

Oceanography and Marine Biology

An Annual Review, Volume 62

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First published 2024

ISBN: 9781032761961 (hbk)

ISBN: 9781032832869 (pbk)

ISBN: 9781003477518 (ebk)

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DOI: 10.1201/9781003477518-4

The funder for this chapter National Environmental Science Program, Australian Research
Council Linkage Project



CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

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Abstract Seagrass meadows are declining globally at alarming rates due to multiple stressors. Efforts are underway to preserve and restore these valuable ecosystems. Several frameworks for seagrass restoration exist, and some restoration attempts are being made at scale; however, poor outcomes are widespread, suggesting our understanding of the processes that drive seagrass performance is still limited. We argue that plant-sediment interactions influence almost all components of restoration, yet they are poorly incorporated in restoration design and frameworks. We synthesise the current information on how belowground interactions influence seagrass health and identify which of these are amenable to manipulation and at what scale they could be employed to improve restoration strategies and decision-making frameworks. We identified three key, interdependent areas by which belowground interactions influence seagrass health and performance. Those three areas include how (1) sediment microbial communities control nutrient and chemical cycling for seagrass, (2) the response of seagrass to sediment processes may be influenced by their life history and genetics of seagrass species targeted for restoration and (3) other species may interact with sediments to promote or inhibit seagrass survivorship and growth. Decision-making frameworks should be extended to include belowground interactions because they are of fundamental concern for determining initial site suitability and affect subsequent decisions and planning for restoration. This, in turn, will improve restoration outcomes and community engagement, critical for the successful management of these endangered ecosystems.

Keywords: Seagrass Restoration; Sediments; Microbes; Seagrass Genetics; Species Interactions; Decision-making Frameworks

Introduction

Seagrass meadows provide critical nursery grounds for fisheries (Whitfield 2017), nutrient cycling (Costanza et al. 2014), coastal protection (Boudouresque et al. 2016) and habitat for many species including those of conservation concern (Hughes et al. 2009). Seagrasses also sequester a globally significant amount of carbon, which is known as blue carbon (Macreadie et al. 2019, Serrano et al. 2019; <https://www.iucn.org/resources/issues-briefs/blue-carbon>). Through these services, seagrasses provide an estimated US\$6.8 trillion to the global economy (Costanza et al. 2014). One of the consequences of human development and exploitation of marine coastal and estuarine ecosystems is the severe reduction (Green et al. 2021, Evans et al. 2018) and, in some instances, the complete loss of seagrasses and the ecological and socio-economic services they provide. Globally, seagrasses are disappearing at an alarming rate of $110 \text{ km}^2 \text{ yr}^{-1}$ (Waycott et al. 2009). Since the 1980s, an estimated 19%–29% of seagrass cover has been lost worldwide (Orth et al. 2006, Waycott et al. 2009, Dunic et al. 2021). As a result of the worldwide decline in seagrass habitat, 14% of the world's 72 seagrass species are now at an elevated risk of extinction (Short et al. 2011). Importantly, this loss of seagrass represents an associated loss of ecosystem services valued at US\$318 million annually (based on 2011 seagrass service values of US\$28,916 ha^{-1} ; Costanza et al. 2014). Enhancing the resilience of seagrasses to environmental stress (i.e. the ability to resist and/or recover from environmental stress) and restoring lost seagrass habitat is critical for improving the health and function of marine coastal and estuarine ecosystems, buffering coastal ecosystems from ongoing climate change and sustaining the coastal communities and industries that depend on them.

Many factors have contributed to seagrass declines (reviewed in Statton et al. 2018) but chiefly responsible among these are massive historical and continuing land-based sediment and nutrient inputs (Orth et al. 2006, Dunic et al. 2021), as well as contemporary climate-related stressors

(Short et al. 2016). For example, following an extreme heatwave event in 2010/11, 1310 km² seagrass habitat was lost from the Shark Bay World Heritage Area (Strydom et al. 2020). In Tampa Bay (USA), large reductions in seagrass coverage were observed in the 1970s mainly due to dredging operations and eutrophication (Johansson & Greening 1999). To date, management actions have mainly focussed on improving light quality by mitigating sediment and nutrient loads (Orth et al. 2006). Previous reviews have highlighted the need for large-scale restoration (van Katwijk et al. 2009, 2016, Sinclair et al. 2021a), discussed how we might achieve that and subsequently developed ecological decision-making frameworks for seagrass restoration (Statton et al. 2021). Similarly, Tan et al. (2020) reviewed the various methodologies employed in seagrass restoration and the relative successes achieved by those methods. Indeed, roadmaps for coordinated landscape-scale coastal and marine ecosystem restoration have been developed in several reviews (Fortes et al. 2018, van Katwijk et al. 2021, Saunders et al. 2022). Belowground interactions that influence critical sediment processes, however, have been largely ignored in restoration and initial decision-making frameworks but are critical to seagrass health because they influence all aspects of restoration, from selecting donor and restoration sites to developing improved methods and monitoring regimes. Here, we review how belowground interactions can be incorporated into these seagrass restoration frameworks to enhance restoration success.

Managements' actions to improve water quality have led to successful restoration of seagrasses (de los Santos et al. 2019, Lefcheck et al. 2018, McLeod et al. 2018, but see Orth et al. 2012 as not all restoration depends on water quality improvements). Yet, seagrass restoration is often seen as a risky undertaking, because restoration trials often fail to deliver the desired outcomes. The perceived lack of restoration success has resulted in hesitancy from policymakers and resource managers to provide the necessary funding to develop adequate restoration methods. This has led to a 'stagnation loop' whereby a lack of funding to improve the science behind restoration leads to a lack of restoration success and community disengagement and continued low restoration success (Abelson et al. 2020). To break this stagnation loop, we need more successful restoration through a better scientific understanding of the factors influencing seagrass performance and growth (Abelson et al. 2016, 2020). Ecological knowledge of seagrasses can then be utilised to develop better tools to accelerate recovery and enhance the resilience of extant and restored seagrass ecosystems.

Fundamentally, successful restoration is contingent on appropriate site selection and removal/abatement of stressors that provide barriers to natural recovery or restoration. In general, high-energy environments (e.g., shallow sediments subject to high bed shear stress due to wind waves and/or tidal currents) may preclude the recruitment of seagrasses due to physical disturbance associated with sediment resuspension and smothering. These sites likely have coarser sediments, with low organic carbon and nutrient contents. In these high-energy environments, sulphide stress will be low; however, nutrients may be limiting, especially before a seagrass meadow is well established (Figure 1). Importantly, sediment and nutrient deposition also affect sediment grain size, nutrient and chemical cycling under microbial control, which can impact seagrass performance and natural recovery long after water quality is improved (Fortes et al. 2018, Zabarte-Maeztu et al. 2021). A particular challenge for the restoration of seagrass meadows is creating conditions that promote the establishment or 'seeding' of critical feedbacks that allow plants to survive and persist in a given site (van Katwijk et al. 2016). For example, better incorporation of sediment quality will determine site selection and whether any environmental intervention/enhancement is required (e.g., microbial or nutrient seeding) which in turn will influence the methods used for restoration.

In addition, many restoration efforts are focused on developing improved methods to stabilise the sediment for seeding and anchoring of shoots (see Tan et al. 2020). These restoration efforts are improving seagrass growth and survivorship, particularly at smaller scales (Tan et al. 2020). For some seagrass systems, these experiments are beginning to lead to larger-scale efforts. Following experimental testing of methodologies (e.g., <https://www.seagrassresearch.net/restoration>), seagrasses are now being restored at scale in Cockburn Sound and Shark Bay, Western Australia, as

SEAGRASS RESTORATION STRATEGIES

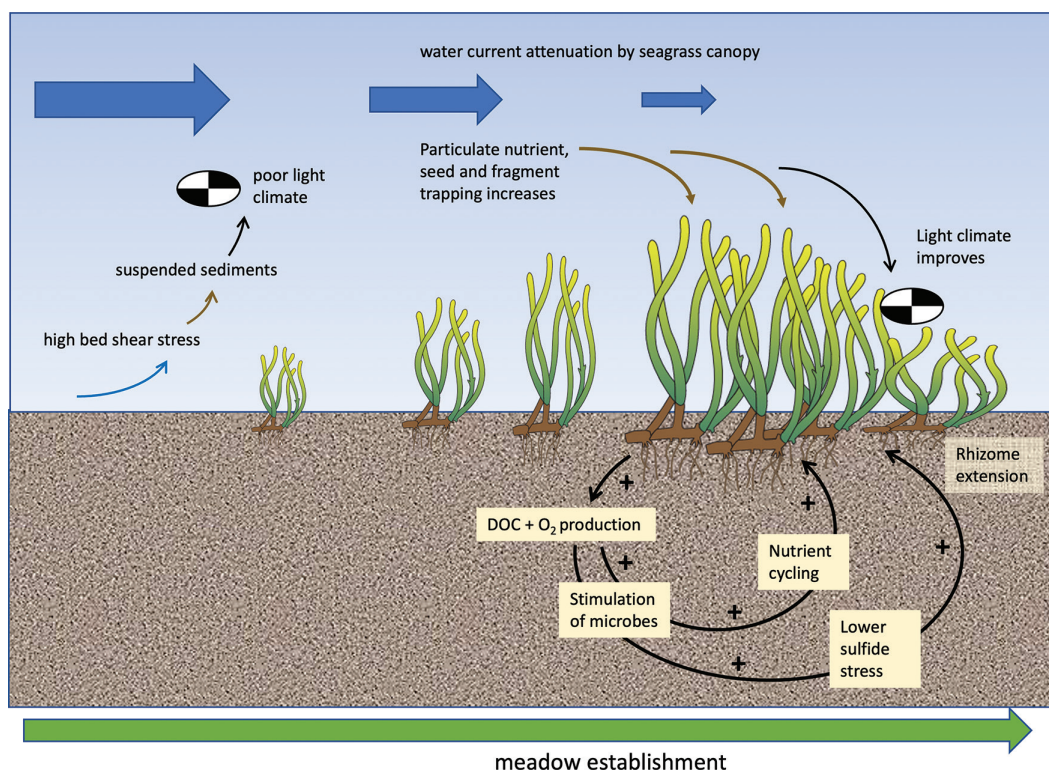


Figure 1 Seagrasses are keystone species that create feedbacks that influence hydrodynamics, particulate trapping, sediment quality, microbial processes and redox-based cycling of sediment chemistry.

well as in The Dutch Wadden Sea (Govers et al. 2022). However, current restoration methods make little provision for the inclusion of sediment processes and belowground interactions in planning restoration. Sediment processes are at the heart of these feedbacks and thus critical for improving seagrass health and restoration outcomes (Figure 2).

Ultimately, the health of seagrass meadows will be determined by their genetic architecture and their interaction with the biotic (e.g., animals and microbes) and abiotic (e.g., light availability, temperature and sediment chemistry) environments. Seagrasses create feedbacks that influence hydrodynamics, particulate trapping, sediment quality, microbial processes and redox-based cycling of sediment chemistry (Figure 1). A growing body of research demonstrates a critical role for belowground microbes in supporting seagrass health by reducing environmental stress (Crump et al. 2018, Martin et al. 2019, Fraser et al. 2023, Fuggle et al. 2023) and controlling interactions with other macrophytes (Gribben et al. 2017, 2018). Importantly, the interactions between seagrass life history, genetics and sediment conditions will likely play an important role in determining restoration success within highly modified environments (de Boer 2007, Kilminster et al. 2015, Pazzaglia et al. 2021), and more consideration needs to be given to genetic provenance when selecting material for restoration (Sinclair et al. 2014). Sediment conditions at restoration sites may have switched to an alternative stable state (McGlathery et al. 2013), requiring careful matching of seagrass species/functional types and/or genotypes to local environmental conditions at restoration sites. Genomic approaches now provide a powerful set of tools to understand adaptive and neutral genetic variation and guide the selection of species/functional types/genotypes best suited for restoration (Wood et al. 2020). In addition, seagrasses do not exist in isolation and interact with many other macro-organisms, and such interactions can influence seagrass survivorship and growth. For

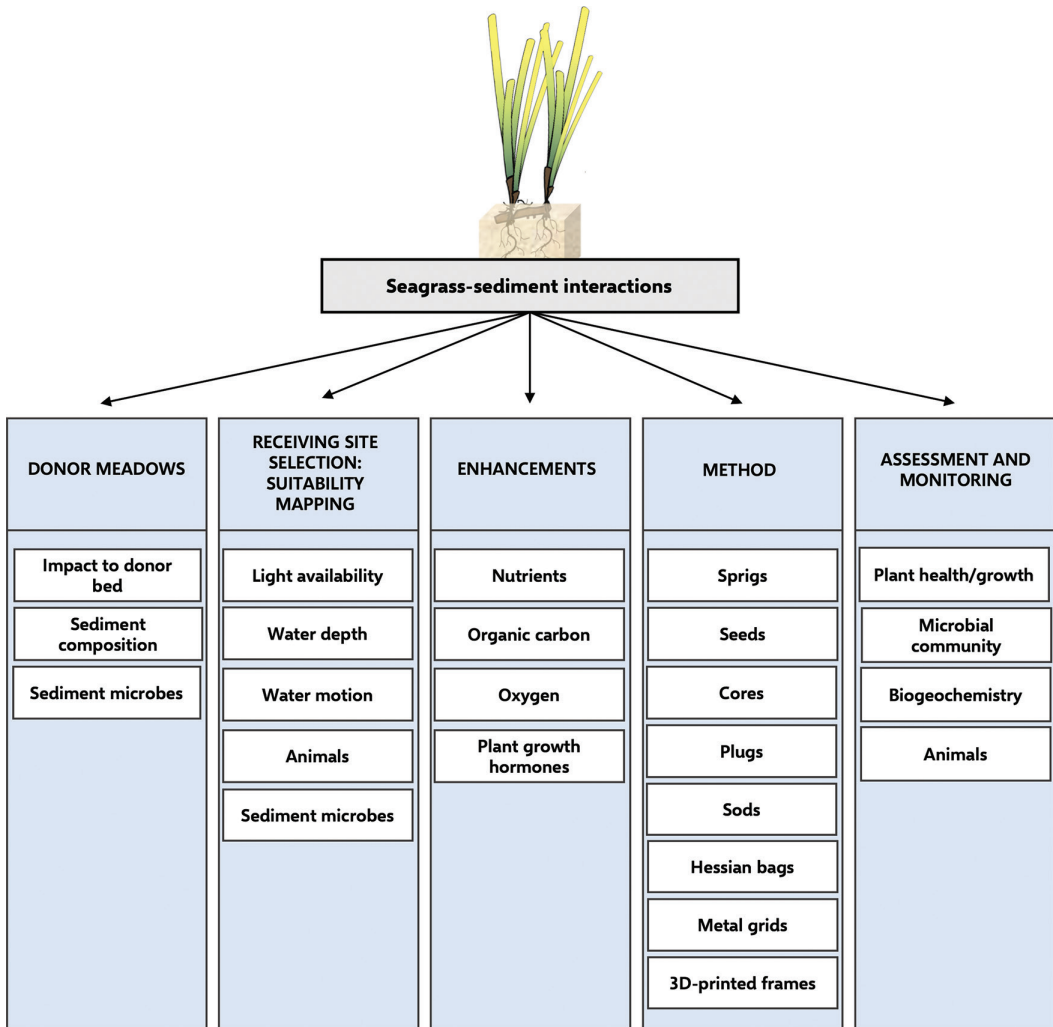


Figure 2 Seagrass-sediment interactions are at the heart of many components involved in restoration success, starting from donor and receiving site selection to methods and enhancements and ending with the assessment and monitoring of restoration success.

example, bioturbating organisms can improve sediment conditions by enhancing belowground oxygen conditions that can enhance seagrass performance (Aller 1988, Webb & Eyre 2004). However, bioturbation can also result in the dislodgement of seagrass seeds decreasing survivorship (Johnson et al. 2018). In addition, the presence of a healthy belowground microbiome can influence the outcomes of interactions with other macrophytes (e.g., Gribben et al. 2017, 2018).

In this review, we synthesise the current information on how belowground interactions influence seagrass health and identify which processes are amenable to manipulation and at what scale they could be employed to improve restoration strategies and decision-making frameworks. To address these questions, we used two approaches: (1) a workshop held in December 2021 with seagrass experts across Australia and (2) a selective literature search. Participants came from a range of backgrounds representing state government agencies charged with managing Australia’s marine estates, university researchers and leading restoration practitioners. Based on the workshop, we identified three key, interdependent areas by which belowground interactions influence seagrass

health and performance. Those three areas included how (1) sediment microbial communities control nutrient and chemical cycling for seagrass, (2) seagrass response to sediment processes may be influenced by their life history and genetics of seagrass species targeted for restoration and (3) interactions with other species that promote and inhibit seagrass survivorship and growth.

For each area, co-authors were divided into groups based on their area of expertise, reviewed the primary published scientific literature and provided a critical overview of the current state of knowledge. We then identified the key opportunities for utilising this knowledge to improve restoration strategies and what the scientific knowledge gaps are to realise their use in restoration. This review is not intended to contain a complete synopsis of the published literature for seagrass restoration as many aspects on frameworks, methodologies and successes have been extensively reviewed elsewhere (van Katwijk et al. 2016, Orth et al. 2020, Sinclair et al. 2021a, Pansini et al. 2022). This review focuses on how to improve restoration outcomes through the inclusion of belowground interactions and identify scientific knowledge gaps in the processes controlling seagrass performance and current knowledge that could be employed to enhance restoration success.

Current state of knowledge

Seagrass sediment microbes

In terrestrial systems, the importance of plant-soil interactions and the link between belowground processes mediated by microbes and aboveground performance is well recognised. As plants germinate and grow in the soil, they can influence the biotic and abiotic properties of the soil, e.g., through the release of chemical compounds and input of organic matter, which can result in changes of the microbial community composition and function (Van der Putten et al. 2013, Veen et al. 2019). These changes in soil properties and its microbiome can in turn affect the establishment and performance of individual plants of the same or a different species, a process known as plant-soil feedbacks (PSF) (Bever et al. 1997). PSF can be negative (resulting in a net growth-reducing effect to individuals of the same species), neutral (the net effect of all influences on plant growth is zero) or positive (growth of the same plants or other individuals of the same species is promoted) (Van der Putten et al. 2013). PSF are now widely recognised as important drivers of plant community dynamics, plant coexistence and plant responses to environmental change (Kardol et al. 2006, Heinen et al. 2020). Given the analogies between seagrasses and their terrestrial counterparts, there is huge potential for using these aboveground-belowground links to advance the field of seagrass restoration.

Our understanding of the effects of microbial communities on seagrass-sediment interactions and feedbacks has only recently started to develop (Piercey et al. 2021). Emerging studies show that seagrasses harbour diverse microbial communities on the surfaces and within their above- and belowground structures (Garcias-Bonet et al. 2012, Ugarelli et al. 2017, Tarquinio et al. 2019), as well as on their seeds (Tarquinio et al. 2021). These studies show that microbes have the potential to strongly influence above- and belowground processes related to carbon-, nitrogen- and sulphur cycling, all of which are linked to seagrass performance and the diverse ecological communities they support. For example, seagrass root-associated and rhizosphere (i.e., the region of sediment in the immediate vicinity of the roots) microbiomes are typically enriched in sulphur cycling bacteria, many of which likely play key roles in sulphide detoxification, ultimately contributing to the ability of seagrasses to persist in high sulphide environments (e.g. Martin et al. 2020, Scholz et al. 2021). Some of these bacteria also possess the genes to fix nitrogen (Petersen et al. 2016, Mohr et al. 2021) and break down organic matter, releasing nutrients that contribute to plant growth in otherwise oligotrophic oceans (Fraser et al. 2018). Epiphytic bacteria on leaf surfaces are a key component in the ability of seagrass to uptake dissolved organic nitrogen from the water column (Tarquinio et al. 2018). Some bacteria that occur on seagrass tissues can help defend against pathogens and saprophytes (Tarquinio et al. 2019). Seagrasses also host diverse fungal communities on and inside

their leaves, roots and rhizomes, although their role in seagrass functioning remains poorly known (Ettinger & Eisen 2019, 2020).

There is significant variation in the composition of the microbiome between seagrass species (Garcias-Bonet et al. 2021), particularly between different functional types of seagrasses (colonising vs opportunistic vs persistent, *sensu* Kilminster et al. 2015). Significant variation can also occur among plants of the same species growing in different locations (Martin et al. 2022), which suggests that microbial composition is mediated by both the host and the environment. There is now experimental evidence that has linked alterations in seagrass microbiomes with changes in light (Martin et al. 2018), sediment organic matter (Fraser et al. 2016, 2023), nutrient enrichment and temperature (Nguyen et al. 2021). Such changes in environmental conditions can not only impact the health of seagrasses directly but also through changes to the associated microbiome.

Seagrass life history, genetics and sediment processes

The loss of seagrass from an area can lead to a rapid change in local sediment conditions that can make it difficult to re-establish the seagrass in those areas. Restoration has typically focused on technical and logistical issues relating to transplanting methods, seed collection and the physical suitability of areas for restoration (Bastyan & Cambridge 2008, Fonseca 2011, Tan et al. 2020). There is, however, a growing realisation that modification of sediment conditions may be needed for successful restoration. Key to this is understanding how seagrass life histories (e.g., Sinclair et al. 2021a,b), growth forms and physiological tolerances (e.g., Kilminster et al. 2015) influence and modify sediment conditions. For example, some seagrasses include short-lived, colonising species with fast growth rates (e.g., those from the genus *Ruppia* and *Halophila*) through to longer lived species with moderate growth rates (e.g., *Zostera*) and long-lived species with relatively slow growth rates that form persistent meadows (e.g., *Amphibolis* and *Posidonia*; Kilminster et al. 2015). We are becoming increasingly aware of how restoration success may be influenced by these different growth strategies and sediment conditions and how seagrasses modify the sediment environment as they colonise and expand within an area. Growth of transplanted *Posidonia australis* rhizomes can vary greatly within and among sites (e.g., 9.1–22.3 cm yr⁻¹ in the same New South Wales (NSW) estuary (Meehan & West 2002) and 10–35 cm yr⁻¹ in Western Australia (Renton et al. 2011). *P. australis* seedlings are slower growing, with rhizome extension ranging from 5 to 17 cm yr⁻¹ in NSW (Meehan & West 2004). Growth rates of leaves and rhizomes can depend on sediment nutrient levels (Cambridge & Kendrick 2009), and it is likely that some genotypes perform better under some sediment conditions. Sediment properties (grain size, nutrients, microbiome) can play a role in influencing rhizome elongation and root architecture, which may in turn influence establishment success. For example, species of *Zostera* tend to produce greater belowground biomass and longer rhizome nodes in oligotrophic sediments (e.g. Ferguson et al. 2016, Song et al. 2021), while sediment type (specifically grain compactness; Statton et al. 2013) and nutrients (Hovey et al. 2011) can affect root architecture and hence anchoring of seagrass.

Similar to patterns in terrestrial plants, weedy fast-growing species (e.g., *Halophila* spp.) that are often first colonisers of disturbed seagrass beds (Smulders et al. 2017) may be less reliant on their microbial communities, and they more quickly overcome adverse sediment conditions (Bauer et al. 2018, Koziol & Bever 2015, 2016; but see Lee et al. (2018) as *Halophila ovalis* might be dependent on microbes for nitrogen acquisition because of the loss of genes encoding NADH dehydrogenase-like complex assembly). Variation in seagrass life histories will also influence the spatial and temporal patterns of genetic diversity and connectivity which may be important for sediment processes within restoration sites. Seagrass life history reflects the ability to disperse either via current-mediated transport of floating propagules along the water surface (e.g., *Posidonia*, *Thalassia*, *Enhalus* and *Zostera*) or the dispersal of negatively buoyant seeds in the water column or the sediment-water interface (e.g. *Halophila* and *Halodule*; Kendrick et al. 2012). The genetic structure

of seagrasses can be heavily influenced by these modes of dispersal resulting in chaotic genetic patchiness, clonality and polyploidy (McMahon et al. 2017, Sinclair et al. 2020, Edgeloe et al. 2022).

Species interactions and their effects on seagrass-sediment interactions

Bioengineers have the capacity to affect seagrass by changing sediment conditions and influencing restoration success. Some bioturbators can rework large amounts of sediments, leading to sediment destabilisation (e.g., sea urchins and rays) negatively affecting seagrass or stabilisation that can have positive effects on seagrasses (e.g., tube building worms; Volkenborn et al. 2009, Figure 3A).

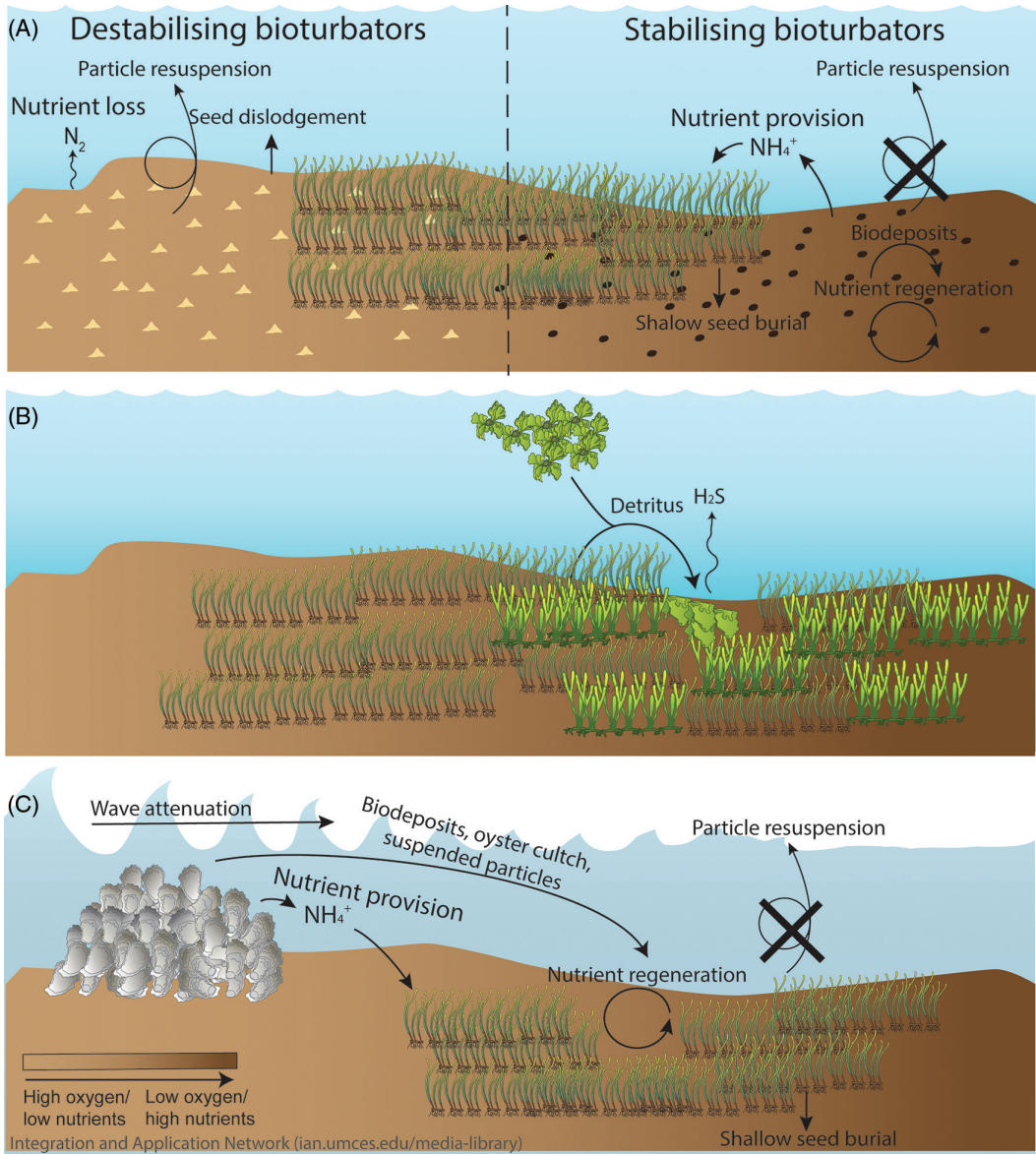


Figure 3 The effect of (A) bioturbators, (B) free-floating seaweed and *Caulerpa* and (C) shellfish reefs on seagrass-sediment interactions.

For example, Callianassid shrimps can reduce seagrass growth via sediment resuspension during burrow creation, reducing light availability and sediment stability (Suchanek 1983, Siebert & Branch 2006), while sea urchins and sand dollars can dislodge seeds (Johnson et al. 2018). For example, coir mats have been successfully used to exclude Callianassid shrimps and improve transplant success and shoot growth of *Zostera muelleri* seagrass in Australia (Wendländer et al. 2019). Studies are now underway to test the applicability of this technique at large scales.

In contrast, the activity of clams and some worms can bury seagrass seeds to a sediment depth suitable for germination within a few days after seed deposition, providing escape from predation and promoting seed retention (Blackburn & Orth 2013, Li et al. 2017, Fales et al. 2020). Alternatively, bioturbators can provide nutrients for seagrass growth in areas where nutrients are limited, such as sandy environments (de Boer 2007, Gilbertson et al. 2012, Stief 2013). Importantly, in eutrophic sediments, Lucinidae and Solemyidae bivalves can reduce sulphide stress in seagrasses by hosting sulphide-oxidising bacteria in their gills (Gagnon et al. 2020, van der Geest et al. 2020).

In general, the effects of macroalgae on sediment-seagrass interactions are not well studied. Macroalgae are likely to affect seagrass-sediment interactions via the modification of sediment chemistry, physical structure and microbial communities due to increased input of seaweed detritus (Fraser et al. 2016). *Caulerpa* species are among the few seaweeds that grow directly in soft sediments, and several species co-occur with seagrass (Ceccherelli et al. 2000, Glasby 2013). At high densities, *Caulerpa* sediments generally have higher organics (due to a high detrital input of fragments (Wright 2005), silt content, anoxia and sulphide concentration compared to seagrass sediments (Holmer et al. 2009, McKinnon et al. 2009). Moreover, there are very different microbial communities in *Caulerpa* and seagrass sediments. *Caulerpa* sediments typically contain bacteria associated with fermentative pathways and sulphate reduction (i.e., low oxygen environments; Chisholm & Moulin 2003, Gribben et al. 2017), whereas seagrass sediments contain bacteria associated with aerobic pathways (i.e., higher oxygen environments; Gribben et al. 2017, 2018). An important role for seagrass sediment in reducing the success of invasive *Caulerpa* species has been demonstrated: *Caulerpa* fragments grow worse in sediments with intact seagrass (*Zostera* and *Posidonia*) sediment microbial communities compared to disturbed seagrass sediments. However, once *Caulerpa* is established in seagrass beds, it creates reduced conditions to which it is tolerant suggesting positive feedback (self-facilitation) between *Caulerpa* sediment and propagule success. Overall, modifications to the sediment caused by *Caulerpa* are likely to influence seagrass-sediment feedbacks via modification of sediment properties and microbial communities. This more anoxic and sulphidic sediment may limit seagrass recovery in areas that may now be occupied by *Caulerpa* and/or may have legacy effects on sediment condition even if *Caulerpa* is removed that impede restoration (Gribben et al. 2017, 2018).

Similarly, high densities of seaweed attached to biogenic structures (including epiphytic on seagrass) trigger chemical and microbial changes to seagrass sediment. For example, in Chesapeake Bay, dense macroalgal canopies growing on *Zostera* had negative effects on seagrass production possibly due to changes in sediments (lowered redox and higher concentrations of ammonium) or light limitation (Hauxwell et al. 2001, 2003). Other studies have also shown negative effects of epiphytic seaweed on seagrass due to a reduction in light (Drouin et al. 2012), but in general, the effects of increased detrital input of epiphytic seaweed on seagrass-sediment interactions are not well tested. In addition, blooms of free-floating seaweed, typically the result of increased nutrient loading to a waterway, can settle on seagrass beds and change water and sediment conditions (Figure 3B, Goodman et al. 1995). Modification of sediment properties in this way, combined with flow-on effects on microbial communities, may hinder seagrass restoration in areas where free-floating seaweeds do not commonly co-exist with seagrasses. Free-floating seaweeds are not always 'bad' as they form a major component of the tropical marine seagrass meadows and coexist with seagrasses in these areas.

Shellfish also affect sediments by the addition of oyster cultch and the release of biodeposits (faeces and pseudo-faeces; Figure 3C), which increases sediment nutrient levels, sediment stabilisation and seed trapping (Meysick et al. 2019, Gagnon et al. 2020). Increases in sediment nutrients can boost growth rates of seagrass *Halodule wrightii* at intermediate oyster densities, which were related to intermediate levels of ammonia and phosphate in sediments (Booth & Heck 2009). Survival of *Zostera marina* transplants was increased by the presence of mussels in high and medium exposure sites, but not in sheltered sites, indicating an effect on sediment stabilisation and storm protection (Bos & Katwijk 2007). Even though most studies assessing interactions between seagrass and reef-building shellfish have found positive effects, negative interactions can also occur mostly due to eutrophication effects, epiphyte growth and competition for space (Gagnon et al. 2020). For example, high biodeposit loads can intensify sediment eutrophication, driving sulphide production and reducing seagrass growth (Vinther & Holmer 2008). Negative effects have mainly been identified when seagrass and shellfish occur in the same habitat, while positive effects have mainly been recorded when they are located in independent, but fringing habitats (Gagnon et al. 2020).

Science needs for increased management and restoration success

Microbes

There are an increasing number of studies that show changes in the seagrass belowground microbiome with changes in environmental conditions (Fraser et al. 2016, Martin et al. 2018, Wang et al. 2020, Nguyen et al. 2021, Fuggle et al. 2023). However, experiments that establish causal effects of microbial changes on seagrass performance are rare (but see Fuggle et al. 2023). Given the fundamental role that microorganisms have in biogeochemical cycling in seagrass ecosystems and their potential effects on plant performance, more experimental studies are needed to gain a detailed understanding of the role of belowground microbes in seagrass health and performance. Incorporating these seagrass-microbiome interactions into restoration planning could significantly improve restoration success rates now and into the future (Wood et al. 2019). In addition, seagrasses also host diverse fungal communities but their role in seagrass functioning is largely unknown (Ettinger & Eisen 2019, 2020). As evidenced from terrestrial ecosystems (Maltz & Treseder 2015, Koziol et al. 2018, Neuenkamp et al. 2019), exploring seagrass-fungal relationships and how they contribute to seagrass performance may be critical for building a holistic understanding of how belowground processes contribute to seagrass health and improving restoration strategies.

The choice of appropriate restoration strategies depends on an assessment of site-specific environmental factors that influence seagrass microbiome interactions, with a view to working within environmental constraints and promoting beneficial microbial processes. Once we have a better idea of which microbes promote or hinder seagrass growth under specific environments, knowledge of seagrass and sediment microbiomes could be used for monitoring and active intervention. Molecular tools can be used to (1) establish a baseline against which the health status of meadows can be assessed and (2) track microorganisms or functional groups linked with poor plant performance as early warning signals to trigger preventative management actions. In addition, information on plant and/or sediment microbiomes can help (3) identify 'healthy' meadows that can be used as donors for restoration, either of shoots, seeds or sediment; (4) select sites where microbiome composition is likely to increase the chances of restoration success; and (5) check that the manipulation of plants, seeds or sediments does not lead to microbial changes that may negatively affect restoration success (van Katwijk et al. 2016, Koziol et al. 2018). Using these molecular tools may in practice be challenging for managers and restoration practitioners depending on the scale of the project and because of the associated costs and expertise that are needed. The cost of DNA sequencing has, however, declined to a point where the generation of large amounts of sequence

data is within the budget of most research groups. A partnership between restoration practitioners and scientists would therefore be the best way forward to deploy these methods.

Seagrass restoration practitioners may still face considerable challenges that require active manipulations of sediments or plants focused on optimising their microbiomes. Restoration of aboveground plant community properties may require steering of belowground ecosystem processes and those organisms that drive them (Wubs et al. 2016). Manipulations may thus focus on promoting the conditions that would facilitate the desired sediment microbiome, for example, by providing appropriate levels and types of nutrients or by manipulating the physical environment (e.g., grain size). An alternative approach for promoting positive seagrass-sediment interactions is to directly inoculate with desired microbiomes, e.g., through inoculations with bulk sediment from sites with healthy seagrass communities, as done in terrestrial systems to enhance the establishment of plants in degraded sites (Wubs et al. 2016, Grman et al. 2020) or through targeted inoculations of beneficial microbes such as by coating seeds or large-scale spraying of these inoculants on degraded sites prior to restoration, a commonly used method in land bioremediation (Kuiper et al. 2004).

The microbiome monitoring and manipulations outlined above rely on new and emerging techniques, such as (1) high-throughput culturing methods to isolate, screen and identify microbes conferring a beneficial trait/function to seagrass and that can be used as probiotic inoculations (e.g., mangrove bacteria; Soldan et al. 2019); (2) enriched bulk or compound-specific stable isotopes (Kaldy et al. 2006, 2013) and isotope probes viewed over highly resolved spatial scales within the rhizosphere or plant tissue (i.e., NanoSIMS; Tarquinio et al. 2018) to understand links between microbial and plant functions; and (3) bioinformatics pipelines for metagenome-assembled genomes (MAGs) and long-read technologies to improve seagrass and sediment-specific sequencing databases that allow the development of specific markers/primers (Duffin et al. 2020). The consistent use of best-practice methodology for sample collection and processing, culturing protocols, primers and bioinformatics pipelines (e.g., BioPlatforms Australia, Earth Microbiome Project; Thompson et al. 2017, Phelps et al. 2021) is critical to facilitate standardisation and to provide a place for sequence deposits and metadata. Integrating these technologies with *in situ* manipulations is key to determine causation and mechanisms that underpin plant performance and health in real-world scenarios.

Life history and genetics

The conditioning of sediments through a succession of different species could provide restoration practitioners with a valuable tool for modifying less suitable sediment conditions at a restoration site to more favourable conditions. Restoration of belowground ecosystem functions may also be achieved by using early colonising plants as tools to promote beneficial microbiomes for subsequent colonisers/desired species that can be planted after the sediment is stabilised and microbial associations are established (Van der Putten et al. 1993, Angers & Caron 1998, Kardol & Wardle 2010). In addition, genetic diversity represents the raw material that natural selection acts on and is likely to be important for seagrass to establish in a range of sediment conditions within restoration sites. There is, however, a lack of knowledge associated with links between genetic diversity in seagrass meadows and their associated microbial communities, despite health and nutrient benefits for seagrasses and adjacent ecosystems (e.g., Hughes & Stachowicz 2004, Reynolds et al. 2012). Further research is needed to understand the interaction between genotype and microbiome and how mixed species and successional approaches can be used in seagrass restoration programmes.

Some genotypes may be locally adapted to particular sediment conditions, and for successful restoration outcomes, we need to match restoration material (seeds or shoots) from environments that more closely match the conditions at the restoration site (van Katwijk et al. 2009). However, detailed range-wide knowledge of patterns of genetic diversity is limited to only several seagrass species (e.g., *Posidonia australis*, *Posidonia oceanica*, *Zostera marina*, *Zostera noltii*, *Thalassia hemprichii*, *Thalassia testudinum* and *Halodule wrightii*; Coyer et al. 2004, Olsen et al. 2004,

Arnaud-Haond et al. 2007, Dijk et al. 2009, Hernawan et al. 2017, Duffy et al. 2022, Sinclair et al. 2023, Tavares et al. 2023). The spatial scale of genetic studies varies considerably from range-wide studies providing overall patterns of genetic diversity and connectivity over hundreds to thousands of kilometres to detailed studies within meadows at the scale of metres. Finer spatial scale studies provide useful estimates within highly modified industrialised environments where active restoration is ongoing, for example, *Zostera muelleri* in Port of Gladstone (Australia; Jackson et al. 2021), *Posidonia australis* in Cockburn Sound (Australia; Sinclair et al. 2014, 2021b) and *Zostera marina* in Bodega Harbor (USA; Kollars et al. 2022). A better understanding of the genetic structure and patterns of local adaptation in relation to sediment conditions is needed both at the local and range-wide scales to guide what restoration material may be best suited for the sediment conditions at a restoration site.

From a restoration perspective, differences in life histories could be exploited by using fast-growing species (of seagrass or even algae) to rapidly colonise an area and modify and improve sediment conditions that then enable longer-lived species to establish and grow in these areas (Williams 1990). Indeed, in small-scale experiments, the growth and survivorship of slower growing species (e.g., *Thalassia testudinum* and *Posidonia sinuosa*) were enhanced when transplanted into sediments containing early colonising species (Van Keulen et al. 2003, Kenworthy et al. 2018).

The rapid development of 'omic' technologies also provides unprecedented opportunities to integrate genetic data to inform and enhance seagrass restoration. For example, the use of population genomic analysis can provide a more detailed understanding of population connectivity and patterns of genetic diversity. In addition, it can provide an understanding of the genetic basis underlying adaptive variation associated with particular environments and how a seagrass species may respond to local sediment conditions. This can assist in identifying and matching genotypes from donor meadows to environmental conditions at restoration sites, or ensuring restoration material contains genetic variants that allow for adaptation to future projected environmental conditions (Coleman et al. 2020). Transcriptomic studies of gene expression also provide significant opportunities for the use of genetic information to inform restoration as they allow for the identification of the genes underlying responses to specific environmental stressors (Mohammadi et al. 2019, Nguyen et al. 2020, Booth et al. 2022). These analyses provide important insights into the tolerance of individuals to different sediment stressors and an understanding of the resilience of restored populations to future environmental change.

Species interactions

To inform restoration, it is important to understand the full array of negative and positive seagrass-bioturbator interactions. For example, the potential beneficial effects of animal bioturbators on seagrass growth, survival and reproduction, including the provisioning of nutrients and microclimates for beneficial microbial community development and microbial function, remain largely unassessed. Moreover, in addition to providing benefits to seagrass health, bioturbators may also affect the provision of ecosystem services by seagrasses. Bioturbators can decrease carbon sequestration in saltmarshes by oxygenating sediments and boosting aerobic decomposition of organic carbon, while at the same time facilitating arbuscular mycorrhizal fungi that promote saltmarsh growth and carbon sequestration capacity (Martinetto et al. 2016). Large-scale field surveys of bioturbators co-occurring with seagrass and how they relate to seagrass health and habitat function are needed.

While studies comparing the effects of a few species of bioturbators have suggested that idiosyncratic effects play a key role in seagrass-bioturbator interactions (Johnson et al. 2018, Lacoste et al. 2018), no studies have experimentally assessed if the nature of these interactions are related to bioturbator functional groups. For example, seed burial capacity has been related to bioturbation rates (as measured by grams of sediment moved per day per individual), but only three species were assessed (Blackburn & Orth 2013). To inform these approaches, studies are needed to identify

taxonomical groups or functional traits associated with positive or negative effects on seagrasses. The information produced can inform global seagrass efforts, as the focus on functional traits will make results transferable between systems, even for new sites where there is little understanding of the ecology of sediment biodiversity.

In addition, more studies are needed to understand which seagrass species benefit from associations with lucinid bivalves, and how widespread these positive interactions are. Lastly, the role of shellfish as nutrient providers for seagrasses has been mostly assessed for those shellfish species that occur in close association with seagrasses, such as the mussel *Modiolus americanus* (Peterson & Heck 1999), *Mytilus edulis* (Reusch et al. 1994) and the oyster *Crassostrea virginica* (Booth & Heck 2009). It is, however, less clear how shellfish reefs occurring in the surrounding areas affect seagrasses. Studies are needed to test how shellfish reefs affect seagrass health and understand context-specific effects to pre-empt any potential negative effects of shellfish on seagrass via eutrophication.

Given the influence bioturbators can have on seagrass restoration success, site suitability models should incorporate information on naturally occurring ‘stabilising’ and ‘destabilising’ bioturbators. A recent study in the Wadden Sea showed that the incorporation of biotic factors such as macro zoobenthos in seagrass habitat suitability models could improve the models and consequently restoration outcomes (Gräfnings et al. 2023). Moreover, in addition to designing strategies to minimise the impact of destabilising bioturbators, for example, by the use of coir mats (Wendländer et al. 2019), harmful bioturbators can be removed at the planting stage in areas where historical records show that the local presence of these species increased after seagrass loss. Strategies can also be developed to harness the beneficial effects of bioturbators to improve restoration outcomes. For example, practitioners can use stabilising bioturbators to pre-condition sediments for seagrass planting which can help exclude harmful bioturbators, increase nutrient availability in low-nutrient sediments, decrease sulphide stress in eutrophic sediments and/or inoculate with or promote the growth of beneficial microbial communities. For example, in areas with high sediment sulphide levels, co-planting seagrass with lucinid bivalves, where available, might help transplants overcome sulphide stress (Derksen-Hooijberg et al. 2018, Chin et al. 2021). The natural capacity for reproduction and dispersal of bioturbators makes this strategy ideal for projects across large scales.

High levels of some benthic and free-floating seaweed are often the result of increased nutrients and other catchment disturbances. Thus, ongoing monitoring and management of nutrient inputs is critical to reduce the biomass of these algae and their potential impacts on sediment conditions for seagrass. Other species such as *Caulerpa* are highly invasive in many areas of the world interacting with local seagrasses (Gribben et al. 2017, 2018). Manual removal of these species and sediment pre-conditioning might be necessary before seagrass restoration efforts begin.

The extensive number of shellfish reef restoration projects worldwide provide opportunities for the development of co-planting initiatives with seagrass. With a better understanding of how shellfish reefs affect seagrass performance, reefs could be used to pre-condition sediments for seagrass planting in wave-exposed areas where there are low levels of nutrients in sediments. In these areas, shellfish reefs attenuate waves promoting sediment stabilisation (Meyer et al. 1997) and contribute biodeposits that can increase nutrient content in sediments at distances up to 100 m away from reefs (Bugnot et al. 2022). Therefore, there is potential for shellfish reefs to enhance seed retention and seagrass growth and reproduction via the provision of nutrients in more exposed and nutrient-deprived areas.

Conclusion

2021–2030 is the *UN Decade on Ecosystem Restoration*, and there are good opportunities and desire from government, community groups and the scientific community to restore degraded ecosystems. However, successful restoration and building climate-resilient coastal ecosystems are contingent on understanding the key environmental processes that both inhibit and promote restoration

and recovery. Despite the well-described influence of seagrass sediment interactions on seagrass performance, they are rarely considered in seagrass restoration, despite their potential to transform restoration success at scale.

This review identified significant opportunities to enhance seagrass restoration by explicitly including seagrass-sediment interactions. This includes enhanced methods for restoration, more effective monitoring and assessment of restoration success. Importantly, we suggest extending decision-making frameworks to include sediment processes as they are of primary concern in determining initial site suitability and affect subsequent decisions and planning for restoration (Figure 4, Panel 1). At the outset, we recognise that hydrodynamics play a key role in determining sediment factors that may both benefit and hinder the successful restoration of seagrasses. We suggest therefore that an assessment of hydrodynamics and its implications for sediment properties and microbial community development is an important first step in site selection, the choice of restoration strategies and the selection of suitable donor material.

Across the areas we identified, it is evident that seagrass sediment interactions are at the heart of many feedback processes influencing seagrass health. It is now more important than ever to understand the role of sediment interactions in seagrass health as climatic changes and human disturbances will increasingly impact these interactions between seagrasses and the sediment. Indeed, emerging research is showing that belowground microbes become even more important to plant performance and resilience with increasing stress (Fuggle et al. 2023). Thus, in the face of ever-increasing environmental changes, we predict that understanding these interactions will only become more important and thus critical for seagrass restoration.

Future studies on seagrasses should focus on a better understanding of (1) the functioning of the seagrass microbiome and its relationship with seagrass genetics; (2) seagrass-sediment interactions across ecological contexts; and especially (3) how the seagrass microbiome, genetics and bioengineers can increase seagrass resilience to environmental changes. These studies not only are critical to broaden our understanding of important aspects of seagrass ecology but will also be extremely

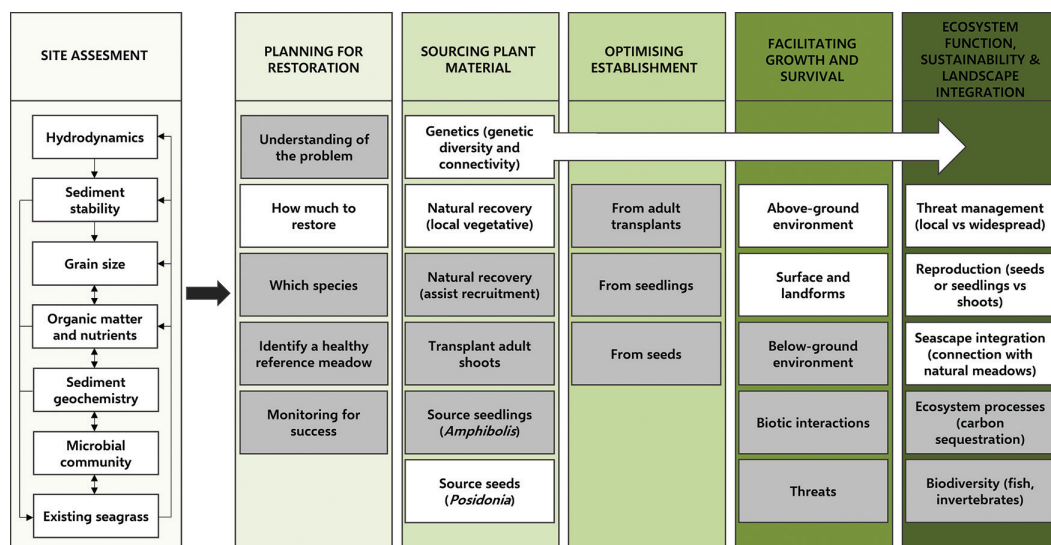


Figure 4 Extended ecological decision-making framework for seagrass restoration that explicitly includes belowground interactions. Boxes in grey indicate which actions or processes of restoration are influenced by belowground interactions. Vertical panels 2–5 to the right adapted from Miller et al. (2017) for marine restoration (Statton et al. 2021). The additional first vertical panel explicitly incorporates the sediment process as a primary consideration into the decision-making framework for seagrass restoration.

useful for seagrass restoration activities. The outcomes of these studies would help us identify how and which seagrass species or habitats will be most affected by climate change and which sediment processes promote or decrease seagrass health under stressful conditions. As a result, we could get an understanding of how to manage sediment conditions that promote the growth of seagrasses across different environments (Birnbaum & Trevathan-Tackett 2022). For example, mutualistic microbes and bioengineers could potentially be used to enhance the resilience of existing seagrass meadows or the survival of transplanted seagrasses. The right experimental strategies aimed at understanding the role of sediment processes in seagrass health will provide evidence-based insight into what management actions, at small and large scales, will improve seagrass restoration efforts now and into the future.

Acknowledgements

This work was funded under the Australian Government's National Environment Science Program (NESP).

References

- Abelson, A., Halpern, B.S., Reed, D.C., Orth, R.J., Kendrick, G.A., Beck, M.W., Belmaker, J., Krause, G., Edgar, G.J., Airoidi, L., Brokovich, E., France, R., Shashar, N., de Blaeij, A., Stambler, N., Salameh, P., Shechter, M. & Nelson, P.A. 2016. Upgrading marine ecosystem restoration using ecological-social concepts. *BioScience* **66**, 156–163.
- Abelson, A., Reed, D.C., Edgar, G.J., Smith, C.S., Kendrick, G.A., Orth, R.J., Airoidi, L., Silliman, B., Beck, M.W., Krause, G., Shashar, N., Stambler, N. & Nelson, P. 2020. Challenges for restoration of coastal marine ecosystems in the anthropocene. *Frontiers in Marine Science* **7**, 544105.
- Aller, R.C. 1988. Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. *Nitrogen Cycling in Coastal Marine Environments* **1988**, 301–338.
- Angers, D.A. & Caron, J. 1998. Plant-induced changes in soil structure: processes and feedbacks. *Biogeochemistry* **42**, 55–72.
- Arnaud-Haond, S., Migliaccio, M., Diaz-Almela, E., Teixeira, S., Van De Vliet, M.S., Alberto, F., Procaccini, G., Duarte, C.M. & Serrão, E.A. 2007. Vicariance patterns in the Mediterranean Sea: east-west cleavage and low dispersal in the endemic seagrass *Posidonia oceanica*. *Journal of Biogeography* **34**, 963–976.
- Bastyan, G.R. & Cambridge, M.L. 2008. Transplantation as a method for restoring the seagrass *Posidonia australis*. *Estuarine, Coastal and Shelf Science* **79**, 289–299.
- Bauer, J.T., Koziol, L. & Bever, J.D. 2018. Ecology of floristic quality assessment: testing for correlations between coefficients of conservatism, species traits and mycorrhizal responsiveness. *AoB Plants* **10**, plx073.
- Bever, J.D., Westover, K.M. & Antonovics, J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* **85**, 561–573.
- Birnbaum, C. & Trevathan-Tackett, S.M. 2022. Aiding coastal wetland restoration via the belowground soil microbiome: an overview. *Restoration Ecology* **31**, e13824.
- Blackburn, N.J. & Orth, R.J. 2013. Seed burial in eelgrass *Zostera marina*: the role of infauna. *Marine Ecology Progress Series* **474**, 135–145.
- de Boer, W.F. 2007. Seagrass-sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. *Hydrobiologia* **591**, 5–24.
- Booth, D.M. & Heck, K.L. 2009. Effects of the American oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. *Marine Ecology Progress Series* **389**, 117–126.
- Booth, M.W., Breed, M.F., Kendrick, G.A., Bayer, P.E., Severn-Ellis, A.A. & Sinclair, E.A. 2022. Tissue-specific transcriptome profiles identify functional differences key to understanding whole plant response to life in variable salinity. *Biology Open* **11**, bio059147.
- Bos, A.R. & Katwijk, M.M.V. 2007. Planting density, hydrodynamic exposure and mussel beds affect survival of transplanted intertidal eelgrass. *Marine Ecology Progress Series* **336**, 121–129.

- Boudouresque, C.F., Pergent, G., Pergent-Martini, C., Ruitton, S., Thibaut, T. & Verlaque, M. 2016. The necromass of the *Posidonia oceanica* seagrass meadow: fate, role, ecosystem services and vulnerability. *Hydrobiologia* **781**, 25–42.
- Bugnot, A.B., Dafforn, K.A., Coleman, R.A., Ramsdale, M., Gibbeson, J.T., Erickson, K., Vila-Concejo, A., Figueira, W.F. & Gribben, P.E. 2022. Linking habitat interactions and biodiversity within seascapes. *Ecosphere* **13**, e4021.
- Cambridge, M.L. & Kendrick, G.A. 2009. Contrasting responses of seagrass transplants (*Posidonia australis*) to nitrogen, phosphorus and iron addition in an estuary and a coastal embayment. *Journal of Experimental Marine Biology and Ecology* **371**, 34–41.
- Ceccherelli, G., Piazzini, L. & Cinelli, F. 2000. Response of the non-indigenous *Caulerpa racemosa* (Forsskål) J. Agardh to the native seagrass *Posidonia oceanica* (L.) delile: effect of density of shoots and orientation of edges of meadows. *Journal of Experimental Marine Biology and Ecology* **243**, 227–240.
- Chin, D.W., de Fouw, J., van der Heide, T., Cahill, B.V., Katcher, K., Paul, V.J., Campbell, J.E. & Peterson, B.J. 2021. Facilitation of a tropical seagrass by a chemosymbiotic bivalve increases with environmental stress. *Journal of Ecology* **109**, 204–217.
- Chisholm, J.R.M. & Moulin, P. 2003. Stimulation of nitrogen fixation in refractory organic sediments by *Caulerpa taxifolia* (Chlorophyta). *Limnology and Oceanography* **48**, 787–794.
- Coleman, M.A., Wood, G., Filbee-Dexter, K., Minne, A.J.P., Goold, H.D., Vergés, A., Marzinelli, E.M., Steinberg, P.D. & Wernberg, T. 2020. Restore or redefine: future trajectories for restoration. *Frontiers in Marine Science* **7**, 237.
- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S. & Turner, R.K. 2014. Changes in the global value of ecosystem services. *Global Environmental Change* **26**, 152–158.
- Coyer, J.A., Diekmann, O.E., Serrão, E.A., Procaccini, G., Milchakova, N., Pearson, G.A., Stam, W.T. & Olsen, J.L. 2004. Population genetics of dwarf eelgrass *Zostera noltii* throughout its biogeographic range. *Marine Ecology Progress Series* **281**, 51–62.
- Crump, B.C., Wojahn, J.M., Tomas, F. & Mueller, R.S. 2018. Metatranscriptomics and amplicon sequencing reveal mutualisms in seagrass microbiomes. *Frontiers in Microbiology* **9**, 388.
- Derksen-Hooijberg, M., Angelini, C., Lamers, L.P.M., Borst, A., Smolders, A., Hoogveld, J.R.H., de Paoli, H., van de Koppel, J., Silliman, B.R. & van der Heide, T. 2018. Mutualistic interactions amplify saltmarsh restoration success. *Journal of Applied Ecology* **55**, 405–414.
- Dijk, J.K.V., Tussenbroek, B.I.V., Jiménez-Durán, K., Márquez-Guzmán, G.J. & Ouborg, J. 2009. High levels of gene flow and low population genetic structure related to high dispersal potential of a tropical marine angiosperm. *Marine Ecology Progress Series* **390**, 67–77.
- Drouin, A., McKindsey, C.W. & Johnson, L.E. 2012. Detecting the impacts of notorious invaders: experiments versus observations in the invasion of eelgrass meadows by the green seaweed *Codium fragile*. *Oecologia* **168**, 491–502.
- Duffin, P., Martin, D.L., Pagenkopp Lohan, K.M. & Ross, C. 2020. Integrating host immune status, *Labyrinthula* spp. load and environmental stress in a seagrass pathosystem: assessing immune markers and scope of a new qPCR primer set. *PLoS One* **15**, e0230108.
- Duffy, J.E., Stachowicz, J.J., Reynolds, P.L., Hovel, K.A., Jahnke, M., Sotka, E.E., Boström, C., Boyer, K.E., Cusson, M., Eklöf, J., Engelen, A.H., Eriksson, B.K., Fodrie, F.J., Griffin, J.N., Hereu, C.M., Hori, M., Hughes, A.R., Ivanov, M.V., Jorgensen, P., Kruschel, C., Lee, K.-S., Lefcheck, J.S., Moksnes, P.-O., Nakaoka, M., O'Connor, M.I., O'Connor, N.E., Orth, R.J., Peterson, B.J., Reiss, H., Reiss, K., Richardson, J.P., Rossi, F., Ruesink, J.L., Schultz, S.T., Thormar, J., Tomas, F., Unsworth, R., Voigt, E., Whalen, M.A., Ziegler, S.L. & Olsen, J.L. 2022. A Pleistocene legacy structures variation in modern seagrass ecosystems. *Proceedings of the National Academy of Sciences* **119**, e2121425119.
- Dunic, J.C., Brown, C.J., Connolly, R.M., Turschwell, M.P. & Côté, I.M. 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. *Global Change Biology* **27**, 4096–4109.
- Edgeloe, J.M., Severn-Ellis, A.A., Bayer, P.E., Mehravi, S., Breed, M.F., Krauss, S.L., Batley, J., Kendrick, G.A. & Sinclair, E.A. 2022. Extensive polyploid clonality was a successful strategy for seagrass to expand into a newly submerged environment. *Proceedings of the Royal Society B* **289**, 20220538.
- Ettinger, C.L. & Eisen, J.A. 2019. Characterization of the Mycobiome of the Seagrass, *Zostera marina*, reveals putative associations with marine chytrids. *Frontiers in Microbiology* **10**, 2476.

- Ettinger, C.L. & Eisen, J.A. 2020. Fungi, bacteria and oomycota opportunistically isolated from the seagrass, *Zostera marina*. *PLoS One* **15**, e0236135.
- Evans, S. M., Griffin, K. J., Blick, R. A., Poore, A. G., & Vergés, A. 2018. Seagrass on the brink: Decline of threatened seagrass *Posidonia australis* continues following protection. *Plos one* **13**(4), e0190370.
- Fales, R.J., Boardman, F.C. & Ruesink, J.L. 2020. Reciprocal interactions between bivalve molluscs and seagrass: a review and meta-analysis. *Journal of Shellfish Research* **39**, 547–562.
- Ferguson, A.J., Gruber, R.K., Orr, M. & Scanes, P. 2016. Morphological plasticity in *Zostera muelleri* across light, sediment, and nutrient gradients in Australian temperate coastal lakes. *Marine Ecology Progress Series* **556**, 91–104.
- Fonseca, M.S. 2011. Addy revisited: what has changed with seagrass restoration in 64 years? *Ecological Restoration* **29**, 73–81.
- Fortes, M.D., Ooi, J.L.S., Tan, Y.M., Prathep, A., Bujang, J.S. & Yaakub, S.M. 2018. Seagrass in Southeast Asia: a review of status and knowledge gaps, and a road map for conservation. *Botanica Marina* **61**, 269–288.
- Fraser, M.W., Statton, J., Hovey, R.K., Laverock, B. & Kendrick, G.A. 2016. Seagrass derived organic matter influences biogeochemistry, microbial communities, and seedling biomass partitioning in seagrass sediments. *Plant and Soil* **400**, 133–146.
- Fraser, M.W., Gleeson, D.B., Grierson, P.F., Laverock, B. & Kendrick, G.A. 2018. Metagenomic evidence of microbial community responsiveness to phosphorus and salinity gradients in seagrass sediments. *Frontiers in Microbiology* **9**, 1703.
- Fraser, M.W., Martin, B.C., Wong, H.L., Burns, B.P. & Kendrick, G.A. 2023. Sulfide intrusion in a habitat forming seagrass can be predicted from relative abundance of sulfur cycling genes in sediments. *Science of the Total Environment* **864**, 161144.
- Fuggie, R.E., Gribben, P.E. & Marzinelli, E.M. 2023. Experimental evidence root-associated microbes mediate seagrass response to environmental stress. *Journal of Ecology* **111**, 1079–1093.
- Gagnon, K., Rinde, E., Bengil, E.G.T., Carugati, L., Christianen, M.J.A., Danovaro, R., Gambi, C., Govers, L.L., Kipson, S., Meysick, L., Pajusalu, L., Tüney Kızılkaya, İ., van de Koppel, J., van der Heide, T., van Katwijk, M.M. & Boström, C. 2020. Facilitating foundation species: the potential for plant-bivalve interactions to improve habitat restoration success. *Journal of Applied Ecology* **57**, 1161–1179.
- Garcias-Bonet, N., Arrieta, J.M., de Santana, C.N., Duarte, C.M. & Marbà, N. 2012. Endophytic bacterial community of a Mediterranean marine angiosperm (*Posidonia oceanica*). *Frontiers in Microbiology* **3**, 342.
- Garcias-Bonet, N., Eguíluz, V.M., Díaz-Rúa, R. & Duarte, C.M. 2021. Host-association as major driver of microbiome structure and composition in Red Sea seagrass ecosystems. *Environmental Microbiology* **23**, 2021–2034.
- Gilbertson, W.W., Solan, M. & Prosser, J.I. 2012. Differential effects of microorganism-invertebrate interactions on benthic nitrogen cycling. *FEMS Microbiology Ecology* **82**, 11–22.
- Glasby, T.M. 2013. *Caulerpa taxifolia* in seagrass meadows: killer or opportunistic weed? *Biological Invasions* **15**, 1017–1035.
- Goodman, J.L., Moore, K.A. & Dennison, W.C. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. *Aquatic Botany* **50**, 37–47.
- Govers, L.L., Heusinkveld, J.H.T., Gräfnings, M.L.E., Smeele, Q. & van der Heide, T. 2022. Adaptive intertidal seed-based seagrass restoration in the Dutch Wadden Sea. *PLoS One* **17**, e0262845.
- Gräfnings, M.L.E., Govers, L.L., Heusinkveld, J.H.T., Silliman, B.R., Smeele, Q., Valdez, S.R. & van der Heide, T. 2023. Macrozoobenthos as an indicator of habitat suitability for intertidal seagrass. *Ecological Indicators* **147**, 109948.
- Green, A. E., Unsworth, R. K., Chadwick, M. A., & Jones, P. J. 2021. Historical analysis exposes catastrophic seagrass loss for the United Kingdom. *Frontiers in plant science* **12**, 629962.
- Gribben, P.E., Nielsen, S., Seymour, J.R., Bradley, D.J., West, M.N. & Thomas, T. 2017. Microbial communities in marine sediments modify success of an invasive macrophyte. *Scientific Reports* **7**, 9845.
- Gribben, P.E., Thomas, T., Pusceddu, A., Bonechi, L., Bianchelli, S., Buschi, E., Nielsen, S., Ravaglioli, C. & Bulleri, F. 2018. Below-ground processes control the success of an invasive seaweed. *Journal of Ecology* **106**, 2082–2095.
- Grman, E., Allen, J., Galloway, E., McBride, J., Bauer, J.T. & Price, P.A. 2020. Inoculation with remnant prairie soils increased the growth of three native prairie legumes but not necessarily their associations with beneficial soil microbes. *Restoration Ecology* **28**, S393–S399.

- Hauxwell, J., Cebrián, J., Furlong, C. & Valiela, I. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* **82**, 1007–1022.
- Hauxwell, J., Cebrián, J. & Valiela, I. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* **247**, 59–73.
- Heinen, R., Hannula, S.E., Long, J.R.D., Huberty, M., Jongen, R., Kielak, A., Steinauer, K., Zhu, F. & Bezemer, T.M. 2020. Plant community composition steers grassland vegetation via soil legacy effects. *Ecology Letters* **23**, 973–982.
- Hernawan, U.E., van Dijk, K., Kendrick, G.A., Feng, M., Biffin, E., Lavery, P.S. & McMahon, K. 2017. Historical processes and contemporary ocean currents drive genetic structure in the seagrass *Thalassia hemprichii* in the Indo-Australian Archipelago. *Molecular Ecology* **26**, 1008–1021.
- Holmer, M., Marbà, N., Lamote, M. & Duarte, C.M. 2009. Deterioration of sediment quality in seagrass meadows (*Posidonia oceanica*) invaded by macroalgae (*Caulerpa* sp.). *Estuaries and Coasts* **32**, 456–466.
- Hovey, R.K., Cambridge, M.L. & Kendrick, G.A. 2011. Direct measurements of root growth and productivity in the seagrasses *Posidonia australis* and *P. sinuosa*. *Limnology and Oceanography* **56**, 394–402.
- Hughes, A.R. & Stachowicz, J.J. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences* **101**, 8998–9002.
- Hughes, A.R., Williams, S.L., Duarte, C.M., Heck Jr, K.L. & Waycott, M. 2009. Associations of concern: declining seagrasses and threatened dependent species. *Frontiers in Ecology and the Environment* **7**, 242–246.
- Jackson, E.L., Smith, T.M., York, P.H., Nielsen, J., Irving, A.D. & Sherman, C.D. 2021. An assessment of the seascape genetic structure and hydrodynamic connectivity for subtropical seagrass restoration. *Restoration Ecology* **29**, e13269.
- Johansson, J.O.R. & Greening, H.S. 1999. Seagrass restoration in Tampa Bay: a resource-based approach to estuarine management. In *Seagrasses*, Stephen A. Bortone (ed.). Boca Raton, Florida: CRC Press, 297–312.
- Johnson, A.J., Statton, J., Orth, R.J. & Kendrick, G.A. 2018. A sediment bioturbator bottleneck to seedling recruitment for the seagrass *Posidonia australis*. *Marine Ecology Progress Series* **595**, 89–103.
- Kaldy, J.E., Eldridge, P.M., Cifuentes, L.A. & Jones, W.B. 2006. Utilization of DOC from seagrass rhizomes by sediment bacteria: ¹³C-tracer experiments and modeling. *Marine Ecology Progress Series* **317**, 41–55.
- Kaldy, J.E., Brown, C.A. & Andersen, C.P. 2013. In situ ¹³C tracer experiments elucidate carbon translocation rates and allocation patterns in eelgrass *Zostera marina*. *Marine Ecology Progress Series* **487**, 27–39.
- Kardol, P. & Wardle, D.A. 2010. How understanding aboveground-belowground linkages can assist restoration ecology. *Trends in Ecology & Evolution* **25**, 670–679.
- Kardol, P., Martijn Bezemer, T. & van der Putten, W.H. 2006. Temporal variation in plant-soil feedback controls succession. *Ecology Letters* **9**, 1080–1088.
- Kendrick, G.A., Waycott, M., Carruthers, T.J.B., Cambridge, M.L., Hovey, R., Krauss, S.L., Lavery, P.S., Les, D.H., Lowe, R.J., Vidal, O.M.I., Ooi, J.L.S., Orth, R.J., Rivers, D.O., Ruiz-Montoya, L., Sinclair, E.A., Statton, J., van Dijk, J.K. & Verduin, J.J. 2012. The central role of dispersal in the maintenance and persistence of seagrass populations. *BioScience* **62**, 56–65.
- Kenworthy, W. J., Hall, M. O., Hammerstrom, K. K., Merello, M., & Schwartzschild, A. 2018. Restoration of tropical seagrass beds using wild bird fertilization and sediment regrading. *Ecological Engineering*, **112**, 72–81.
- Kilminster, K., McMahon, K., Waycott, M., Kendrick, G.A., Scanes, P., McKenzie, L., O'Brien, K.R., Lyons, M., Ferguson, A., Maxwell, P., Glasby, T. & Udy, J. 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment* **534**, 97–109.
- Kollars, N.M., Abbott, J.M. & Stachowicz, J.J. 2022. Hidden biodiversity: spatial mosaics of eelgrass genotypic diversity at the centimeter to meadow scale. *Ecology* **103**, e3813.
- Koziol, L. & Bever, J.D. 2015. Mycorrhizal response trades off with plant growth rate and increases with plant successional status. *Ecology* **96**, 1768–1774.
- Koziol, L. & Bever, J.D. 2016. AMF, phylogeny, and succession: specificity of response to mycorrhizal fungi increases for late-successional plants. *Ecosphere* **7**, e01555.
- Koziol, L., Schultz, P.A., House, G.L., Bauer, J.T., Middleton, E.L. & Bever, J.D. 2018. The plant microbiome and native plant restoration: the example of native mycorrhizal fungi. *BioScience* **68**, 996–1006.

- Kuiper, I., Lagendijk, E.L., Bloemberg, G.V. & Lugtenberg, B.J. 2004. Rhizoremediation: a beneficial plant-microbe interaction. *Molecular Plant-Microbe Interactions* **17**, 6–15.
- Lacoste, É., Piot, A., Archambault, P., McKindsey, C.W. & Nozais, C. 2018. Bioturbation activity of three macrofaunal species and the presence of meiofauna affect the abundance and composition of benthic bacterial communities. *Marine Environmental Research* **136**, 62–70.
- Lee, H., Golicz, A.A., Bayer, P.E., Severn-Ellis, A.A., Chan, C.-K.K., Batley, J., Kendrick, G.A. & Edwards, D. 2018. Genomic comparison of two independent seagrass lineages reveals habitat-driven convergent evolution. *Journal of Experimental Botany* **69**, 3689–3702.
- Lefcheck, J.S., Orth, R.J., Dennison, W.C., Wilcox, D.J., Murphy, R.R., Keisman, J., Gurbisz, C., Hannam, M., Landry, J.B., Moore, K.A., Patrick, C.J., Testa, J., Weller, D.E. & Batiuk, R.A. 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proceedings of the National Academy of Sciences* **115**, 3658–3662.
- Li, C.-J., Li, W.-T., Liu, J., Zhang, X. & Zhang, P. 2017. *Zostera marina* seed burial can be enhanced by Manila clam *Ruditapes philippinarum*: a microcosm study. *Ocean Science Journal* **52**, 221–229.
- Macreadie, P.I., Atwood, T.B., Seymour, J.R., Fontes, M.L.S., Sanderman, J., Nielsen, D.A. & Connolly, R.M. 2019. Vulnerability of seagrass blue carbon to microbial attack following exposure to warming and oxygen. *Science of The Total Environment* **686**, 264–275.
- Maltz, M.R. & Treseder, K.K. 2015. Sources of inocula influence mycorrhizal colonization of plants in restoration projects: a meta-analysis. *Restoration Ecology* **23**, 625–634.
- Martin, B.C., Statton, J., Siebers, A.R., Grierson, P.F., Ryan, M.H. & Kendrick, G.A. 2018. Colonizing tropical seagrasses increase root exudation under fluctuating and continuous low light. *Limnology and Oceanography* **63**, S381–S391.
- Martin, B.C., Bougoure, J., Ryan, M.H., Bennett, W.W., Colmer, T.D., Joyce, N.K., Olsen, Y.S. & Kendrick, G.A. 2019. Oxygen loss from seagrass roots coincides with colonisation of sulphide-oxidising cable bacteria and reduces sulphide stress. *The ISME Journal* **13**, 707–719.
- Martin, B.C., Alarcon, M.S., Gleeson, D., Middleton, J.A., Fraser, M.W., Ryan, M.H., Holmer, M., Kendrick, G.A. & Kilminster, K. 2020. Root microbiomes as indicators of seagrass health. *FEMS Microbiology Ecology* **96**, fuz201.
- Martin, B.C., Middleton, J.A., Skrzypek, G., Kendrick, G.A., Cosgrove, J. & Fraser, M.W. 2022. Composition of seagrass root associated bacterial communities are linked to nutrients and heavy metal concentrations in an anthropogenically influenced estuary. *Frontiers in Marine Science* **8**, 768864.
- Martinetto, P., Montemayor, D.I., Alberti, J., Costa, C.S.B. & Iribarne, O. 2016. Crab bioturbation and herbivory may account for variability in carbon sequestration and stocks in south west Atlantic salt marshes. *Frontiers in Marine Science* **3**, 122.
- McGlathery, K.J., Reidenbach, M.A., D'odorico, P., Fagherazzi, S., Pace, M.L. & Porter, J.H. 2013. Nonlinear dynamics and alternative stable states in shallow coastal systems. *Oceanography* **26**, 220–231.
- McKinnon, J.G., Gribben, P.E., Davis, A.R., Jolley, D.F. & Wright, J.T. 2009. Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. *Marine Ecology Progress Series* **380**, 59–71.
- McLeod, I.M., Boström-Einarsson, L., Johnson, C.R., Kendrick, G., Layton, C., Rogers, A.A. & Statton, J. 2018. *The Role of Restoration in Conserving Matters of National Environmental Significance in Marine and Coastal Environments*. Hobart, Tasmania: NESP Marine Biodiversity Hub.
- McMahon, K.M., Evans, R.D., van Dijk, K., Hernawan, U., Kendrick, G.A., Lavery, P.S., Lowe, R., Puotinen, M. & Waycott, M. 2017. Disturbance is an important driver of clonal richness in tropical seagrasses. *Frontiers in Plant Science* **8**, 2026.
- Meehan, A.J. & West, R.J. 2002. Experimental transplanting of *Posidonia australis* seagrass in Port Hacking, Australia, to assess the feasibility of restoration. *Marine Pollution Bulletin* **44**, 25–31.
- Meehan, A.J. & West, R.J. 2004. Seedling development and patch formation of the seagrass *Posidonia australis* in a southeast Australian estuary. *Aquatic Botany* **79**, 1–14.
- Meyer, D.L., Townsend, E.C. & Thayer, G.W. 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restoration Ecology* **5**, 93–99.
- Meysick, L., Infantes, E. & Boström, C. 2019. The influence of hydrodynamics and ecosystem engineers on eelgrass seed trapping. *PLoS One* **14**, e0222020.

- Miller, B.P., Sinclair, E.A., Menz, M.H., Elliott, C.P., Bunn, E., Commander, L.E. & Stevens, J.C. 2017. A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. *Restoration Ecology* **25** (4), 605–617.
- Mohammadi, N.S., Buapet, P., Pernice, M., Signal, B., Kahlke, T., Hardke, L. & Ralph, P.J. 2019. Transcriptome profiling analysis of the seagrass, *Zostera muelleri* under copper stress. *Marine pollution bulletin* **149**, 110556.
- Mohr, W., Lehnen, N., Ahmerkamp, S., Marchant, H.K., Graf, J.S., Tschitschko, B., Yilmaz, P., Littmann, S., Gruber-Vodicka, H., Leisch, N., Weber, M., Lott, C., Schubert, C.J., Milucka, J. & Kuypers, M.M.M. 2021. Terrestrial-type nitrogen-fixing symbiosis between seagrass and a marine bacterium. *Nature* **600**, 1–5.
- Neuenkamp, L., Prober, S.M., Price, J.N., Zobel, M. & Standish, R.J. 2019. Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. *Fungal Ecology* **40**, 140–149.
- Nguyen, H.M., Kim, M., Ralph, P.J., Marín-Guirao, L., Pernice, M. & Procaccini, G. 2020. Stress memory in seagrasses: first insight into the effects of thermal priming and the role of epigenetic modifications. *Frontiers in Plant Science* **11**, 494.
- Nguyen, H.M., Bulleri, F., Marín-Guirao, L., Pernice, M. & Procaccini, G. 2021. Photo-physiology and morphology reveal divergent warming responses in northern and southern hemisphere seagrasses. *Marine Biology* **168**, 129.
- Olsen, J.L., Stam, W.T., Coyer, J.A., Reusch, T.B., Billingham, M., Boström, C., Calvert, E., Christie, H., Granger, S. & Lumiere, R.L. 2004. North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology* **13**, 1923–1941.
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M. & Williams, S.L. 2006. A global crisis for seagrass ecosystems. *BioScience* **56**, 987.
- Orth, R.J., Moore, K.A., Marion, S.R., Wilcox, D.J. & Parrish, D.B. 2012. Seed addition facilitates eelgrass recovery in a coastal bay system. *Marine Ecology Progress Series* **448**, 177–196.
- Orth, R.J., Lefcheck, J.S., McGlathery, K.S., Aoki, L., Luckenbach, M.W., Moore, K.A., Oreska, M.P.J., Snyder, R., Wilcox, D.J. & Lusk, B. 2020. Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. *Science Advances* **6**, eabc6434.
- Pansini, A., Bosch-Belmar, M., Berlino, M., Sarà, G. & Ceccherelli, G. 2022. Collating evidence on the restoration efforts of the seagrass *Posidonia oceanica*: current knowledge and gaps. *Science of The Total Environment* **851**, 158320.
- Pazzaglia, J., Nguyen, H.M., Santillán-Sarmiento, A., Ruocco, M., Dattolo, E., Marín-Guirao, L. & Procaccini, G. 2021. The genetic component of seagrass restoration: what we know and the way forwards. *Water* **13**, 829.
- Peterson, B.J. & Heck, K.L. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. *Journal of Experimental Marine Biology and Ecology* **240**, 37–52.
- Petersen, J.M., Kemper, A., Gruber-Vodicka, H., Cardini, U., Van Der Geest, M., Kleiner, M., Bulgheresi, S., Mußmann, M., Herbold, C. & Seah, B.K. 2016. Chemosynthetic symbionts of marine invertebrate animals are capable of nitrogen fixation. *Nature microbiology* **2**, 1–11.
- Phelps, C.M., McMahon, K., Bissett, A., Bernasconi, R., Steinberg, P.D., Thomas, T., Marzinelli, E.M. & Huggett, M.J. 2021. The surface bacterial community of an Australian kelp shows cross-continental variation and relative stability within regions. *FEMS Microbiology Ecology* **97**, fiab089.
- Piercey, R.S., Gribben, P.E., Hanley, T.C., Moles, A.T. & Hughes, A.R. 2021. Incorporating marine macrophytes in plant-soil feedbacks: emerging evidence and opportunities to advance the field. *Journal of Ecology* **109**, 614–625.
- Renton, M., Airey, M., Cambridge, M.L. & Kendrick, G.A. 2011. Modelling seagrass growth and development to evaluate transplanting strategies for restoration. *Annals of Botany* **108**, 1213–1223.
- Reusch, T.B.H., Chapman, A.R.O. & Gröger, J.P. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Marine Ecology Progress Series* **108**, 265–282.
- Reynolds, L.K., McGlathery, K.J. & Waycott, M. 2012. Genetic diversity enhances restoration success by augmenting ecosystem services. *Plos One* **7**, e38397.

- de los Santos, C.B., Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C.M., van Katwijk, M.M., Pérez, M., Romero, J., Sánchez-Lizaso, J.L., Roca, G., Jankowska, E., Pérez-Lloréns, J.L., Fournier, J., Montefalcone, M., Pergent, G., Ruiz, J.M., Cabaço, S., Cook, K., Wilkes, R.J., Moy, F.E., Trayter, G.M.-R., Arañó, X.S., de Jong, D.J., Fernández-Torquemada, Y., Auby, I., Vergara, J.J. & Santos, R. 2019. Recent trend reversal for declining European seagrass meadows. *Nature Communications* **10**, 3356.
- Saunders, M., Waltham, N., Cannard, T., Sheppard, M., Fischer, M., Twomey, A., Bishop, M., Boody, K., Callaghan, D. & Fulton, B. 2022. A roadmap for coordinated landscape-scale coastal and marine ecosystem restoration. Report to the Reef and Rainforest Research Centre, Cairns, Queensland.
- Scholz, V.V., Martin, B.C., Meyer, R., Schramm, A., Fraser, M.W., Nielsen, L.P., Kendrick, G.A., Risgaard-Petersen, N., Burdorf, L.D. & Marshall, I.P. 2021. Cable bacteria at oxygen-releasing roots of aquatic plants: a widespread and diverse plant-microbe association. *The New Phytologist* **232**, 2138–2151.
- Serrano, C., Lovelock, C.E.B., Atwood, T., Macreadie, P.I., Canto, R., Phinn, S., Arias-Ortiz, A., Bai, L., Baldock, J., Bedulli, C., Carnell, P., Connolly, R.M., Donaldson, P., Esteban, A., Ewers Lewis, C.J., Eyre, B.D., Hayes, M.A., Horwitz, P., Hutley, L.B., Kavazos, C.R.J., Kelleway, J.J., Kendrick, G.A., KilmiVnster, K., Lafratta, A., Lee, S., Lavery, P.S., Maher, D.T., Marbà, N., Masque, P., Mateo, M.A., Mount, R., Ralph, P.J., Roelfsema, C., Rozaimi, M., Ruhon, R., Salinas, C., Samper-Villarreal, J., Sanderman, J., J. Sanders, C., Santos, I., Sharples, C., Steven, A.D.L., Cannard, T., Trevathan-Tackett, S.M. & Duarte, C.M. 2019. Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications* **10**, 4313.
- Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpang, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freeman, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Judson Kenworthy, W., La Nafie, Y.A., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., Tussenbroek, B. van, Vergara, S.G., Waycott, M. & Zieman, J.C. 2011. Extinction risk assessment of the world's seagrass species. *Biological Conservation* **144**, 1961–1971.
- Short, F.T., Kosten, S., Morgan, P.A., Malone, S. & Moore, G.E. 2016. Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany* **135**, 3–17.
- Siebert, T. & Branch, G.M. 2006. Ecosystem engineers: interactions between eelgrass *Zostera capensis* and the sandprawn *Callinassa kraussi* and their indirect effects on the mudprawn *Upogebia africana*. *Journal of Experimental Marine Biology and Ecology* **338**, 253–270.
- Sinclair, E.A., Krauss, S.L., Anthony, J., Hovey, R. & Kendrick, G.A. 2014. The interaction of environment and genetic diversity within meadows of the seagrass *Posidonia australis* (Posidoniaceae). *Marine Ecology Progress Series* **506**, 87–98.
- Sinclair, E.A., Edgeloe, J.M., Anthony, J.M., Statton, J., Breed, M.F. & Kendrick, G.A. 2020. Variation in reproductive effort, genetic diversity and mating systems across *Posidonia australis* seagrass meadows in Western Australia. *AoB Plants* **12**, plaa038.
- Sinclair, E.A., Sherman, C.D.H., Statton, J., Copeland, C., Matthews, A., Waycott, M., van Dijk, K.-J., Vergés, A., Kajlich, L., McLeod, I.M. & Kendrick, G.A. 2021a. Advances in approaches to seagrass restoration in Australia. *Ecological Management & Restoration* **22**, 10–21.
- Sinclair, E.A., Sherman, C.D.H., Statton, J., Copeland, C., Matthews, A., Waycott, M., van Dijk, K.-J., Vergés, A., Kajlich, L., McLeod, I.M. & Kendrick, G.A. 2021b. Advances in approaches to seagrass restoration in Australia. *Ecological Management & Restoration* **22**, 10–21.
- Sinclair, E.A., Hovey, R.K., Krauss, S.L., Anthony, J.M., Waycott, M. & Kendrick, G.A. 2023. Historic and contemporary biogeographic perspectives on range-wide spatial genetic structure in a widespread seagrass. *Ecology and Evolution* **13**, e9900.
- Smulders, F.O.H., Vonk, J.A., Engel, M.S. & Christianen, M.J.A. 2017. Expansion and fragment settlement of the non-native seagrass *Halophila stipulacea* in a Caribbean bay. *Marine Biology Research* **13**, 967–974.
- Soldan, R., Mapelli, F., Crotti, E., Schnell, S., Daffonchio, D., Marasco, R., Fusi, M., Borin, S. & Cardinale, M. 2019. Bacterial endophytes of mangrove propagules elicit early establishment of the natural host and promote growth of cereal crops under salt stress. *Microbiological Research* **223**, 33–43.
- Song, X., Zhou, Y., Zeng, J., Shou, L., Zhang, X., Yue, S., Gao, W., Feng, W., Wang, Z. & Du, P. 2021. Distinct root system acclimation patterns of seagrass *Zostera japonica* in sediments of different trophic status: a research by X-ray computed tomography. *Journal of Oceanology and Limnology* **39**, 2267–2280.
- Statton, J., Cambridge, M.L., Dixon, K.W. & Kendrick, G.A. 2013. Aquaculture of *Posidonia australis* seedlings for seagrass restoration programs: effect of sediment type and organic enrichment on growth. *Restoration Ecology* **21**, 250–259.

- Statton, J., Dixon, K.W., Irving, A.D., Jackson, E.L., Kendrick, G.A., Orth, R.J. & Sinclair, E.A. 2018. Decline and restoration ecology of Australian seagrasses. In *Seagrasses of Australia: Structure, Ecology and Conservation*, A.W.D. Larkum et al. (eds.). Cham: Springer International Publishing, 665–704.
- Statton, J., Sinclair, E.A., McNear, S., Kendrick, A. & Kendrick, G.A. 2021. Assisting recovery of seagrass in Shark Bay, Gathaagudu. Final Report to the National Environmental Science Program, Marine Biodiversity Hub, 89.
- Stief, P. 2013. Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic macrofauna: mechanisms and environmental implications. *Biogeosciences* **10**, 7829–7846.
- Strydom, S., Murray, K., Wilson, S., Huntley, B., Rule, M., Heithaus, M., Bessey, C., Kendrick, G.A., Burkholder, D., Fraser, M.W. & Zdunic, K. 2020. Too hot to handle: unprecedented seagrass death driven by marine heatwave in a world heritage area. *Global Change Biology* **26**, 3525–3538.
- Suchanek, T.H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *Journal of Marine Research* **41**, 281–298.
- Tan, Y.M., Dalby, O., Kendrick, G.A., Statton, J., Sinclair, E.A., Fraser, M.W., Macreadie, P.I., Gillies, C.L., Coleman, R.A., Waycott, M., van Dijk, K., Vergés, A., Ross, J.D., Campbell, M.L., Matheson, F.E., Jackson, E.L., Irving, A.D., Govers, L.L., Connolly, R.M., McLeod, I.M., Rasheed, M.A., Kirkman, H., Flindt, M.R., Lange, T., Miller, A.D. & Sherman, C.D.H. 2020. Seagrass restoration is possible: insights and lessons from Australia and New Zealand. *Frontiers in Marine Science* **7**, 617.
- Tarquino, F., Bourgoire, J., Koenders, A., Laverock, B., Säwström, C. & Hyndes, G.A. 2018. Microorganisms facilitate uptake of dissolved organic nitrogen by seagrass leaves. *The ISME Journal* **12**, 2796–2800.
- Tarquino, F., Hyndes, G.A., Laverock, B., Koenders, A. & Säwström, C. 2019. The seagrass holobiont: understanding seagrass-bacteria interactions and their role in seagrass ecosystem functioning. *FEMS Microbiology Letters* **366**, fnz057.
- Tarquino, F., Atlan, O., Vanderklift, M.A., Berry, O. & Bissett, A. 2021. Distinct endophytic bacterial communities inhabiting seagrass seeds. *Frontiers in Microbiology* **12**, 14.
- Tavares, A.I., Assis, J., Larkin, P.D., Creed, J.C., Magalhães, K., Horta, P., Engelen, A., Cardoso, N., Barbosa, C., Pontes, S., Regalla, A., Almada, C., Ferreira, R., Abdoul, B.M., Ebaye, S., Bourweiss, M., dos Santos, C.V.-D., Patrício, A.R., Teodósio, A., Santos, R., Pearson, G.A. & Serrao, E.A. 2023. Long range gene flow beyond predictions from oceanographic transport in a tropical marine foundation species. *Scientific Reports* **13**, 9112.
- Thompson, L.R., Sanders, J.G., McDonald, D., Amir, A., Ladau, J., Locey, K.J., Prill, R.J., Tripathi, A., Gibbons, S.M., Ackermann, G., Navas-Molina, J.A., Janssen, S., Kopylova, E., Vázquez-Baeza, Y., González, A., Morton, J.T., Mirarab, S., Zech Xu, Z., Jiang, L., Haroon, M.F., Kanbar, J., Zhu, Q., Jin Song, S., Kosciulek, T., Bokulich, N.A., Lefler, J., Brislawn, C.J., Humphrey, G., Owens, S.M., Hampton-Marcell, J., Berg-Lyons, D., McKenzie, V., Fierer, N., Fuhrman, J.A., Clauset, A., Stevens, R.L., Shade, A., Pollard, K.S., Goodwin, K.D., Jansson, J.K., Gilbert, J.A. & Knight, R. 2017. A communal catalogue reveals Earth’s multiscale microbial diversity. *Nature* **551**, 457–463.
- Ugarelli, K., Chakrabarti, S., Laas, P. & Stingl, U. 2017. The seagrass holobiont and its microbiome. *Microorganisms* **5**, 81.
- van Katwijk, M.M., Bos, A.R., de Jonge, V.N., Hanssen, L.S.A.M., Hermus, D.C.R. & de Jong, D.J. 2009. Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Marine Pollution Bulletin* **58**, 179–188.
- van Katwijk, M.M., Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A., Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K.-S., Meinesz, A., Nakaoka, M., O’Brien, K.R., Paling, E.I., Pickerell, C., Ransijn, A.M.A. & Verduin, J.J. 2016. Global analysis of seagrass restoration: the importance of large-scale planting. *Journal of Applied Ecology* **53**, 567–578.
- van Katwijk, M.M., van Tussenbroek, B.I., Hanssen, S.V., Hendriks, A.J. & Hanssen, L. 2021. Rewilding the Sea with domesticated seagrass. *BioScience* **71**, 1171–1178.
- Van Keulen, M., Paling, E. I., & Walker, C. J. 2003. Effect of planting unit size and sediment stabilization on seagrass transplants in Western Australia. *Restoration Ecology* **11**(1), 50–55.
- van der Geest, M., van der Heide, T., Holmer, M. & de Wit, R. 2020. First field-based evidence that the seagrass-lucinid mutualism can mitigate sulfide stress in seagrasses. *Frontiers in Marine Science* **7**, 11.
- Van der Putten, W.H., Van Dijk, C. & Peters, B.A.M. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* **362**, 53–56.

- Van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Voorde, T.F.J.V. de & Wardle, D.A. 2013. Plant-soil feedbacks: the past, the present and future challenges. *Journal of Ecology* **101**, 265–276.
- Veen, G.F., Fry, E.L., ten Hooven, F.C., Kardol, P., Morriën, E. & De Long, J.R. 2019. The role of plant litter in driving plant-soil feedbacks. *Frontiers in Environmental Science* **7**, 168.
- Vinther, H.F. & Holmer, M. 2008. Experimental test of biodeposition and ammonium excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance. *Journal of Experimental Marine Biology and Ecology* **364**, 72–79.
- Volkenborn, N., Robertson, D.M. & Reise, K. 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. *Helgoland Marine Research* **63**, 27–35.
- Wang, L., Tomas, F. & Mueller, R.S. 2020. Nutrient enrichment increases size of *Zostera marina* shoots and enriches for sulfur and nitrogen cycling bacteria in root-associated microbiomes. *FEMS Microbiology Ecology* **96**, fiae129.
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T. & Williams, S.L. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12377–12381.
- Webb, A.P. & Eyre, B.D. 2004. Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Marine Ecology Progress Series* **268**, 205–220.
- Wendländer, N.S., Lange, T., Connolly, R.M., Kristensen, E., Pearson, R.M., Valdemarsen, T. & Flindt, M.R. 2019. Assessing methods for restoring seagrass (*Zostera muelleri*) in Australia's subtropical waters. *Marine and Freshwater Research* **71**, 996–1005.
- Whitfield, A.K. 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries* **27**, 75–110.
- Williams, S.L. 1990. Experimental studies of Caribbean seagrass bed development. *Ecological Monographs* **60**, 449–469.
- Wood, G., Marzinelli, E.M., Coleman, M.A., Campbell, A.H., Santini, N.S., Kajlich, L., Verdura, J., Wodak, J., Steinberg, P.D., Vergés, A., Wood, G., Marzinelli, E.M., Coleman, M.A., Campbell, A.H., Santini, N.S., Kajlich, L., Verdura, J., Wodak, J., Steinberg, P.D. & Vergés, A. 2019. Restoring subtidal marine macrophytes in the Anthropocene: trajectories and future-proofing. *Marine and Freshwater Research* **70**, 936–951.
- Wood, G., Marzinelli, E.M., Vergés, A., Campbell, A.H., Steinberg, P.D. & Coleman, M.A. 2020. Using genomics to design and evaluate the performance of underwater forest restoration. *Journal of Applied Ecology* **57**, 1988–1998.
- Wright, J.T. 2005. Differences between native and invasive *Caulerpa taxifolia*: a link between asexual fragmentation and abundance in invasive populations. *Marine Biology* **147**, 559–569.
- Wubs, E.R.J., van der Putten, W.H., Bosch, M. & Bezemer, T.M. 2016. Soil inoculation steers restoration of terrestrial ecosystems. *Nature Plants* **2**, 1–5.
- Zabarte-Maeztu, I., Matheson, F.E., Manley-Harris, M., Davies-Colley, R.J. & Hawes, I. 2021. Fine sediment effects on seagrasses: a global review, quantitative synthesis and multi-stressor model. *Marine Environmental Research* **171**, 105480.