



To restore coastal marine areas, we need to work across multiple habitats simultaneously

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Restoration of coastal marine habitats—often conducted under the umbrella of "nature-based solutions"—is one of the key actions underpinning global intergovernmental agreements, including the Paris Agreement and the 2021–2030 United Nations (UN) Decade of Restoration. To achieve global biodiversity and restoration targets, such as the Kunming-Montreal Global Biodiversity Framework, which aims to restore 30% of degraded ecosystems by 2030, we need methods that accelerate and scale up restoration activities in size and impact. Part of the solution is crosshabitat facilitation—positive interactions that occur when processes generated in one habitat benefit another. These interactions involve physical, biological, and biogeochemical processes, such as wave energy dampening, competition reduction, and nutrient cycling.

To date, positive cross-habitat interactions, henceforth known as "facilitative interactions," underpin coastal ecosystem development, resilience, and expansion (1–3), but have received little attention in coastal marine restoration practice beyond small-scale studies. We found that only 6 of 2,145 coastal marine restoration studies addressed restoration of multiple habitats concurrently, and just 3 explicitly aimed to harness cross-habitat facilitation. In contrast, terrestrial ecosystem restoration often employs multihabitat restoration approaches (4).

And yet, these interactions are incredibly important for habitat formation. Without cross-habitat facilitation via oyster and coral reefs that baffle waves, for example, saltmarshes, seagrasses, and mangroves cannot naturally develop in many locations. Biotic interactions, such as species migrations, can mediate long-distance cross-habitat facilitation (5, 6). Cross-habitat facilitation can extend beyond coastal marine seascape interactions to interactions across marine-terrestrial borders. For example, nutrient exchange between land and sea can increase sand dune or reef productivity (7).

Coastal habitats, like this one in Tacilevu, Fiji, are highly productive and diverse, supporting livelihoods and biodiversity. Facilitative, or positive, cross-habitat interactions, such as wave breaking by coral reefs or sediment trapping by seagrass and mangroves, enable other habitats to persist and thrive. And yet, restoration activities are not usually planned across multiple habitat types. Image credit: Joey Crosswell (CSIRO, Dutton Park, Australia).

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We argue that successful scaling of coastal marine restoration requires a conceptual and practice-based shift from single-habitat practices to restoration endeavors that focus on rebuilding multiple, connected habitats across seascapes. An emerging field of restoration research and practice is demonstrating that cross-habitat facilitation can improve restoration outcomes and yield multiple cobenefits, often for minimal cost (1). Only when large- and small-scale facilitative interactions are both included in restoration can we systematically harness their benefits (1, 8). Practitioners, scientists, and natural resource managers may achieve this by basing multihabitat restoration design on the patterns and spacings observed between habitats in natural seascapes, measuring or using models to quantify the distances over which cross-habitat facilitation occurs, integrating restoration programs across agencies, and genuine commitments to global agreements that reduce the underlying causes of habitat loss (e.g., climate change, urbanization).

Special Roles

Physical, chemical, and biological connections among coastal marine habitats determine how they are characteristically distributed in seascapes. For instance, seagrass and mangroves are found in quiescent waters, which in the tropics are often formed by offshore coral reefs that act as a "wave break" (9). In turn, seagrass and coral reefs are often located offshore of mangroves, which trap sediments to create water

clear enough to support photosynthesis (10). These close connections among habitats mean that the loss or degradation of one habitat type can have negative outcomes on adjacent ecosystems (9). To promote resilience and sustainability, restoration designs should consider how the spatial configurations and dependencies of multiple habitat types affect one another in positive ways.

Facilitative interactions between coastal marine habitat types are well-documented. We found 116 studies that have reported facilitative interactions between pairs of coastal marine habitat-forming species (SI Appendix, Tables S1 and S2). Wave attenuation, provision of hard substrate for settlement and growth of other species, and nutrient regulation are among the most common mechanisms by which one habitat helped a second habitat thrive (Fig. 1A). For instance, shading and substrate abrasion by transplanted kelp on restored oyster reefs reduced the settlement of competitive turfing algae and increased oyster recruitment 26-fold in the area immediately beneath the kelp (11). The underlying mechanisms of cross-habitat facilitation have been well-documented (2, 3), yet their translation into restoration practice, particularly over larger spatial scales, has rarely been attempted, demonstrated, or systematically called for.

A variety of barriers can hinder the adoption of multihabitat restoration. They include insufficient understanding of how multiple restored habitat types interact over different temporal and spatial scales, stakeholder conflicts, inadequate funding to achieve multihabitat restoration, a lack of cross-discipline

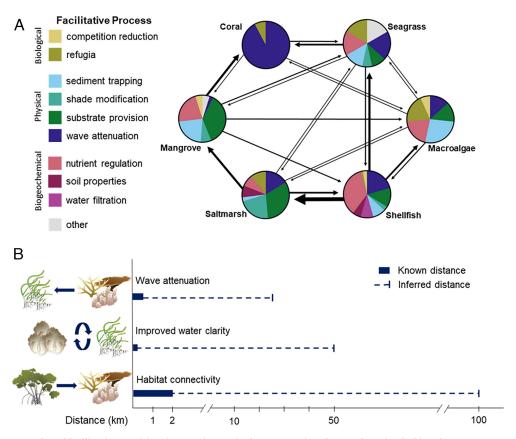


Fig. 1. (A) Over 200 examples of facilitative (positive) interactions exist between pairs of coastal marine habitat formers (SI Appendix, Tables S2 and S3). Arrows point to the directionality of interactions and are weighted according to the proportion of interactions reported between each pair, relative to the total number of interactions recorded from this review. (B) The maximum reported distance of facilitative interactions for each of three types of interaction (solid bars) is much smaller than the distances over which these processes operate as inferred from other studies (dashed lines), highlighting potential to harness large-scale facilitative interactions in restoration practice (SI Appendix, Table S4). Image credit: T. Saxby, C. Collier, and T. Carruthers (Integration and Application Network, University of Maryland, Cambridge, MD).

perspectives when planning and designing restoration, and permits that do not consider multiple habitat types and may ultimately prevent incorporation of multiple habitat types in restoration designs (12, 13). Furthermore, the current paradigm in restoration practice among permitting bodies and practitioners seeks to minimize negative interactions, such as competition, rather than harness positive interactions (1). Although most restoration is done on single habitats, at the seascape scale, this may result in intentionally spacing restored habitats away from other habitats to reduce the chance that restoration of one habitat might negatively impact adjacent habitats.

Although interactions among different habitat types are not universally positive, we can avoid negative interactions in multihabitat restoration practice by identifying the distances between habitats where facilitative interactions are most common and use these to design the spacing and configuration of restoration. Understanding how environmental conditions may exacerbate unwanted negative interactions also needs to be accounted for [e.g., sea-level rise exacerbating mangrove encroachment of saltmarshes (14)]. By better understanding interactions among habitat types, researchers and managers can scale up the benefits of multihabitat restoration and improve coastal marine habitat restoration efforts.

Scale Matters

Small-scale facilitative interactions are frequently observed between pairs of habitat-forming species (Fig. 1 and SI Appendix, Fig. S1). However, incorporating large-scale facilitative interactions across habitats and seascapes is needed to scale up coastal marine restoration efforts. In restoration, the spatial scales of documented examples of multihabitat restoration to date are orders of magnitude smaller than those of singlehabitat restoration activities reported for mangrove and kelp habitats (SI Appendix, Fig. S2 and Table S3). Despite this, there still appears to be strong evidence for cross-habitat facilitation in restoration. For example, planting mangrove propagules and simultaneously constructing oyster reefs within 20 meters led to overall increased survival and settlement of habitat-formers and their associated communities (15). Cross-habitat facilitation can operate at larger scales, greater than 1 kilometer. One study found that reinstating tidal flows to impounded areas of modified coastal land allowed for the natural rehabilitation of multiple wetland habitat types (e.g., mangrove and saltmarsh). This enhanced nutrient cycle functioning over at least 2 square kilometers, the area over which it was measured (16). Lessons learned from these cases may help guide future multihabitat restoration efforts to achieve success on similar scales.

To better implement large-scale and long-term multihabitat restoration will require policy changes.

Ecological modeling provides mechanisms to estimate cross-habitat interactions occurring over scales much larger than previously quantified. For example, empirical studies have shown that oysters and seagrass cycle nutrients and stabilize sediments at the scale of a few meters (17, 18). In contrast, modeling of filtration by oysters and sediment

stabilization by seagrass suggests that these biogeochemical and physical processes contribute to improved water clarity and may occur on the scale of entire estuaries [e.g., >50 kilometers (19); Fig. 1B). By modeling these interactions, we can better understand the large distances over which they occur.

Migratory animals can play a role as well. The feeding, defecation, and migratory patterns of large marine mammals such as whales, for instance, contribute substantially to nutrient cycling and productivity in the ocean—both vertically within the water column and latitudinally over thousands of kilometers (20). Likewise, diurnal migrations of reef fish to nearby seagrass to feed on invertebrates at night results in beneficial nutrient inputs to reefs during the day when fish return to rest and defecate under the corals (reviewed by ref. 5). Further investigation of biotic cross-habitat connections may reveal the large-scale potential of these interactions and opportunities to align species recovery and habitat restoration programs.

Facilitative interactions can also extend beyond coastal marine seascapes to terrestrial landscapes, mediated by biotic or physical connections. This, in turn, enhances biogeochemical processes. In one example, nutrient supply on desert islands with low productivity is enhanced by onshore accumulation of wrack and carrion, which, in turn, supports high abundances of terrestrial invertebrates and community biomass (7). Seabirds can similarly influence marine-to-terrestrial and terrestrial-to-marine dynamics. On the same desert island, organic deposits of guano from nesting or feeding seabirds supported more biodiverse terrestrial communities (7). These land-sea linkages can extend up to 1,000 kilometers. Pacific salmon migrate from marine to freshwater ecosystems, where nutrients from the salmon are deposited within streams (i.e., excretion) or in nearby riparian and forest areas (i.e., decomposition of carcasses from predator foraging). This, in turn, can enhance riparian vegetation that is important habitat for juvenile salmon (6). Such dynamics suggest that there may be ways to anticipate, account for, and harness large-scale positive interactions within and beyond coastal marine ecosystems as part of large-scale ecological restoration efforts.

Getting Results

To better implement large-scale and long-term multihabitat restoration will require policy changes. These include developing a coordinated seascape policy that articulates sea tenure through time, marine spatial planning to reconcile stakeholder conflict, adaptive management of restored sites to manage any unintended outcomes, coordination of restoration across agen-

> cies, and sufficient funding and resources to implement and monitor large-scale restoration. Successful single-habitat restoration—done at large scales and over long durations while delivering social and ecological benefits—can provide useful lessons (21). Innovation and technologies that accel-

erate and scale up restoration, such as industrial-scale harvesting, incubation, and deployment of coral larvae on coral reefs (22), can help us achieve more cost-effective solutions. Restoration practices should incorporate facilitative interactions at all scales and multiple habitat types, using conservationplanning approaches.

Multihabitat restoration approaches will underpin a new and emerging chapter in our efforts to conserve and restore coastal marine ecosystems. We found just six examples of multihabitat restoration in peer-reviewed studies, all published since 2015. In order to design future multihabitat restoration projects, we should draw guidance from naturally occurring configurations and spacing in seascapes and strive to understand how these configurations influence or are influenced by different biotic, biogeochemical, or physical interactions across different distances and between habitat types. In order to learn from nature, however, we do need more accurate local, regional, national, and global habitat distribution maps (23).

Climate change makes scaling up restoration efforts even more urgent. Blue carbon ecosystems, including seagrass, saltmarshes, and mangroves, can sequester large amounts of CO₂, thus mitigating some effects of climate change, and restoration of biodiverse coastal habitats can increase their resilience (24). Effectively restoring blue carbon habitats will require multihabitat approaches in many contexts; for example, the reinstation of tidal inundation of impounded lands can bring back saltmarshes and mangroves (16). Sea-level rise and warming are already causing shifts in the distribution of blue carbon ecosystems, sometimes resulting in conflicts from a management perspective [e.g., mangrove encroachment on saltmarshes (14)]. Plus, the capacity of blue carbon ecosystems to counteract the effects of climate change will become less effective once global temperatures increase by 1.5 °C, which will happen by 2050, based on current emissions trajectories (25, 26). We therefore have a small window of opportunity to implement ecological restoration over large scales to achieve global targets as set by the UN Conference of Parties on Climate Change and the UN Convention on Biological Diversity.

Clearly, there are real opportunities to improve coastal marine ecosystems through multihabitat restoration. The challenges in coastal marine ecosystems are sizeable. But the alternative is worse. As the symptoms of climate change worsen, the livelihoods, wellbeing, and safety of at least a billion people (26) are at stake due to coastal ecological degradation.

Fortunately, there is some evidence of greater awareness and initiatives. For example, the International Union for Conservation of Nature Great Blue Wall aims to develop a connected network of conserved and restored coastal habitats to protect livelihoods and conserve biodiversity in the western Indian Ocean by 2030. But there's plenty more that can be done. In line with the UN Decade on Ecosystem Restoration and the Kunming-Montreal Global Biodiversity Framework targets, we call on international agencies, governments, nonprofits, research organizations, contractors, and Indigenous groups to collaborate. To achieve real and lasting effects, we must try to forge policies that advance the restoration of multiple habitats within these connected seascapes at a wide range of scales. This will be a crucial step in the battle to fight climate change and conserve biodiversity.

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