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Combining co-introduction with patch-size optimization as a novel strategy to maximize seagrass restoration

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Abstract

Coastal ecosystem engineers, such as mussels, oysters, salt marsh grasses, and seagrasses, typically shape their environment by ameliorating stressors when they grow beyond a critical population size. In doing so, they not only facilitate themselves but also provide habitat for diverse communities, which in turn, can engage in reciprocal interspecific facilitation. Over the last decades, anthropogenic disturbances have caused rapid degradation of coastal ecosystems, emphasizing the need for their restoration. Although the importance of both inter- and intraspecific positive interactions has been confirmed in small-scale experiments, their combined potential remains to be tested in restoration-scale experiments. Here, we examine whether restoration aimed at simultaneous recovery of both facilitation types can increase restoration yields of the seagrass *Zostera marina*. We conducted a full factorial experiment by manipulating patch size to test for intraspecific facilitation effects and co-introduced the epiphyte-grazing snails *Littorina littorea* to investigate interspecific facilitation. We found that the effect of including intraspecific facilitation on restoration yields was highly dependent on the hydrodynamic exposure conditions at the restoration site. Large patches in the most exposed sites showed a 40% increase in seagrass restoration yield compared to small patches, while at sheltered sites, large patches counted up to 60% less surviving plants compared to small ones. Interspecific facilitation, on the other hand, increased success yields by 73% on average. Moreover, in some plots where *L. littorea* survived through the winter, we counted 20 times more shoots than plots without co-introduction. Our study is the first to demonstrate that co-introduction can serve as a successful large-scale restoration strategy. Additionally, we highlight that integration of both inter- and intraspecific facilitation into restoration designs can be a powerful approach to increase coastal restoration success. However, we emphasize that these strategies should be applied

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specifically to counter environmental stressors as they may have adverse effects themselves in environments without such stressors.

KEYWORDS
coastal ecosystems, food web, interspecific facilitation, intraspecific facilitation, mutualism, patch size effect, periwinkle, plant–animal interaction, positive feedback, restoration

INTRODUCTION

Coastal ecosystems such as salt marshes, mangroves, shellfish reefs, seagrass meadows, coral reefs, and kelp forests provide vital ecosystem services including carbon sequestration, wave attenuation, and habitat provisioning (Costanza et al., 1997; Whitfield, 2017). These ecosystems are shaped by ecosystem engineering species that ameliorate stress in harsh environments through positive feedbacks (sensu Jones et al., 1994). These intraspecific feedbacks are generated through direct modifications of the abiotic environment (e.g., sediment accretion, reduction of hydrodynamic forcing) or by reducing biotic stressors (e.g., protection against predation) (Bouma et al., 2009; Donadi et al., 2013; Hunt & Scheibling, 2001; Huxham et al., 2010; Maxwell et al., 2017; Silinski et al., 2018; van der Heide et al., 2011). A consequence of such intraspecific positive interactions is that the realized niche may exceed the organism's fundamental niche in high-stress conditions (Bruno et al., 2003). However, to enable settlement under high-stress conditions, a critical population size threshold must be met as the strength of intraspecific facilitation is patch size and/or density dependent (Bouma et al., 2009; Silliman et al., 2015; Suykerbuyk, Govers, et al., 2016). For example, high hydrodynamic stress, which limits the restoration success of the mussel *Mytilus edulis* and the seagrass *Zostera marina*, was ameliorated by intraspecific facilitation. This was achieved through the formation of aggregated spatial mussel configurations and, respectively, planting of high versus low seagrass density patches (Bos & van Katwijk, 2007; Schotanus et al., 2020).

By modifying their environment, coastal ecosystem engineers do not only facilitate themselves but benefit associated species as well. Hence, these engineers are often also called foundation species (Angelini et al., 2011; Borst et al., 2018; Ellison et al., 1996). These associated species, in turn, can engage in reciprocal positive interactions with their foundation species. Such interspecific interactions can be direct or indirect. Direct reciprocal interspecific facilitation (i.e., facultative mutualisms), for example, occurs when sponges rely on mangrove roots for attachment, while mangroves receive carbon from the sponges (Ellison et al., 1996). Other examples are mussels that use cordgrasses for attachment and shading, while enhancing nutrients and alleviating drought stress for the grasses (Angelini et al., 2016); and lucinid bivalves that detoxify sediment for seagrasses, while receiving oxygen and predation shelter from the seagrasses (de Fouw et al., 2018; van der Heide et al., 2012). Indirect interspecific facilitation, on the other hand, can manifest via trophic facilitation (Estes et al., 2004; Valdez et al., 2020). An example of trophic facilitation is the maintenance of seagrass beds by sea otters (*Enhydra lutris*) and cod (*Gadus morhua*) through their consumption of mesopredators such as crabs. This increases the abundance of small, epiphytic algae-grazing invertebrates which, in turn, reduce competition for light and nutrients for the seagrasses (Hughes et al., 2013; Whalen et al., 2013).

Over the last decades, anthropogenic disturbances such as eutrophication, infrastructure development, climate change, and overfishing have increasingly disrupted positive interactions (Aguilera et al., 2020; Jackson et al., 2001; Lotze et al., 2005, 2006; Waycott et al., 2009). This has, in turn, contributed to a rapid worldwide decline of coastal foundation species (Coleman & Williams, 2002; van der Heide, Angelini, et al., 2021; Waycott et al., 2009; Worm et al., 2006). Especially when disrupting cascading effects, removal of one species can have detrimental consequences on the community level (Casini et al., 2009; Coleman & Williams, 2002; Hughes et al., 2013) and potentially prevent natural recovery (Bellwood et al., 2004; Casini et al., 2009; Valdemarsen et al., 2011). In an attempt to halt and reverse coastal ecosystem losses, substantial efforts are made to restore foundation species (Lefcheck et al., 2018; van Katwijk et al., 2016). Thus far, however, success has been limited (Bayraktarov et al., 2016; van Katwijk et al., 2016), highlighting the need for innovations to increase the efficacy of restoration strategies. Recently, evidence is mounting that harnessing emergent traits by clustering of plant transplants (Silliman et al., 2015; van Katwijk et al., 2016) or mimicry of traits by temporarily simulating dense patches of stems or roots (Temmink et al., 2020) can increase restoration success by over 100% (Schotanus et al., 2020; Silliman et al., 2015; Temmink et al., 2020). Moreover, recent studies suggest that

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integration of facultative mutualistic interactions through co-introduction can result in similar increases in restoration yields (Derksen-Hooijberg et al., 2018; de Fouw et al., (2023); Gagnon et al., 2020; Gribben et al., 2019; Shaver & Silliman, 2017; Sievers et al., 2022; Valdez et al., 2020; Zhang et al., 2021). Yet, although both inter- and intraspecific positive interactions have been successfully tested, these studies did not combine the inclusion of both interaction types or remained theoretical or relatively small in scale.

In this study, we examined whether the implementation of inter- and intraspecific facilitation and their interaction can be used as a successful strategy for the restoration of the seagrass *Z. marina* in Lake Grevelingen. This lake is known for its lack of natural grazers and stochastic hydrodynamic events limiting seagrass restoration (Cronau et al., 2022; Cronau et al., unpublished data). Previous work showed that the periwinkle *Littorina littorea* grazes epiphytes from seagrass leaves without discriminating between algae and abandoned algae-covered dwelling tubes built by *Platynereis dumerilii* (Cronau et al., 2023). Epiphytic algae compete with the seagrasses for light and nutrients (Östman et al., 2016), whereas the ragworm *P. dumerilii* restricts leaf movement and reduces effective leaf surface by gluing leaves together when creating dwelling tubes. Through grazing, *L. littorea* inhibits the negative effects of epiphytic algae growth as well as gluing together of leaves by *P. dumerilii*, thus protecting the seagrass via two distinct pathways (Figure 1; Cronau et al., 2023). *Z. marina*, in turn, indirectly provides a food source for *L. littorea* in the form of epiphytic algae growing on its leaves and provides refuge habitat against predators and hydrodynamic exposure. We experimentally combined a patch size (testing intraspecific facilitation) and co-introduction (testing interspecific facilitation) treatment (Figure 1), using *Z. marina* transplants at three sites within Lake Grevelingen, varying in level of hydrodynamic exposure. We specifically tested the following hypotheses: (1) co-introduction of *Z. marina* and *L. littorea* will provide indirect positive interactions through trophic facilitation, as well as through inhibition of gluing by *P. dumerilii*, increasing *Z. marina* restoration success, (2) increasing patch size will increase *Z. marina* restoration success by enhancing intraspecific facilitation and ameliorating hydrodynamic exposure, (3) a larger patch size will decrease edge effects and concomitant *L. littorea* loss, increasing *Z. marina* restoration success. We use our findings to address the importance of an intact trophic structure and a network of positive inter- and intraspecific interactions for seagrass restoration. Finally, we discuss the implications of our findings for coastal restoration and conservation policies in areas where community shifts have been detected.

MATERIALS AND METHODS

Study area

Our experiment was conducted in Lake Grevelingen, situated in the south of the Netherlands (Figure 2). Formerly an estuary of the Rhine–Meuse delta, it was transformed into an artificial saltwater lake in 1971 by damming off the connections to both fresh and seawater, as a protective measure after a catastrophic flood in 1953 (Nienhuis et al., 1996). It covers about 108 km^2 made up of shallow sandy flats intersected by deep channels. Water level fluctuates about 20 cm between winter and summer, and the daily amplitude is mainly wind driven, and the salinity varies between 27.7 and 31.6 throughout the lake (van Donk et al., 2021).

Historically, Lake Grevelingen was an estuary with intertidal flats where *Z. marina* occurred in low abundance. Then, when it got dammed off from the sea, the estuary turned into a lake in 1971. The damming resulted in a considerable drop in salinity, after which the seagrass started expanding in the now permanently submerged shallow zones to a maximum areal cover of 4600 ha in 1978. After the lake was reconnected to the North Sea via a small passage in 1978, *Z. marina* gradually went extinct as salinity slowly rose again during the second half of the 1980s and 1990s (Nienhuis et al., 1996). Both the increase and decline most likely were the result of these human-driven salinity shifts that caused the initial selection and subsequent extinction of a low salinity *Z. marina* ecotype (van Katwijk et al., 2023). After the disappearance of seagrass, ephemeral short-lived macroalgae became the main primary producers, showing yearly bloom and die-off events (Tangelder et al., 2019). Also, during and following these environmental changes, shifts in faunal community occurred in which multiple natural epiphyte grazers all but disappeared (Hoeksema, 2002; Troost et al., 2018). Although salinity levels in Lake Grevelingen are still relatively high, *Z. marina* as a species is well known to thrive in these conditions, and the lake's abiotic conditions seem suitable for Northwest European *Z. marina* populations in general (van der Heide et al., 2009). Therefore, multiple seagrass restoration efforts have been undertaken during the past few years using donor plants from different localities (Cronau et al., 2022, 2023). These projects, however, have shown that a lack of epiphyte grazers causes multiple problems for newly introduced plants.

For our experiment, we selected three sites within the lake (Figure 2a): (1) Slikken van Flakkee North (SFN: 51°47′4.8″ N, 3°58′28.8″ E), (2) Veermansplaat (VP: 51°44′55.6″ N, 4°0′10.5″ E), and (3) Slikken van Flakkee South (SFS: 51°44′27.2″ N, 4°01′30.4″ E). The selected sites ranged in depth from 50 to 110 cm with SFS at

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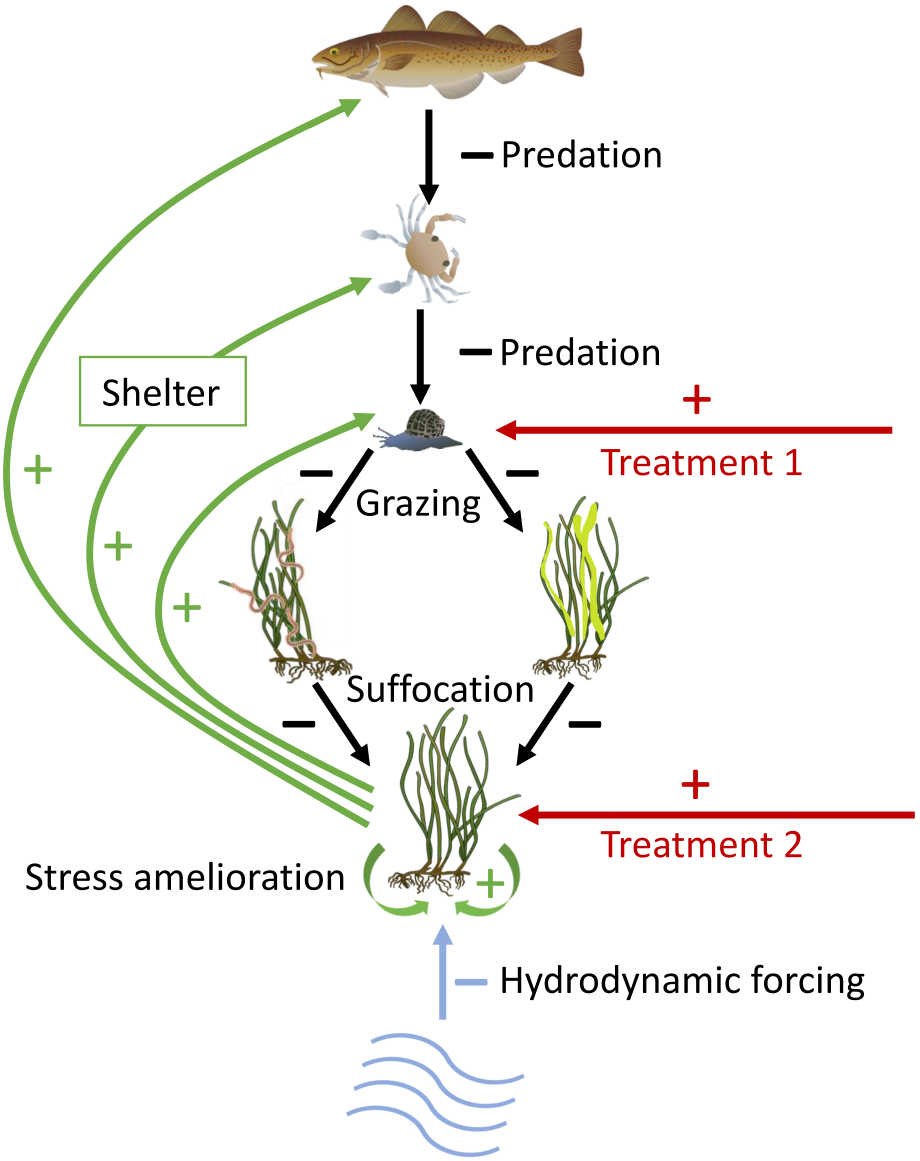


FIGURE 1 Schematic illustration of the multitrophic interactions important to the study system in Lake Grevelingen. Black arrows indicate negative interspecific interactions. Green arrows indicate the non-trophic inter- and intraspecific facilitating interactions of seagrass. The blue arrow indicates the negative interaction of hydrodynamic forcing on seagrass. The red arrows indicate the two study treatments: Treatment 1 involves interspecific facilitation through *Littorina littorea* addition, while Treatment 2 involves intraspecific facilitation by increasing patch size. Symbols are courtesy of Tracey Saxby, Dieter Tracey, Kim Kraeer, and Lucy Van Essen-Fishman, IAN (ian.umces.edu/imagelibrary/). Modifications were made to the symbols in accordance with a Creative Commons Attribution-ShareAlike 4.0 International license (https://creativecommons.org/licenses/by-sa/4.0/).

50 cm and VP at 110 cm deep. Sites were selected based on a long history of *Z. marina* presence up to the total extinction in Lake Grevelingen in the 1990s (Nienhuis et al., 1996). Moreover, these sites showed a range in hydrodynamic exposure and contained the longest surviving seagrasses during field restoration experiments in 2019 and 2020 (Cronau et al., 2022, 2023; Cronau et al., unpublished data). Although most seagrasses from previous experiments had mostly disappeared at the start of this study, few plants survived throughout the monitoring period at SFN and VP.

Experimental design and setup

To measure how inter- and intraspecific facilitation, and their interaction, affect *Z. marina* restoration, we conducted a full factorial grazer and patch size experiment at each of the three selected sites. At each site, we constructed six small and two large plots of 1 and 25 m^2 (5×5 m^2), respectively (Appendix S1: Figure S1). Half of each of the plots at each site was treated with the addition of 200 *L. littorea* (periwinkles) m^{-2} on the day of transplantation. The addition was repeated one and three

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FIGURE 2 Map of the Netherlands with a detailed view of the study area Lake Grevelingen and the three study sites Slikken van Flakkee North (SFN), Veermansplaat (VP), and Slikken van Flakkee South (SFS).

months after transplantation. *L. littorea* were initially collected from the donor seagrass meadow site and afterward supplemented with local individuals from the adjacent Eastern Scheldt (51°40′06.9″ N, 4°07′06.6″ E).

Z. marina ramets were harvested in the Limfjorden, Denmark (57°0′57.7″ N, 9°29′23.0″ E) at a depth of 60–80 cm on 16–17 July 2021. This donor site with perennial *Z. marina* plants was selected due to its relative proximity to the study site (687 km), its density of seagrass shoots, and similar growing conditions to Lake Grevelingen regarding depth, limited tidal amplitude, salinity, and hydrodynamic exposure (Maar et al., 2023). Ramets were carefully removed by hand after which sediment was rinsed of within the fjord. The bare root ramets were stored in crates covered by wet cloths to keep them moist during transport. Transplants were then transported to Lake Grevelingen (51°43′35.2″ N, 3°58′14.9″ E), where planting units were constructed by bundling four vegetative shoots, each with 7.5 ± 2.5 cm of intact rhizome, using iron wire attached to a 15-cm iron nail (according to Tan et al., 2020). After construction, they were stored in crates with flowthrough water in Lake Grevelingen until transplantation.

Transplantation was conducted from 19 to 21 July 2021. To prevent cross intervention between treatments, small plots (of 1 m^2) were spaced at least 3 m apart, and large plots (of 25 m^2) were spaced 10 m apart from small plots and 25 m apart from the other large plot (Appendix S1: Figure S2). Planting units were placed in a 5×5 m^{-2} grid, spacing the plants 20 cm apart with the first planting slot empty, resulting in 24 transplants and 72 shoots m^{-2} (Cronau et al., 2023). A total of 4032 planting units (16,128 shoots) were transplanted this way.

Measurements

Modified effective fetch was calculated for each of the three sites after Howes et al. (1994), resulting in a sheltered, intermediately exposed, and exposed site. All field sites were monitored from July to November 2021 and in April 2022. Monitoring was done via snorkeling, which allowed close examination while minimizing disturbance. At each site, the number of *Z. marina* shoots, glued shoots (glued by *P. dumerilii* cocoons), *L. littorea* snails, and cover of algae were determined within a 0.25-m^2 quadrat for all

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six small plots and within ten 0.25-m^2 quadrats evenly distributed within each of the two large plots. From the second monitoring round onward, crushed *L. littorea* shells were also counted within the quadrats since shore crabs (*Carcinus maenas*) were observed predating on the snails. To determine sediment characteristics, we took a single sediment core from the top 5 cm (26 mm diameter) per small plot and used a rhizon sampler (Eijkelkamp Agrisearch Equipment, The Netherlands) to extract porewater from the top 5 cm (November 2021). Sediment cores and porewater samples were extracted in the same manner for the first 4 of the 10 monitoring quadrats within the large plot. For each rhizon and core taken within the 1- and 25-m^2 plots, another was taken 1 m outside of the plot. After collection, sediment cores and porewater samples were stored at −18°C. To determine plant characteristics, a core containing a single planting unit was extracted from each 1-m^2 plot and the first 4 quadrats of the 25-m^2 plots. Transplant rhizomes were carefully rinsed from sediment, after which the plants were placed in plastic bags.

Sample processing

Sediment cores were freeze-dried for 96 h. After homogenization, organic content (in percentage) was determined as dry mass (DM) loss after ignition (4 h, 550°C). Furthermore, median grain size was determined on a subsample of 10 g using a particle size analyzer (Coulter LS 13320). Ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^{3-}) concentrations in the porewater were analyzed using an Auto Analyzer (Seal Analytical XY-Z sampler, Bran + Luebbe GmbH, Norderstedt, Germany).

Belowground tissue from the extracted planting unit was further rinsed free from sediment, after which a single plant was randomly selected from the planting unit. Shoot and leaf count, as well as the longest leaf length, were measured, after which epiphytes and *P. dumerilii* were removed. Epiphytes were removed by carefully scraping them off with a sharp razor, and *P. dumerilii* were removed by hand together with their cocoon. Lastly, above- and belowground tissue, as well as removed epiphytes, were dried at 60°C for 24 h for DM measurements.

Statistical analysis

We used mixed-effects models for the statistical analyses of shoot count, epiphyte DM, *P. dumerilii* numbers, above- and belowground DM, median grain size, organic matter content, and nutrient concentrations. For each of these response variables, we used the following general approach. These models contained at least both treatments as interactive independent variables and plot as a random variable to account for pseudoreplication within the plots. We started by constructing two variants. The first variant of the model contained site as an added random effect to account for potential site effect. In the second variant, site was replaced with fetch (which was calculated per site; see *Measurements*) as an interactive independent variable. Fetch, as a proxy for hydrodynamic exposure, is a known stressor to seagrass restoration in Lake Grevelingen. Seagrasses, however, are capable of mitigating hydrodynamic stress through intraspecific facilitation. By including fetch in our model, we expect to infer a fetch-dependent effect of our patch size treatment. We selected the best-fitting model based on AIC. Finally, whenever the fetch model was selected and fetch showed an interaction with one of the treatments, separate models were run per site to analyze the effect of the treatment in each of the sites. See Appendix S1: Table S1 for an overview of used fetch and site models and their corresponding AIC scores.

Following the above general approach, we analyzed the dependent variables epiphyte DM, *P. dumerilii* numbers, above- and belowground DM, median grain size, organic matter content, and nutrient concentrations using linear mixed-effects models (LMMs).

L. littorea count was analyzed using a generalized linear mixed-effects model (GLMM) with a Poisson distribution, following the general approach, but only using co-introduction treatment plots since the other ones did not contain any *L. littorea*. Shoot counts were also analyzed using GLMMs with a Poisson distribution. Before winter, shoot count was analyzed following our general approach with the addition of time as an interactive independent variable to account for multiple measurements over time. For the shoot count after winter, we used the general approach, but without time as an added variable. Furthermore, after selecting the best-fitting model, we added *L. littorea* count to the model as an interactive independent explanatory variable to account for the differences in co-introduction treatment durability after winter.

The independent variables fetch and time were scaled for equal contribution to the analyses and to reduce multicollinearity produced by higher order terms within the models. Type 3 Wald chi-square test ANOVAs were applied on the GLMM models when testing for interactions, whereas type 3 ANOVAs with the Satterthwaite's method were applied for LMM models. Dependent variables were log, log + 1, or square root transformed when necessary to meet the corresponding models' assumptions. All tests were considered significant and reported at an alpha level of $p \leq 0.05$. Alpha levels of $p > 0.05$ were considered nonsignificant and only reported as such

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(for a full overview of all test results, see Appendix S1: Table S2). Means in text and figures are followed by the SE of the mean (SEM). All statistical analyses were conducted in R v4.2.0 (R Core Team, 2021).

RESULTS

Zostera marina

We found that *L. littorea* positively affected shoot density of *Z. marina*, while a large patch size was only beneficial at exposed conditions and became disadvantageous in sheltered conditions. Average shoot density decreased over time, with densities between sites diverging from a shared average of 24 shoots per 0.25 m^2 at the onset of transplantation to 16.75 ± 1.79 for SFN, 15 ± 1.79 for VP, and 21.81 ± 2.8 for SFS at the end of the growing season (Appendix S1: Figure S3a). Differences were best explained by the treatments combined with the site-specific calculated fetches of 2.15 (SFN; exposed), 1.69 (VP; intermediately exposed), and 0.23 (SFS; sheltered). The fetch model proved to best predict shoot density (see Appendix S1: Table S1 for AIC comparisons). It showed a significant positive effect of the co-introduction treatment interaction with time ($\chi^2 = 38.59$, $p < 0.001$), a positive effect of co-introduction independently ($\chi^2 = 6.43$, $p = 0.011$), and an interaction between the treatment patch size and environmental variable fetch over time ($\chi^2 = 40.91$, $p < 0.001$; Figure 3a). This interaction between patch size and fetch on shoot density was explained by individual models per site showing a positive effect of increased patch size over time in SFN with the highest fetch ($\chi^2 = 6.69$, $p = 0.009$), no effect at VP with the intermediate fetch, and a negative effect in SFS ($\chi^2 = 36.81$, $p < 0.001$) with the lowest fetch. At SFS, small patches started performing better than large patches after an algae bloom had occurred (Appendix S1: Figure S3b).

At the end of the growing season, *Z. marina* aboveground DM was predicted best by the fetch model, while belowground DM was best predicted by the site model. We found that aboveground DM was increased by co-introduction, whereas it correlated negatively with fetch ($F_{(1,34)} = 7.51$, $p < 0.018$ and $F_{(1,34)} = 10.44$, $p = 0.007$, respectively). Meanwhile, belowground DM was significantly increased by the co-introduction treatment ($F_{(1,34)} = 11.70$, $p = 0.005$; Figure 3b) while showing no effect from patch size.

Littorina littorea

We found that at the end of the growing season, *L. littorea* had reduced epiphyte biomass on seagrass leaves as well as *P. dumerilii* numbers. Patch size, meanwhile, had no apparent effect on epiphyte biomass nor on *P. dumerilii* numbers, while fetch positively correlated

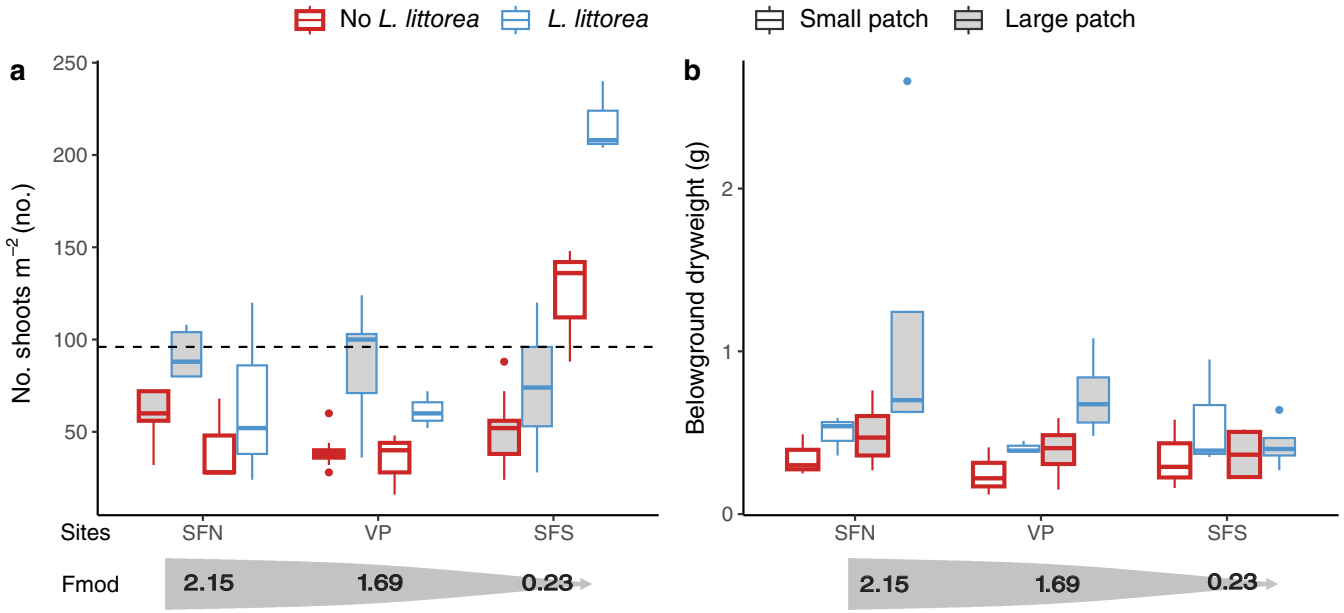


FIGURE 3 (a) Number of *Zostera marina* shoots per square meter and (b) the belowground dry mass per ramet. Both plots represent data 107 days after transplantation for each of the three sites, differentiating between the patch size and co-introduction treatments. The variability within the boxplots for the large-plot treatment is based on pseudo-replication, with 10 non-independent measurements taken within the same plot. The gray arrow represents the modified effective fetch (Fmod) per site. The horizontal dashed line depicts the initial transplanted number of shoots.

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with *P. dumerilii* numbers. Epiphyte DM (in grams per gram of DM *Z. marina*) was best predicted by the site model and was reduced by *L. littorea* addition ($F_{(1,36)} = 14.61$, $p < 0.001$; Figure 4a), whereas patch size did not show a significant effect and fetch no significant correlation. *P. dumerilii* density (in individuals per gram of DM *Z. marina*) was best predicted by the fetch model and was reduced by *L. littorea* addition ($F_{(1,34)} = 21.92$, $p < 0.001$; Figure 4b). Fetch also positively correlated with *P. dumerilii* numbers ($F_{(1,34)} = 23.61$, $p < 0.001$), with the highest amount of *P. dumerilii* at the location with the highest fetch.

Many of the added *L. littorea* migrated out of their plots after introduction. The number of remaining *L. littorea* was best predicted by the fetch model, and abundance was positively affected by increased patch size

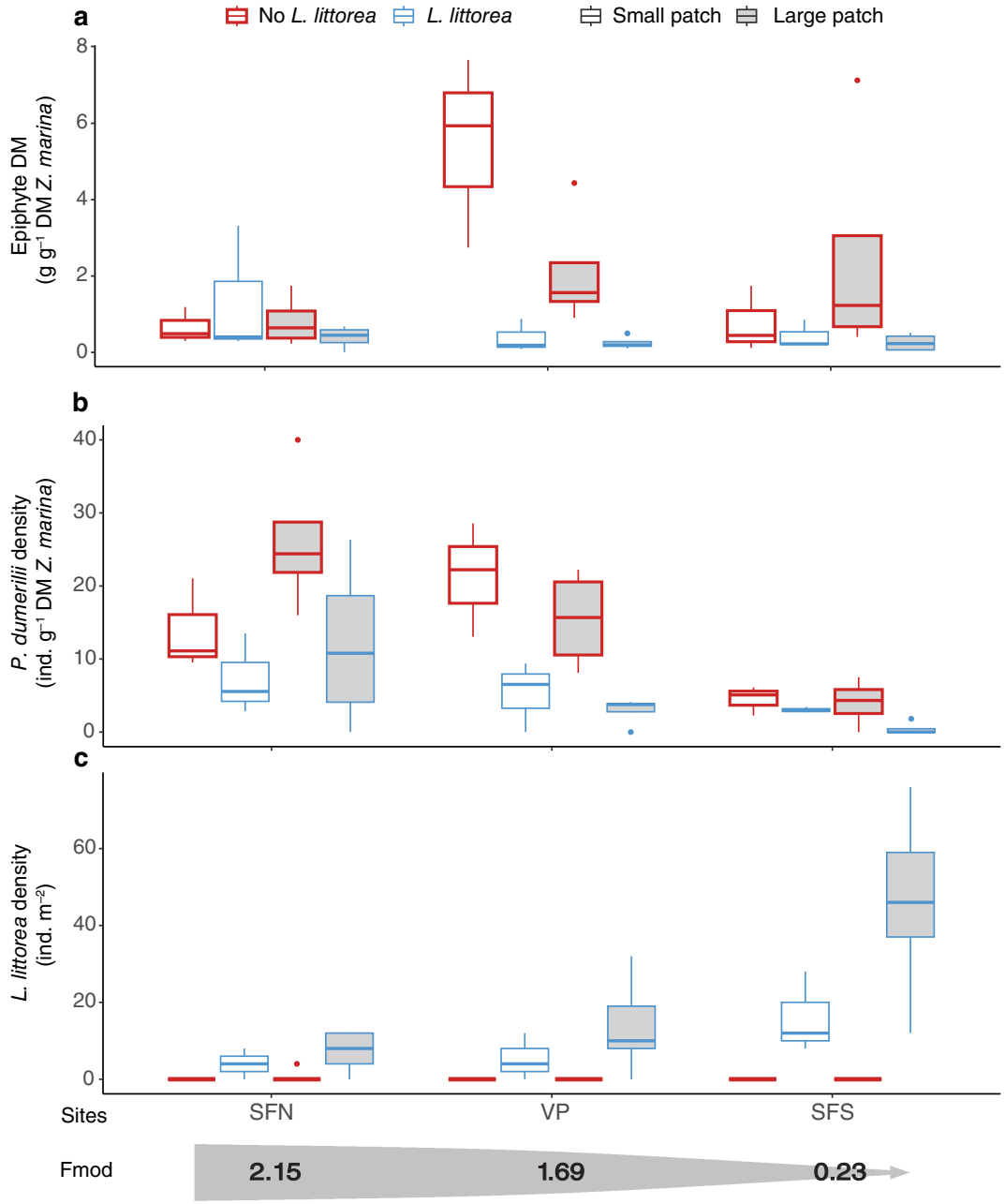


FIGURE 4 (a) Epiphyte dry mass (DM) per aboveground *Zostera marina* shoot DM, (b) the number of *Platynereis dumerilii* per aboveground *Z. marina* shoot DM, and (c) number of *Littorina littorea* per square meter. Both plots represent data 107 days after transplantation for each of the three sites, differentiating between the patch size and co-introduction treatments. The variability within the boxplots for the large-plot treatment is based on pseudo-replication, with 10 non-independent measurements taken within the same plot. The gray arrow represents the modified effective fetch (Fmod) per site.

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($\chi^2 = 16.62$, $p < 0.001$), whereas fetch negatively correlated with *L. littorea* numbers ($\chi^2 = 70.28$, $p < 0.001$; Figure 4c). No effect of the patch size treatment was found. Also, predation of *L. littorea* by *C. maenas* took place at least at one of the sites where the shorecrab was observed predating on added *L. littorea*, and crushed shells were found within the treatment plots (Appendix S1: Figure S4).

Winter survival

After winter, shoot density was still positively affected by the co-introduction treatment, whereas patch size had no effect at the exposed site and intermediate exposed site and a negative effect at the sheltered site. Overall, mean shoot density declined over the winter from 72.1 ± 5.3 shoots m^{-2} in November to 11.1 ± 1.7 shoots m^{-2} in April. The fetch-model best explained shoot numbers, with patch size and co-introduction treatment significantly affecting shoot density ($\chi^2 = 7.42$, $p = 0.001$; $\chi^2 = 21.64$, $p < 0.001$, respectively; Figure 5a). Like pre-winter conditions, a significant interaction between the treatment patch size and the environmental variable fetch occurred ($\chi^2 = 6.82$, $p = 0.009$). Now, however, only a significant negative effect from increased patch size remained at SFS with the lowest fetch ($\chi^2 = 19.71$, $p < 0.001$). The co-introduction treatment, contrastingly, increased shoot density in all conditions even when no *L. littorea* remained after winter (Figure 5b). *L. littorea* survival was generally low, with only Veermansplaat showing numbers equal to pre-winter conditions. *L. littorea* count, when added to the fetch-model, showed an additional interaction with the co-introduction treatment ($\chi^2 = 5.43$ $p = 0.002$) and independently increased shoot density ($\chi^2 = 7.78$, $p = 0.005$). Small and large co-introduction treatment plots without *L. littorea* surviving the winter still counted 269% and 400% more surviving shoots than their non-co-introduction treatment counterparts, respectively, whereas small and large plots with surviving *L. littorea* counted 850% and 2375% more surviving shoots than their local non-co-introduction treatment counterparts.

DISCUSSION

Our experimental results show that the inclusion of inter- and intraspecific facilitation, and their combination, can increase seagrass restoration success, particularly in exposed conditions. Within saltwater Lake Grevelingen, we found that co-introducing *Z. marina* with the epiphyte-grazing snail *L. littorea* improved plant survival and increased belowground biomass. We also found that increased patch size improved seagrass survival through intraspecific facilitation but only in relatively exposed conditions (Figure 6). Moreover, large

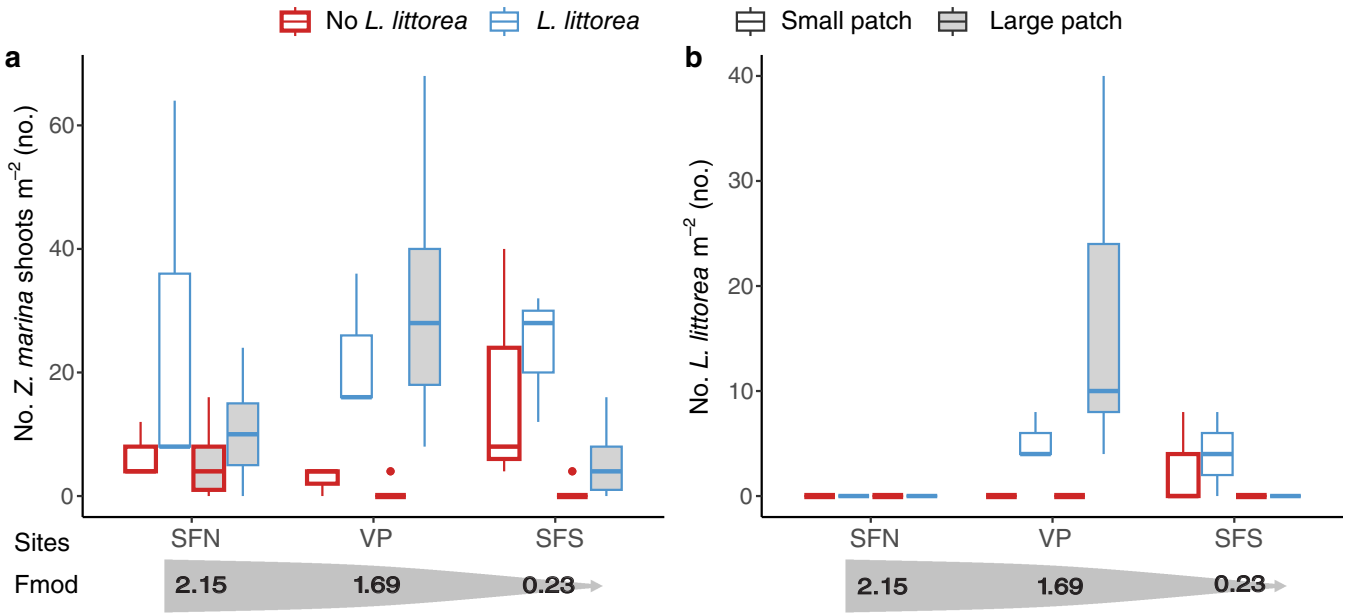


FIGURE 5 (a) Number of *Zostera marina* shoots per square meter and (b) number of *Littorina littorea* per square meter. Both plots represent data 107 days after transplantation for each of the three sites, differentiating between the patch size and co-introduction treatments. The variability within the boxplots for the large-plot treatment is based on pseudo-replication, with 10 non-independent measurements taken within the same plot. The gray arrow represents the modified effective fetch (Fmod) per site.

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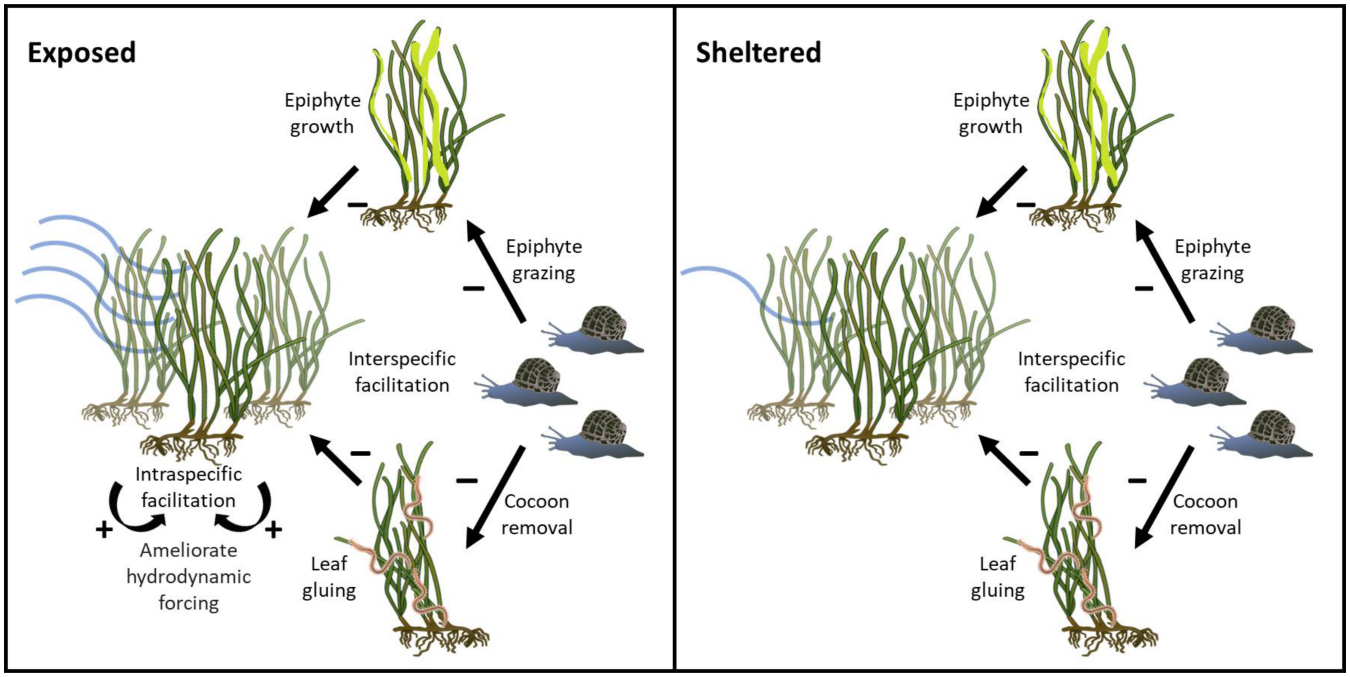


FIGURE 6 Schematic illustration representing intraspecific facilitation due to positive feedbacks at exposed sites and interspecific facilitation by grazers through epiphyte grazing (top) and anti-gluing (bottom) protection at exposed as well as sheltered sites. Symbols are courtesy of Tracey Saxby and Dieter Tracey, IAN (ian.umces.edu/imagelibrary/). Modifications were made to the symbols in accordance with a Creative Commons Attribution-ShareAlike 4.0 International license (https://creativecommons.org/licenses/by-sa/4.0/).

patches had a retaining effect on *L. littorea* numbers in all exposure conditions. After winter, plots with the co-introduction treatment continued to perform significantly better than those without, even in the plots where *L. littorea* had disappeared over time. Large plots where *L. littorea* had not disappeared during winter counted over 20 times more surviving shoots than those without the co-introduction treatment. These findings are the first to show the positive effect of co-introduction in large-scale seagrass restoration projects and more generally indicate the importance of including positive interspecific interactions for the restoration of degraded coastal ecosystems where such key interactions disappeared.

Interspecific interactions

The co-introduction of *Z. marina* with the epiphyte-grazing *L. littorea* consistently increased shoot density, as well as above- and belowground DM, by mitigating light limitation caused by epiphytes and leaf gluing. These effects were observed across all hydrodynamic exposure conditions by the end of the growing season. The success of this new seagrass restoration strategy is in accordance with earlier findings in cordgrass salt marshes by Derksen-Hooijberg et al. (2018), seagrass patches by Zhang et al. (2021), and coral reefs by Biggs (2013), who were the first and to date only attempts of co-introduction in coastal ecosystem restoration projects. In our work, at least two distinct mechanisms were likely responsible for the increased *Z. marina* performance in co-introduced plots (Figure 6). First, epiphyte grazing is well known to increase seagrass performance by reducing competition between eelgrass and faster growing algae for light and nutrients (Duffy et al., 2015; Whalen et al., 2013). Multiple experiments have shown a direct impact of grazer addition to growth and survival of *Z. marina* plants (Cronau et al., 2023; Whalen et al., 2013), and the absence of a healthy grazer population has frequently been suggested to endanger the longevity of existing seagrass meadows (Baden et al., 2012; Hughes et al., 2013; Östman et al., 2016). Second, *L. littorea* grazing counteracted gluing of *Z. marina* leaves by *P. dumerilii*, which entangles the leaves and poses a direct threat to the survival of *Z. marina* plants (Cronau et al., 2022, 2023).

We indeed found support for the occurrence of this dual-protective interaction as co-introduced plots had a considerably lower epiphyte load and lower *P. dumerilii* densities during harvest at the end of the growing season. This indicates that the epiphytes on seagrasses served as a suitable food source for *L. littorea*, which is supported by the relative sedentary behavior of *L. littorea* inside seagrass plots. However, some environmental factors influenced their behavior. First, *C. maenas* was found to

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predate on *L. littorea*, crushing their shells. *C. maenas* is known to predate on *L. littorea*, and the fact that the only naturally occurring *L. littorea* were large individuals points to high predation pressure (Perez et al., 2009). Second, hydrodynamic exposure was an important driver for *L. littorea* loss, most likely due to active migration or hydrodynamics-related losses. The occurrence of active migration is supported by sporadic *L. littorea* being observed within non-periwinkle treatment plots. Sensitivity of grazers to hydrodynamic forcing has been documented before as *Hydrobia ulvae* densities were observed to be lower on seagrass in relatively exposed sites (Schanz et al., 2002). Third, death through natural causes or stress-induced death could also have occurred since the periwinkles were collected, transported, and introduced from another environment.

After winter, both the co-introduction treatment and the remaining *L. littorea* numbers contributed strongly to a higher *Z. marina* shoot density. Since over half of the plots had lost their snails during winter, the legacy and continued effects of the co-introduction treatment could be elucidated. Co-introduced plots that lost their *L. littorea* presence over winter still counted four times more shoots than non-co-introduced plots. Meanwhile, co-introduced plots that maintained a continuous *L. littorea* presence, contained over 20 times more shoots than their non-co-introduced counterparts. The increased belowground biomass in the co-introduction treatment during the growing season most likely contributed to the increased survival over the winter, even when the introduced *L. littorea* had disappeared. The even better performing co-introduction plots which had retained *L. littorea* indicate that *L. littorea* continued protecting the seagrass during winter. Although algae cover is minimal during winter, *P. dumerilii* is known to maintain high densities during winter months (Bedford & Moore, 1985). Since *Z. marina* plants are generally less resilient during the winter (Eriander et al., 2016), protection during this period might also be vitally important. As *L. littorea* densities could already be related to hydrodynamic exposure during the growing season, stochastic storm events may have been the most important determinant for *L. littorea* survival during winter.

Intraspecific interactions

The effect of the patch size on plant survival varied across the three sites in Lake Grevelingen. This site-specific effect is likely due to differences in hydrodynamic exposure. Larger patches exhibited higher shoot densities at the most exposed site, while the opposite was observed at the sheltered site (Figure 6). Our experimental design, however, only included three unmanipulated exposure levels. Therefore, conclusions drawn on the role of hydrodynamic exposure should only be seen as correlative, and variation in other environmental factors per site could have played crucial roles also. Despite this, our shoot density model including fetch provided greater explanatory power than the model containing site as a random effect, reinforcing the presumed importance of hydrodynamic exposure. A general positive effect of plot size is expected, as intraspecific facilitation increases with both plant density and patch size (Silliman et al., 2015; van der Heide, Angelini, et al., 2021; van Katwijk et al., 2016), due to mechanisms such as soil stabilization or attenuation of hydrodynamic energy (Bouma et al., 2005, 2009; Christianen et al., 2013; Suykerbuyk, Bouma, et al., 2016; van der Heide et al., 2007). Earlier work, however, indicates that these facilitating interactions are only essential in harsh environmental conditions (Maxwell et al., 2017; van der Heide, Temmink, et al., 2021), which is supported by our results on plant survival that only showed a positive effect of increased patch size at the most exposed sites. Aboveground DM of *Z. marina*, on the other hand, was not amplified by increased patch size but only negatively correlated with hydrodynamic exposure, with the highest DMs at the most sheltered site. This effect is well documented (Schanz & Asmus, 2003) and reinforces our assumption about the importance of hydrodynamic exposure in our experiment. No significant patch size effects were detected on granulometry, organic matter, or porewater nutrients. This is likely due to the limited duration of the experiment since slight effects on median grain size and nitrate concentrations were noted (Appendix S1: Figure S5a,b).

Although higher shoot densities in large plots at exposed sites are according to our expectations, the absence of a harsh environment and thus a reduced need for intraspecific facilitation does not explain why large plots underperformed at the sheltered site. Initially, large plots at the sheltered site performed similarly to small plots. However, following a spike in algae cover at this site, small plots began to outperform the large ones (Appendix S1: Figure S3a,b). During this spike, algae covered all plots at the sheltered site (Appendix S1: Figure S3a), but detached shoots were observed only in large plots. The detached shoots may have died through suffocation caused by the algae (den Hartog, 1994), which may have been more severe in the large plots because they retained the algae better. Where the relatively large edge effect of small plots is normally considered a disadvantage in exposed areas (van Katwijk et al., 2016), within the sheltered site the small patch size might have allowed enough water movement in and around the plots to prevent suffocation of plants. A similar negative effect

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of an otherwise facilitating trait was observed in a field study where the addition of structures, mimicking intraspecific-facilitating traits, improved seagrass survival in mildly hydrodynamically exposed environments but hindered seagrass expansion in environments with low exposure (van der Heide, Temmink, et al., 2021). An alternative explanation can be that, in accordance with the stress gradient hypothesis (Bertness & Callaway, 1994; Chin et al., 2021), in the absence of a need for facilitative interactions in benign conditions, competition overrules any beneficial effects of facilitation. This has been observed in mussel beds, where a depletion of resources can create banded structures (Liu et al., 2014), and in common reed (*Phragmites australis*), where intraspecific facilitation in stressful saline conditions shifts to intraspecific competition in freshwater conditions (Reijers et al., 2019).

Conditional outcomes of combined inter- and intraspecific facilitation

Although we observed no direct interactions between inter- and intraspecific facilitation, we did find that large patches maintained higher *L. littorea* densities over time, which could be attributed to increased food availability or shelter (Duffy et al., 2015), or the decreased edge effects with respect to hydrodynamic exposure (Boström et al., 2006). Higher *L. littorea* densities would logically result in increased protection against algae growth and ragworm gluing, increasing seagrass survival rates. The fact that no direct interactions between the co-introduction and patch size treatment were observed, despite large patches retaining *L. littorea* more effectively, could be because high densities were not needed to suppress epiphytes and gluing. *L. littorea* is even known to be potentially harmful to seagrasses when in high densities relative to epiphyte cover (Jaschinski & Sommer, 2008). Another option is that a larger experimental scale might be required to demonstrate such interactions. After winter, at site VP where most *L. littorea* remained, we found a larger difference in shoot count between the co-introduction and non-co-introduction treatment between large and small plots, although not significant.

Inter- and intraspecific interactions as coastal ecosystem restoration strategies

Previous studies suggest that inter- and intraspecific facilitation can be powerful tools for restoration when used in the correct environmental settings (Chin et al., 2021; Derksen-Hooijberg et al., 2018; Gagnon et al., 2020; Renzi et al., 2019; Shaver & Silliman, 2017; Sievers et al., 2022; Silliman et al., 2015; Valdez et al., 2020; van Katwijk et al., 2016). Our study is the first to provide experimental evidence that co-introduction (interspecific facilitation) can successfully be applied as a large-scale restoration strategy for seagrass meadows and is positively affected by increased patch size (intraspecific facilitation). Specifically, we demonstrated that within a year (i.e., one growing season and subsequent winter), restoration success can be increased by 23 times upon co-introduction of *L. littorea*. Moreover, increased patch size resulted in higher grazer abundances as well as increased restoration success at the exposed site. This obviously gives the transplantation a head start during the first year, enhancing the chances for long-term restoration success. It is advisable to introduce grazers during the second growing season in case the grazer densities have dropped, until the grazer populations and patch sizes are sufficiently large to sustain themselves. Application of co-introduction therefore seems of high importance for management, and we suggest its application in combination with increased meadow size in exposed areas. The positive effect of intraspecific facilitation in harsh abiotic environmental conditions was also shown by Bouma et al. (2009), Jaschinski and Sommer (2008), and van der Heide, Temmink, et al. (2021). Moreover, a negative effect of intraspecific interaction in sheltered conditions was suggested in the study by van der Heide, Temmink, et al. (2021). Interspecific facilitation, on the other hand, most likely reaches its highest potential where the consequences of *L. littorea*'s absence (e.g., epiphyte growth and leaf gluing) are greatest. Co-introduction might even, on exceptional occasions, work counterproductively. For example, when grazing pressure on epiphytes is already high, grazing by *L. littorea* may damage the outer layer of seagrass while scraping off epiphytes in enclosed conditions (Jaschinski & Sommer, 2008). In addition, unchecked marsh periwinkles have been documented to potentially leave mudflats barren due to high grazing pressure (Silliman & Bertness, 2002). But these might be the rare exceptions, as many coastal ecosystems experience community shifts and massive loss of natural grazers (Baden et al., 2010; Hughes et al., 2013; Östman et al., 2016; Waycott et al., 2009) or are exposed to harsh environmental conditions and can therefore benefit from one or a combination of both presented restoration strategies based on the conditions of the specific system.

AUTHOR CONTRIBUTIONS

Rens J. T. Cronau: Conceptualization; investigation; formal analysis; visualization; writing—original draft. **Leon P. M. Lamers:** Conceptualization; writing—review and editing. **Jimmy de Fouw:** Conceptualization;

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formal analysis; writing—review and editing. **Marieke M. van Katwijk:** Conceptualization; writing—review and editing. **Tjeerd J. Bouma:** Writing—review and editing. **Jannes H. T. Heusinkveld:** Conceptualization; investigation. **Thijs Poortvliet:** Writing—review and editing. **Tjisse van der Heide:** Conceptualization; formal analysis; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Cronau, 2024) are available in Data Archiving and Networked Services (DANS) Data Station Life Sciences at https://doi.org/10.17026/LS/DFT8VG.

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