RESEARCH ARTICLE

Life cycle informed restoration: Engineering settlement substrate material characteristics and structural complexity for reef formation

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Abstract

1. Ecosystems are degrading world-wide, with severe ecological and economic consequences. Restoration is becoming an important tool to regain ecosystem services and preserve biodiversity. However, in harsh ecosystems dominated by habitat-modifying organisms, restoration is often expensive and failure prone. Establishment of such habitat modifiers often hinges on self-facilitation feedbacks generated by traits that emerge when individuals aggregate, causing density- or patch size-dependent establishment thresholds. To overcome these thresholds, adult or juvenile habitat-forming species are often transplanted in clumped designs, or stress-mitigating structures are deployed. However, current restoration approaches focus on introducing or facilitating a single life stage, while many habitat modifiers experience multiple bottlenecks throughout their life as they transition through sequential life stages.

2. Here, we define and experimentally test 'life cycle informed restoration', a restoration concept that focuses on overcoming multiple bottlenecks throughout the target species' lifetime. To provide proof of concept, and show its general applicability, we carried out complementary experiments in intertidal soft-sediment systems in Florida and the Netherlands where oysters and mussels act as reef-building habitat modifiers. We used biodegradable structures designed to facilitate bivalve reef recovery by both stimulating settlement with hard and fibrous substrates and post-settlement survival by reducing predation.

3. Our trans-Atlantic experiments demonstrate that these structures enabled bivalve reef formation by: (a) facilitating larval recruitment via species-specific settlement substrates, and (b) enhancing post-settlement survival by lowering predation. In the Netherlands, structures with coir rope most strongly facilitated mussels by providing fibrous settlement substrate, and predation-lowering spatially complex hard attachment substrate. In Florida, oysters were greatly facilitated by hard substrates, while coir rope proved unbeneficial.

4. *Synthesis and applications*. Our findings demonstrate that artificial biodegradable reefs can enhance bivalve reef restoration across the Atlantic by mimicking emergent traits that ameliorate multiple bottlenecks over the reef-forming organism' life cycle. This highlights the potential of our approach as a cost-effective and practical tool for nature managers to restore systems dominated by habitat modifiers whose natural recovery is hampered by multiple life stage-dependent bottlenecks. Therefore, investment in understanding how to achieve life cycle informed restoration on larger scales and whether the method it is applicable to restore other ecosystems is now required.

1 | INTRODUCTION

Natural ecosystems generate many important ecosystem services, including carbon storage, shoreline protection, improved water quality, food provisioning and support for biodiversity (Zedler & Kercher, 2005). However, these services and the ecosystems that sustain them are rapidly declining due to overexploitation, land-use change, eutrophication and other climate and human stressors (IPBES, 2019). Supported by the United Nations' call to action in the 'UN Decade on Ecosystem Restoration', governments, industry and nature organizations increasingly elevate restoration as a vital tool to reverse these losses (Suding et al., 2015). However, restoration of ecosystems that occur in hash environments, such as drylands, peat bogs, coastal dunes, salt marshes, seagrasses and marine reefs is currently expensive and prone to failure (e.g. Bayraktarov et al., 2016). Mounting evidence shows that establishment of the habitat-forming organisms shaping these ecosystems—often termed ecosystem engineers, habitat-forming species or foundation species (Jones et al., 1994, hereafter called habitat-forming species)—hinges on the initiation of self-facilitating feedbacks generated by emergent traits (Silliman et al., 2015; Temmink et al., 2020; Temmink, Cruijsen, et al., 2021). These traits are not expressed by individuals or small clones but emerge when individuals aggregate or form large clones or patches. Emergent traits in turn facilitate conspecifics for instance by enhancing local rainwater infiltration in drylands (Tirado et al., 2015), or by stabilizing soils and providing attachment substrate in hydrodynamically exposed coastal zones (Bersoza Hernández et al., 2018; Maxwell et al., 2016). However, because these emergent traits

require a certain minimum organism density and patch size to operate adequately, establishment of these organisms is impeded below such density or size thresholds (Temmink et al., 2020).

To overcome establishment thresholds, restoration practitioners either transplant adult or juvenile habitat-forming species in clumped rather than more commonly used dispersed designs or deploy temporary or permanent structures (Bakrin Sofawi et al., 2017; Johnson et al., 2019; Silliman et al., 2015). The first approach is often used to restore both terrestrial and aquatic vegetation (Silliman et al., 2015), while the latter technique involving permanent structures is often pursued to support marine reef formation (Bersoza Hernández et al., 2018; van der Heide et al., 2014; Zu Ermgassen et al., 2020). Although these stress-mitigating techniques are important advancements, they typically only facilitate a single life stage, such as transplanting of adults, seeding propagules or stimulating recruitment (Bersoza Hernández et al., 2018; Silliman et al., 2015; van Katwijk et al., 2016; Zu Ermgassen et al., 2020). Yet, many habitat-forming organisms experience multiple bottlenecks throughout their life as they transition from seed/larvae to recruits, recruits to juveniles and juveniles to adults (Figure 1; Balke et al., 2011; de Paoli et al., 2015). Moreover, for many habitat-forming species, an individual's ability to overcome consecutive bottlenecks often depends on intraspecific facilitation by established conspecifics or requires a window of opportunity (i.e. a sufficiently long period of calm low-stress conditions during which individuals can either establish or grown enough to advance to the next life stage; Balke et al., 2011; Tirado et al., 2015).

In this study, we hypothesize that by alleviating survival bottlenecks across multiple life stages—via mimicry of emergent traits
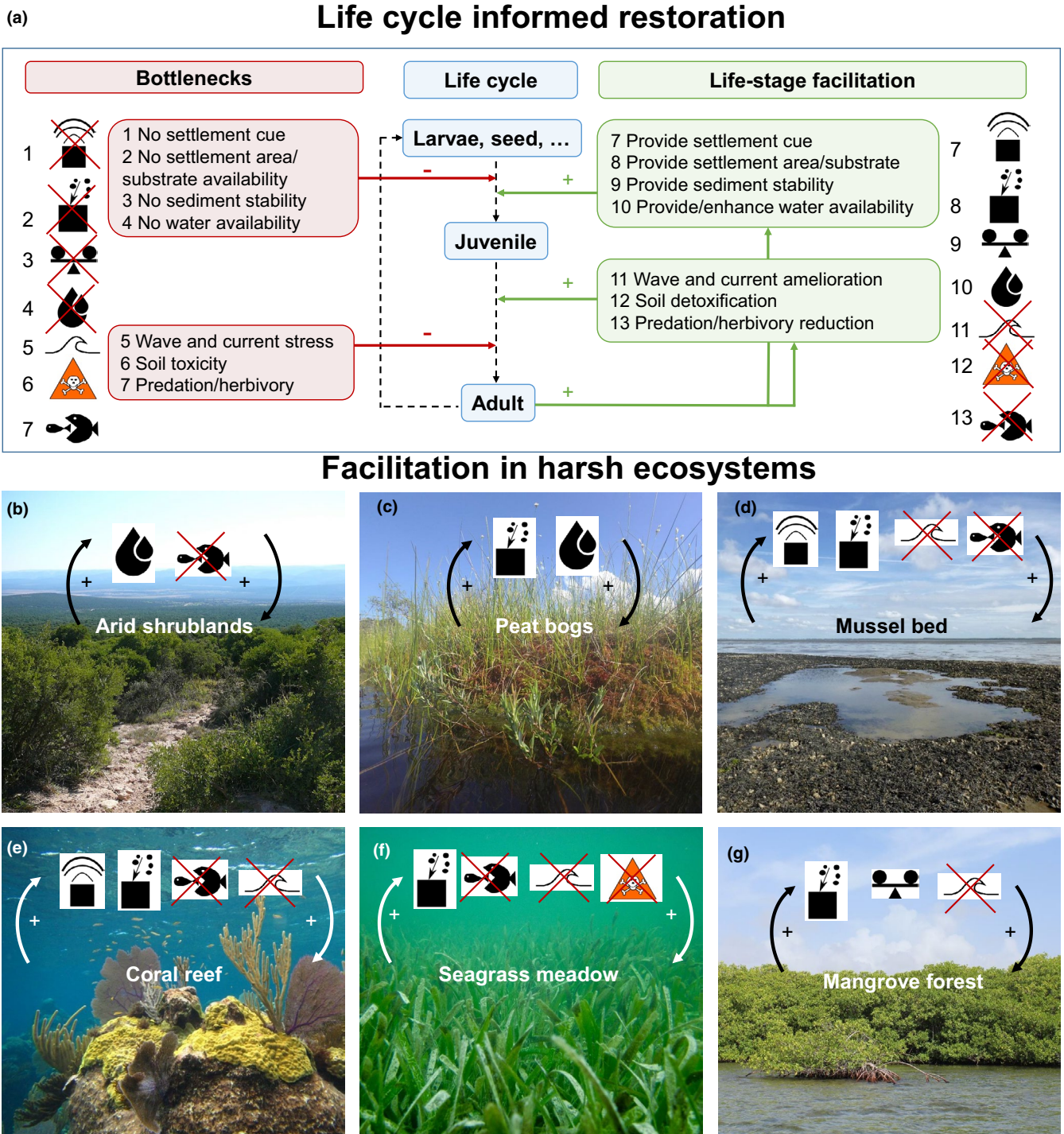
FIGURE 1 Life cycle informed restoration. Habitat-modifying species often face multiple bottlenecks as they mature from seeds/propagules to juveniles to adults (assuming there are sufficient seeds/broodstock), life stage-specific bottlenecks are often ameliorated by adult conspecifics (a, numbers show the definition of each symbol representing a bottleneck on the left and mechanism of facilitation on the right). Note: the list of limiting factors and faciliation mechanisms is not exhaustive. Arid shrublands (b), peat bogs (c), mussel beds (d), coral reefs (e), seagrass meadows (f) and mangrove forests (g) are all examples of habitats where adults facilitate the recruitment, survival and growth of conspecifics by alleivating multiple, ecosystem-specific, bottlenecks. To rejuvenate degraded ecosystems or create new habitats, life cycle informed restoration approaches thus mimick adult habitats by strategically facilitating habitat-modifying species across multiple life stages to reduce bottlenecks to their establishment. Pictures: (b) Han Ollf, (c and d) R.J.M.T., (e) Jimmy de Fouw (f and g) L.P.M.L.

that generate facilitation among conspecifics in naturally established larger clones or patches—restoration practitioners can stimulate ecosystem recovery. Such a 'life cycle informed restoration'

approach would eliminate the need for transplanting adults to regenerate facilitation (Figure 1), and thus any dependence on often limiting donor source populations. To investigate our hypothesis and

FIGURE 2 Field sites and experimental setup. Location of the field site near Ameland in the Netherlands (a) and near Cedar Key in Florida US (b). Overview of the experimental units in the Netherlands (c) and Florida (d) with a closeup of a cage, fully covered in fine mesh to exclude predators (e), and a cage control (one side open, the rest covered in fine mesh) with a structure with rope inside in the Netherlands (f). The green mesh is the gabion that supports the fine mesh (f). Schematic of the experimental treatments, and details regarding the experiment duration and plot dimensions for each of the three experiments (g). (1) Do engineered establishment structures (ESS) facilitate reef development? (2) Are species-specific settlement substrates required for reef development? (3) What is the importance of post-settlement predation in controlling reef development and can engineered ESS reduce this stress? Gabions (square lattice panels) were used for structural support for the ropes and mesh. Pictures: R.J.M.T. (c, d and f) and G.S.F. (e). Map data made with Natural Earth

test our approach as a general proof of concept—to show whether we can initiate reef formation by facilitating settlement by providing suitable substrate and subsequently enhance post-settlement survival by reducing predation, we carried out a trans-Atlantic experiment in which we aim to facilitate reef formation by aggregating epibenthic bivalves in intertidal soft-sediment ecosystems. As model systems, we focused on reefs naturally formed by oysters or mussels in Florida and the Netherlands. Specifically, in Florida, we aimed to facilitate the primary reef-building native Eastern oyster *Crassostrea virginica*, and potentially also the native hooked mussel *Ischadium recurvum* that is often found growing on oyster beds. In the Netherlands, we targeted the primary reef-building native blue mussel *Mytilus edulis*. In addition, our approach could also facilitate native European flat oysters *Ostrea edulis*, or the non-native invasive Pacific oyster *Crassostrea gigas* that was introduced by fishermen when the native oyster declined (see study system description; Fey et al., 2010). World-wide, bivalve reefs have deteriorated in extent and quality over the last centuries (Lotze et al., 2006). Restoration is challenging because of multiple bottlenecks that occur throughout these organism's life cycles as highlighted below.

Although each bivalve species needs to overcome multiple bottlenecks to form reefs, the requirements of these species differ due to their own distinct life-history and functional traits. In many bivalve species, adults release eggs and sperm into the water column where fertilization occurs and embryos develop into free-swimming larvae that (except e.g. *O. edulis*, where fertilization occurs internally in the females), after several weeks, settle as spat on the seafloor. Oyster spat preferentially settle on hard, stable substrates on which they cement themselves in place, such as oyster shells or concrete (Bersoza Hernández et al., 2018; Christianen et al., 2018; Preston et al., 2020; Rodriguez-Perez et al., 2019). After this, they are sessile filter feeders and highly dependent on the quality of the local environment for their survival, growth and reproduction (Burreson & Ragone, 1996; Peyre et al., 2016; Pogoda et al., 2019). Mussel spat, in constrast, typically settle in/on fibrous substrates for refuge, such as byssal threads of adult conspecifics or natural fiber-based substrates (Carl et al., 2012; van der Heide et al., 2014; Walters & Wethey, 1996). They remain mobile to some extent and gradually move outward from the small crevices they settle in as they grow larger in later life stages (Bayne, 1964). After settlement, mussel and oyster recruits are often at risk of being dislodged by currents and waves and can be heavily predated, severely hampering juvenile survival of both species (Brown et al., 2008; de Paoli et al., 2015; van der Heide et al., 2014). On established reefs, adult conspecifics provide attachment substrate, ameliorate physcial stress and provide

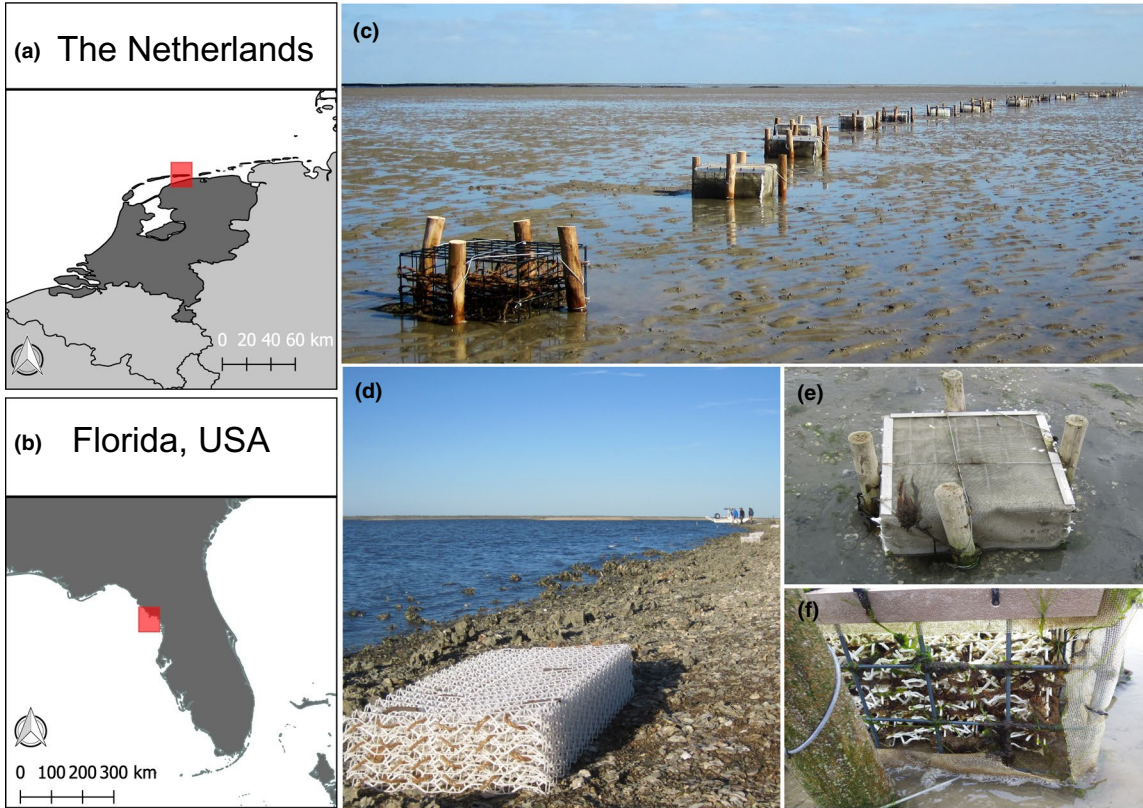shelter from predation by forming spatially complex habitats (Carl et al., 2012; Donadi et al., 2013).

To succesfully apply life cycle informed restoration for our model systems, we propose that the different life stages and species-specific requirements need to be considered and integrated to create self-sustaining ecosystems (Figure 1). As a general proof of concept, we deployed biodegradable engineered establishment structures to temporarily simulate emergent traits found in established bivalve reefs (Figure 2d,f). Specifically, we aim to use the structures to both facilitate settlement by providing a suitable substrate, and thereafter enhance post-settlement survival by reducing predation to levels that allow reef formation (e.g. by birds and crabs). Eventually, a reef should develop such that it sustains its own suitable settlement and growing conditions, at which point the structure itself naturally biodegrades. To investigate our concept and its generality, we implemented various complementary field experiments (Figure 2). First, we determined whether the structures can initiate reef formation in two contrasting ecosystems across the Atlantic (Trans-Atlantic reef formation experiment). Second, we tested if we differentially can stimulate bivalve recruitment depending on their requirements by incorporating a second, distinct settlement substrate—fibrous coir rope—into the structure (which itself provides hard, stable substrate; Settlement substrate experiment). Last, we determined whether the structures reduce predation by excluding predators (Predation experiment). We demonstrate that restoration yields can be greatly enhanced through the amelioration of multiple bottlenecks with temporary structures throughout an organism's life.
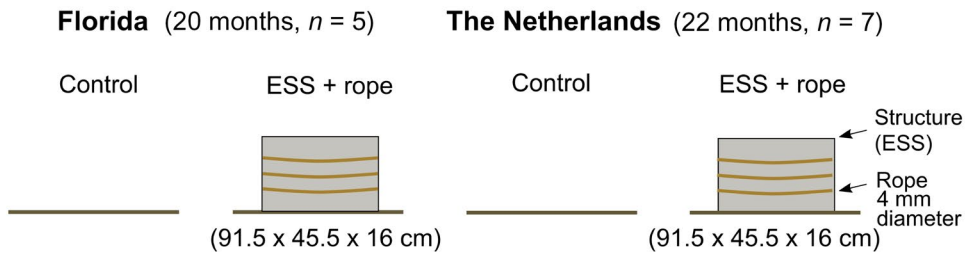
2 | MATERIALS AND METHODS

2.1 | Study sites

To provide proof of concept for life cycle informed restoration, we carried out experiments with biodegradable engineered establishment structures on the intertidal flats of the Gulf of Mexico (Cedar Key, Florida, US, 29°9′48.03″N, 82°59′46.59″W) and the Wadden Sea (Ameland, the Netherlands, 53°25′9.57″N, 5°40′9.20″E) between 2016 and 2018 (Figure 2).

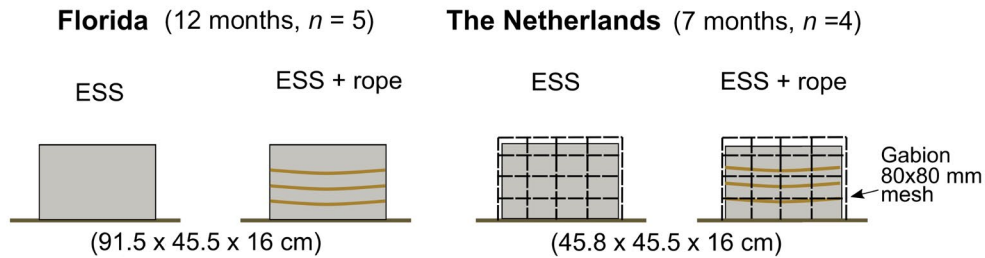In Florida, we targeted the native Eastern oyster *C. virginica*, which is the primary reef-building species, and potentially also the native hooked mussel *I. recurvum* that is often found growing on native oyster beds or other hard structures. In the Netherlands, we targeted the reef-building native blue mussel *M. edulis*. In addition, the structures could also facilitate the native European flat

(a) The Netherlands

(b) Florida, USA

(g) ① **Trans-Atlantic reef formation experiment**

Florida (20 months, $n = 5$)   **The Netherlands** (22 months, $n = 7$)

Control   ESS + rope   Control   ESS + rope

Structure (ESS)
Rope 4 mm diameter

(91.5 x 45.5 x 16 cm)   (91.5 x 45.5 x 16 cm)

② **Settlement preference experiment**

Florida (12 months, $n = 5$)   **The Netherlands** (7 months, $n = 4$)

ESS   ESS + rope   ESS   ESS + rope

Gabion 80x80 mm mesh

(91.5 x 45.5 x 16 cm)   (45.8 x 45.5 x 16 cm)

③ **Predation experiment**

The Netherlands (7 months, $n = 4$)

Control cage + rope   Control cage + ESS + rope   Cage + rope   Cage + ESS + rope

Cage 1x1 mm mesh

(45.8 x 45.5 x 16 cm)
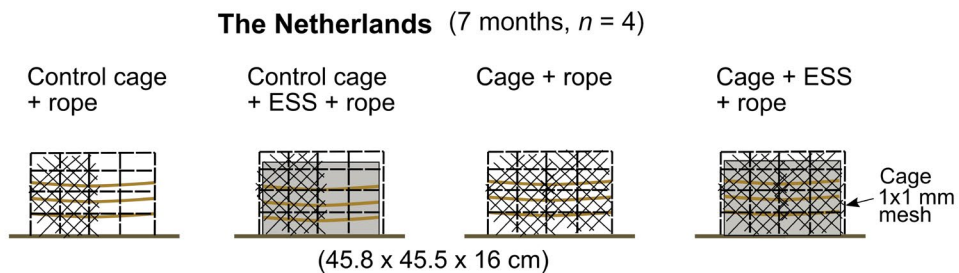
oyster *O. edulis*, or the non-native pacific oyster *C. gigas* that was introduced in 1983. Fishermen actively introduced the non-native *C. gigas* as an alternative to the native *O. edulis* when this species became virtually extinct due to a combination of disease and a very cold winter in 1960s (Fey et al., 2010). As a consequence, most reefs in the Netherlands now consist of mixed beds of native *M. edulis* and non-native *C. gigas*, assemblages that are, on rare occasions complemented by a native *O. edulis* individual.

Larvae of *C. virginica*, *I. recurvum*, *M. edulis* and *C. gigas* were generally abundant in the water column of their respective ecosystems and could potentially settle as spat in our experiment. Larval densities of the native *O. edulis* were virtually absent as this species is functionally extinct in the Wadden Sea (e.g. De Vooys, 1999; Johnson et al., 2019). Course shell hash sediment typified the site in Florida, with small clumps of the native Eastern oyster *C. virginica* that were found scattered in a very low density. Bare, sandy sediment characterized the site in the Netherlands. Here, a small intertidal mixed mussel–oyster bed consisting of native *M. edulis* and non-native *C. gigas*, respectively, was located 300 m from the experiment.

2.2 | Experimental setups

2.2.1 | Trans-Atlantic reef formation experiment

To investigate whether our temporary structures can facilitate reef natural establishment and survival of reef-forming bivalves (native *C. virginica* or native *I. recurvum* in Florida, and native *M. edulis*, native *O.* edulis or non-native *C. gigas* in the Netherlands), we carried out a reef structure experiment (the trans-Atlantic experiment) in Florida US and the Netherlands (experiment 1 in Figure 2g). At each site, we constructed the experiment as a randomized block design with control (bare flat) and structure addition as the two treatments. Specifically, we constructed five replicate blocks in Florida in April 2017 and seven replicates in the Netherlands in April 2016. Following a 20- and 22-month period, we terminated the experiments in Florida and the Netherlands in November 2018 and February 2018 respectively.

Each engineered structure consisted of eight stacked Biodegradable Ecosystem Engineering Elements (BESE) sheets resulting in a 16 cm high module (sheet: 91.5 × 45.5 × 2 cm [L × W × H]; Figure 2d; BESE Ecosystem Restoration Products, Culemborg, The Netherlands). A BESE sheet is composed of biodegradable potato-waste-derived Solanyl C1104 M (Rodenburg Biopolymers, Oosterhout, the Netherlands, BESE Ecosystem Restoration Products). Through each module, we braided 70 m of fibrous coir rope (∅: 0.5–1 cm), which we added to serve as a potential settlement substrate. The rope mimicked byssus threads of byssus-forming bivalves (van der Heide et al., 2014), such as blue mussels in the Netherland and hooked mussels in Florida. These structures were intended to (a) facilitate establishment by providing a hard substrate in a soft-sediment ecosystem, as well as fibrous substrate that may act as a settlement cue for mussels, and (b) reduce predation

pressure post-settlement because of its complex matrix, physically obstructing larger predators (>3 cm). We placed the resulting establishment units in the intertidal. In Florida, we secured each unit using four 1.5-m long L-shaped rebar anchors. In the Netherlands, we fixed the units between four 1.4-m long wooden poles (∅: 6–8 cm) that were hammered 1 m into the ground and were cross-connected over the units with 3-mm PVC-coated steel wire. We placed the plots at least 3 m spaced apart at 86% and 75% inundation frequency for Florida (1.2 ± 0.0007 ft. North American Vertical Datum of 1988; NAVD88) and the Netherlands (−0.35 ± 0.002 m Normaal Amsterdams Peil; NAP) respectively (Fivash, Stüben, et al., 2021).

At the termination of the experiment, we took one subsample of each plot using a custom-made soil sampler (diameter 15 cm, length: 48 cm). To clean-slice through structures, it had small teeth (height: 25 mm). Controls were checked visually but supported no mussel or oysters' individuals. We placed every sample in a plastic bag, after which we separated bivalves from the structure in a laboratory. Next, as a first general metric of reef formation, we determined oysters or mussels (shell + soft tissue) dry mass. Oysters were dried at 70°C to constant weight (after at least 74 hr). Mussel biomass was calculated based on a mussel length to biomass calibration. Furthermore, to examine whether distinct age cohorts recruited during the experiment, we determined length frequencies (Beukema & Dekker, 2007). Oyster lengths were measured from samples gathered in November 2018 (*n* = 100), while mussel lengths were measured from samples obtained in February 2018 (*n* = 122).

2.2.2 | Settlement substrate experiment

To unravel if species-specific (oyster–mussel) settlement preferences are required for reef development (experiment 2 in Figure 2g), we performed a second experiment (Settlement substrate experiment) in which we manipulated the presence/absence of the fibrous coir rope within the structures in both Florida and the Netherlands. In Florida, this experiment was carried out by adding a structure without rope to each of the five replicate blocks of the trans-Atlantic experiment (see Section 2.2.1). In the Netherlands, we constructed an entirely new experiment in a four-replicate randomized block design at the same site and elevation as the trans-Atlantic experiment, which ran from April 2016 to October 2016. For this experiment, we used halved establishment modules (i.e. 45.8 × 45.5 × 16 cm [L × W × H]) with and without 35 m of coir rope. We fixed these modules with cable ties to plastic-coated gabions to provide structural support (dimensions: 52.5 × 52.5 × 22.5 cm [L × W × H] with a 7.5 cm mesh size, including a lid on top). We secured the gabions to 1.4-m long wooden poles (∅: 6–8 cm) with 3 mm thick coated steel wire in the same fashion as the first experiment.

We sampled the plots in Florida following the methods described above. In the Netherlands, each entire plot with its respective gabion, was placed in a separate plastic bag. Next, we transported the samples to the laboratory and stored at −20°C until further analyses. For analysis, each plot was thawed, and carefully deconstructed,

while all mussels were collected. All samples (shell and soft tissue) were oven dried at 70°C to constant weight and weighed. We measured oyster lengths from samples gathered in Florida in April 2018 ($n = 74$), while we measured mussel lengths from samples obtained in the Netherlands in October 2016 ($n = 1,960$). We counted oyster individuals, while for mussels, we calculated the individuals based on a mussel length to biomass calibration.

2.2.3 | Predation experiment

Finally, to examine the importance of post-settlement predation in controlling reef development and whether structures can reduce this stress (experiment 3 in Figure 2g), we performed a third experiment (Predation experiment). In this experiment, we factorially manipulated predation pressure and substrate type in the Netherlands. This experiment ran from April 2016 to October 2016. In the study area, we constructed a new experiment in a four-replicate randomized block design at the same site and elevation as the trans-Atlantic experiment using halved establishment modules (see Section 2.2.1). The treatments consisted of (1) control cage with rope, (2) control cage with structure with rope, (3) exclosure cage with rope and (4) exclosure cage with structure with rope.

We constructed the structures in the same fashion as the settlement preference experiment in the Netherlands (see Section 2.2.2). For the rope treatment, we braided 35 m of coir rope over three

layers inside a gabion. Both gabion with ropes and the structure with rope were then covered with mesh. We fully covered exclosure cages in mesh to exclude predators (width of mesh: 1,000 μm; wire thickness: 515 μm, nylon, Kabel Zaandam, The Netherlands, Figure 2e), while allowing bivalve larvae to enter (Widdows, 1991). Control cages were partially covered in mesh, but open on one side to allow predators to enter and to also influence hydrodynamics and food delivery to mussels a similar extent as the exclosure cages (Figure 3f). The seams of the mesh used to construct the open and fully covered exclosures were glued with Bison poly max express. In the field, we placed the open side of control cages most sheltered from waves (northeastern direction). We secured the structures following the method described in Section 2.2.1 for the Netherlands. During the experiment, we monitored the outside of all cages for fouling every month from spring to autumn, but this turned out to be minimal. We did not observe signs of predators breaching the cages. We obtained the mussel biomass data using the same method as described for the settlement substrate experiment for the Netherlands (see Section 2.2.2).

2.3 | Statistical analyses

Due to non-normality, bivalve biomass data from the trans-Atlantic experiment were non-parametrically analysed using Wilcoxon tests for Florida and the Netherlands. Student's *t* tests were used
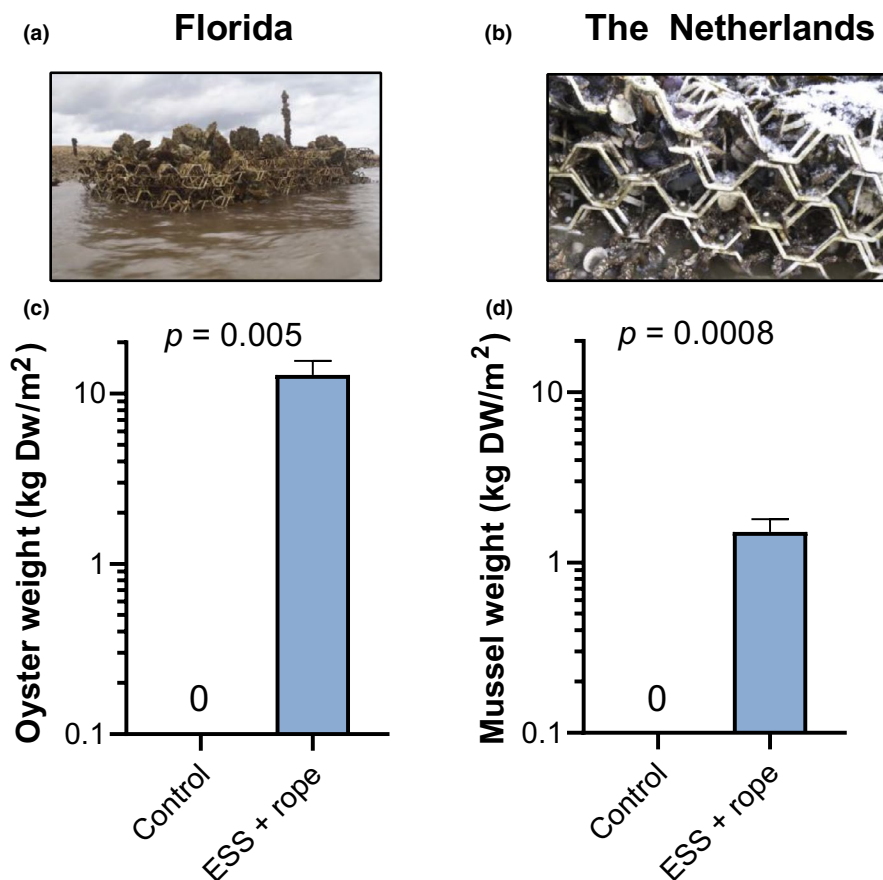

FIGURE 3 Effects of structures on oyster and mussel establishment. Structures at the end of the experiment in Florida (a) and in the Netherlands (b). Effects of establishment conditions (engineered establishment structure [EES] with rope or bare sediment) on oyster (c) and mussel (d) biomass (kg DW/m^2 ±*SEs* for $n = 5$ and $n = 7$ replicate plots in Florida and the Netherlands respectively). Dry biomass is shell + tissue weight after two growing seasons. Note: *y*-axes are shown on log scales. Pictures: M.T. and R.J.M.T

to analyse the magnitude and significance of differences in bivalve biomass in the settlement preference experiment for each country. These data were log-transformed. A linear mixed-effects model (LMER) with Gaussian error distribution was used to assess main and interactive effects of structure and predator exclusion treatment (i.e. full cage or cage control) on mussel biomass in the third experiment (data were log-transformed; Kuznetsova et al., 2019). Block number, treated as random factor in the analyses of the third experiment, proved not significant, and was thus removed from the analyses. All analyses were performed in R studio (version 3.6) statistical and programming environment (R Core Team, 2020). All results are shown with their standard error of the arithmetic mean ($\pm SEM$).

3 | RESULTS

3.1 | Trans-Atlantic reef formation experiment

The formation of the reefs was stimulated by the structures on intertidal flats of both Florida and the Netherlands, while no reef formation took place in the controls without structures (Figure 3). We found no mussels on the structures in Florida, and no native or non-native oysters in the Netherlands. Specifically, formed reefs consisted of 12.9 ± 3 kg DW/m^2 oysters or 1.5 ± 0.3 kg DW mussels/m^2 on the structure in Florida and the Netherlands, respectively, after 20 and 22 months of growth (Florida: $Z = 2.79$, $p = 0.005$, the Netherlands: $Z = 3.34$, $p = 0.0008$). Oyster biomass on these adult habitat mimics in Florida was almost an order of magnitude higher compared to mussel biomass in the Netherlands. Additionally, the length of both the oysters and the mussels varied in time (Figure S2). Histograms of mussel biomass show growth from April 2018 to November 2018 for oysters and from October 2016 to February 2018 for mussels.

3.2 | Settlement substrate experiment

The addition of a natural substrate that mimics mussel byssal threads (fibrous rope) increased mussel biomass and the number of individuals relative to the structure alone in the Netherlands, while oyster biomass and number of individuals were similar in the two treatments in Florida (Figure 4). In the Netherlands, we found no non-native and native oysters, and in Florida no mussels. Specifically in Florida, oyster biomass in the structure without rope was 12.4 ± 2.7 kg DW oyster/m^2, which was higher but not significantly different from structures with rope (6.6 ± 1.1 kg DW oysters/m^2, $t = 1.9$, $p = 0.09$). By contrast, mussel biomass was 12 times higher (0.9 ± 0.3 kg DW mussels/m^2) in the structures with rope relative to structures without rope in the Netherlands (0.08 ± 0.007 kg DW mussels/m^2, $t = -8.18$, $p = 0.0002$). The number of oyster individuals also did not differ between treatments ($2,900 \pm 840$ and $1,470 \pm 364$ m^{-2} for structure and structure with rope, respectively, $t = 1.8$, $p = 0.07$), while the number of mussel individuals was 12 times higher in the structure with rope compared to the structure alone ($4,600 \pm 1,500$ and 380 ± 40 m^{-2}, $t = -8.18$, $p = 0.0002$).

3.3 | Predation experiment

Excluding predators stimulated mussel settlement and growth, while establishment in open control cages benefited most from the combination of the structure with rope (Figure 5). The exclusion of predators did not stimulate native or non-native oyster establishment. In closed cages, mussel biomass did not differ between rope (10.4 ± 2.7 kg DW/m^2) and structure with rope treatments (7.8 ± 1.8 kg DW/m^2). In contrast, in control cages accessible to predators, the structure with rope that provides some predator protection yielded seven times more mussel biomass (0.7 ± 0.3 kg DW/m^2) than the rope only in the control cage treatment (0.1 ± 0.03 kg DW/m^2; Figure 5).

4 | DISCUSSION

Current restoration approaches typically focus on overcoming a single bottleneck obstructing ecosystem recovery (Bayraktarov et al., 2016; Renzi et al., 2019, see Appendix S1 in Supprting Information). Our results provide proof of concept that through life cycle informed restoration, large restoration gains and reduced reliance on donor populations can be achieved in areas that are substrate limited, and where recruitment limitation is not an issue. Specifically, our field experiments demonstrate that this technique can initiate mussel and oyster reef formation, in the Netherlands and Florida respectively. We engineered species-specific settlement substrates, and subsequently facilitated post-settlement survival, using materials that are biodegrade. Therefore, we argue that a life cycle informed restoration approach using materials that temporarily mimic emergent traits of adult populations, and that most likely do not leave behind a legacy of waste, may offer a viable and sustainable approach for large-scale restoration of bivalve reefs globally. Moreover, this approach may also be suitable to increase restoration success of other important ecosystems dominated by habitat modifiers that face multiple life stage-dependent bottleneck when establishing.

4.1 | Engineering settlement substrate and post-settlement survival for reef formation

Our experiments clearly show that the establishment structures, engineered to mimic emergent traits, facilitate reef formation. Plots with the structure matured into reefs, while bare flats remained bare throughout the experimental period in both Florida and the Netherlands (Figure 3; Appendix S2). The addition of coir rope to the structures stimulated blue mussel establishment, because this species prefers to settle in fibrous and complex, rather than smooth,
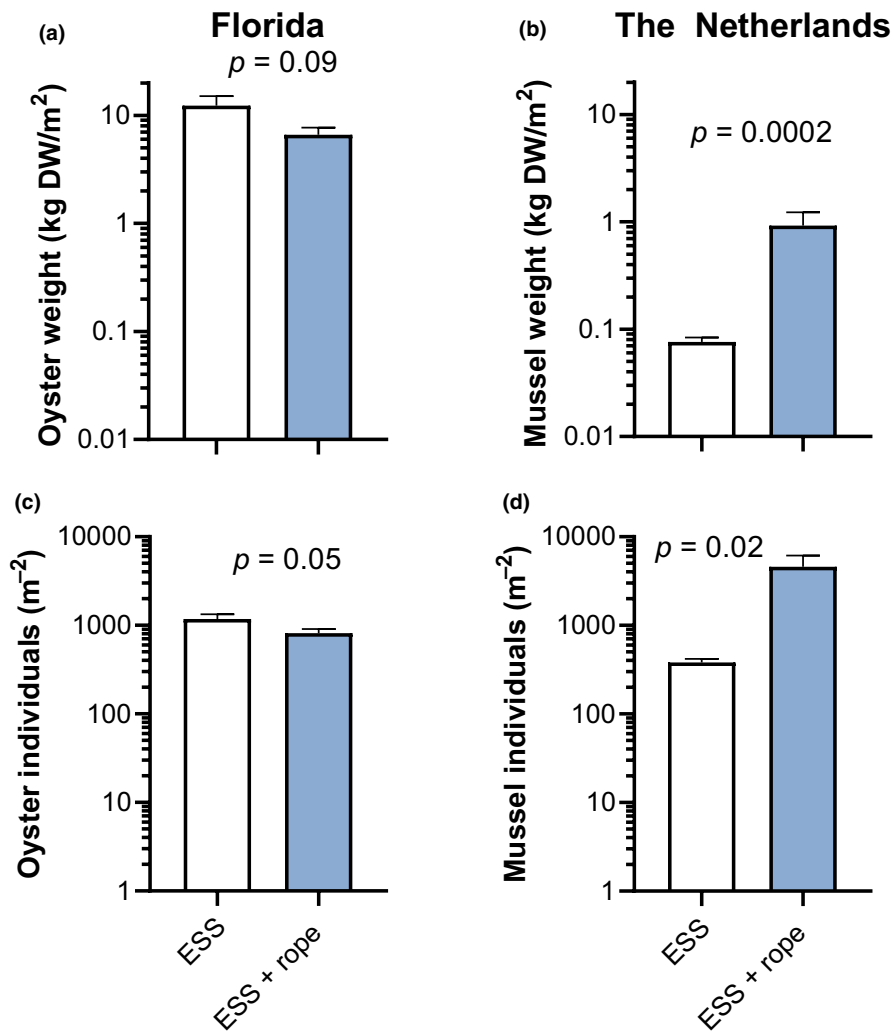
(a) Florida
p = 0.09

(b) The Netherlands
p = 0.0002

FIGURE 4 Effect of substrate on oyster and mussel reef establishment. Effect of engineered establishment substrates (engineered establishment structure [EES] and structure with rope) on oyster (a) and mussel weight (g DW/ m^2 ±SEs, n = 5 and n = 4 replicate plots in Florida and the Netherlands respectively, dry biomass is shell + tissue weight) (b), and oyster (c) and mussel (d) individuals m^{-2} after one season for Florida and the Netherlands respectively. Note: *y*-axes are shown on log scales

(c)
p = 0.05

(d)
p = 0.02

substrates (Carl et al., 2012; Dobretsov & Wahl, 2001). The combination of hard and fibrous substrate most closely resembles established mussel reefs formed by hard mussel shells intertwined with fibrous byssal threads. In addition to blue mussels, this settlement preference is likely to be important for other species of mussels that are known to settle on fibrous substrates, such as the Northern horse mussel, Mediterranean mussel and the Asian green mussel (Karayücel et al., 2002; Sanderson et al., 2008; Ramírez & Martinez, 1999). Importantly, in these conditions, post-settlement mussel recruits remain mobile, and can migrate into interstitial spaces to avoid predation and migrate out of them at larger sizes (Carl et al., 2012). Although the non-native *C. gigas* and native *O. edulis* could have established on the structures in the Netherlands, we found no non-native and native oysters. Furthermore, oysters did not benefit from fibrous rope addition in Florida and the Netherlands, most likely because oyster spat require hard and stable substrate for attachment to cement unto (Pogoda et al., 2019). Post-settlement, oysters are sessile for the rest of their lives. Therefore, a stable surface that prevents self-burial or burial by moving sediment/substrate, such as that provided by the structures, is vital to their success. These findings suggest that by incorporating different substrates for species-specific settlement that are inspired by traits of the adult

organism, it is possible to stimulate different bivalve species with contrasting settlement strategies. This might be a useful tool for selecting substrates suitable for native bivalves, but not for invasive and non-native ones (Colsoul et al., 2020; Troost, 2010). We further anticipate that incorporating species-specific chemical cues into restoration designs could both benefit bivalves and other habitat modifiers like stony corals and tubeworms, as previous work demonstrated that larvae of these species positively respond to specific chemicals as cues for settlement (Callaway, 2003; Rodriguez-Perez et al., 2019; Tebben et al., 2015).

Results from the predation experiment clearly indicate that by excluding predators, recruitment of mussels to ropes was an order of magnitude higher compared to control cages with ropes accessible to predators, while it did not facilitate native and non-native oyster establishment. However, in control cages, the presence of the structure did reduce predation, as evidenced by recruitment success on structures with rope being seven times higher than treatments with only rope. Hence, our results support earlier work demonstrating that successful mussel recruitment requires a combination of suitable attachment substrate and low predation pressure—conditions typically created within established mussel beds (van der Heide et al., 2014). Predation is also a common pressure limiting restoration
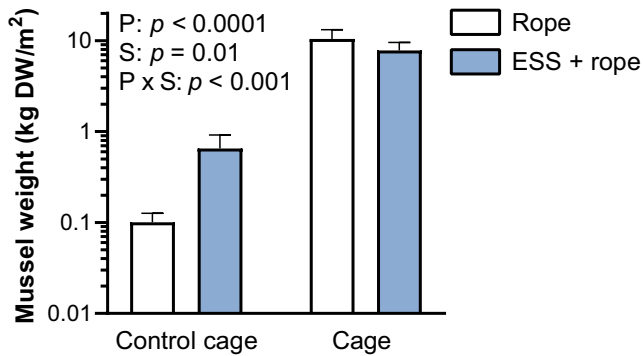
FIGURE 5 Predation effects on mussel reef development. The effect of rope alone (grey bars) and engineered establishment structures (EES) woven with rope (blue bars) in control cages that were accessible to predators—cage covered with fine mesh that was open on one side—or cages that excluded predators—completely covered with fine mesh (kg DW/m^2 ±SEs, $n = 4$, dry biomass is shell + tissue weight) after one season in the Netherlands (2016). The main (P, predation, $\chi^2 = 142.4$; S, substrate type, $\chi^2 = 6.1$) and interactive (P × S, $\chi^2 = 11.8$) effects are shown with p values in the inset. Note: y-axis is shown a log scale

success of oyster reefs (Kimbro et al., 2017; Newell et al., 2007). Oysters are often most susceptible to predation by crabs, flatworms and predatory gastropods in the first few month's post-settlement (Kimbro et al., 2017; Newell et al., 2007). In our experiment, the oysters were present in high densities on both on the inside as well as on the outside of the engineered establishment substrates (Figure 3a). Combined with the observations that we found no boring sponges that are detrimental to their survival and a very low density of predatory sea snails; this suggests that predation was of limited importance at our study site during the timeframe of our experiments.

Although our results clearly highlight that natural bivalve recruitment can be greatly enhanced by structures, it is important to note that our experiments were performed in two ecosystems with ample supply of larvae. Larval densities in the water column are, at least periodically, very high. Obviously, this may not always be the case in other systems. Therefore, placement of structures that mimic emergent traits to ameliorate bottlenecks must either be where settlement of juveniles is possible or otherwise, additional interventions should be carried out to overcome this very first bottleneck. For instance, the structures could be 'primed' with spat from native species in hatchery facilities (Theuerkauf et al., 2015), after which an inoculated module can be transferred to the restoration site. Beyond bivalves, using seed/propagules in restoration reduces the need for adult transplants that are often used in restoration (Silliman et al., 2015; van Katwijk et al., 2016). Structures can be designed to first trap and protect plant seeds, as lack of seed retention is often limiting establishment on bare intertidal flats or in the riparian zone of fast flowing rivers (Fivash, Temmink, et al., 2021; Wang et al., 2019). Once seeds are trapped, the structures should help to overcome subsequent bottlenecks, by mimicking emergent traits found in patches of adult plants that facilitate juveniles. For instance, in dynamic ecosystems, such as salt marshes,

seagrass meadows or mangroves, the growth and survival of juvenile plants are severely hampered by waves or currents. Seedlings may thus benefit from wave and current amelioration by adult plants or structures that mimic this facilitation (Chang et al., 2008; Huxham et al., 2010; Maxwell et al., 2016). Furthermore, in both fresh and saltwater wetlands, juvenile plants may suffer from unfavourable soil conditions due to a lack of oxygen (Lamers et al., 2013). Oxygenation of the root zone, typically performed by adults, may ameliorate such stress. Finally, in drylands, shrubs may benefit from increased water infiltration, shading or hydraulic lift created by conspecifics (Tirado et al., 2015), mechanisms that could also be simulated by artificial structures.

4.2 | Life cycle informed restoration

In this paper, we provide proof of concept of the idea that facilitation of multiple life stages by mimicking key emergent traits, can initiate reef formation using biodegradable structures (Appendix S3). To illustrate the potential scalability of life cycle-based restoration as a general approach, we calculated construction costs for four scenarios for bivalve ecosystems in which we upscale our specific experimental technique as an example. The costs to restore intertidal bivalve ecosystems based on our approach range from 86,000 to 318,000 US$/ha (Appendix S4). The creation of a low-density oyster reef with a 10% initial cover (Folmer et al., 2014, see Appendix S4 for details regarding initial cover %) is cheapest at 86,000 US$/ha. Costs are highest (318,000 US$/ha) when using a high initial cover (30%, Liu et al., 2014) with structures that include coir rope to enhance mussel settlement. Both estimates, however, are on the low end compared to the median (189,000 US$) and mean (860,000 US$) reported costs to restore oyster reefs (Bayraktarov et al., 2016).

While our experimental results show that the engineered establishment structures used here can enhance reef formation, the current design is of course a relatively crude simulation of real reef structures. This highlights a potential for optimization, including its spatial complexity, size, specifically targeting native over non-native species, and methods to secure the structures in the field. Beyond bivalves, further development of materials and designs that mimic emergent traits of other habitat modifiers shaping terrestrial, fresh and saltwater ecosystems is likely required. In such cases, 3D printing of biodegradable, but temporarily stable, structures may open many design possibilities, allowing the development of tailor-made structures to facilitate the specific needs of habitat modifiers in degrading ecosystems. Once a design is optimized, structures should be industrially produced, making large-scale outplacement of the structures feasible (Temmink et al., 2020). Before doing so, however, it is vital to understand the long-term behaviour and ecological fate of the biodegradable material as well as the effect of any large-scale structures on abiotic conditions.

Apart from understanding the basic behaviour of temporary structures in the environment, it is of course vital to understand

the most-crucial life stage-dependent bottlenecks related to self-facilitation to successfully implement life cycle informed restoration in other ecosystems dominated by habitat modifiers (Balke et al., 2011). Next, each bottleneck naturally mitigated by emergent traits should be carefully eliminated using trait mimics or other techniques, and most preferably should facilitate native over invasive species (Pogoda et al., 2019; Troost, 2010; Zu Ermgassen et al., 2020). Our work highlights that ecosystems can be initiated from early life stages (e.g. seed or propagules), and thus do not require adult transplants (Silliman et al., 2015; Temmink et al., 2020) or a natural window of opportunity (Balke et al., 2011). This is only true when restoration designs account for the multiple mechanisms of facilitation required to enable those early life stages to establish and grow to maturity. In many harsh ecosystems dominated by habitat modifiers, seeds and propagules often require stable substrates and some relief from physical, chemical and/or biotic stress. These systems include freshwater bogs, submerged aquatic vegetation beds, reed marshes, as well as coral reefs, seagrass beds, salt marshes and mangroves in marine systems. The use of renewable and biodegradable materials to temporarily perform those functions may offer an environmental-friendly, scalable and viable solution for future restoration relative to conventional restoration techniques (Balestri et al., 2019). In a broader perspective, the widespread degradation of ecosystems critically requires the need to conduct large-scale restoration. Approaches such as life cycle informed restoration, which deals with overcoming multiple bottlenecks, may be vital to achieving this grand societal challenge.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

R.J.M.T., C.A., G.S.F., K.D., W.L., T.J.B. and T.v.d.H. designed the experiments; All authors were involved in carrying out the field experiments; R.J.M.T. analysed the data; R.J.M.T., C.A. and T.v.d.H. wrote the first draft of the manuscript and all authors contributed to the subsequent drafts.

DATA AVAILABILITY STATEMENT

Data available via Archiving and Networked Services (DANS) EASY https://doi.org/10.17026/dans-xxt-muff (Temmink, Angelini, et al., 2021).

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SUPPORTING INFORMATION

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

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