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Review

Restoration ecology meets design-engineering: Mimicking emergent traits to restore feedback-driven ecosystems

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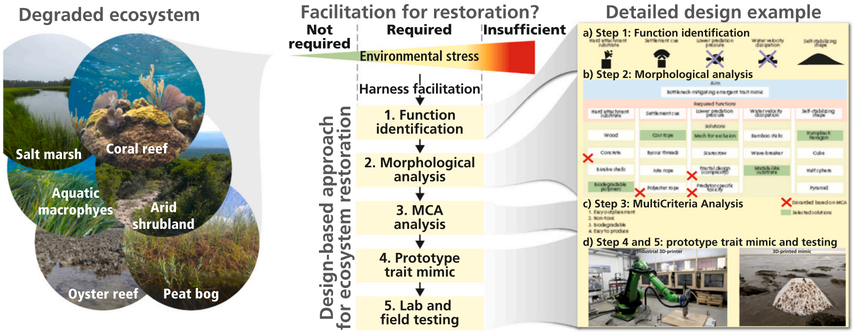
HIGHLIGHTS

- Positive feedback interactions play a key role in harsh environments.
- Harnessing positive feedbacks interactions can kickstart ecosystem restoration.
- Explicit trait-mimicry that generate feedbacks can further enhance restoration.
- Combining ecology and engineering approaches allow innovative restoration designs.
- We present a five-step design process for novel restoration approaches.

GRAPHICAL ABSTRACT



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ABSTRACT

Ecosystems shaped by habitat-modifying organisms such as reefs, vegetated coastal systems and peatlands, provide valuable ecosystem services, such as carbon storage and coastal protection. However, they are declining worldwide. Ecosystem restoration is a key tool for mitigating these losses but has proven failure-prone, because ecosystem stability often hinges on self-facilitation generated by emergent traits from habitat modifiers. Emergent traits are not expressed by the single individual, but emerge at the level of an aggregation: a minimum patch-size or density-threshold must be exceeded to generate self-facilitation. Self-facilitation has been successfully harnessed for restoration by clumping transplanted organisms, but requires large amounts of often-limiting and costly donor material. Recent advancements highlight that kickstarting self-facilitation by mimicking emergent traits can similarly increase restoration success. Here, we provide a framework for combining expertise from ecologists, engineers and industrial product designers to transition from trial-and-error to emergent trait design-based, cost-efficient approaches to support large-scale restoration.

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1. Introduction

Ecosystems generate ecosystem services to humanity, including supporting public health, biodiversity, water purification, coastal defense, and carbon sequestration (Costanza et al., 1997; De Groot et al., 2013). However, many of these services and the ecosystems that sustain them are degrading at a rapid pace worldwide due to land-use changes, pollution, eutrophication, and overexploitation (Millennium Ecosystem Assessment, 2005). Currently, 20–75 % of boreal and temperate forests, 40–60 % of tropical and temperate peatlands, 40 % of salt marshes, 35 % of mangroves, 30 % of seagrass, 85 % of oyster reefs, and 20 % of coral reefs worldwide are lost or degraded (Wilkinson, 2008; Gedan et al., 2009; Waycott et al., 2009; Beck et al., 2011; Ellis et al., 2013; Atwood et al., 2017; Leifeld and Menichetti, 2018; Fluet-Chouinard et al., 2023). Policy agreements at the national, regional, and global level set clear goals to halt ongoing degradation and restore lost ecosystems and their associated services (Higgs et al., 2014; Suding et al., 2015). The most prominent example is the UN Decade on Ecosystem Restoration 2021–2030, which aims to restore degraded ecosystems within the current decade (Waltham et al., 2020). Recent advancements in terrestrial ecosystems with low abiotic and biotic stress such as planting forests or seeding grasslands highlight that restoration can be successful at low costs (De Groot et al., 2013; Höhl et al., 2020). However, applying such approaches in ecosystems defined by high abiotic and biotic stress has led to many project failures and the cost to restore such stressful systems can be up to 10-fold higher per unit area (Silliman et al., 2015; Bayraktarov et al., 2016).

Physically harsh environments encompass challenging conditions often created by stochastic disturbances, such as dynamic sediments, powerful waves, variable moisture levels, acidity, low sediment oxygen, and nutrient scarcity. While such conditions are occasionally created for the restoration of unique biodiversity, these conditions pose difficulties for many plants and animals to thrive. Examples of ecosystems occurring in harsh environments include peat bogs, semi-arid drylands, coral reefs, salt marshes, seagrasses, mangroves, and bivalve reefs. In such harsh environments positive species interactions play a key role in establishment, stability, and survival (Stachowicz, 2001; Bruno et al., 2003; Renzi et al., 2019; Temmink et al., 2022b; Zobel et al., 2022) (Fig. 1). These ecosystems are often shaped by habitat-modifying organisms. Jones et al. (1994) coined the term 'ecosystem engineer' for such habitat modifying organisms and split them into two categories: allogenic and autogenic. Allogenic modifiers change their environment by transforming their environment (e.g., dam building by beavers), while autogenic modifiers change the environment via their own structure (e.

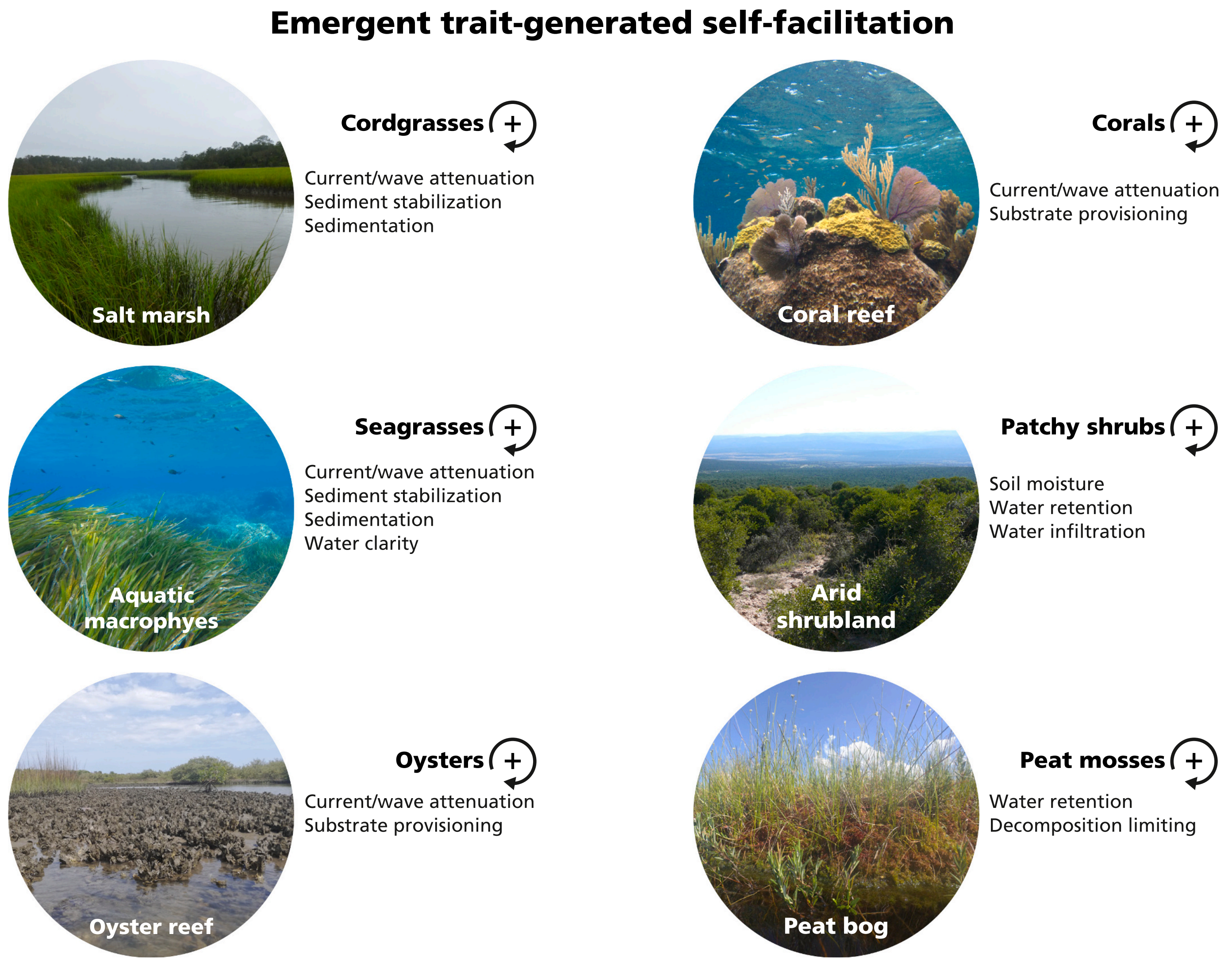


Fig. 1. Six examples of facilitation-driven systems in which habitat modifying organisms generate self-facilitation with emergent traits. The examples are not exhaustive.
(Photo credits: Coral reef: Jimmy de Fouw, Arid shrubland: Han Olff, Oyster reef, Aquatic macrophytes, salt marsh, peat bog: R.J.M. Temmink.)

g., sediment trapping between cordgrass leaves) (Jones et al., 1994). Because autogenic ecosystem engineers are typically spatially dominant and facilitate many associated species through their environmental modifications, they are often also considered foundation species (Dayton, 1972; Ellison, 2019).

Ecosystems shaped by autogenic habitat modifiers are commonly patchy in nature especially ones that are undergoing succession or recovery (Rietkerk and van de Koppel, 2008; Siteur et al., 2023). Within the patch, autogenic habitat-modifiers ameliorate the external prevailing conditions – i.e., conditions outside the patch – to facilitate their own growth (Van Breemen, 1995; Silliman et al., 2015; Maxwell et al., 2016). Such aggregations modify environmental conditions by emergent traits, which are traits not expressed by the single individual, but only emerge at the organizational level of the group (Smaldino, 2014; Temmink et al., 2020). This intraspecific facilitation (hereafter called self-facilitation) is typically positive-density and patch-size dependent, resulting in a positive feedback that increases in strength with increasing density and patch size. Under harsh conditions, that can result in a situation where growth and survival of the habitat modifier is only possible the when density and patch-sizes are sufficient (Bertness and Shumway, 1993; Bruno et al., 2003; Bouma et al., 2009b, 2013; Angelini and Silliman, 2012), while establishment thresholds hamper survival or establishment when patch sizes remain too small (Silliman et al., 2015; van Katwijk et al., 2016). This characteristic makes restoration of harsh ecosystems failure-prone and costly (De Groot et al., 2013; Silliman et al., 2015; Bayraktarov et al., 2016). However, recent inclusion of self-facilitation in restoration experiments highlighted the potential to greatly improve restoration success in ecosystems shaped by habitat-forming organisms (Silliman et al., 2015; van Katwijk et al., 2016; Fischman et al., 2019; Temmink et al., 2020).

Here, we first explore the mechanisms underlying self-facilitation generated by autogenic habitat modifiers in physically harsh conditions across a range of coastal, freshwater wetland and terrestrial ecosystems, and highlight how such self-facilitation can result in non-linear ecosystem responses and establishment thresholds. Second, we discuss how self-facilitation can be harnessed to overcome establishment thresholds to kickstart ecosystem restoration. Third, we synthesize recent advancements on how emergent traits that generate self-facilitation can be mimicked to enhance ecosystem restoration effectiveness. Finally, based on the previous steps, we present a novel stepwise framework based on ecology, industrial design and engineering techniques which allows for rapid design and cost-effective production of species-specific trait-mimicking structures that generate self-facilitation to kickstart restoration in habitat-modifier dominated ecosystems.

2. Self-facilitation, feedbacks and establishment thresholds

Autogenic habitat modifiers alter their physical environment, for instance by attenuating water or airflow, altering nutrient cycling, allelopathy, trapping sediment or accumulating organic matter (Dayton, 1972; Jones et al., 1994; Stachowicz, 2001; Chiapusio et al., 2013). Through these mechanisms, they commonly improve living conditions for themselves and their conspecifics (Van Breemen, 1995; Lamers et al., 2000; van de Koppel et al., 2005; Hirota et al., 2011; Scheffer et al., 2012; Maxwell et al., 2016). Such self-facilitation is generated via positive density-dependence (in some fields commonly defined as Allee-effect, Courchamp et al., 2008) yielding a positive feedback, in which the within-patch habitat quality improves compared to the unmodified baseline with increasing density and/or patch-size (Bertness and Callaway, 1994; Bruno et al., 2003; Bouma et al., 2009b; Licci et al., 2019). For example, sufficiently dense and large tropical forests generate a humid microclimate by stimulating local rainfall through evapotranspiration, thereby stabilizing tree-dominance and preventing encroachment of savanna's or grasslands that would inhabit a drier unmodified state (Hirota et al., 2011; De Frenne et al., 2021). In coastal ecosystems, dense and large patches of coastal vegetation such as cordgrasses, seagrasses and mangroves lower flow velocity and stimulate sedimentation, creating more benign growing conditions within the patch (Bouma et al., 2007, 2009b; Maxwell et al., 2016). Oyster, mussel and coral reefs dissipate wave energy and provide complexity for settlement of larvae, enhancing habitat quality (Dobretsov and Wahl, 2001; Costa et al., 2016). In freshwater wetlands, large patches of bog-forming peatmosses increase water retention during drought thus reducing stress (Robroek et al., 2009), while terrestrial forbs in arid drylands increase water holding capacity and water infiltration through its roots structure (Chirino et al., 2011). In otherwise hostile conditions, such self-facilitating feedback loops can be essential to a species' survival, growth and reproduction as they can alleviate physical, chemical or biotic stress, thereby extending the foundation species' own realized niche (Bruno et al., 2003; Crotty and Bertness, 2015).

Positive feedbacks generated by self-facilitation can make ecosystems respond in a nonlinear fashion to environmental change, because these mechanisms buffer external stress (i.e., prevailing conditions outside habitat modifier-formed patches) until a certain threshold is exceeded. Once a level of external stress is exceeded, the habitat modifiers can no longer maintain their favourable conditions, resulting in mass mortality of the habitat modifying species (van der Heide et al., 2020). Moreover, sufficiently strong feedbacks can lead to alternative stable states (i.e., bistability). Bistability is a condition where, depending on the initial state, both a habitat modifier-dominated and an alternative state are stable under the same environmental conditions (Scheffer et al., 2001). Such stable states can include a habitat-modifier dominated with an associated community that benefits from the modified conditions or a community without habitat modifiers exposed to unmodified conditions. A consequence of such dynamics is that natural recovery to the same state is challenging once the habitat modifier is unable to modify the abiotic environmental conditions to an extent that is within the tolerance limit range of a species to allow establishment (van der Heide et al., 2020) (Fig. 2). Under natural conditions, establishment can occur during a window of opportunity – a sufficiently long period of exceptionally favourable conditions with for example no disturbances during which isolated individuals or small clones can establish and grow large enough to initiate self-facilitating feedbacks (Balke et al., 2011, 2014). However, such windows are relatively rare and stochastic and natural re-establishment of the habitat-modifier dominated ecosystem may therefore take decades or longer (Balke et al., 2011, 2014). Consequently, bottlenecks for natural establishment can emerge in degraded ecosystems where habitat modifiers are unable to achieve patch sizes or densities high enough to generate the facilitative interactions required to create abiotic environmental conditions that lie within the tolerance limits of a species (Renzi et al., 2019). In such common cases, ecological restoration may require approaches designed to intentionally jumpstart self-facilitation normally generated by the habitat modifying organism to overcome establishment thresholds (Robroek et al., 2009; Silliman et al., 2015; Katwijk et al., 2016; Temmink et al., 2020).

In ecosystems shaped by autogenic habitat modifiers, self-facilitation is often generated when individual allogenic habitat-modifiers spatially organize in large patches and in dense aggregations. Such aggregations generate emergent traits (Smaldino, 2014; Temmink et al., 2020). For example, at an individual level it is possible to measure traits such as length, biomass and shell thickness of a mussel, but only after aggregation into a mussel bed traits emerge that lower predation pressure, ameliorate waves, and provide 3D-complexity for settlement of conspecifics (Costa et al., 2016; Colden et al., 2017). The positive effect of emergent traits is context dependent and are most important where habitat modification through self-facilitation is both required and sufficiently strong to allow the aggregation of organisms to inhabit conditions otherwise unsuitable for an individual or a small clone (Bruno et al., 2003; Silliman et al., 2015; van der Heide et al., 2021) (Fig. 2). For example, large aggregations of stiff cordgrass can reduce hydrodynamic disturbances (Bouma et al., 2009a; Licci et al., 2019), resulting in higher

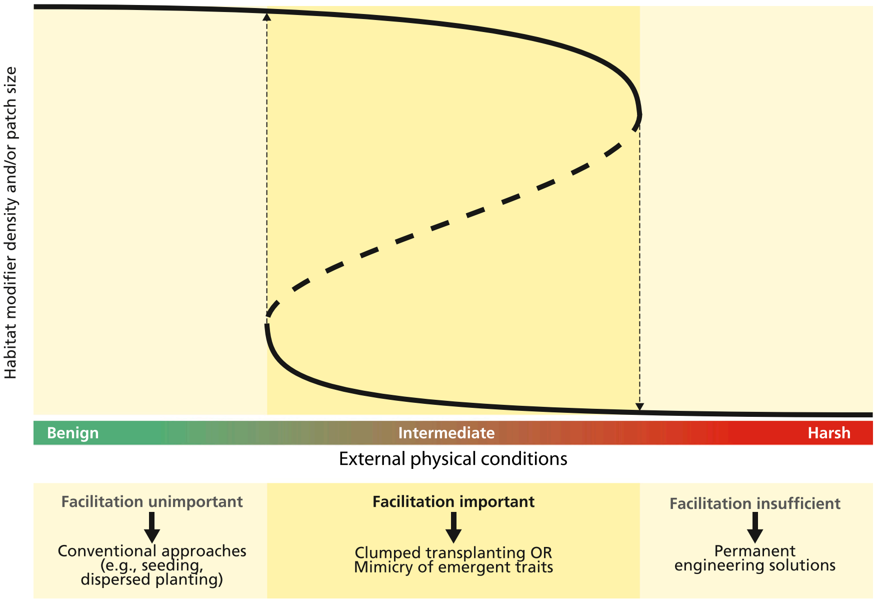


Fig. 2. Conceptual overview showing stable equilibria across a stress gradient of external physical conditions. Under intermediate harshness of external physical conditions, density and/or patch-size-dependent emergent traits generate self-facilitation, which make conditions within a patch less harsh to many organisms (relative to unmodified baseline conditions). This mechanism enhances growth and survival beyond a certain critical threshold for density and patch size, but makes both natural recovery and restoration very difficult below it. In such situations, restoration effectiveness can be improved by harnessing self-facilitation to enable a shift to a habitat modifier-dominated state. The concept is based on the alternative states theory and hysteresis (Scheffer et al., 2001).

survival and plant performance (Silliman et al., 2015). However, if external physical conditions are too harsh, habitat modification is insufficient to mitigate stress, yielding systems without the habitat modifier (van der Heide et al., 2021) (Fig. 2). When conditions are benign, self-facilitation to mitigate environmental stress is of minor importance, as the organism is generally able to survive irrespectively of its patch-size or density (Bruno et al., 2003; van der Heide et al., 2021).

3. Harnessing self-facilitation for ecosystem restoration

Only recently researchers and restoration practitioners started to intentionally harness self-facilitation with the aim of kickstarting positive feedbacks in ecosystems naturally shaped by habitat modifiers. In general, such attempts encompass the reintroduction of habitat modifiers in groups that are sufficient in density and/or patch size to allow emergent traits to modify the local ‘within-patch’ environment such that the reintroduced organisms can thrive. A clear example comes from tropical forest ecosystems where landscape-scale replanting actions attempt to kickstart vegetation-atmosphere microclimate feedbacks which should in turn stimulate tree germination (Hirota et al., 2011; De Frenne et al., 2021).

In coastal zones where hydrodynamic, sediment burial and physical stresses associated with the exchange of ocean and freshwater create strong stress gradients, self-reinforcing feedbacks are pervasive and been shown to improve restoration outcomes. In salt marshes, for example, simple clumping of cordgrass transplants at a scale of 4 m^2 instead of classically applied forestry-style dispersed planting resulted in a doubling of overall restoration success expressed as survival, shoot density and expansion (Silliman et al., 2015). Notably, mechanisms underlying self-facilitation were context dependent, with larger patches mitigating wave stress under hydrodynamically exposed conditions, while clumping mitigated soil anoxia via enhanced radial-oxygen loss from the dense root mat in sheltered conditions (Silliman et al., 2015). Similar positive but also context dependent-effects of aggregation were observed in seagrass restoration, where large-scale transplantation actions clearly outperform smaller scale efforts (van Katwijk et al., 2016). Moreover, also in coastal reefs both clumping (de Paoli et al., 2017) and massive upscaling of restoration actions (Schulte et al., 2009) demonstrated clear positive effects on restoration effectiveness.

In freshwater systems, feedbacks occur at similar spatial scales compared to coastal systems. In open water, introducing water soldier, a floating plant, at high densities resulted in higher growth compared to low densities. High density stands alleviated nitrogen stress through shared uptake and facilitated plant growth through the decrease of oxygen concentration in the water. This in turn stimulated sediment phosphorus mobilisation and increased carbon dioxide concentrations, which enhanced underwater photosynthesis (Harpenslager et al., 2016). Positive effects of aggregation were observed in raised bogs, where larger-scale introduction of peat mosses outperform smaller scale introduction. In this study, larger peat moss patches were better able to maintain their own wet micro-hydrology during drought, which resulted in higher growth and more successful establishment (Robroek et al., 2009).

Although harnessing self-facilitation via large-scale reintroduction or increasing patch size, can enhance transplant survival, such approaches require more donor material per unit area to achieve restoration success within the same time span. For example, transplanting larger aggregations reduces the ability of clonal plants to spread laterally because the relative edge length along which the vegetation can spread decreases isometrically with patch size. As a result, more transplant units are required in larger aggregations to achieve lateral outgrowth rates sufficient for recolonization (Silliman et al., 2015; Temmink et al., 2020). As a consequence, restoration is much more expensive in feedback-driven ecosystem – ranging from 5000 to 5,500,000 US$/ha (de Groot et al., 2012; Bayraktarov et al., 2016) – while donor material may also become a limiting factor.

4. Mimicry of emergent traits in restoration

As harnessing self-facilitation benefits ecosystem restoration but increases demand for often limited donor material, it raises the question whether traits that generate self-facilitation can be mimicked to kickstart restoration. When successful, mimicry could lower the demand of donor material, increase overall efficacy, and reduce restoration costs. (Bio)mimicry is a long-utilized concept that learns from and mimics nature that has evolved over hundreds of millions of years to solve design challenges. This has yielded major technological advancements for humanity, such as the design of the Japanese high-speed bullet train after the beak of kingfishers or the application of passive cooling in architecture inspired by termite mounts (Benyus, 1997; Speck and Speck, 2021).

While biomimicry has found wide application in product development, it was only recently explicitly considered in ecosystem restoration, when it was introduced by Temmink et al. (2020) as a means to

Table 1
Examples of ecosystems where emergent traits were implicitly or explicitly mimicked for restoration. This list is not exhaustive.

Ecosystem	Habitat modifier	Self-facilitation through emergent traits	Nature of biomimicry	Key references
Salt marsh	Cordgrasses	Wave and current reduction, sedimentation (stems), sediment stability (root mat)	Implicit: with brush-filled breakwalls or living shorelines Explicit: with biopolymer-based biodegradable structures	(Hofstede, 2003; Safak et al., 2020) (Temmink et al., 2020; Fivash et al., 2021b)
Seagrass meadow	Seagrasses	Wave and current reduction, sedimentation (stems), sediment stability (root mat)	Implicit: with bio-container from seagrass wrack or anchoring with iron, cement, plastics and geo-textiles Explicit: with biopolymer-based biodegradable structures	(van Katwijk et al., 2016; Balestri et al., 2019) (Temmink et al., 2020; van der Heide et al., 2021; MacDonnell et al., 2022)
Mangrove forest	Mangrove trees	Wave and current reduction, sedimentation (pneumatophores, stems), sediment stability (roots)	Implicit: with wave attenuation structures, planting design and techniques Explicit: n.a.	(Kusmana, 2017; Winterwerp et al., 2020; Gijsman et al., 2021)
Bivalve reef	Mussels or oysters	Settlement substrate provisioning (shell, byssus threads), wave and current reduction (reef, self-stabilizing shape)	Implicit: with bagged bivalve shell, mixed shell substrates (oyster, scallop, clam shells), concrete structures, and mixed concrete structures (crab traps coated with concrete) Explicit: with biopolymer-based biodegradable structures	(Bersoza Hernández et al., 2018; Johnson et al., 2019; Goelz et al., 2020; Safak et al., 2020) (Fivash et al., 2021a; Gilby et al., 2021; Temmink et al., 2021a)
Coral reef	Corals	Settlement substrate provisioning (coral), wave and current reduction (reef)	Implicit: with artificial reefs made of concrete (reefballs), or rubber, metal or plastic Explicit: with 3D-printed clay structures	(Meesters et al., 2015; Higgins et al., 2022) (Levy et al., 2022)
Arid dryland	Perennial forbs	Water holding capacity (soil organic matter), shade (canopy), water infiltration (roots), soil stabilization (roots)	Implicit: with bunds dug by humans Explicit: with clay or wood obstruction/shade-providing structures	(e.g. JustDiggit, Moore et al., 2020) (Chirino et al., 2011; Minnick and Alward, 2012, Johnston and Garbowski, 2020; Oreja et al., 2020)
Raised bog	Peatmosses	Water holding capacity (pore space, capillary rise), shading (vegetation) floatability by gas trapping (complexity)	Implicit: *Sphagnum* with straw introduction Explicit: – with biopolymer-based biodegradable structures	(Rochefort et al., 2003; Günther et al., 2017) (Temmink et al., 2021b)

mimic emergent traits that generate self-facilitation. Implicitly, however, biomimicry has been applied in restoration for several decades (Table 1). Here, we discuss relatively well-studied examples in vegetated coastal systems (salt marsh, seagrass meadow, and mangroves), bivalve and coral reefs, freshwater bogs and arid drylands in more detail to illustrate how emergent traits that generate self-facilitation were implicitly and explicitly mimicked for the purpose of ecological restoration (Fig. 1, Table 1).

4.1. *Implicit emergent trait mimicry*

Over the course of the last decades, there were many restoration studies that implicitly mimicked emergent traits for ecosystem restoration (Table 1). In coastal ecosystems, such attempts mostly focus on mimicking traits that mitigate stress from waves and currents. In salt marshes and mangrove forests, artificial shelters were created using (brush-filled) breakwalls, living shorelines, bamboo poles or 'guludans' with the aim of stimulating sedimentation. Implicitly, these approaches mimic well-described sediment-stabilizing and flow dissipating emergent traits generated by the stems and root mats of the vegetation (Hofstede, 2003; Kusmana, 2017; Safak et al., 2020; Gijsman et al., 2021). In seagrass restoration, anchoring of rhizome fragments or plants is an often-used and successful approach to prevent uprooting when revegetating degraded sites (van Katwijk et al., 2016; Balestri et al., 2019). These anchoring methods implicitly mimic the increased anchoring naturally generated by larger, established seagrass patches (Maxwell et al., 2016). For coral, oyster and bivalve reef restoration, the introduction of a wide variety of hard substrates ranging from bagged shells, to concrete blocks to 'reefballs' is a common practise to stimulate natural larval or polyp settlement (Meesters et al., 2015; Bersoza Hernández et al., 2018; Strain et al., 2018; Johnson et al., 2019; Goelz et al., 2020; Safak et al., 2020). These hard and often permanent substrates offer suitable space for settlement and provide habitat complexity that can reduce predation similar to natural, established reefs.

In freshwater ecosystems such as peat bogs, scientists and restoration practitioners implicitly mimicked emergent traits to stimulate the establishment of peat moss vegetation. In degraded bogs the introduction of peat moss fragments covered by straw helps to create a microclimate. Small peat moss fragments easily dry out and straw provides shading and creates a microclimate with a higher relative humidity and more stable temperatures. Such a stable microclimate is normally generated inside large patches by the bog vegetation itself (Rochefort et al., 2003; Gaudig et al., 2018). Such implicit mimicry was found to increase vegetation cover seven times compared to controls (Rochefort et al., 2003). In regreening projects in (sub)tropical countries, the digging of bunds increase water retention and infiltration (e.g., JustDiggit) (Moore et al., 2020), which in turn facilitates the establishment of vegetation. This method implicitly mimics the increased water infiltration and retention naturally generated by larger vegetation patches (D'Odorico et al., 2007).

4.2. *Explicit emergent trait mimicry*

Explicit mimicry of emergent traits was only recently advanced. Specifically, in 2020 Temmink et al. (Temmink et al., 2020) show that biodegradable mimics that simulate dense patches of stiff stem canopies greatly enhance survival and growth cordgrass transplants. These results are like those obtained by clumping transplants of Silliman et al. (2015). The benefit of this new mimicry approach is that small transplants are now protected by temporary mimics rather than conspecific in a clump, thus greatly reducing the amount of required donor material. Moreover, similar results were found for seagrass transplants, with the difference that mimics were most effective when they simulated sediment stabilization by dense root mats instead of the seagrass canopies that are flexible instead of stiff (Temmink et al., 2020). Notably, follow-up work highlighted that the obtained benefits strongly depend on the environmental conditions. No clear benefits were found in sheltered conditions were self-facilitation is unimportant, while in extremely exposed conditions mimicry proved insufficient (van der Heide et al., 2021), confirming the context dependency highlighted in Fig. 2. Finally, in addition to facilitating cord- and seagrass transplants, these mimics also benefitted natural establishment of annual pioneer vegetation by stabilizing the sediment, thus creating an artificial Window of Opportunity of these species (Fivash et al., 2019, 2021b).

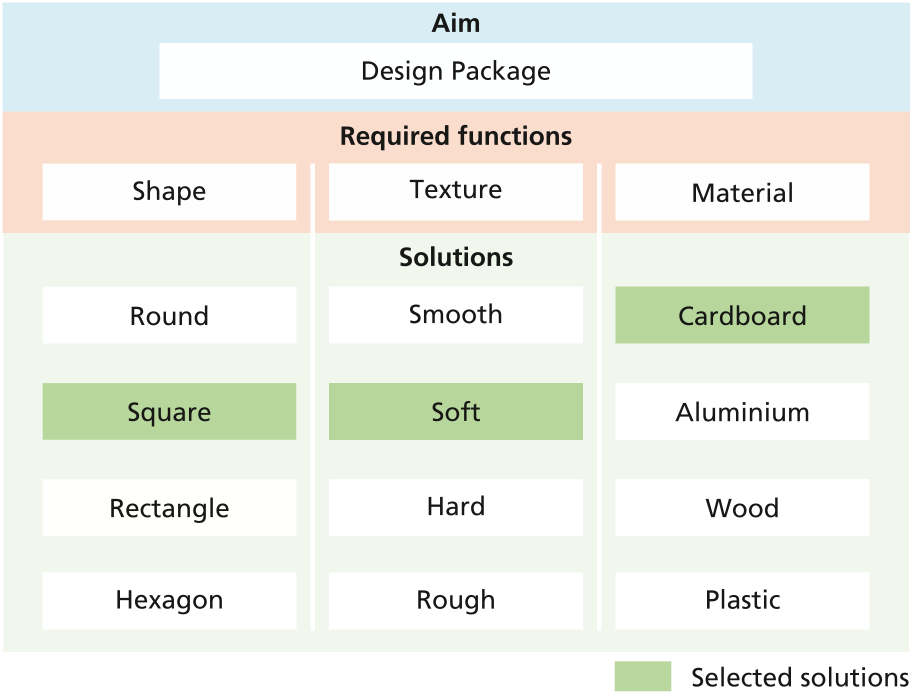
Apart from facilitating coastal vegetation, emergent trait-based mimicry was also found to enhance bivalve reef-establishment. In Florida and the Netherlands, biodegradable mimics simulated structurally complex established oyster reefs. The mimics were found to greatly enhance settlement of oyster recruits by providing stable hard substrate and predation-limiting 3D-complexity that is naturally generated by adult reefs (Fivash et al., 2021a; Temmink et al., 2021a). Moreover, in the Dutch Wadden Sea such structures also successfully generated mass settlement of mussel recruits when supplemented with coir rope serving as a mimic of the settlement cue naturally provided on adult reefs by mussel byssal threads (Temmink et al., 2021a, 2022a). Similarly, mimicking the complexity of coral reefs with 3D-scanned and 3D-printed reef tiles showcase explicit mimicry for these systems (Levy et al., 2022).

Beyond coastal systems, emergent trait-based mimicry also stimulated the establishment of floating peat moss vegetation in raised bogs. At high densities, peat mosses growing in open water trap methane and carbon dioxide between their leaves, enabling the formation of floating vegetation mats that support moss growth and patch expansion at or above the water surface. Here, they are exposed to more light and atmospheric carbon dioxide, which enhances their growth compared to submersed growth. Biodegradable structures that mimic dense patches of floating peat moss vegetation greatly enhanced the survival and growth of introduced peat mosses. These yields were possible as the floating mimics artificially created conditions without light and carbon limitation, which are normally generated by the habitat modifier (Temmink et al., 2021b). In arid drylands, emergent traits were successfully mimicked to enhance vegetation establishment. The addition of clay to enhance water retention facilitated short-term plant survival (Chirino et al., 2011). Furthermore, the use of wooden obstruction tailored to reduce water runoff resulted in long-term plant survival (Minnick and Alward, 2012) or constructed pine log piles softened microclimatic conditions and accelerated plant establishment (Oreja et al., 2020). This mimicry was successful, because in arid drylands plants typically enhance water retention and infiltration through their aboveground and belowground biomass and higher soil organic matter.

5. A trait-based industrial design-based framework for restoration

The examples highlight that it is possible to harness self-facilitation by using temporary or permanent structures or techniques that, either explicitly or implicitly, mimic emergent traits that generate self-facilitation to enhance restoration success. Thus far, however, mimics are typically not specifically designed for the target species or even the overall restoration application (see Perricone et al., 2023 for nature-based and bioinspired solutions for coastal protection). Often, they result from relatively unstructured trial-and-error experiments with haphazardly selected existing materials or products. Clear examples are concrete for reefs or anti-erosion mat for soil stabilization of coastal vegetation (Table 1). Consequently, these solutions are often (i) sub-optimal in supporting the target species, (ii) difficult to upscale in terms of labour, or (iii) expensive to implement. Therefore, we argue that restoration science needs to move toward a generalized mechanism- and design-based approach to advance overall restoration success of ecosystems shaped by habitat modifiers.

Here, we propose to apply structured design approaches used in engineering and bioinspired design (Rossin, 2010) to solve complex restoration challenges. A major complicating factor for the restoration of ecosystems dominated by habitat modifiers is that they require ecosystem and species-specific solutions to explicitly harness emergent traits that generate self-facilitation. This results in a large array of possible challenges and solutions to design restoration approaches. In engineering, such a situation is often defined as a complex problem, which requires a design-based approach to solve (Ritchey, 1998). Engineers are trained to solve such complex problems, because the design of industrial or consumer products consist of many possible techniques,



Aim

Design Package

Required functions

Shape	Texture	Material
Solutions		
Round	Smooth	🟩 Cardboard
🟩 Square	🟩 Soft	Aluminium
Rectangle	Hard	Wood
Hexagon	Rough	Plastic

🟩 Selected solutions

Fig. 3. Example of a morphological matrix with the aim (design a package), required functions, solutions, and a selection yielding a possible prototype. When the problem at hand is the creation of a package, the functions can be defined as (i) the shape of the package, (ii) the texture of the package, and (iii) the chosen material. For each function, many solutions can be formulated (material: cardboard, aluminum, wood, et cetera). All solutions are then visualized in a morphological matrix from which different designs can emerge through the combinations of solutions for each function (for example, [i] square-soft-cardboard or [ii] round-rough-aluminum package). A round package might be excluded based on a pre-determined criterium ‘space-effectiveness’.

materials and functions (Zwicky, 1947; Ritchey, 1998).

An often-used structured way to deal with an overabundance of problems and solutions is the morphological analysis (Zwicky, 1947; Ritchey, 1998). This method allows the identification and investigation of the total set of possible relationships or configurations for a complex problem (for an example, see Fig. 3). Briefly, the first step is defining the problem, after which step two involves dividing the problem into different functions that together should solve the problem. The third step entails a matrix-based cross-consistency assessment in which combinations of solutions for the various required functions are assessed for their mutual compatibility (Zopounidis and Pardalos, 2010), resulting in the exclusion of incompatible combinations. Finally, a fourth step involves a multicriteria analyses to select desirable solutions to the problem.

Morphological analyses were applied in astronomy, engineering design (e.g. jet and rocket propulsion systems), industrial product design, architecture, scenario development and security, safety and defense studies (Álvarez and Ritchey, 2015). However, such an approach has not yet been applied to solve complex restoration challenges. Inspired by the work from these other disciplines (Zwicky, 1947; Ritchey, 1998; Zopounidis and Pardalos, 2010; Álvarez and Ritchey, 2015), we propose the following systematic, five-step design-based approach that purposefully uses species-specific emergent traits in mimicry solutions to enhance restoration success (Fig. 4):

1. **Function identification**. The first step identifies establishment thresholds for the target habitat-modifying organism within the context of the environmental setting where it should be restored, and what emergent traits of the target species could mitigate them. Organisms can experience different establishment thresholds depending on site-specific environmental conditions (e.g., wave-stress, predation pressure). It is therefore key to identify relevant stressors and whether the target habitat former possess the emergent traits to ameliorate them. This should inform whether establishment thresholds can be overcome by emergent trait-based mimicry or whether alternative solutions, such as permanent engineering solutions should be considered (Figs. 4, 5a). From the identified establishment thresholds and mitigating emergent traits, a set of key emergent traits to be emulated can then be defined as required functions for the mimic.
2. **Morphological analysis**. The second step uses emergent trait-derived functions identified in step 1 in a creative process with brainstorm sessions and the morphological analysis. For each function derived from a required emergent trait, a set of solutions is listed in a morphological matrix (Figs. 4, 5b). At this stage, the idea is to come up with many original solutions; participants should therefore not be limited by normative constraints (Ritchey, 2011). Finally, a cross-consistency assessment is made on the matrix to exclude incompatible combinations of solutions.
3. **Multi-criteria analysis (MCA)**. In the third step, possible solutions in the morphological matrix are considered based on pre-determined

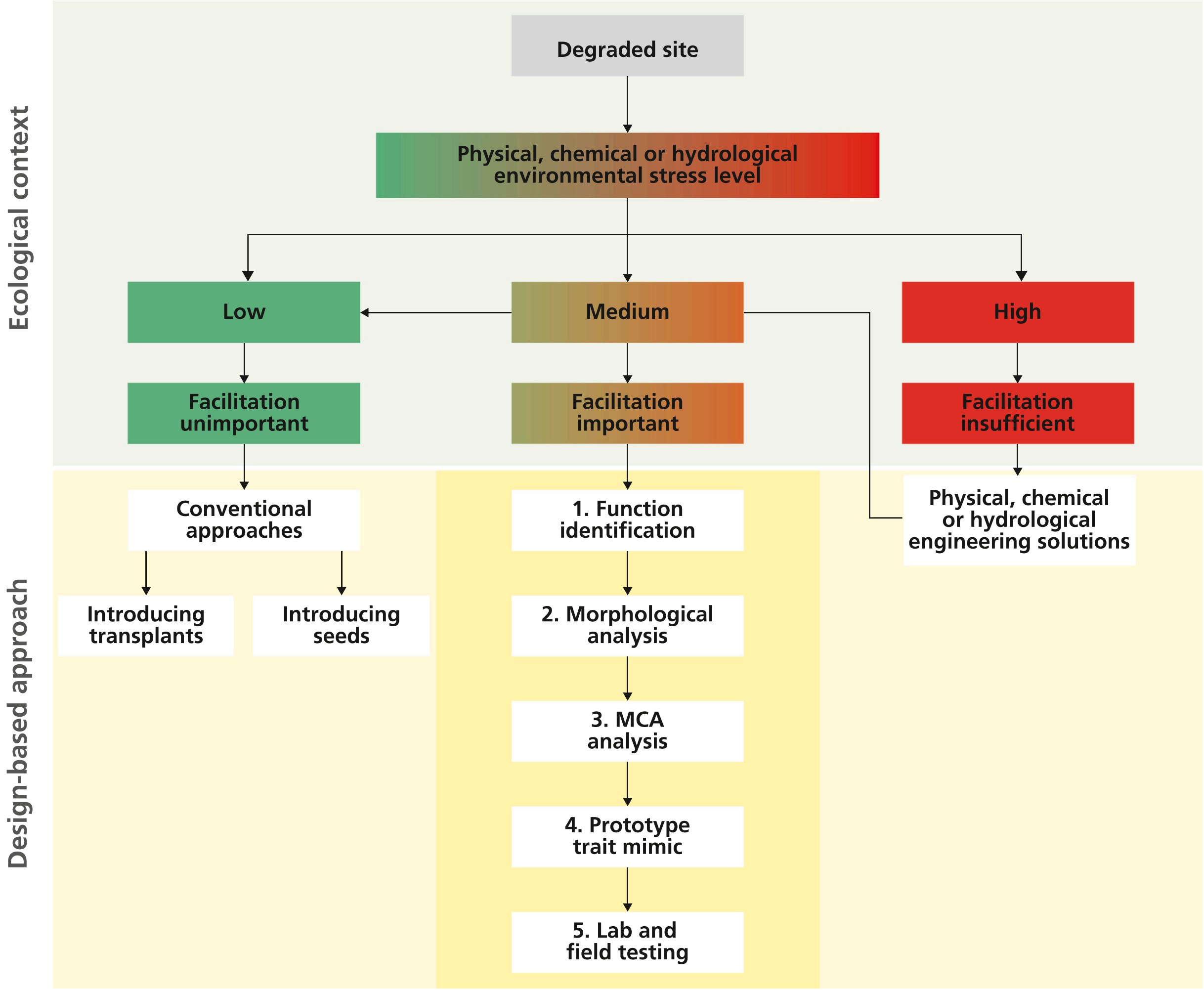


Fig. 4. Possibilities and environmental context of emergent trait-based restoration. The flow chart depicts routes to restore ecosystems characterized either by low, medium or high stress levels. Yellow blocks depict required steps to design a trait-based restoration solution with ecologists, industrial designers and engineers.

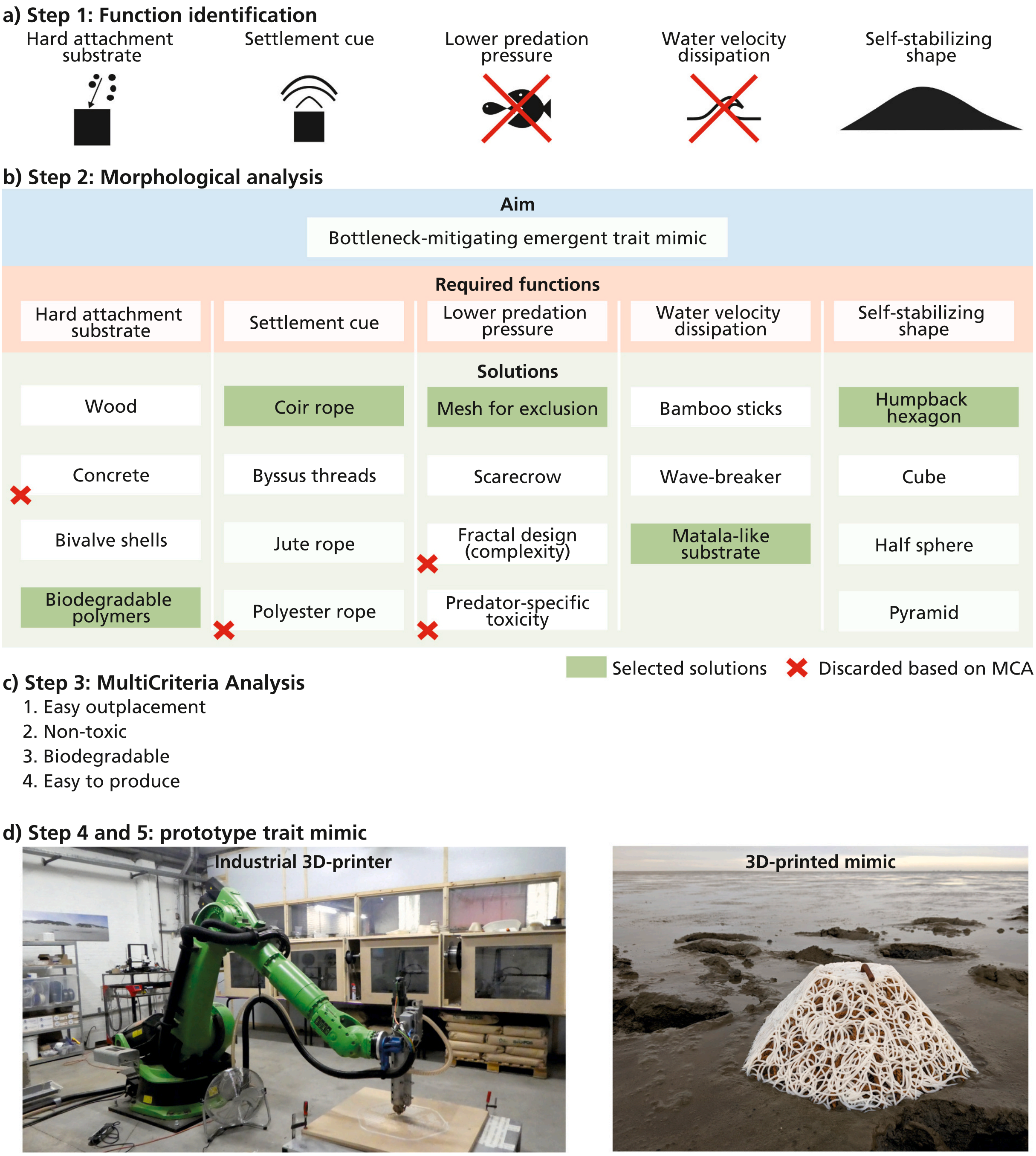


Fig. 5. An example of the five-step design process for a mussel bed case. The prototype was produced using an industrial 3D-printer with biodegradable biopolymers. (Photo credits: 3D-printer: R.J.M. Temmink and mimic: Tom van Leusden.)

criteria (Zopounidis and Pardalos, 2010) and possibly assigned weighing factors according to their importance (Mardani et al., 2015). For temporary emergent trait mimics to be applied in coastal restoration, the following criteria will be considered as essential: non-toxic, biodegradable, easy to produce and outplace. Based on the MCA's criteria, solutions with undesirable properties will be excluded, yielding a constrained set of potential solutions (Figs. 4, 5c).

4. **Design potential emergent trait-based solutions.** In the fourth step, multiple prototypes can be designed by combining solutions for each function generated at step 2 and constrained at step 3 (Figs. 4, 5d). Various combinations of solutions resulting in multiple designs can be evaluated and compared here. For example, which mimic design is likely to be most effective, and how cost-efficient can each design be manufactured? Finally, design-rules can be applied to further optimize the solution, such as applying correct angles of overhang, material thickness, and bridging (Gibson et al., 2010) and machine learning models could aid to cluster designs according to conditions of degraded ecosystems. This step thus results in a selection of viable prototypes.
5. **Prototypes construction, field test and optimization.** The fifth step entails the construction of product concepts and their testing. First, simple, small-scale tests should be conducted to assess purpose-specific characteristics of the applied materials, such as its strength, biodegradability, and/or erodibility. Second, to show ecological proof of concept various competing prototypes should be constructed

and compared in field experiments. The outcomes of these field experiments will (1) select the best candidate prototype, and (2) allow further refinement of the selected prototype, yielding a typical development cycle (Figs. 4, 5d).

6. Future opportunities and challenges

Emergent trait-based restoration has the potential to provide species-specific and context-dependent solutions for the inclusion of self-facilitation into restoration design. This approach can enhance restoration success via two pathways: (i) protect transplanted organisms, and (ii) enhance natural establishment and survival of seedlings, larvae or mature organisms (Temmink et al., 2020; Fivash et al., 2021b). This method results in higher restoration success at market costs even at experimental scale (Bayraktarov et al., 2016; Temmink et al., 2020, 2021a). In this paper, we provide a step-by-step design-framework to structure and elucidate numerous choices when designing restoration mimics. Moreover, our work highlights the necessity for restoration ecologists and practitioners to collaborate with scientific fields such as engineering and industrial design to overcome practical problems.

The current design-based framework only includes intraspecific-generated facilitation of the main habitat modifier, ignoring community-level interactions (i.e., intraspecific facilitation). In seagrass meadows for example, epiphytes grazers and sulfide-consuming lucinid bivalves facilitate seagrasses (Baden et al., 2012; van der Heide et al., 2012), while mussels facilitate cordgrasses in US coastal marshes through the local increase of nutrients and decrease of soil toxins (Derksen-Hooijberg et al., 2018). Following this, our current framework should be expanded by incorporating such community-level interactions, for instance by temporarily mimicking their function until these natural interactions re-establish. Moreover, trophic cascades as seen in many ecosystems (Estes et al., 2011), including the facilitative interactions of predators that control herbivory pressure of habitat modifiers, could be included as well (Maxwell et al., 2016).

Another step toward successful emergent trait-based restoration is to define an optimal risk-reward strategy. For example, large-scale planting ensures mitigation of risk because of higher survival due to strong self-facilitation, while simultaneous planting at multiple sites mitigates risks from local stochastic disturbances (van Katwijk et al., 2016; Fivash et al., 2022). In this light, the spread of risks becomes increasingly important when information about a restoration site is insufficient and disturbances are highly stochastic. In such cases, restoration practitioners can reduce the risk of failure by combining various patch-sizes into their designs (Fivash et al., 2022). A risk strategy also affects restoration costs, as small units are typically cheaper than larger ones, due to required material usage, transport, and installation on site. Therefore, it is pivotal to explicitly include designs of spatial configuration into trait-based restoration, because trait-mimics might influence each other on larger spatial scales, especially in highly dynamic areas such as intertidal ecosystems (Marin-Diaz et al., 2021; Temmink et al., 2022a).

The large-scale degradation of facilitation-driven ecosystems and the loss of ecosystem services calls for rapid restoration on a large scale worldwide. We argue that emergent trait-based restoration can be used as a tool to kickstart restoration of some iconic and threatened facilitation-driven ecosystems worldwide. The successful application of this approach and the systematic restoration approach presented calls to include disciplines not previously engaged, including material scientists, industrial engineers, manufacturing specialists, industrial engineers, construction management help to solve restoration challenges and should be included in the practice of ecological restoration (Gann et al., 2019).

CRediT authorship contribution statement

R.J.M.T. and T.v.d.H conceived the presented idea. R.J.M.T., T.v.d.H., C.A., and M.V. developed the idea. R.J.M.T. and T.v.d.H wrote the first draft of the manuscript and all authors contributed to the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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