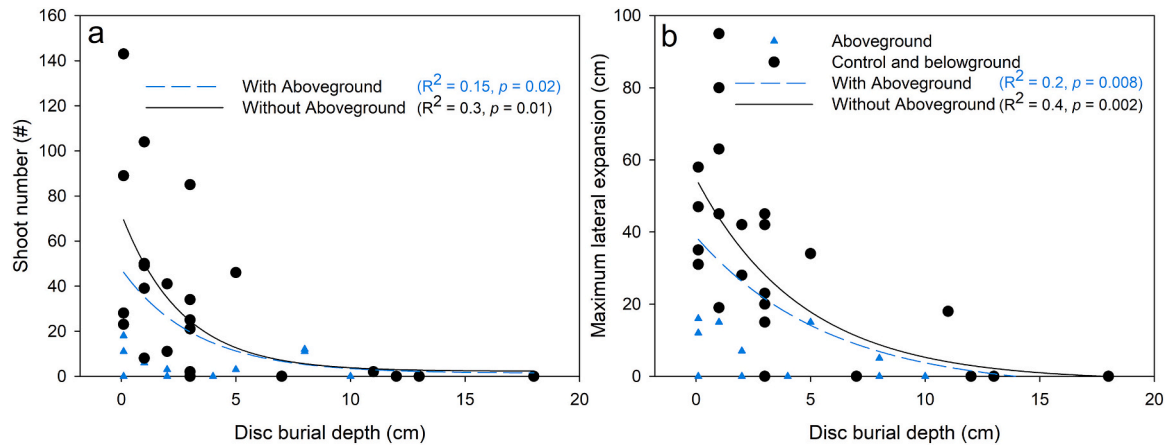
Fig. 4. Correlative analyses of how disc burial depth affects shoot number (a) and maximum lateral expansion (b). The analyses were carried out twice – once with all data (n = 36), and once with aboveground structures excluded (n = 24) as other treatment-related factors than sediment mobility seem to affect seagrass transplant performance in our experiment.

show that the survival and expansion of small transplants within biodegradable establishment structures that mimic dense roots mats or vegetation canopies is context specific and depends on local hydrodynamic intensity. By mimicking sediment-stabilizing root mats, seagrass transplant survival, growth and expansion can be strongly enhanced in hydrodynamically exposed environments. However, results also show that positive effects of this approach decrease and may even turn negative at restoration sites with low wave and current exposure conditions (Finland). At such sites, sediment stabilization from naturally generated feedback by emergent traits is also of less importance. Contrastingly, the structures were unable to sufficiently mitigate physical stress in extremely exposed environments (UK), conditions where natural feedbacks might also be overwhelmed. In addition, we found that aboveground structures, designed to attenuate hydrodynamic energy and trap suspended sediments, clearly underperformed in seagrass systems than belowground structures, to the point where they provide no clear benefits regardless of exposure conditions. Overall, our results suggest that, within upper and lower limits, reduction of sediment mobility by the belowground structures increase overall restoration yields at exposed sites, while the sediment-stabilizing effect of the aboveground structures appears to be negated.

Our work is in agreement with a growing body of literature that identifies sediment dynamics as a key parameter hampering establishment of species in physical environments (Balke et al., 2013; Bouma et al., 2016; Maxwell et al., 2017; Cao et al., 2018). Moreover, our results support recent findings that the placement of aboveground establishment structures hardly provides any benefit to seagrass transplants (Temmink et al., 2020). In contrast, salt marsh-forming cordgrass transplants benefitted more from aboveground structures, emphasizing the importance of mimicking species-specific emergent traits that mitigate the relevant stressors. In the case of cordgrass, mimicry of dense and stiff aboveground stems that attenuate hydrodynamic energy proved more important for cordgrasses than mimicking their sediment-stabilizing root system. In contrast to cordgrass stems, however, seagrass stems are flexible and avoid drag by bending (Bouma et al., 2005; Peralta et al., 2008; Bouma et al., 2010). Temmink et al. (2020) demonstrated that, whereas the rigid aboveground structures served as support for the stiff cordgrass stems, they in fact obstructed seagrass shoot movement, thereby preventing them to bend down towards the sediment surface and avoid drag. In addition, our field observations suggest that the rigid aboveground structures can also serve as a stable and thus suitable attachment substrate for macroalgae that, once settled, compete with the seagrasses for space and light (Fig. A4). More generally, such unintended facilitation of undesired organisms is not only relevant for seagrasses, but is a risk that can also occur in other ecosystem types

when applying trait mimicry. For instance, Teminnk et al. (2021a) and Fivash et al. (2021b) found that reef mimics meant to facilitate mussel settlement in the Netherlands, could also serve as a potential settlement substrate for invasive Pacific oysters. Combined, our findings emphasize the importance of identifying the correct species-specific emergent traits and stressors they mitigate, and target those for simulation in restoration actions.

In addition to correctly mimicking species-specific emergent traits, our work demonstrates that understanding how the importance of these traits varies in relation to local conditions, is vital for applying them in a restoration context. Combined with the earlier results from Temmink et al. (2020), our findings highlight that trait-based mimicry with the aim of reducing physical stress from hydrodynamic energy, is most useful in relatively exposed conditions. In such conditions, it may be a viable alternative to e.g., clumped planting (Silliman et al., 2015) or sod transplantation (van Katwijk et al., 2016). Indeed, results from the Finnish site illustrate that belowground sediment-stabilizing structures may even hamper seagrass growth in environments with low wave and current exposure, conditions where sediment stabilization from emergent traits are likely also unimportant. Here, the structures provide no clear benefit as losses due to currents and waves are limited, while they may physically obstruct the expanding transplants. In such conditions, seeding or dispersed planting are likely sufficient from a hydrodynamics perspective, provided that other environmental conditions (e.g., nutrient loading, water transparency) are also suitable. In addition, the approach is also unsuitable in highly exposed situations such as the UK site, where conditions are simply too harsh to be mitigated by the temporary establishment structures or by feedbacks from emergent traits of an established population. In such cases, permanent protection measures, such hard defense structures, may provide a more feasible option to allow long-term vegetation development.

Although our current establishment structure focus on mimicking sediment stabilization by root mats, or attenuation of hydrodynamics energy by the canopy, clonally growing coastal plants have been found to generate many more density-dependent positive interactions. For instance, both cordgrass and seagrass release oxygen via their roots, thereby oxygenating the sediment – a process that gains in strength with increasing root density (Lamers et al., 2013; Maxwell et al., 2017). Seagrasses also limit development of competing algae by absorbing nutrients from the water layer and providing shelter to algae grazers – effects that both increase with increasing patch and shoot density (Maxwell et al., 2017). Moreover, by aggregating into dense clusters, seagrass and cordgrass patches stimulate settlement of mutualistic lucinid bivalves and ribbed mussels, respectively, that in turn again facilitate the plants (van der Heide et al., 2012a, 2012b; Derksen-

Hooijberg et al., 2018). These examples illustrate that both cordgrasses and seagrasses can generate multiple species-specific emergent traits that, depending on the prevailing conditions may facilitate vegetation establishment and resilience. Clearly, our current mimicry approach is still relatively crude, focusing on a limited set of emergent traits. This highlights not only a potential for optimization of mimicking emergent traits, but also for the development of entirely new establishment aids with the ability to mimic other traits that are useful under a different set of conditions. Depending on the properties required, multiple solutions may be envisioned to emulate certain emergent traits. This is particularly the case when the aim is to combine multiple traits, such as combining attachment substrate with chemical settlement cues and/or predation reducing complexity for bivalve or coral reef development. In engineering design, morphological analysis – a method that allows exploration of all possible solutions for the combinations of functions one aims to achieve – is an often-used approach (Ritchey, 1998). We argue that, once the required functions and goals are clear, this methodology may also be very suitable for (emergent) trait-based restoration approaches, particularly in combination with flexible construction platforms such as 3D-printers (Pérez-Pagán and Mercado-Molina, 2018).

Overall, we conclude that mimicking key emergent traits may allow upscaling of restoration by constraining biological material requirements and implementation costs in many ecosystems that depend on size or density-dependent self-facilitation for persistence. These systems occur across a wide range of conditions, and include iconic but declining ecosystems such as seagrasses, mangroves, salt and freshwater marshes, coral and shellfish reefs, peatlands, and (semi-)arid ecosystems (van der Heide et al., 2021; Temmink et al., 2021b). However, our findings emphasize the importance of understanding the conditions at the restoration site as well as the growth requirements and self-facilitating traits that target organisms may employ. Specifically, for our emergent trait-mimicry approach to be useful, the stressor that is temporarily mitigated should be strong enough to cause an establishment threshold for small transplants, while a sufficiently large established population should be able to mitigate this stressor by itself. In addition, other critical environmental conditions that are not mitigated or improved by the target organism itself (e.g., salinity, temperature) should of course be suitable as well. Moreover, it is likely that the strength of self-facilitation also depends on such stressors as they affect the general health and vigor of the organisms, and thus also their habitat-modifying capacity (van der Heide et al., 2007; de Fouw et al., 2016; Maxwell et al., 2017; de Fouw et al., 2018). Finally, large-scale application should also be carefully considered from an environmental risk perspective, particularly regarding the intermediate-term fate of any chemically or biologically degradable material. We therefore argue that further experimental testing focusing on large-scale designs and restoration success over multiyear timescales in contrasting environmental settings is required prior to wide range application of establishment structures that mimic emergent traits.

CRediT authorship contribution statement

Tjisse van der Heide: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - Original Draft, Supervision, Project administration, Funding acquisition;

Ralph J.M. Temmink: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - Review & Editing, Visualization, Supervision, Project administration;

Greg S. Fivash: Conceptualization, Methodology, Investigation, Writing - Review & Editing;

Tjeerd J. Bouma: Conceptualization, Methodology, Writing - Review & Editing, Supervision, Funding acquisition;

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Declaration of competing interest

The material presented in this manuscript is based on original research carried out by the authors and has not been previously published or submitted elsewhere. All authors agree with the contents of the manuscript and its submission to *Biological Conservation*. Funding sources are credited in the manuscript's acknowledgement section, and none of the authors have any financial benefits resulting from the publication of this manuscript. Appropriate ethics, permits and other approvals were obtained for the research included in this manuscript. The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109373.

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