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Nature-Based Coastal Defenses: Can Biodiversity Help?

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Abstract

The rapid degradation of ecosystems jeopardizes the services they provide. Among the most valuable of these services is protection of coastlines by shoreline ecological communities, such as coral reefs, mangroves and salt marshes. Currently, coastal protection potential of ecosystems is estimated primarily as a function of their spatial extent and type. The degree to which coastal protection depends on aspects of biodiversity within and across these ecosystems is, however, much less explored. Here we synthesize evidence from multiple sources to evaluate whether aspects of biodiversity may influence the degree of coastal protection afforded by coastal ecosystems. We discuss relevant biodiversity theory and the few studies that have investigated how species identity affects shoreline protection, as a first attempt to identify the aspects of biodiversity that are likely to be important in enhancing coastal protection efforts. This synthesis should empower ecologists, conservation scientists and practitioners to test for and then harness the unrealized, but high yield potential, of incorporating biodiversity into coastal defense planning.

Glossary

Biodiversity Variety of life forms often expressed in total number of species, on a specific spatial scale. Also includes genetic diversity.
Disturbance Events that affect ecosystems and their functioning.
Ecosystem functions Processes of energy exchange in ecosystems, such as the production of biomass and the fixation of carbon.
Ecosystem services Ecosystem functions that benefit people.
Facilitation One species benefiting another by mediating stresses.
Fetch Distance that wind can freely blow over water and creates waves.
Niche Position of species in an ecosystem in relation to other species and with respect to resource use, habitat requirement, etc.
Resilience The potential for recovery of an ecosystem after disturbances.

Key Points

The rapid degradation of ecosystems jeopardizes the services they provide. Among the most valuable of these services is protection of coastlines by shoreline ecological communities, such as coral reefs, mangroves and salt marshes. Here we synthesize evidence from multiple sources to evaluate whether aspects of biodiversity may influence the degree of coastal protection afforded by particular coastal ecosystems. This synthesis should empower ecologists, conservation scientists and practitioners to test for and then harness the unrealized, but high yield potential, of incorporating biodiversity into coastal defense planning.

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Introduction

Ecosystems provide humans with a host of valuable services, including food provisioning, water purification, carbon sequestration, climate regulation and natural protection (Costanza *et al.*, 1997; Daily, 1997; Barbier *et al.*, 2011). Among the most valuable of these services is protection of coastlines by natural shoreline communities, such as coral reefs, mangroves and salt marshes (MEA, 2005; Gedan *et al.*, 2011; Silliman *et al.*, 2019). By baffling water movement and dampening potentially destructive waves before they hit the terrestrial shoreline, the biotic structures created by organisms that make up coastal ecosystems reduce flooding and coastal erosion (Das and Vincent, 2009; Koch *et al.*, 2009). These valuable coastal ecosystem services are, however, being threatened because coastal ecosystems are suffering from widespread degradation through habitat destruction and species extinctions and the resultant reduction in biodiversity benefits that enhance system functions (Lotze *et al.*, 2006; Byrnes *et al.*, 2007; Worm *et al.*, 2007; Waycott *et al.*, 2009). Meanwhile, we are facing an increasing number of severe storms (Munich, 2011) and accelerated rates of sea-level rise are predicted (Mousavi *et al.*, 2011). Of all natural disasters, flooding events are second only to earthquakes as causes of fatalities and financial losses (Munich, 2010), and future costs for moving and protecting human shoreline communities are expected to be massive (Parry, 2009; Hinkel *et al.*, 2014). Consequently, understanding, conserving and harnessing the full benefits of natural ecosystems for coastal protection is a high conservation priority as global change stressors increase (He and Silliman, 2019).

Although the value of nature-based coastal storm protection is increasingly recognized (Sutton-Grier *et al.*, 2018; Menéndez *et al.*, 2020; Sun and Carson, 2020; Zhu *et al.*, 2020), our understanding of how to value this service remains largely based on measurements and models that do not account for physical or ecological complexities inherent in coastal ecosystems. Research, however, has begun to refine these models, yielding important implications for ecosystem service management strategies. For example, while the potential for a given coastal ecosystem to protect the coastline was traditionally thought to increase linearly with its size, evidence is mounting that this relationship is non-linear (Barbier *et al.*, 2008; Koch *et al.*, 2009; Narayan *et al.*, 2016; van Wesenbeeck *et al.*, 2017) and that below ground roots and above ground plant surface area are vital traits generating shoreline protection (Silliman *et al.*, 2016; Hijuelos *et al.*, 2019; Vuik *et al.*, 2018; Silliman *et al.*, 2019). Appreciation of this nonlinearity can guide ecosystem-based land use planning strategies that successfully integrate development and conservation goals. Despite these advances, scientists have yet to explicitly consider the possible role of other key system characteristics, such as biodiversity within ecosystems, in determining the quantity of coastal protection they provide.

The last 20 years have witnessed an explosion in research dedicated to understanding links between various aspects of biodiversity and ecosystem functioning (Loreau *et al.*, 2001; Balvanera *et al.*, 2006; Cardinale *et al.*, 2006; Reiss *et al.*, 2009; Bardgett and van der Putten, 2014; Gamfeldt *et al.*, 2014; Brose and Hillebrand, 2016). To date, the clearest message to emerge from this large body of work is that the identity of species (i.e., those with key functional traits that enhance focal processes) within an ecosystem can have strong influences on basic ecosystem functions, such as resource-uptake and productivity. While the identity of species can be a dominant determinant of ecosystem functioning, biodiversity-ecosystem functioning research has also shown that the richness (i.e., number) of biodiversity components (usually species, but also alleles or genotypes) can boost ecosystem functions and, therefore, may also boost associated services (Balvanera *et al.*, 2006; Cardinale, 2011; Tilman *et al.*, 2006). Although the precise ecological mechanisms underlying these effects are yet to be determined, there is growing evidence that "niche complementarity" (ecological differences among species such as phenology, response to disturbance, resource use etc.), plays a key role (Dimitrakopoulos and Schmid, 2004; Kahmen *et al.*, 2005; Cardinale *et al.*, 2011). Theory and growing empirical evidence suggest that such ecological differences among species will become increasingly important over large spatial and temporal scales and where more than one ecological function is considered (Gamfeldt *et al.*, 2008; Griffin *et al.*, 2009a,b; Isbell *et al.*, 2011). Differences among species in their responses to environmental conditions can help to maintain a steady level of ecosystem functioning in the face of environmental changes, as different species act as ecological "insurance" (Yachi and Loreau, 1999; Griffin and Silliman, 2011). In addition to increasing the breadth of ecological niches occupied and providing ecological insurance, a greater richness of species also increases the probability that particular key species (and combinations of species) will be present in a community.

A key, as yet largely unmet, challenge is to translate known effects of biodiversity on basic ecosystem functions (e.g., primary productivity, nutrient cycling) at local scales, to ecosystem services that are provisioned over larger scales and have a direct value to human society (Díaz *et al.*, 2006). In this article, we take the first step toward this goal, asking how aspects of biodiversity may affect nature-based coastal defenses. Specifically, we first provide an overview of the history of coastal protection and the increasing appeal of nature-based strategies; we then give examples of how aspects of biodiversity can be important at multiple scales, how ecosystem diversity across landscapes may be key for harnessing synergies, and even how diversity of trophic levels can be important. We end with a call for large-scale experiments and replicated comparative studies to test how diversity within different levels of ecological organization (species, genetic, ecosystem, and landscape) impacts coastal shoreline protection.

A Short History of Coastal Protection Strategies

Human populations are becoming increasingly concentrated in flood prone areas (e.g., along coasts and rivers; Cohen *et al.*, 1997), and losses of life and property from floods are expected to increase. Therefore, innovative methods for flood protection that maintain access to fresh water or aquatic food resources, while not hindering economic development, are urgently needed.

Incorporating naturally functioning ecosystems as part of coastal land development strategies has emerged as one of the most economically viable and effective ways to defend against floods while maintaining other ecosystem services (Barbier *et al.*, 2008; Feagin, 2008; Gedan *et al.*, 2011; Narayan *et al.*, 2016; Menéndez *et al.*, 2020; Sun and Carson, 2020).

Historically, flood management was a decentralized effort charged to individuals or small communities, and solutions often focused more on adapting to periodic flooding rather than flood prevention (van Koningsveld *et al.*, 2008). For example, many people living in seasonally flooded areas in the Netherlands and in Southeast Asia and Africa have traditionally restricted their domiciles to mounds or to floating rafts and often have economies that are intertwined with flooding events. In much of the world, however, economic development and technological advancements have led to increased centralization of flood management. Consequently, traditional solutions have become ever more displaced by the installation of complex flood defense systems that require large financial investments, large-scale construction, and long term management and maintenance strategies (Duxbury and Dickinson, 2007), and these often come at the cost of ecosystem integrity and biodiversity (Titus, 1998; van Wesenbeeck *et al.*, 2014; Gittman *et al.*, 2016).

Early efforts to develop flood management systems were singly focused on preventing floods without consideration of ecological impacts. In the 1970s, however, increasing environmental awareness and a response to more aggressive flood management approaches lead to legislation ensuring that environmental impacts were considered in flood management activities. In the 1980s, flood management decisions continued to take environmental impacts into consideration but weighed potential socioeconomic impacts of floods more heavily than environmental impacts when making flood control decisions (van Koningsveld *et al.*, 2008). It was not until the mid 1990s that integrated and multidisciplinary design and planning efforts began to emerge as policy makers started to fully appreciate that protecting socioeconomic interests was not necessarily in opposition to protecting ecosystems. Indeed, it was during this time that Integrated Coastal Zone Management (ICZM) (launched in 1994), was developed as a way to guarantee safety against flooding while maintaining other functions of coastal ecosystems. Over the past 15 years, managers have begun to fully embrace this integrative planning process, and innovative solutions to coastal flooding, such as "living shorelines" (Gedan *et al.*, 2011; Scyphers *et al.*, 2011; Smith *et al.*, 2020), Engineering with Nature (Bridges *et al.*) and "Building with Nature" (Borsje *et al*, 2011) have emerged that simultaneously enhance the protection of coastal populations, economic development and ecosystem integrity (Sutton-Grier *et al.*, 2015).

Initiatives and incentives that prioritize nature-based solutions to coastal flooding are being observed across a variety of organizations including conservation-minded organizations (e.g., the Audubon- Coastal Resilience initiative, The Nature Conservancy- Coastal Resilience initiative, IUCN's Commission on Ecosystem Management, etc.), engineering-minded groups (e.g., The Army Corps of Engineers partnership with Engineering with Nature, Slinger and Vreugdenhil (2020)), and governmental entities (e.g., Maryland, USA's New Tidal Wetland Regulations for Living Shorelines Act, 2008 and Victoria, Australia's Marine and Coastal policy). Moreover, as nature-based solutions bridge several sectors of interest, including ecosystem preservation and restoration, these initiatives will likely increase with a renewed call for global restoration (i.e., UN's "Decade of Ecosystem Restoration").

Nature-Based Coastal Defense: Where are We?

The need for sustainable and cost-effective flood and storm mitigation for coastal human communities has renewed interest in coastal protection provided by natural ecosystems. A variety of coastal and riparian ecosystems, including dunes, mangroves, marshes, seagrass beds, and coral and shellfish reefs, are recognized for their provision of coastal protection (UNEP-WCMC, 2006; MEA, 2005; Barbier *et al.*, 2008, 2011; Menéndez *et al.*, 2020; Zhu *et al.*, 2020). These coastal ecosystems form physical structures that attenuate waves, decrease water velocities, stabilize sediments, block winds and reduce erosion, and therefore function in a similar way as man-made coastal defense structures such as levees and dams (**Table 1**).

Coastal ecosystems that attenuate waves diminish coastal flooding and increase shoreline stability (Gedan *et al.*, 2011; Koch *et al.*, 2009; Borsje *et al.*, 2011; Temmerman *et al.*, 2013). The physical structure of coral and shellfish reefs, salt marshes, and mangroves create friction (i.e., drag), which slows water velocities (Christiansen *et al.*, 2000; Mazda *et al.*, 1997) and attenuates waves (marsh Coops *et al.*, 1996; Möller *et al.*, 1999, 2014; mangrove Mazda *et al.*, 1997; Bao, 2011; shellfish reefs Borsje *et al.*, 2011; coral reefs, Hardy and Young, 1996; Lugo-Fernandez *et al.*, 1998). Mangrove and marsh canopies and dunes block wind and

Table 1 Listing ecosystems, their coastal defense properties and additional services

Ecosystem	*Coastal defense properties*	*Additional services*
Coral reef	Wave dampening	Nature, tourism, food provisioning (fish)
Shellfish reef	Wave dampening	Nature, food provisioning (fish and shellfish)
Salt marsh	Wave dampening	Nature, nursery for seafood species
Riverine wetland	flood defense, water retention	Nature, nursery, water purification
Dunes and sandy beaches	flood defense	Tourism and recreation, water purification
Seagrasses	Mediation of currents and waves	Nature, nursery for fish, clam habitat
Mangroves	Reducing wave impact and current velocities	Nature, nursery, provisioning of food and firewood, tourism

reduce fetch and can further reduce wave heights (Campbell *et al.*, 2009). The structure created by organisms in these coastal ecosystems also reduces erosion of bed sediments and helps to stabilize shorelines by reducing water velocities and turbulence (marsh, Neumeier and Ciavola, 2004; mangrove, Mazda *et al.*, 1997 drag; oyster reefs Piazza *et al.*, 2005). Additionally, biotic structures such as roots, rhizomes, and shell debris provide a physical barrier between sediments and erosive water flow (mangrove, Mazda *et al.*, 2006). For example, the presence of belowground salt-marsh biomass has been shown to reduce lateral marsh erosion (Silliman *et al.*, 2016; Silliman *et al.*, 2019). Also, combinations of marshes and levees have proven effective for centuries, where the marsh presence reduces risk on levee failure, but also reduces the depth and width of levee breaches in case of failure (Zhu *et al.*, 2020).

A significant feature of all of these coastal ecosystems is that they are biogenic, or built over time by organisms. Modification of the coastal environment by shellfish, corals, seagrasses, dune plants, salt-marsh grasses, and mangroves bears indirectly on sediments and bathymetry in ways that reduce wave heights and shoreline erosion, beyond the direct effects of drag reduction. Because wave heights are largely determined by water depth (Le Hir *et al.*, 2000), mangrove and marsh plants that affect the elevation of intertidal surfaces by building peat platforms, or oysters and corals which grow vertically, have strong indirect effects on wave heights (Fagherazzi *et al.*, 2006). Biogenic structures can accumulate over decades and centuries, accreting meters in elevation over the underlying substrate (*marsh*, Marani *et al.*, 2007; Kirwan and Murray, 2007), and some organisms, like oysters, can accrete vertically at rates that keep pace with sea level rise (Rodriguez *et al.*, 2014). The sediment deposition facilitated by plants and animals can also affect the stability of the coastal system. In salt marshes, the decay of a dense root mass enriches soil organic content, which is associated with slower erosion than more mineral rich wetland soils (Feagin *et al.*, 2009). Particles bound by mussels and oysters as pseudo-feces increase sediment cohesion and reduce erosion o intertidal flats (Borsje *et al.*, 2011 and citations within).

While, in general, the evidence that biogenic coastal habitats protect shorelines is overwhelming, we still lack important information for predicting when and where these services are effective and can be used for coastal engineering. One major knowledge gap is the scale at which shoreline protection services of different ecosystems are applicable. For example, changes in the shoreline across very large scales along the Thai coastline can be explained by the presence of mangrove forests (Thampanya *et al.*, 2006), while oyster reef restorations and salt marsh vegetation at smaller scales have failed to have a detectable effect on shoreline change in some contexts (oyster, Scyphers *et al.*, 2011; saltmarsh, Feagin *et al.*, 2009), but have been shown to significantly reduce erosion in other contexts (oysters, Stricklin *et al.*, 2010; Chowdhury *et al.*, 2019; saltmarshes, Silliman *et al.*, 2019 and citations within). Similarly, seagrass meadows do not protect the shoreline in every location and scenario (Ondiviela *et al.*, 2014). There are several reasons these discrepancies occur and may impede the generalization and scaling up of shoreline protection services.

Shoreline protection services exhibit stark non-linearities over space and time, due to variation in biotic structures over seasons or years (**Fig. 1**, multiple habitats, Koch *et al.*, 2009; coral reefs, Wilkinson *et al.*, 1999; Sheppard *et al.*, 2005) and due to physical effects that are strongest at the habitat fringe (Kennedy and Mayer, 2002; Möller and Spencer, 2002; Gedan *et al.*, 2011), or in certain environmental contexts, such as shallow water (Ondiviela *et al.*, 2014). These non-linearities have been considered more thoroughly for some coastal ecosystems, for example, seagrass beds (Koch *et al.*, 2009), mangrove forests (Barbier *et al.*, 2008) and marshes (Kennedy and Mayer, 2002; Möller and Spencer, 2002; Silliman *et al.*, 2016), than for others. Spatial non-linearity can prove a valuable asset by reducing large ranges of wave heights to narrow ranges, thereby making wave impact behind the vegetation field more or less constant and independent of external forcing (van Wesenbeeck *et al.*, 2016). Still, due to the lack of controlled measurements on realistic scales, reliability of generic rules for wave reduction by vegetation is poor (Fonseca and Cahalan, 1992; Mendez and Losada, 2004; but see Möller *et al.*, 2014). Temporal non-linearity can also impact shoreline protection services in habitats that exhibit large seasonal fluctuations in above or belowground biomass or rigidity, like salt marshes and seagrasses (Bos *et al.*, 2007; Koch *et al.*, 2009; Schulze *et al.*, 2019). Furthermore, restored ecosystems often take time to fully develop and mature, which impacts their protection capabilities when they are young (Brückner *et al.*, 2019). For example, newly planted marsh grass may lack the extensive root structure needed to sufficiently stabilize sediments and withstand intense wave action, and similarly oyster restoration projects often need multiple years for oysters to recruit and grow; therefore, coastal protection may be low at young restoration sites and increase over time (Manis *et al.*, 2015).

Depending on the biological requirements of the dominant organisms, coastal ecosystems are constrained in their development and self-sustainability by environmental conditions such as elevation, currents, and wave exposure (Piazza *et al.*, 2005; Borsje *et al.*, 2011; Gedan *et al.*, 2011), and better definition of these constraints are necessary to apply natural shoreline protection services more broadly. Additionally, climatic and tidal stage conditions and storm track can have a large impact on the effectiveness of coastal ecosystems in shoreline protection (Resio and Westerink, 2008), making it difficult to predict the effectiveness of ecosystems for a given storm or flooding event until after the event occurs, though emerging research suggests that salt marshes can significantly attenuate waves even under storm surge conditions (Möller *et al.*, 2014; Garzon *et al.*, 2019). Moreover, there are few scientific studies of wave attenuation or coastal protection during catastrophic wave events such as tsunamis, making it even more difficult to establish, with any level of certainty, the effectiveness of coastal ecosystems in protection from these events, which impedes inclusion of ecosystems in coastal protection schemes. Nevertheless, damage analyses do often show protection of communities situated adjacent to coastal ecosystems from even these catastrophic events (Laso Bayas *et al.*, 2011; Danielson *et al.*, 2005; Das and Vincent, 2009). Finally, as we present in this article, the roles of species identity and species composition in coastal protection services have been insufficiently investigated. However, through mechanisms identified in studies of biodiversity and ecosystem function and of natural coastal protection, it is likely that mixtures of species and habitats can increase the effectiveness of natural shoreline protection services.

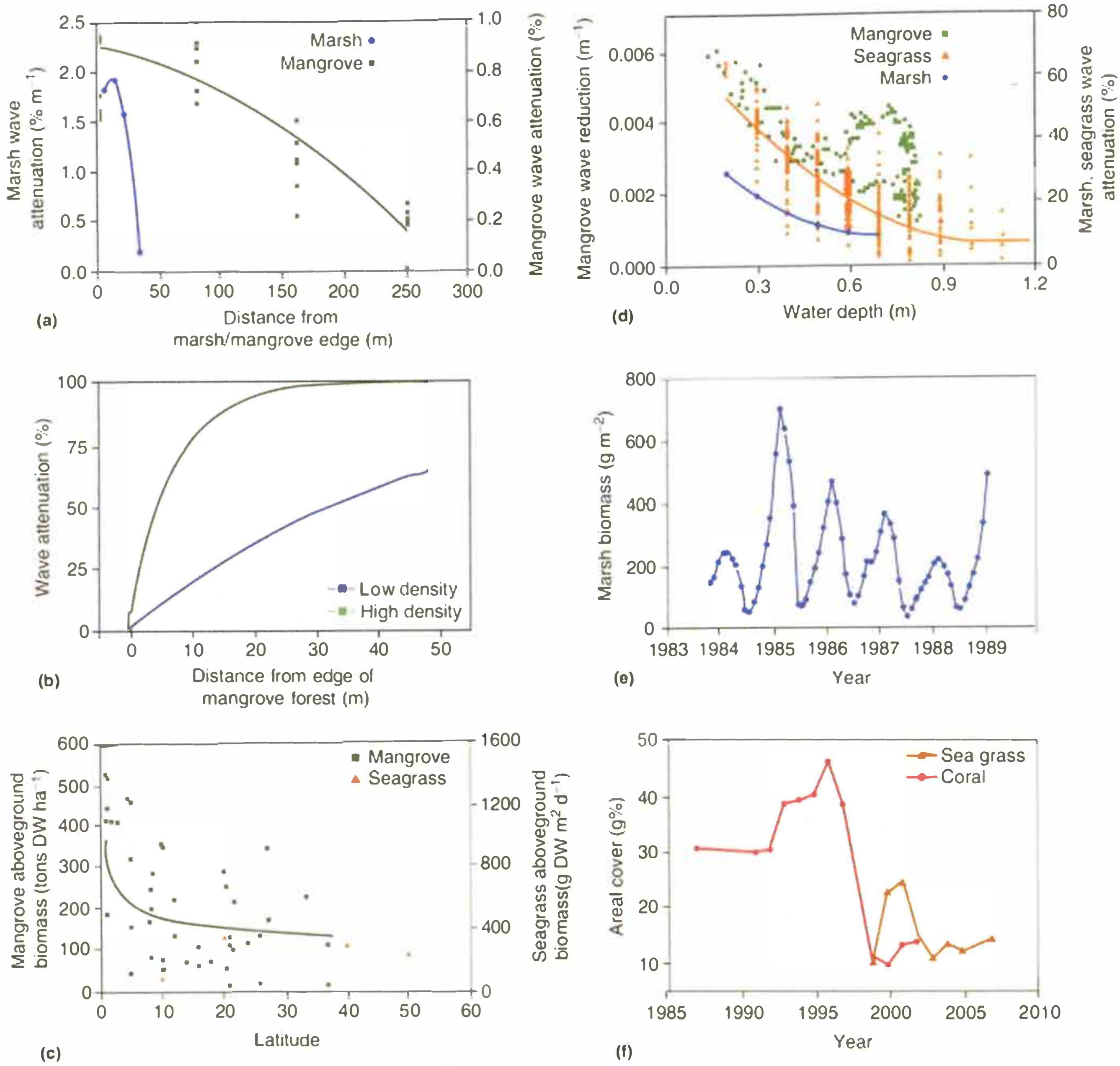

Fig. 1 Examples of non-linearities in wave attenuation for a variety of habitats. Direct measurements of wave attenuation only exist for the smallest spatial (a) and temporal (d) scales. Wave attenuation for different mangrove densities (b) has been modeled. Latitudinal wave attenuation (c) is estimated, based on the aboveground biomass of mangroves and seagrasses, i.e., obstructions to water flow. Wave attenuation over different seasons is also assumed to change with marsh aboveground biomass (e). Inter-annual variability in coral (modified from McClanahan *et al.*) and seagrass area cover (f) is used to estimate long term trends in wave attenuation. Figure and caption reprinted from Koch, E. W., Barbier, E. B., Silliman, B. R., *et al.*, 2009. Non-linearity in ecosystem services: Temporal and spatial variability in coastal protection. Frontiers in Ecology and the Environment 7, 29–37. Massel, S. R., Furukawa, K., Brinkman, R. M., 1999. Surface wave propagation in mangrove forests. Fluid Dynamic Research 24, 219–249. Möller, I., 2006. Quantifying saltmarsh vegetation and its effect on wave height dissipation: Results from a UK East coast saltmarsh. Estuarine Coastal and Shelf Science 69, 337–351. Mazda, Y., Magi, M., Ikeda, Y., Kurokawa, T., Asano, T., 2006. Wave reduction in a mangrove forest dominated by Sonneratia sp. Wetlands Ecology and Management 14, 365–378. Chen, S. N., Sanford, L. P., Koch, E. W., Shi, F., North, E. W., 2007. A nearshore model to investigate the effects of seagrass bed geometry on wave attenuation and suspended sediment transport. Estuaries 30, 296–310. Twilley, R. R., Chen, R. H., Hargis, T., 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. Water, Air and Soil Pollution 64, 265–288. Duarte, C. M., Chiscano, C. L., 1999. Seagrass biomass and production: A reassessment. Aquatic Botany 65, 159–174. Morris, J. T., Haskin, B., 1990. A 5-yr record of aerial primary production and stand characteristics of Spartina alterniflora. Ecology 71, 2209–2217. McClanahan, T. R., Mwaguni, S., Muthiga, N. A., 2005. Management of the Kenyan coast. Ocean and Coastal Management 48, 901–931. Merke, K., 2008. Eelgrass Habitat Surveys for the Emeryville Flats and Clipper Cove, Yerba Buena Island (October 1999–2005, and 2007). California Department of Transportation, Sacramento, CA.

How Biodiversity Matters on Different Scales

A range of ecosystem types contribute to coastal protection (e.g., oyster reefs, coral reefs, salt marshes), and although all these systems damp incoming physical stress from water and wind, the type and combinations of ecosystems present are likely to be an important determinant of the degree of coastal protection provided. For example, existing studies provisionally suggest that, while shellfish reefs and mangroves both contribute to wave dampening and shoreline stabilization, mangroves are substantially more effective in both (shellfish reefs; mangroves; Quartel *et al.*, 2007; Ellison, 2000). Within ecosystem types, the efficacy of shoreline protection can additionally vary with the identity of species. For example, in controlled laboratory settings, differences in effectiveness of wave dampening and sediment trapping have been observed for single-species beds within both marsh plants and sea grasses (Fonseca and Cahalan, 1992; Coops *et al.*, 1996; Peralta *et al.*, 2008). These observed differences between species suggest that the identity of the dominant species may be an important determinant of the degree of coastal protection provisioned by a specific coastal ecosystem, which is consistent with a large body of experimental work examining the effects of species richness on ecosystem functions (reviewed by Hooper *et al.* (2005)). The identity of dominant species can change across time and space within any single coastal ecosystem type and should thus be considered in assessments and predictions of coastal protection potential.

Drawing on theory and past experiments linking biodiversity and ecosystem function (e.g., Balvanera *et al.*, 2006), we predict that the ecosystem services of wave dampening and sediment trapping should also be enhanced by species diversity (the number of species present), not simply as a function of species identity (i.e., a sampling effect). More precisely, although the elevation of these services with increased diversity could stem directly from the greater probability of including one or more exceptional species, it may also result from emergent effects of diversity per se, through the inclusion of species that inhabit complimentary niches. Although this hypothesis has yet to be explicitly tested for shoreline protection services, there is evidence that combinations of different species on local scales can have greater impacts on hydrodynamics and sedimentation rates than any species in isolation (e.g., via differences in stoichiometry; Bouma *et al.*, 2005; Bouma *et al.*, 2010; Manis *et al.*, 2015). Species also clearly show complementarity across space, especially in coastal ecosystems that are often characterized by steep physical gradients and marked zonation of species. It remains unclear how small scale studies might scale up to explain patterns at larger spatial scales; however, we know from some systems that small-scale interactions can influence landscape patterns over larger scales (e.g., salt marshes; Kirwan and Murray, 2007; van Wesenbeeck *et al.*, 2008).

Niche complementarity is likely to be most important, when multiple ecosystem functions or services are considered simultaneously (Gamfeldt *et al.*, 2008; Isbell *et al.*, 2011). This theory may well apply to shoreline protection, as this service involves multiple ecological effects – wave dampening, soil trapping, reduction of water velocity, accretion and soil effects all contribute to shoreline protection – and even if certain species contribute more to one aspect of coastal protection (e.g., wave dampening by a rigid-bodied species), others contribute to another (e.g., soil stabilization by a soft-bodied species) and no single species (or group of similar species) is sufficient to sustain the multi-pronged service of coastal protection. For example, Ewel *et al.* (1998) speculate that fringe and riverine mangroves may be more effective at wave attenuation than basin mangrove forests, but basin mangrove forests may be more important for flood storage capacity.

At the landscape level, different kinds of coastal ecosystems have different functional roles in coastal defense, and so cross ecosystem linkages may be very important for shoreline protection. For example, coral reefs have large implications for wave dampening by functioning as submerged breakwaters (Ferrario *et al.*, 2014) and mangroves are efficient sediment trappers, thereby stabilizing the shoreline (Ellison, 2000). Additionally, a wave tank study demonstrated that the combination of a fringing oyster reef with a landward salt marsh attenuated waves significantly better than either habitat on its own (Manis *et al.*, 2015). Often these systems are found co-occurring along coastlines, as mangroves and marshes are generally restricted to low wave energy environments (Knutson *et al.*, 1981; Ewel *et al.*, 1998), but the presence or placement of an oyster or coral reef at the seaward margin may allow the wetland to persist in a more wave exposed environment (**Fig. 2**). Indeed it seems intuitive that waves are dampened more if they meet a shellfish reef and a mangrove forest than if they meet a mudflat and an eelgrass meadow due to the rigidity and the relative height of their biotic structures. However, there are surprisingly few data to support this idea (see discussion in Barbier *et al.*, 2008). Thus, we are limited in our ability to predict if and to what extent different combinations of coastal communities can enhance or hinder coastal shoreline protection services. A recent review of living shoreline projects highlighted the fact that, to date, approximately only one quarter of restoration projects for coastal protection have included the restoration of more than one habitat simultaneously (Smith *et al.*, 2020). Adopting a larger-scale perspective towards restoration focusing both on ameliorating abiotic conditions at the landscape scale and on a range of habitats may lead to unprecedented results in restoration ecology.

The extent to which different coastal ecosystem types can influence coastal defense properties is dependent upon having natural, functioning and stable food webs within each and on management regimes. For example, salt marshes that have experienced significant grazing have distinct features (Bakker and Ruyter, 1981; Bakker, 1985) that change their effects on wave attenuation. The lower standing biomass of grazed marshes (**Fig. 3**) significantly reduces wave-dampening properties of marshes (Hijuelos *et al.*, 2019). Further, intensive grazing was shown to reduce the strength of marsh soils (Zhang, 1993), which might make marshes more vulnerable to wave erosion. Further, food web complexity and structure are also important because they influence ecosystem stability. For example, large die-backs of salt marshes in the southeast US have been linked to declines of a keystone predator, the blue crab (Silliman and Bertness, 2002). Reductions in blue crab numbers releases fungal-farming snails from predation allowing snail numbers to increase to levels high enough to graze down marsh grasses and transform the tidal marsh into mudflats (Silliman and Bertness, 2002). The ecosystem service of coastal protection offered by a healthy salt marsh is

Fig. 2 New restorations are pairing multiple habitat types for greater effectiveness in shoreline protection (B. Silliman). Reprinted from Gedan, K. B., Kirwan, M. L., Wolanski, E., Barbier, E. B., Silliman, B. R., 2011. The present and future role of coastal wetland vegetation in protecting shorelines: Answering recent challenges to the paradigm. Climatic Change 106, 7–29.

Fig. 3 Grazed marshes (front) differ considerably from non-grazed marsh systems (back). Evidence from effects of different vegetation types on wave dampening suggests that intensive grazing and trampling may have a negative effect on their coastal defense properties. Photo published with permission from Martin Stock.

considerably greater than that offered by an intertidal mudflat. This example shows that food web interactions are often complex and that understanding these interactions is crucial for successful implementation of nature-based coastal defenses. Further, it highlights the value of maintaining biotic diversity and food web structure in ecosystems to maximize their effectiveness in providing coastal protection.

An advantage of natural shoreline protection over man-made coastal defenses is that natural shoreline protection is self-sustaining. Natural shorelines require less maintenance and can naturally adapt to changing environmental conditions such as rising sea levels over time (Smith *et al.*, 2017; Rodriguez *et al.*, 2014). Therefore, applications of nature-based shoreline protection strategies should also attempt to maximize ecosystem resilience. Maintaining greater species diversity is expected to maximize ecosystem output (Cardinale *et al.*, 2006) and increase ecosystem stability over time (Cottingham *et al.*, 2001; Griffin *et al.*, 2009a,b), and more diverse ecosystems are therefore likely to improve the provision of shoreline protection services over the long term.

Harnessing coastal protective services of natural habitats will rely on combined conservation and restoration efforts. While conservation is almost always preferred, restoration of coastal habitats may provide a unique opportunity to build back better, by choosing optimal ecosystems and species that achieve the desired functions and services. Moreover, nature-based techniques that merge habitat restoration with gray infrastructure can capitalize on the strengths of each, while also allowing for innovation and development of new techniques for urban areas or locations where space may be otherwise limiting (Sutton-Grier *et al.*, 2015). The promotion and success of nature-based coastal protection schemes will rely in part on advances in marine ecosystem restoration techniques, especially development of effective scalable methods and updated tools that address future climate change scenarios (Abelson *et al.*, 2020).

While biodiversity is often a goal of restoration, it is rarely incorporated into restoration design in marine systems. Recent research and reviews suggest that incorporating a diverse species assemblage into restoration schemes may enhance restoration outcomes (Hughes *et al.*, 2018; Renzi *et al.*, 2019; Valdez *et al.*, 2020), thus enhancing the likelihood of provisioning coastal protection services down the line. For example, in a seagrass restoration experiment comparing seagrass monocultures to polycultures, plots with the highest species richness had the highest survivorship and increase in percent cover (Williams *et al.*, 2017). A study of mangrove reforestation did not find any effect of species richness on survival after 1 year (Kirui *et al.*, 2008); however, a similar study showed that tree species richness enhanced belowground root biomass after four years (Lang'at *et al.*, 2013), which could ultimately impact sediment stabilization and coastal protection. At the landscape scale, the co-transplantation of mussels and salt marshes has been shown to increase salt-marsh survival three-fold (Derksen-Hooijberg *et al.*, 2018) and the restoration of kelp forests can accelerate the recovery of oyster reefs (McAfee *et al.*, 2021). Interestingly, the effect of kelp on oyster recovery was observed even when using synthetic kelp mimics, which suggests that the simulation of diversity effects, rather than the true incorporation of diversity, can also assist with ecosystem restoration. This mimicry of emergent traits can potentially be used to lower costs and upscale restoration (Temmink *et al.*, 2020).

Genetic diversity, when applied to restoration design, has been shown to increase ecosystem services (Reynolds *et al.*, 2012). While only briefly mentioned here, genetic diversity research has made significant strides in recent years and has potential ecological implications for foundation species (Hughes *et al.*, 2008) that could enhance coastal protection services. For example, in seagrass restoration, the incorporation of genetic diversity has been shown to increase restoration success (Williams, 2001; van Katwijk *et al.*, 2009; Jahnke *et al.*, 2015) and both seagrass response to stress and resistance to and recovery from disturbance are improved with increased genetic diversity (Hughes and Stachowicz, 2004, 2009). Improved restoration success and increased ecosystem resiliency to stress and disturbance will help to provide and maintain ecosystem services such as coastal protection in changing environments. Additionally, intraspecific diversity in oyster cohorts has been positively correlated with growth, recruitment, and survivorship (Smee *et al.*, 2013; Hanley *et al.*, 2016). Although these studies are not directly concerned with coastal protection, there are conceivable benefits that could be relevant. In areas where a single or a few foundation species provide much of the coastal protection, it is possible that genetic diversity within monospecific stands could be crucial for maintaining and restoring habitats and genetic diversity is therefore an important area where much additional research is needed.

Using coastal ecosystems for reducing disaster risk and adapting to climate change effects, such as sea level rise, represents an elegant compromise for achieving the goals of maintaining biodiversity and ecosystem integrity while also providing shoreline protection as well as many other benefits to human communities. Still, to improve applicability of nature-based flood defenses, more knowledge needs to be collected on design, maintenance, management and governance. Preferably, this knowledge should be derived from real-scale applications that are accompanied by a thorough monitoring program. Conserving and promoting biodiversity in coastal ecosystems conserved or created for shoreline protection will help to maximize the myriad ecosystem services they provide, including benefits of fisheries and other natural resources, recreational activities, and water and nutrient regulation.

Conclusions

(1) Awareness is rising that functioning and intact coastal ecosystems offer valuable coastal protection services. By implementing ecosystem management in planning designs for coastal defenses, we can make use of the unique organisms that have evolved in and are well adapted to shoreline stressors. This requires an integrated planning and design process and a solid understanding of natural processes and ecosystem functioning. Making use of general ecological theory is indispensable for adequate restoration and conservation of ecosystems in general.

(2) The effectiveness of coastal ecosystems for wave dampening, reducing current velocities, slowing erosion, and facilitating biotic diversity depends on the types of coastal communities that are present (e.g., oyster reef, coral reef, mangrove, etc.) and on the spatial configuration of these communities.

(3) Degenerated ecosystems, that lack natural species assemblages, are not likely to be as robust, stable and resilient as intact ecosystems and therefore are less likely to provide the valuable ecosystem services that many coastal communities depend on. In general, higher diversity is thought to increase ecosystem stability, enhance resilience to perturbations and increase productivity. Therefore, managing coastal ecosystems to promote diverse and natural species assemblage will enhance the effectiveness of these systems as protection. However, the exact implications for management and conservation depend on whether species-specific effects and possible positive interactions are well understood; if they are, managing for particular species diversity in order to maximize the yield of certain services may be more efficient than managing for diversity per se.

(4) There is a need for large-scale experiments and replicated comparative studies to test how diversity within different levels of ecological organization (species, genetic and ecosystem) and at different scales (within and across habitats) impacts coastal shoreline protection. We cannot advance our understanding of biodiversity-ecosystem service relationships unless proper controls are utilized when assessing impacts of proposed nature-based coastal protection plans.

(5) Incorporating the construction and maintenance of functional coastal ecosystems as a part of coastal defense strategies will require greater collaboration between ecologists, geologists and engineers. It will also require innovation and advances in restoration techniques and research efforts aimed at documenting and quantifying the flood defense properties of ecosystems. Such data are needed to develop predictive models that will allow coastal managers to assess the level of protection provided by specific coastal ecosystem configurations and therefore, also estimate the potential socioeconomic impacts of ecosystem loss.

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