Climate Change, Human Impacts, and Coastal Ecosystems in the Anthropocene

Qiang He[1,*] and Brian R. Silliman[2,3,*]
[1]Coastal Ecology Lab, MOE Key Laboratory of Biodiversity and Ecological Engineering, School of Life Sciences, Fudan University, 2005 Songhu Road, Shanghai 200433, China
[2]Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA
[3]Commonwealth Scientific and Industrial Research Organization, Marine and Atmospheric Research, Cleveland, Queensland 4163, Australia
*Correspondence: he_qiang@hotmail.com (Q.H.), brian.silliman@duke.edu (B.R.S.)
https://doi.org/10.1016/j.cub.2019.08.042

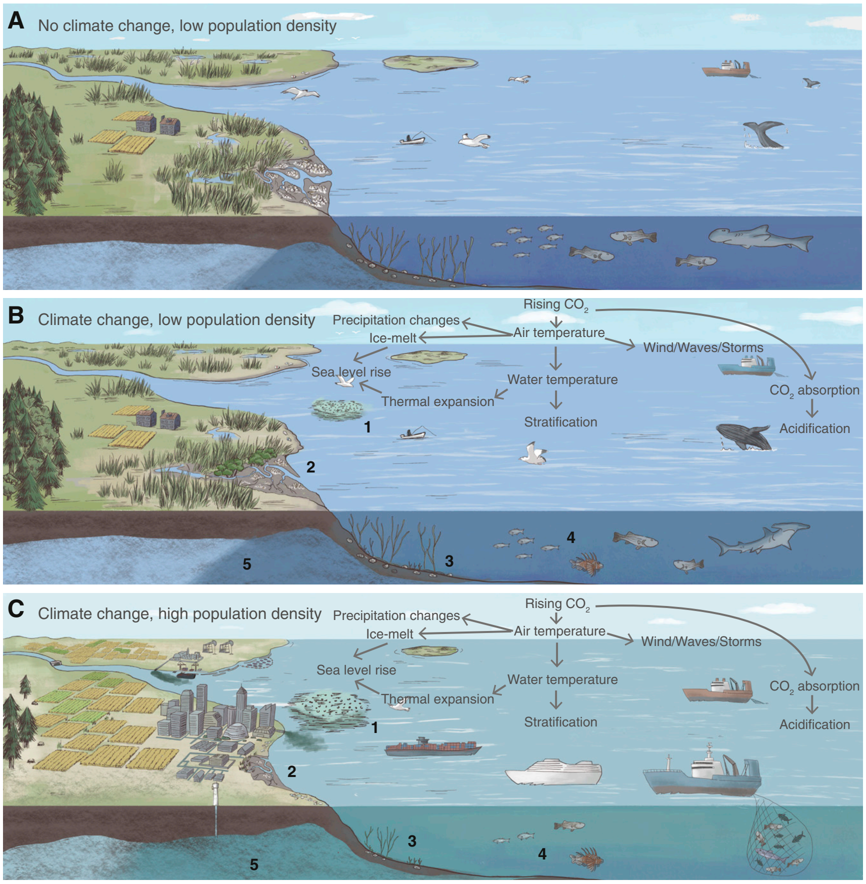
Coastal zones, the world's most densely populated regions, are increasingly threatened by climate change stressors — rising and warming seas, intensifying storms and droughts, and acidifying oceans. Although coastal zones have been affected by local human activities for centuries, how local human impacts and climate change stressors may interact to jeopardize coastal ecosystems remains poorly understood. Here we provide a review on interactions between climate change and local human impacts (e.g., interactions between sea level rise and anthropogenic land subsidence, which are forcing Indonesia to relocate its capital city) in the coastal realm. We highlight how these interactions can impair and, at times, decimate a variety of coastal ecosystems, and examine how understanding and incorporating these interactions can reshape theory on climate change impacts and ecological resilience. We further discuss implications of interactions between climate change and local human impacts for coastal conservation and elucidate the context when and where local conservation is more likely to buffer the impacts of climate change, attempting to help reconcile the growing debate about whether to shift much of the investment in local conservation to global CO_2 emission reductions. Our review underscores that an enhanced understanding of interactions between climate change and local human impacts is of profound importance to improving predictions of climate change impacts, devising climate-smart conservation actions, and helping enhance adaption of coastal societies to climate change in the Anthropocene.

Introduction

Coastal zones, the world's most densely populated areas, are increasingly threatened by global climate change [1]. Contemporary climate change is largely recognized as an anthropogenic phenomenon that began and is sustained by human industrial activities that produce enormous amounts of greenhouse gas (e.g., CO_2 and methane) emissions. Rising atmospheric greenhouse gas concentrations have in turn triggered a suite of rapid physiochemical changes in the air, land and sea. Some of the most concerning physiochemical changes in coastal ecosystems include increasing air and water temperatures, rising sea levels, and ocean acidification (Figure 1), and over recent decades these changes have accelerated. Global average surface air temperature increased by 0.85°C between 1880 and 2012, while the rate of increase has been much higher since 1971 (~0.2°C/decade) [2]. Global mean sea level rose by 0.11 m between 1901 and 2010, and the rate of rise was particularly high starting in the 1980s (3.2 mm/yr) [2]. The pH of the global ocean has decreased by 0.1 pH units since the preindustrial period and by a much faster rate since 1980 (~0.02 pH units/decade) [3]. These changes, especially for sea level rise when the loss of Antarctic ice sheets is incorporated [4], are projected to accelerate even further in coming decades under the 'business-as-usual' scenario [2].

Besides these long-term trends, spatiotemporal variability in the physiochemical environment of coastal seas and oceans is also being exacerbated by climate change, leading to more frequent extreme climate events (e.g., droughts, storms, and heat waves) and spatiotemporal redistributions of climatic conditions (e.g., altered upwelling and ocean circulation) [5]. The consequences of these physicochemical changes for the biota and functioning of coastal ecosystems have been studied intensively, and there is now overwhelming evidence that climate change is driving changes in virtually all coastal ecosystems [6,7].

Climate change can bring cumulative effects to every environmental issue [8]. Although climate change is the most broadly occurring threat to coastal ecosystems, coastal zones have also been undergoing intense local human impacts for centuries [9]. Many coastal ecosystems, for example, receive inputs of excessive nutrients, heavy metals, and other forms of land-derived pollutants (e.g., microplastics and sediments), are reclaimed or blocked from the sea for urban/industrial development, agriculture, and aquaculture, are harvested for food, wood, and other natural resources, and are extracted for groundwater (leading to saltwater intrusion) (Figure 1C). These local human impacts can all drive degradation or collapse of coastal ecosystems [10] and are still intensifying in many regions [11]. Increased co-occurrences of local human impacts and climate change in the coastal zone amplify the likelihood of interactions. Some of those interactions have been widely recognized, such as those between warming and nutrients on algae



Current Biology

Figure 1. Impacts of climate change and local human activities on coastal ecosystems.
Shown is a temperate estuary adjoining land and ocean. (A) Scenario when the system is not affected by climate change. (B) Scenario when the system is pressured primarily by climate change. (C) Scenario when the system is pressured by both climate change and intense local human impacts. In (B), 1, climate warming promotes algal blooms [129]; 2, seaward loss and landward movement of coastal wetland as a result of sea level rise [102], and mangrove replacement of salt marsh grasses as a result of climate warming [105]; 3, warming-driven replacement of temperate seagrasses by subtropical seagrasses [130], and loss of bivalves due to ocean acidification [131]; 4, invasion of tropical fishes into temperate coastal waters and changes in fish species abundance and composition with warming [132]; 5, saltwater intrusion due to sea level rise [28]. In (C), 1, impacts of warming on algal blooms and hypoxia are exacerbated by eutrophication [12]; 2, loss of coastal wetlands due to the compounding effects of sea level rise and sea reclamations for urban, industrial and agricultural expansion [133]; 3, seagrass/bivalve loss is exacerbated due to synergistic/additive interactions between warming/ocean acidification and eutrophication [33,75]; 4, collapse of fisheries due to synergistic interactions between overfishing and warming [134]; 5, intense groundwater withdrawal exacerbates saltwater intrusion driven by sea level rise [28].

in coastal waters [12]. However, despite the ubiquity of interactions between climate change and local human impacts in coastal zones, multifactorial studies on these interactions are much fewer relative to single-factor studies on either climate change or local human impacts. An inclusive framework for understanding, predicting and managing interactions between climate change and local human impacts in coastal ecosystems has yet to be formulated.

Here, following a brief overview of climate change impacts in coastal ecosystems, we synthesize the literature on interactions between climate change and local human impacts, exemplify how these interactions affect major coastal ecosystems that include salt marshes, mangrove forests, seagrass beds, kelp forests, coral reefs, soft sediments, and oyster reefs (Table 1), and examine how understanding and incorporating these interactions can reshape theory on climate change impacts and ecological resilience. We further discuss the implications of these interactions for coastal conservation. Managing local human impacts through local conservation actions (e.g., marine protected areas, mitigation of terrestrial stressor input, and restoration) has been considered to be an important strategy to buffer the impact of climate change and boost resilience in coastal ecosystems. Whether local conservation actions can help buffer coastal ecosystems from climate change and whether to shift much of the investment in local conservation to global CO_2 emission reductions has been recently debated, however. We attempt to help reconcile this debate, by highlighting the context of when and where investing in local conservation can buffer against climate change (e.g., in areas with high human impacts). Our review may thereby serve as a framework for incorporating local human impacts into understanding, predicting, and managing the effects of climate change on coastal ecosystems.

Climate Change Impacts on Coastal Ecosystems

The impacts of climate change on coastal ecosystems have been extensively reviewed (e.g., [1,6,7]). Briefly, these syntheses have found that climate change can strongly affect coastal ecosystems at all levels of biological organization. First, climate change can have strong impacts on gene expression, cellular and whole-organism physiology, driving changes in their survival, growth, reproduction, and behavior (see Box 1 for case studies). Recent advancements in molecular techniques (e.g., DNA-sequencing technologies and quantitative genetics) are allowing for in-depth characterization of the genomic and physiological responses of coastal organisms to climate change and for deciphering the genetic basis underlying their disparate capacities to acclimatize, adapt and evolve under climate change [13]. Such studies can provide mechanistic bases for understanding biological responses to climate change.

Climate change further leads to global redistribution of coastal biota via physiologically driven species range shifts and altered species interactions. To match their physiological tolerances,

Table 1. Major coastal ecosystems and their main climate change and local human stressors.

Ecosystem	Definition	Climate change stressors	Local human stressors	References
Salt marshes	Saline or brackish intertidal areas dominated by salt-tolerant plants, such as herbs, grasses, or low shrubs, occurring primarily in sheltered or depositional coasts in temperate zones.	Sea level rise, warming, rising atmospheric CO_2, climate extremes (drought, storms)	Pollutant input, biological invasion, coastal development, coastal engineering, nutrient input, sediment input, fishing, grazing	[117,118]
Mangrove forests	Coastal intertidal areas dominated by woody halophytes (trees or shrubs), occurring mainly in the tropics and subtropics worldwide.	Sea level rise, warming, rising atmospheric CO_2, ocean acidification, climate extremes (heat waves/cold, drought, storms)	Fishing, forest logging, coastal development, coastal engineering, aquaculture, freshwater input, sediment input, nutrient input, pollutant input, recreation, biological invasion, mining	[117,119]
Seagrass beds	Marine flowering plant-dominated systems found in shallow salty and brackish waters worldwide. Some seagrass beds can occur in low intertidal areas.	Warming, sea level rise, ocean acidification, climate extremes (storms)	Nutrient input, coastal development, sediment input, coastal engineering, fishing, physical disturbance, disease, aquaculture	[117,120]
Soft sediments	Un-vegetated, muddy or sandy marine systems dominated by macrofauna, such as polychaetes, crustaceans, echinoderms, and molluscs.	Warming, sea level rise, ocean acidification	Pollutant input, coastal development, coastal engineering, biological invasion, nutrient input, fishing, aquaculture, sediment input, nourishment/grooming, mining, recreation	[117,121]
Rocky shores	Wave-exposed sea coasts where solid rock (e.g., boulders, cobbles and exposed bedrock) predominates.	Warming, ocean acidification, sea level rise, climate extremes (heat waves, drought, storms)	Fishing, pollutant input, biological invasion, coastal development, coastal engineering, sediment input, aquaculture, nutrient input, thermal effluent, collecting and gathering, recreation	[117,122,123]
Kelp forests	Shallow marine ecosystems covered by densely growing kelp species (large brown algae) and found in temperate and arctic regions worldwide.	Warming, ocean acidification, climate extremes (heatwaves, storms)	Fishing, kelp harvesting, pollutant input, nutrient input	[117,124]
Coral reefs	Underwater tropical marine ecosystems characterized by reef-building corals.	Warming, sea level rise, ocean acidification, climate extremes (heat waves, storms)	Fishing, coastal development, sediment input, nutrient input, coastal engineering, pollutant input, disease, recreation, collecting and gathering	[117,125,126]
Oyster reefs	Reefs formed due to dense aggregations of bivalve shellfish in temperate and subtropical estuaries	Warming, sea level rise, ocean acidification, climate extremes (drought)	Pollutant input, coastal development, coastal engineering, fishing, nutrient input, biological invasion, sediment input, disease	[117,127,128]

Climate change and local human stressors are based on [117] (those with a score of greater than 2 are considered). Additional stressors are added when needed according to reviews on a specific type of coastal ecosystem.

organisms tend to shift distributions to higher latitudes, deeper depths (in subtidal systems), or higher elevations (in intertidal systems). Rates of range expansion/contraction differ dramatically among species [7]. Consequently, species may not necessarily interact with the same assemblage as they have in recent history. Climate change may also directly alter species interactions by, for example, changing species behavior and diet, introducing novel and more potent herbivores, breaking down mutualisms, or reversing winners and losers in competition [14]. Range shifts and altered species interactions then act together to reshuffle communities, leading to tropicalization of temperate zones and borealization of polar zones (see Box 1 for case studies). Effects of climate change on community dynamics, however, can vary greatly among tropical, temperate, and polar zones, and global- and regional-scale comparative studies are needed to assess large-scale variation in the effects of climate change on distributional and compositional changes in coastal marine communities.

Population- and community-level impacts of climate change often propagate to ecosystem levels, affecting ecosystem functions and the provision of important ecosystem services, such as coastal protection, fisheries maintenance, pollution mitigation, and carbon sequestration [15]. Both positive and negative effects have been reported (see Box 1 for case studies).

Box 1. Impacts of climate change on coastal ecosystems: case studies.

Here we review cases where climate change has been demonstrated to affect gene expression and cellular/whole-organism physiology, population and community dynamics, and ecosystem functions and services in coastal ecosystems. These not only represent areas where scientific understanding is rapidly advancing, but are also areas of ecological or economic importance.

Impacts on organism genes and physiology: Climate change can have strong impacts on gene expression and cellular and whole-organism physiology. Heat stress, for example, has been found in both coastal animals and plants (e.g., seagrasses) to up-regulate genes that encode heat-shock proteins [97,98]. A range of other physiological/metabolic processes, including photosynthesis and respiration, increase with temperature within the range of species tolerance (before the tolerance threshold is reached and acute thermal death occurs) [6]. This explains, in part, the increased likelihood of phytoplankton blooms and disease outbreaks with ocean warming [12,99]. For heterotrophic organisms such as salmon in the Pacific Northwest, increased respiratory rates in warmer waters can lead to energy demand exceeding energy intake, reducing their aerobic scope for activity and their growth and reproduction [6,100]. Warming temperatures may more strongly affect polar and tropical marine species than temperate marine species, because polar and tropical marine species have evolved in some of the most temperature-stable marine environments on Earth and have very narrow tolerances to temperature variation [101]. Rising sea levels can increase inundation stress, reducing the photosynthesis and growth of salt marsh grasses and mangroves on their seaward edge [102]. Ocean acidification is thought to increase the energetic cost of calcification and deplete carbonate ions, reducing calcification in most calcifiers (except crustaceans), including commercially valuable shellfish and habitat-forming species, such as oysters and corals [103].

Reshuffling and shifting of tropical, temperate and polar communities: Reshuffling and shifting of coastal marine communities with climate change have been increasingly documented. Mangroves, for example, are replacing their temperate analogues — salt marshes, tropical seagrasses are expanding and replacing temperate seagrasses, invasive lionfish are increasingly found in temperate waters, and tropical herbivorous reef fishes are intruding and, at times, decimating temperate kelp forests, leading to tropicalization of temperate zones (some of those processes are depicted in Figure 1B). Similarly, boreal fish communities are expanding into the Arctic [104], leading to borealization of polar zones. Range-shifting habitat-forming species [105] and keystone consumers [106] can even drive sudden community phase shifts. Range shift is not clear for all systems, however. Coral reefs' poleward expansion, for example, can be constrained due to limited solar radiation that is required for corals to sustain their symbiotic photosynthetic algae [107]. Indeed, in the tropics where species with limited thermal tolerance are living close to their temperature optima [108], increased mortality and extinction may lead to simplification of biodiversity and even collapse of tropical communities, as seen in some coral reefs [47], mangrove forests [109], and tropical seagrass beds [110].

Alteration in ecosystem function and services: Mangrove encroachment in salt marshes under warming, for example, can promote wetland carbon stock [111]. Sea level rise may increase the lateral extent of coastal wetlands (Figure 1) and enhance their carbon stock, especially in areas where wetland landward movement is not blocked by human infrastructure [112]. Sea level rise, however, has also been found to reduce the production, nitrogen sequestration and denitrification functions of tidal marshes [113]. Drought, heat, and storm-driven die-offs of salt marshes, mangroves, and coral reefs reduce the coastal protection services those ecosystems provide [114]. Furthermore, climate change can disrupt the fisheries ecosystem services valuable for many coastal societies. While some fish populations may be able to escape warming via range shifts, fishes, including commercially valuable shellfish and finfish, cannot escape ocean acidification [115]. Predicted collapses of marine capture fisheries and coral reefs driven by ocean acidification by 2200 have been valued at 97 to 301 billion 2014 dollars per year [116].

How climate change affects the full suite of functions and services of coastal ecosystems, however, remains relatively underexplored, and comprehensive assessments have yet to be conducted.

Interactions with Local Human Impacts

The impacts of climate change on coastal ecosystems, as summarized above and investigated in the majority of existing studies on one or two climate change stressors, tend to reflect average conditions and do not account for interactions with local human impacts. On sparsely populated coasts, these impacts may hold true (Figure 1B). But great stretches of the world's coasts today are densely populated by humans, and human impacts can extend further from areas directly modified by humans. For example, many large rivers that discharge enormous amounts of nutrients to the coastal ocean have plumes extending 50–400 km seaward [16]. In such cases, larger-scale interactions with local human impacts are likely to occur and should not be neglected (Figure 1C). Local human impacts can interact with climate change in two different, nonexclusive mechanisms. First, local human impacts can mediate the susceptibility of organisms to a climate change stressor, and vice versa, a climate change stressor can mediate the susceptibility of organisms to a local human stressor (e.g., heavy metal pollution). Second, local human impacts can directly modify the climate change stressor itself (e.g., relative sea level rise and seawater pH).

Some of the best evidence for interactions between climate change and local human impacts in coastal ecosystems has come from studies on climate warming. It is well known that eutrophication can interact with climate warming to exacerbate harmful algal blooms (Figure 1C), such as in the Baltic Sea

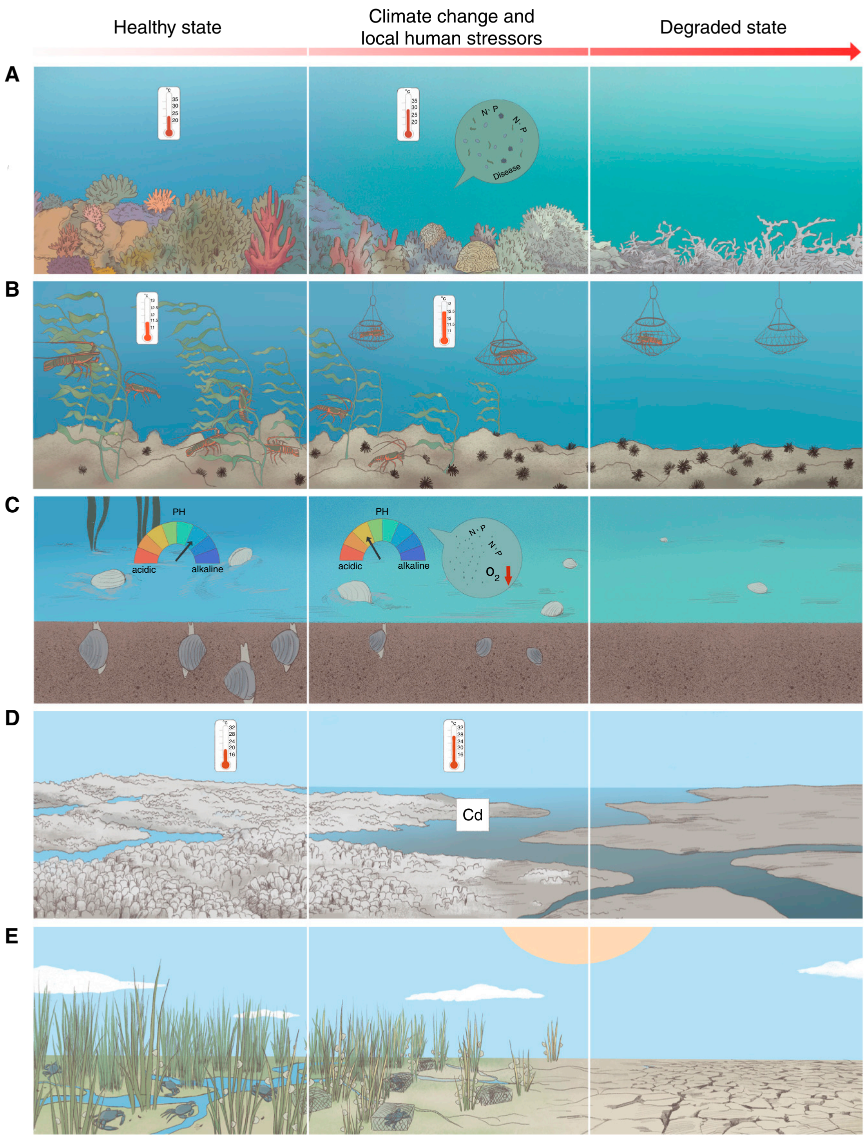


Figure 2. Empirically tested synergistic interactions between climate change and local human impacts in a variety of coastal ecosystems.
(A) Warming and eutrophication on coral reefs. (B) Warming and overfishing in kelp forests. (C) Ocean acidification and hypoxia on hard clams in soft sediments. (D) Warming and heavy metal pollution on oyster reefs. (E) Drought and overfishing in salt marshes. These illustrations are mainly to exemplify some of the climate change and local human stressors that have been demonstrated to interact to cause coastal ecosystem degradation. These climate change and local human stressors may take effect at different timescales. See main text and references therein for details and the mechanisms of these interactions.

and Gulf of Mexico. Harmful algal blooms often result from anthropogenic nutrient enrichment. As phytoplankton optimize growth with increasing temperature, harmful algal blooms often benefit from climate warming and longer seasons of elevated temperatures [12]. On coral reefs including those in Florida Keys, eutrophication, as well as overfishing [17], can make corals more sensitive to elevated seawater temperatures by increasing turf and macroalgal cover, destabilizing microbiomes, and elevating pathogen loads [18,19], thereby exacerbating the potential for phase shifts to an algal barren state (Figure 2A). In kelp forests in eastern Tasmania, Australia, sea urchins, a prominent benthic herbivore, are expanding into eastern Tasmania under climate warming. Fishing, by removing large predatory lobsters and releasing sea urchin populations from predator control, can amplify overgrazing of kelps, thereby increasing risk of climate warming-driven phase shifts from productive kelp beds to sea urchin barrens [20] (Figure 2B). Vice versa, climate warming can increase the susceptibility of organisms to a local human stressor (e.g. Methylmercury and hypoxia). On oyster reefs, for example, warming, by increasing energy limitation and causing failure of energetically costly detoxification mechanisms, can elevate sensitivity of oysters to trace metal (e.g., cadmium) pollution, leading to increased oyster mortality (Figure 2D) [21].

For sea level rise, local human impacts are more likely to directly modify the rate of relative sea level rise. Local human activities can actually be more important than climate change in driving relative sea level rise, especially in coastal zones where subsurface fluids (e.g., groundwater and gas) are heavily exploited [22]. Along the Italian coast, for example, the sea rose on average by ~10 cm over the 20th century. In Venice where local human activities, largely groundwater pumping for industrial activities, led to sinking ground, relative sea level rise over the same time period was >100% higher, increasing flood frequency by more than seven times [23]. This type of relative sea level rise amplified by local human impacts (e.g., local land subsidence and/or decreased accretion) has been even more dramatic in other coastal megacities such as Shanghai [24] and Manila [25] and has been observed in nearly 90% of the world's river deltas [26]. These elevated rates of relative sea level rise not only increase flooding risk in coastal man-made systems, but can also accelerate vegetation changes in coastal wetlands, such as intrusion of salt-tolerant plants [27]. Furthermore, local human activities can exacerbate sea level rise-driven saltwater intrusion. Groundwater extraction, for example, can make coastal aquifers more vulnerable to saltwater intrusion than predicted by models using sea level rise as the major driver of inland movement of seawater (Figure 1C) [28].

Relative to climate warming and sea level rise, ocean acidification, as a chemical process, is often more strongly affected by local human impacts. Unlike the open ocean, pH of coastal waters is often substantially more variable, due to local human impacts that include inputs from land [29] (note that the pH of coastal waters is also affected by upwelling and interactions between the sea floor and the water column). High levels of eutrophication, for example, can exacerbate acidification of coastal waters, especially subsurface waters, because eutrophication fuels algal blooms, which deplete oxygen and release CO_2 during bacterial respiration of the organic matter from blooms [30]. Inputs of other pollutants (e.g., heavy metals) can also exacerbate acidification in coastal waters, as pollutants generally decrease the rate of photosynthesis and the efficiency of CO_2 removal from the atmosphere, thereby increasing the amount of CO_2 available for absorption by seawater [31]. Such terrestrial inputs can be primarily driven by watershed human activities. Watershed deforestation, mining, and agricultural activities can release large amounts of acids in tropical and subtropical acid sulphate soils, the delivery of which by river run-off can acidify coastal waters at higher rates than atmospheric CO_2 alone [32]. Besides directly modifying pH changes, local human impacts can also interact with ocean acidification by increasing the susceptibility of biota to ocean acidification. In coastal soft sediments, for example, hypoxia can lower metabolism and internal gas exchange and exacerbate intracellular oxygen deficiency and respiratory CO_2 retention in hard clams, thereby amplifying the negative effects of ocean acidification on their growth and survival (Figure 2C) [33].

Other climate change stressors can also interact with local human impacts. In salt marshes, for example, drought, by compromising plant defense condition, can increase the susceptibility of cordgrass to overgrazing by periwinkle snails (*Littorina littorea*), whose predators — blue crabs (*Callinectes sapidus*) — have undergone population decline due to overfishing (Figure 2E) [34,35]. Similarly, freshwater withdrawal can exacerbate the collapse of oyster fisheries driven by increased predation pressure during droughts [36].

It is important to note that while synergistic interactions between climate change and local human impacts are increasingly reported and emphasized in the literature, additive and antagonistic interactions are also found in coastal ecosystems. For example, heavy metal pollution can weaken the toxicological effects of ocean acidification on coastal meiobenthic copepods due to competition between H^+ and heavy metals for binding sites [37]. Watershed agricultural activities, such as the use of lime in agriculture to reduce soil acidity, may counteract pH decline from ocean acidification driven by rising anthropogenic CO_2 [29]. Hypoxia and warming can have additive and opposing effects on the growth of Olympia oyster (*Ostrea lurida*) [38]. While all those forms of interactions between climate change and local human impacts have important ecological implications and need to be recognized [39], synergistic and additive interactions are typically more devastating for coastal ecosystems where they occur [40].

In summary, interactions with global climate change can occur with many local human impacts, across a suite of diverse marine species, and in a variety of marine ecosystems along great stretches of the world's coasts [41]. These interactions can be synergistic, antagonistic, or additive, and occur when either a climate change stressor can mediate the susceptibility of organisms to a local human stressor (and vice versa) or when local human impacts directly modify the climate change stressor itself.

Predicting Impacts and Resilience

Despite accumulating studies on interactions between climate change and local human impacts, the question of when and where local human impacts are more likely to compound impacts of climate change is still open. Resolving this question is necessary to refine predictions of climate change impacts and coastal ecosystem resilience within the context of local human impacts. Below we outline pathways and hypotheses with which we can begin to synthesize and help resolve this question.

Climate Change Impacts along Human Population Gradients

Local human impacts are more likely to interact with climate change in coastal areas that are densely populated, since increasing human density often escalates the magnitude of local human stressors. Increasing human density contributes to eutrophication, pollution, and habitat destruction, owing to increased outputs of human waste and sewage, increased land development for housing, industrial and agricultural activities, and increased resource extraction (e.g., fisheries, wood, freshwater and other raw materials) (Figure 3A–C) [42–44]. Human population density has thus been used widely as a reasonable proxy of the relative magnitude of local human impacts [28,44,45]. Some human activities, however, can occur even in very remote regions of the world (e.g., fishing) or generate unusual amounts of per capita impacts (e.g., industrial and agricultural use of freshwater), implying that the relationships between human population density and local human impacts can be context-dependent and more nuanced. Despite its simplicity, it is reasonable to hypothesize that human population density (or activity intensity) can predict the interactive impacts of climate change with local human impact. Combining this hypothesis with different types of interactions (synergistic, additive, and antagonistic), the following predictions can be made. Assuming that local human impacts increase with human density until an asymptote is reached at very high densities, the impact of climate change is predicted to increase exponentially with increasing human density when its interaction with local human impact is synergistic (Figure 4A). When the interaction is additive, the impact of climate change is predicted to increase exponentially at low human densities and reaches an asymptote at very high densities (Figure 4A). In contrast, when the interaction is antagonistic, the impact of climate change is predicted to decrease with increasing human density (Figure 4A).

These new hypotheses haven't been tested specifically, but existing empirical data are lending support for variation in the impact of climate change along human density gradients. For example, due to groundwater and gas extraction, land subsidence, a proxy for relative sea level rise within a region, increases significantly with human density across western Indonesia, a country forced by rapid land subsidence to relocate its capital city from Jakarta to Borneo (Figure 3D) [46]. In the contiguous US, saltwater intrusion into coastal aquifers driven by the combination of sea level rise and groundwater pumping is predicted to increase exponentially with human density (Figure 3E) [28]. For coastal waters that are weakly affected by freshwater inputs, annual mean pH decreases with increasing human density (Figure 3F). Declines in herbivore grazing, a result of overfishing, can substantially amplify the negative impacts of ocean acidification and warming on corals [17], and fishing intensity often

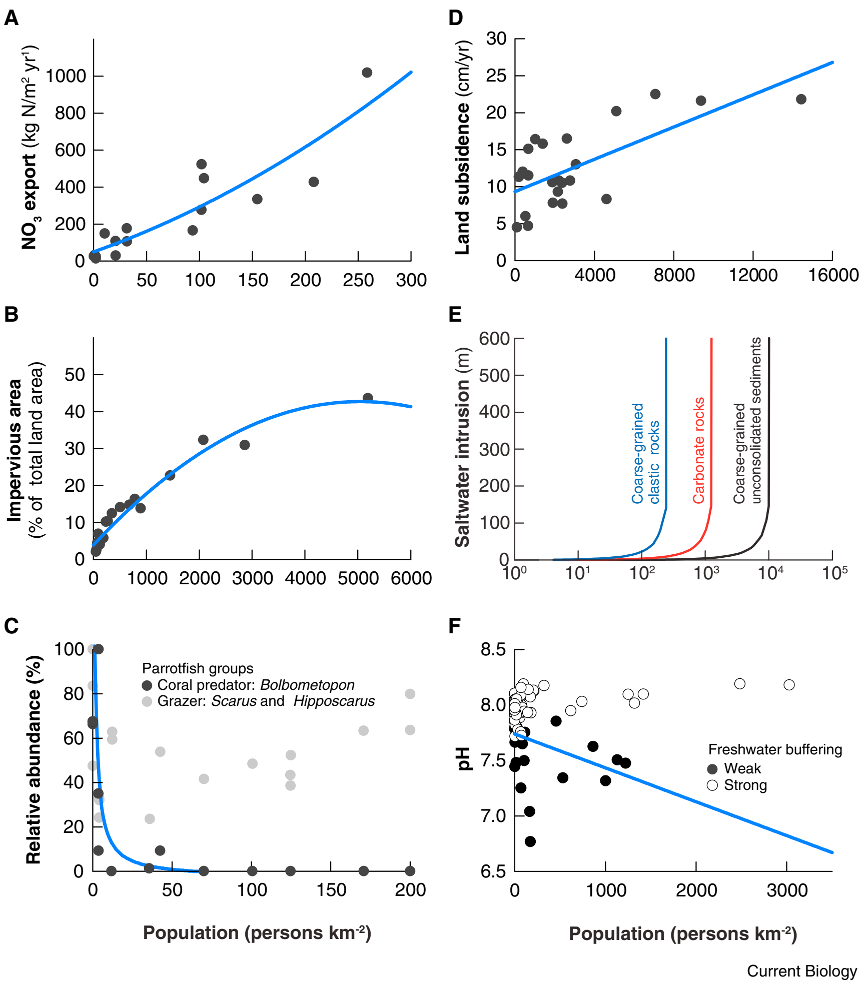


Figure 3. Empirical data showing variation in local human impacts and climate change impacts along human population density gradients.
(A) NO_3 export intensity in the world's major watersheds (redrawn from [42]). (B) Impervious area as a percentage of total land area in different counties in New Jersey, USA (redrawn from [43]). (C) Relative abundances of two functionally different parrotfish groups across the Indian and Pacific Oceans (humans primarily fish coral predators that are of large body size, rather than grazers that are typically of small body size; republished with permission from The Royal Society [44] © 2011). (D) Rate of land subsidence (owing to groundwater and gas extraction) in western Indonesia (the two dots with highest human densities indicate sites located in Jakarta, the soon-to-be-past capital city of Indonesia; data from [46]). (E) Saltwater intrusion (due to sea level rise and groundwater extraction) simulated for three different types of coastal aquifers in the contiguous US (reprinted with permission from Springer Nature: Nature Climate Change [28] © 2012). (F) Mean seawater pH for 80 coastal sites that were either strongly or weakly affected by freshwater inputs (data from [29]; two sites were excluded due to missing information on freshwater effects and one due to much higher population density; the exclusion of the latter didn't affect the relationship with human population density shown here). Population density data in D and F were extracted from [135] (estimated within 5 km diameter; population data in 2005 and 2000 were used in D and F, respectively). In all panels, lines show linear (D, F), quadratic (A, B) or inverse polynomial (C) regressions ($P < 0.057$ in all cases), except that model predictions are shown in E. In C and F, only significant regressions are shown. The regressions for grazers in C and for sites with strong freshwater buffering in F were insignificant and so are not shown.

increases with human density [44]. Understanding how climate change impacts vary, linearly or nonlinearly, along human density gradients certainly requires more specific investigation.

Human density gradients can provide a useful tool to begin to gain a predictive understanding of the impacts of climate change on the structure and functioning of coastal ecosystems. Human density, however, is not the only predictor for spatiotemporal variation in the impact of climate change. Other factors, such as magnitude of climate stress and geographic attributes, could be at work, too. For magnitude of climate stress, local human impacts should generally dominate at low levels of climate stress (Figure 4A). At high levels of climate stress, interactions with local human impacts (either synergistic, additive or antagonistic) are likely to be most pronounced, and when the interaction is synergistic, climate change may cause the greatest loss of species or ecosystems at intermediate human densities (Figure 4B). At extreme levels of climate stress, climate change is likely to overwhelm any local human impacts (Figure 4A). This may explain why water quality and fishing were found to synergistically interact with heat stress in previous coral bleaching events on the Great Barrier Reef but not in the record extreme warming event in 2015–2016 [47,48]. Geographic attributes can also dictate where climate change may be more likely to interact with local human impact. This could explain why a decreasing trend in pH with increasing local human density was found for coastal waters weakly affected by estuarine freshwater run-off but not for those strongly affected (Figure 3F).

Are Synergistic, Additive, or Antagonistic Interactions Predictable?

Can the nature (synergistic, additive, or antagonistic) of interactions between climate change and local human impacts be predicted? The nature of stressor interaction has been shown to vary with a range of ecological factors including ecosystem type, stressor type, and species functional traits [41,49], and it is challenging to screen for the best predictors [39]. However, it might be more feasible to predict interactions between climate change and local human impacts by understanding the underlying processes and mechanisms. The co-tolerance (co-sensitivity) concept can be a valuable tool for this [39]. According to the co-tolerance concept [50], when tolerance to a climate change stressor confers tolerance to a local human stressor, because both stressors act on the same ecological or physiological processes, antagonistic interactions are expected when they occur simultaneously. Conversely, when a local human stressor and a climate change stressor act on two different processes and species are equipped to resist one but not both stressors, the local human stressor is more likely to increase

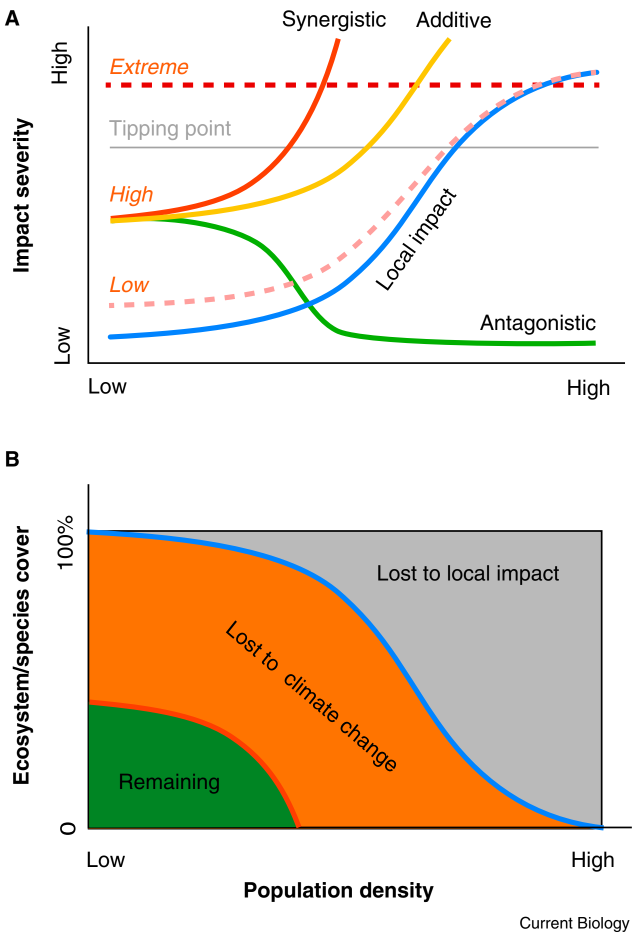


Figure 4. Conceptual models of climate change impacts as a function of human population density.
(A) Variation in synergistic, additive, and antagonistic interactions between climate change and local human impacts. Also shown is how magnitude of climate stress (low, high, and extreme) can affect interactions between climate change and local human impacts. (B) Relative loss of coastal ecosystem/species to climate change and local human impacts when they interact synergistically.

their susceptibility to the climate change stressor, leading to synergistic or additive interactions. The co-tolerance concept can be applied to both individual species and community levels (Figure 5A).

The co-tolerance concept, recently redefined as a more inclusive 'correlated response' theory [51], has been well developed in studies of heavy metal contamination. Co-tolerance has been shown to dictate types of interactions between heavy metal and temperature [52]. Studies on co-tolerance in coastal ecosystems remain few. In Kenyan coral reefs, neither a positive nor negative relationship between sensitivities to warming and fishing pressure across different coral species was found (Figure 5B), partly explaining the absence of synergistic interactions between fishing and warming [53]. In another study on coral reef fishes [54], a negative convex relationship between sensitivities to climate change and fishing pressure was found (Figure 5B), which might indicate potential synergistic interactions between climate change and fishing. Whether co-tolerance

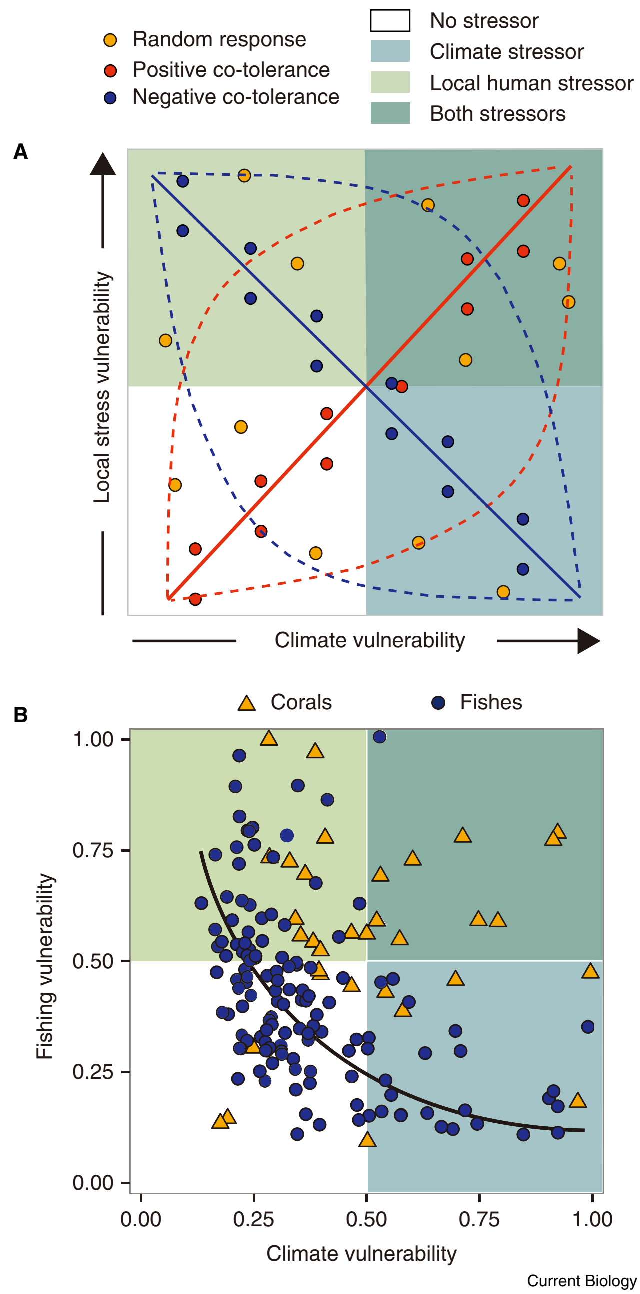


Figure 5. Co-tolerances to climate change and local human stressors.
(A) Theoretical co-tolerance relationships. (B) Tolerances of corals and fishes to climate and fishing stressors on coral reefs. In (A), for random responses, species are randomly distributed in their vulnerability to both stressors. When both stressors occur (shown as shaded areas), 75% of the species will be affected. For positive co-tolerances, species' vulnerability to one stressor is similar to their vulnerability to the other stressor. When both stressors occur, 50% of the species will be affected. For negative co-tolerances, species' vulnerability to one stressor is negatively related to their vulnerability to the other stressor. When both stressors occur, 100% of the species will be affected. The solid lines in (A) show the ideally linear positive and negative co-tolerances, respectively. If the positive or negative co-tolerance relationships are nonlinear, the proportion of species affected may change more or less. In (B), there is a downward curvilinear negative co-tolerance relationship among reef fishes (black line), while no clear co-tolerance relationship exists among corals. Figure 5A and 5B adapted from [136].

can predict the nature of interactions between climate change and local human impacts, however, needs to be tested more broadly.

Incorporating Local Human Impacts Alters Predictions of Resilience to Climate Change

How will local human impacts alter resilience of coastal ecosystems to climate change? Synergistic and additive interactions may reduce resilience to climate change by increasing the risk that the tipping points (i.e., the thresholds over which sudden, drastic ecosystem shifts occur) of ecosystems to climate stress are exceeded (Figure 4A). Overfishing, for example, can substantially increase the likelihood that the tipping points of coral reefs to ocean acidification [17] and those of kelp forests to climatic warming [20] are exceeded, causing shifts from productive ecosystems to algal barrens. Eutrophication can increase the likelihood that the tipping points of coral reefs to ocean acidification are exceeded [17]. Conversely, antagonistic interactions with local human impacts are predicted to enhance resilience to climate stress by lowering the risk that tipping points are exceeded (Figure 4A). Empirical demonstrations, however, are still lacking.

Local human impacts can also alter resilience of coastal ecosystems to climate change via other mechanisms. First, local human impacts can affect ecological factors (e.g., species diversity, competition/facilitation, and food web interactions) that govern the resistance of coastal ecosystems to climate change [55,56]. Overfishing, for example, can simplify food webs in kelp forests and coral reefs, and simplification of food webs and decreases in number of links per species are predicted to decrease ecosystem resistance [57]. Also, local human impacts can influence recovery following climate events. Depletion of large herbivorous fishes, for example, has been demonstrated to impede coral recovery in the aftermath of the 1998 bleaching event by permitting macroalgal overgrowth, resulting in phase shifts on the Great Barrier Reef [58].

Protection, Restoration, and Recovery Potential

Increasing empirical evidence is making it clear that the impacts of climate change on coastal ecosystems are often modulated by local human impacts. But can local conservation, by managing local human impacts, compensate for the impacts of climate change? And when and where is local conservation more likely to buffer the impacts of climate change? These are questions central to the growing debate of whether we should shift much of our investment in local conservation to global greenhouse gas emission reductions. Over the last few decades, at least billions of US dollars per year have been invested into local conservation actions including designation and enforcement of marine protected areas (MPA), mitigation of terrestrial pollutant input, and ecosystem restoration [59,60]. While the number of local conservation actions has increased exponentially [60], their performance in buffering coastal ecosystems from climate change has been questioned [61].

Can MPAs that Reduce Local Human Impacts Help Save Coastal Ecosystems from Climate Change?

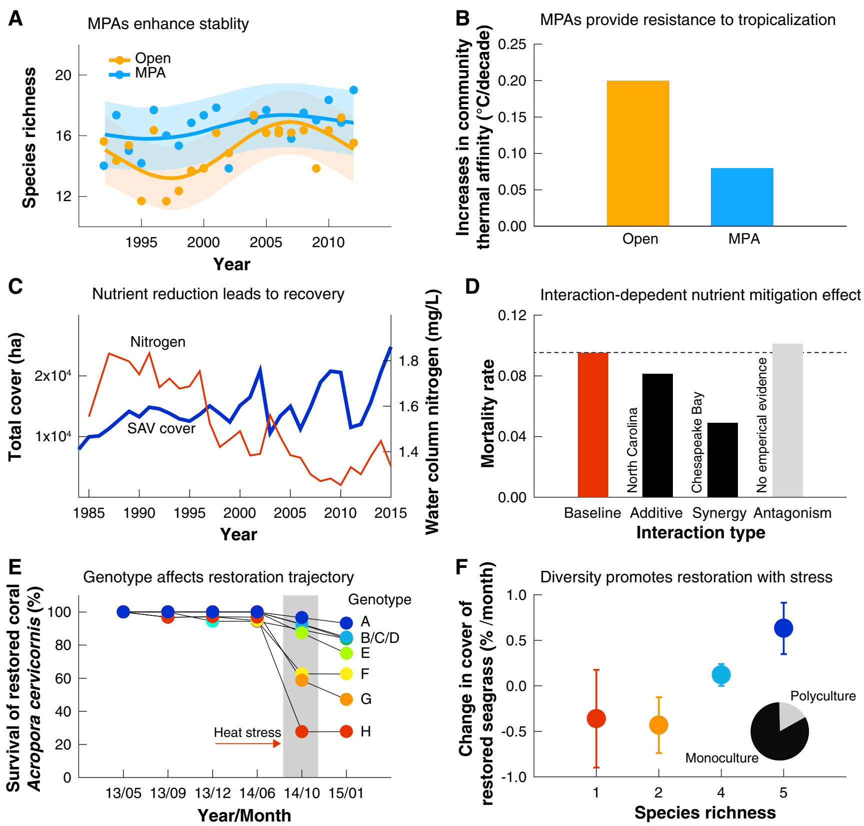
MPAs are a leading conservation tool for mitigating local human impacts on coastal ecosystems, especially for fishing when fishing is properly managed [62]. MPAs have been shown to enhance the resilience of multiple types of coastal ecosystems to climate change [63]. On the rapidly warming Tasmanian east coast, for example, MPAs enhanced resilience of kelp forests to climate warming-driven sea urchin expansion by reinstating top-down control of urchin populations by predators [64], increased the temporal stability of temperate reef fish communities over 20 years (Figure 6A), and helped resist the initial stages of tropicalization by limiting the intrusion of range-extending species (Figure 6B). In Baja California, Mexico, MPAs increased the resilience of marine invertebrates to mass mortality likely caused by climate-driven hypoxia, since large body size and high egg production in MPAs led to greater resistance and faster recovery of marine invertebrates [65]. On the Great Barrier Reef, MPAs have been found in multiple studies to enhance the capacity of coral reefs to withstand warming, floods, and storms, due to greater herbivory, trophic cascades, faster recovery, and portfolio effects within MPAs [58,66,67]. In the Bahamas, corals also recovered from mass bleaching and hurricane impacts faster inside than outside MPAs [68]. In the Line Islands affected by the strong 1997–1998 El Niño, corals recovered in fully protected reefs within a decade, whereas they did not recover in unprotected reefs [69,70].

Despite broad recognition of MPAs' positive effects on resilience to climate change, their performance on coral reefs is a matter of recent debate. No effects of MPAs on coral resistance to the record 2015–2016 mass bleaching on the Great Barrier Reef [47] triggered widespread concerns that MPAs would fail to save ecosystems from climate change. These concerns are apparently supported by more than a dozen other empirical studies and meta-analyses where no effects of MPAs on resilience of coral reefs to climate change were found (see a list in [61], although most of these meta-analytical studies were not comparisons of paired MPAs and fished sites).

Disparity in the effect of MPAs on coral resilience to climate change may have resulted from multiple sources. First, the performance of MPAs varies greatly with multiple management-related factors. Only well-enforced, older, larger MPAs, currently accounting for a small fraction of all the MPAs established globally, can achieve the best conservation performance [71]. Second, even some well-enforced, fishing-excluded MPAs, such as those in New Caledonia, South Pacific [72] and Florida Keys, USA [73], still face major chronic local human impacts (e.g., watershed nutrient inputs). In both places, regulation of watershed human impacts has been recommended to improve the resilience of protected coral reefs to climate change [72,74]. MPAs should indeed only be considered as part of a portfolio of local conservation strategies (e.g., along with enhanced sewage treatment) used to reduce local human impacts, rather than the 'silver bullet' to increase climate change adaption. Furthermore, the performance of MPAs in enhancing resilience to climate change may vary with species tolerance to climate stress. For corals and other tropical species with limited thermal tolerance, the probability for climate stress to overwhelm local human impacts can be high (Figure 4A).

Managing Terrestrial Human Impacts to Increase Coastal Resilience to Climate Change

Reducing terrestrial stressor inputs to coastal ecosystems can indeed be important or even necessary to increase resilience to climate change, especially when terrestrial human impacts and climate change interact additively and synergistically. In Chesapeake Bay where synergistic interactions between



Current Biology

Figure 6. Local conservation promotes resilience and restoration under climate change.
All are empirical evidence. (A) Marine protected areas (MPAs) enhanced stability in coral reef fish species richness in the Maria Island Marine Reserve, Tasmania, Australia (reprinted with permission from Springer Nature: Nature Climate Change [137] © 2014). (B) MPAs also provided resistance of coral reef fish communities to tropicalization (data from [137]). (C) Long-term nutrient reduction led to recovery of submerged aquatic vegetation (SAV) in Chesapeake Bay, USA (redrawn from [76]). (D) Effects of nutrient reduction on seagrass mortality rate are predicted to depend on type of warming and nutrient interaction (adapted from [77]). Synergistic and additive interactions between warming and nutrients on seagrass mortality have been found in Chesapeake Bay [75] and North Carolina [78] (USA), respectively, while we are unaware of a study that reported antagonistic interactions between warming and nutrients on seagrass mortality. (E) Genotype identity determined the success and resistance of restored corals to heat stress (adapted from [138] © Inter-Research 2017). (F) Plantings of higher species richness can promote seagrass recovery in habitats with ongoing intense human disturbance (inset: proportions of monoculture and polyculture seagrass restoration studies; adapted from [89]). Only 17% of current seagrass restoration studies used mixtures of two or more seagrass species.

eutrophication and warming have driven seagrass loss [75], long-term watershed nutrient reductions led to recent recovery of submersed aquatic vegetation including seagrasses (Figure 6C) [76]. This agrees with the prediction that reducing nutrient inputs can lower seagrass mortality when warming and nutrients interact synergistically (Figure 6D) [77]. This effect of nutrient reduction might be weaker but remains positive when warming and nutrients interact additively as has been observed for seagrasses [78]. Although reducing nutrient inputs has also been predicted to exacerbate seagrass mortality when warming and nutrients interact antagonistically, we know of no empirical studies showing such interactions in seagrasses. On the Great Barrier Reef, 6–17% improvement in water quality has been found to be necessary to counteract future thermal stress expected by 2050 among inshore and mid-shelf reefs, although it may have little effect on outershelf reefs dominated by fast-growing, thermally sensitive corals [48] (also see [79]). Similarly, reducing nutrient inputs can increase resilience to climate change in other coastal ecosystems (e.g., rocky shores dominated by kelps and fucoids) [80,81].

Using Restorations to Enhance Ecosystem Recovery from and Resistance to Climate Change

For coastal ecosystems that have been degraded or destroyed, active restoration may assist recovery where natural recovery is stalled. Although some restoration strategies can have negative consequences or provide a dis-service (which needs to be recognized) [82], restoration is becoming a major intervention in coastal conservation [60]. Restoration may be especially applicable where ecosystems are recruitment-limited (e.g., seagrasses) or where population regrowth is only possible through expansion by adults (e.g., salt marsh clonal grasses). However, for habitat restoration to work over large spatial and temporal scales, interactions between climate change and local human impacts must be considered as they have strong implications for when and where restoration will work [83].

First, restoration must not only mitigate past and existing environmental stressors, but must also be conceived to endure recurrent and new environmental obstacles to recovery. Restoration of overexploited oyster populations in Chesapeake Bay, for example, can be impaired by accelerating ocean acidification. And due to a synergistic effect of pH and salinity on calcification, this impairment can be more severe in low salinity areas often preferred by oyster restoration practitioners [84]. Following a catastrophic die-off triggered by drought, restoration of salt marsh vegetation in temperate China has been shown to be restricted by grazing pressure likely elevated by overfishing [56]. Restoration of mangrove forests destroyed by hurricanes can be slowed by biological invasions [85] and recurrent hurricanes [86]. Furthermore, setting historical ecosystem conditions as restoration targets and references can be questionable when climate and human impacts are constantly changing and almost all temperate zones are experiencing tropicalization. Thus, to be most effective, restoration will also need to establish species and assemblages that are most tolerant of these increasing stressors, in areas where local human impacts are being reduced, and in their new ranges predicted by future climate scenarios [83].

For tools that can be used in restoration, we must expand beyond those typically employed to those that are becoming available with rapid advances in technology and ecology. For example, innovative physiological, genetic, and population tools, such as assisted stress acclimation, evolution, and relocation, have been recently advocated for rebuilding warming-resilient coral populations (Figure 6E) [87], even if these tools pose ethical questions. A natural tool to rebuilding resilient assemblages is harnessing positive species interactions (e.g., facilitation, mutualism, and trophic cascade) in restorations via clumping outplants [88], using species polycultures (Figure 6F) [89], or reintroducing top predators. By ameliorating existing local human impacts that limit regrowth, neighbors can positively affect target species, aid their recovery, and give them a greater chance of overcoming increasing climate stressors, as has been demonstrated in a variety of coastal ecosystems [88,90]. Positive species interactions can also make an ecosystem self-reinforced by positive feedbacks, enhancing its resistance to changing local and global environmental conditions. Such ecosystem self-reinforcing processes deserve more investigation and incorporation into climate-smart restoration measures and will be most important where local human impacts and global climate stressors interact additively and synergistically.

Don't Scale Back Local Conservation; Increase Investment at All Scales

Local conservation actions, including MPAs, mitigation of terrestrial stressor input, and restoration, have been clearly shown in a variety of cases to buffer the impact of climate change and boost resilience in coastal ecosystems, providing more time for species to evolve. Local conservation, however, is not a cure-all, and its performance is context-dependent. It may be especially important for saving coastal ecosystems from intermediate to high levels of climate stress [48], while extreme levels of climate stress will decimate coastal ecosystems regardless of local conservation (Figure 4A), although it could be essential for recovery after climate extremes subside. Also, local conservation might be especially important when the target local human impact interacts with climate change synergistically or additively; when the interaction is antagonistic, local conservation may be more promising in climate change refugia [91]. Furthermore, the major local human stressors and their magnitude often vary from place to place, and local conservation strategies may not be applied universally without adaption. And different local conservation strategies might be required for different places (e.g., place-based conservation [92]). Finally, favoring one local conservation measure is likely to be insufficient [62], given that coastal ecosystems often face multiple types of local human impacts, such as offshore fishing and watershed nutrient inputs. To optimize the performance of local conservation, more investments are clearly needed to increase coverage, install complementary measures, and enhance enforcement. Instead of reducing investment in local conservation in favor of heavy investment in global greenhouse gas emission reductions [47,61], we call for increased investments in both to provide a dual guard against climate change and to maximize the potential for coastal ecosystem recovery.

Evolving Coastal Management

Global climate change is accelerating at high rates, pressuring all of Earth's ecosystems including those on coasts. Mitigating the impacts of climate change on coastal ecosystems, however, is particularly challenging because of interactions with local human impacts that are intense in densely populated coasts. Coastal management strategies need to consider those interactions to optimize performance. Another challenge for coastal management is that climate change and human impacts are constantly changing. Thus, an adaptive, evolving management strategy is required. A prototype of such evolving coastal management might be two thousand years of coastal adaption to encroaching seas in the Netherlands, which has evolved from coastal armament, walling off estuaries to currently giving land back to the sea, restoring and creating coastal ecosystems as natural, sustainable flood defenses [93,94]. The Dutch approach, however, does not necessarily transfer to other coasts. In developing coastal regions/countries, adaption capacity can be severely limited by socioeconomic and technical constraints [95]. Coastal societies will have to develop innovative coastal management strategies appropriate for their socioeconomic status and ecosystem condition, potentially including community-based fisheries management and ecosystem-based management, an integrated management approach that considers all types of interactions within an ecosystem (e.g., climate change, human impacts, and stakeholders) [96]. Other innovative coastal management strategies may emerge with advances in ecological understanding of coastal processes and in technologies (e.g., genetic modification, remote sensing, and telecommunication). The impact of climate change on coastal ecosystems in the Anthropocene simply cannot be understood and managed as constant and in isolation. Understanding interactions between climate change and local human impacts has profound and far-reaching implications for the future of coastal ecosystems and civilization along the increasingly human-populated coasts.

ACKNOWLEDGEMENTS

Q.H. was supported by National Natural Science Foundation of China (31870414) and B.R.S. by the US National Science Foundation (1445834), Lenfest Ocean Program, and a Distinguished Fulbright Chair from CSIRO in Australia.

REFERENCES

1. Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., and Williams, S.L. (2006). The impacts of climate change in coastal marine systems. Ecol. Lett. *9*, 228–241.
2. IPCC. (2014). Climate Change 2014: Mitigation of Climate Change, *Volume 3* (USA: Cambridge University Press, Cambridge, United Kingdom and New York, NY).
3. Doney, S.C., Fabry, V.J., Feely, R.A., and Kleypas, J.A. (2009). Ocean acidification: the other CO2 problem. Annu. Rev. Mar. Sci. *1*, 169–192.
4. Golledge, N.R., Kowalewski, D.E., Naish, T.R., Levy, R.H., Fogwill, C.J., and Gasson, E.G.W. (2015). The multi-millennial Antarctic commitment to future sea-level rise. Nature *526*, 421–425.
5. Garcia, R.A., Cabeza, M., Rahbek, C., and Araujo, M.B. (2014). Multiple dimensions of climate change and their implications for biodiversity. Science *344*, 1247579.

6. Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., *et al*. (2012). Climate change impacts on marine ecosystems. Annu. Rev. Mar. Sci. *4*, 11–37.

7. Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., *et al*. (2013). Global imprint of climate change on marine life. Nat. Clim. Chang. *3*, 919–925.

8. Schindler, D.W. (2001). The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci. *58*, 18–29.

9. Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., and Jackson, J.B.C. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. Science *312*, 1806–1809.

10. Crain, C.M., Halpern, B.S., Beck, M.W., and Kappel, C.V. (2009). Understanding and managing human threats to the coastal marine environment. Ann. N.Y. Acad. Sci. *1162*, 39–62.

11. He, Q., Bertness, M.D., Bruno, J.F., Li, B., Chen, G., Coverdale, T.C., Altieri, A.H., Bai, J., Sun, T., Pennings, S.C., *et al*. (2014). Economic development and coastal ecosystem change in China. Sci. Rep. *4*, 5995.

12. Paerl, H.W., and Scott, J.T. (2010). Throwing fuel on the fire: synergistic effects of excessive nitrogen inputs and global warming on harmful algal blooms. Environ. Sci. Technol. *44*, 7756–7758.

13. Munday, P.L., Warner, R.R., Monro, K., Pandolfi, J.M., and Marshall, D.J. (2013). Predicting evolutionary responses to climate change in the sea. Ecol. Lett. *16*, 1488–1500.

14. de Fouw, J., Govers, L.L., van de Koppel, J., van Belzen, J., Dorigo, W., Cheikh, M.A.S., Christianen, M.J.A., van der Reijden, K.J., van der Geest, M., Piersma, T., *et al*. (2016). Drought, mutualism breakdown, and landscape-scale degradation of seagrass beds. Curr. Biol. *26*, 1051–1056.

15. Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., and Silliman, B.R. (2011). The value of estuarine and coastal ecosystem services. Ecol. Monogr. *81*, 169–193.

16. Rabouille, C., Conley, D.J., Dai, M.H., Cai, W.J., Chen, C.T.A., Lansard, B., Green, R., Yin, K., Harrison, P.J., Dagg, M., *et al*. (2008). Comparison of hypoxia among four river-dominated ocean margins: The Changjiang (Yangtze), Mississippi, Pearl, and Rhone rivers. Cont. Shelf Res. *28*, 1527–1537.

17. Anthony, K.R.N., Maynard, J.A., Diaz-Pulido, G., Mumby, P.J., Marshall, P.A., Cao, L., and Hoegh-Guldberg, O. (2011). Ocean acidification and warming will lower coral reef resilience. Glob. Chang. Biol. *17*, 1798–1808.

18. Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., *et al*. (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat. Commun. *7*, 11833.

19. Shaver, E.C., Burkepile, D.E., and Silliman, B.R. (2018). Local management actions can increase coral resilience to thermally-induced bleaching. Nat. Ecol. Evol. *2*, 1075–1079.

20. Ling, S.D., Johnson, C.R., Frusher, S.D., and Ridgway, K.R. (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc. Natl. Acad. Sci. USA *106*, 22341–22345.

21. Lannig, G., Cherkasov, A.S., and Sokolova, I.M. (2006). Temperature-dependent effects of cadmium on mitochondrial and whole-organism bioenergetics of oysters (*Crassostrea virginica*). Mar. Environ. Res. *62*, S79–S82.

22. Ingebritsen, S.E., and Galloway, D.L. (2014). Coastal subsidence and relative sea level rise. Environ. Res. Lett. *9*, 091002.

23. Carbognin, L., Teatini, P., Tomasin, A., and Tosi, L. (2010). Global change and relative sea level rise at Venice: what impact in term of flooding. Clim. Dynam. *35*, 1055–1063.

24. Wang, J., Gao, W., Xu, S., and Yu, L. (2012). Evaluation of the combined risk of sea level rise, land subsidence, and storm surges on the coastal areas of Shanghai, China. Clim. Chang. *115*, 537–558.

25. Rodolfo, K.S., and Siringan, F.P. (2006). Global sea-level rise is recognised, but flooding from anthropogenic land subsidence is ignored around northern Manila Bay, Philippines. Disasters *30*, 118–139.

26. Ericson, J.P., Vorosmarty, C.J., Dingman, S.L., Ward, L.G., and Meybeck, M. (2006). Effective sea-level rise and deltas: Causes of change and human dimension implications. Glob. Planet. Chang. *50*, 63–82.

27. Warren, R.S., and Niering, W.A. (1993). Vegetation change on a northeast tidal marsh - interaction of sea-level rise and marsh accretion. Ecology *74*, 96–103.

28. Ferguson, G., and Gleeson, T. (2012). Vulnerability of coastal aquifers to groundwater use and climate change. Nat. Clim. Chang. *2*, 342–345.

29. Carstensen, J., and Duarte, C.M. (2019). Drivers of pH variability in coastal ecosystems. Environ. Sci. Technol. *53*, 4020–4029.

30. Cai, W.-J., Hu, X., Huang, W.-J., Murrell, M.C., Lehrter, J.C., Lohrenz, S.E., Chou, W.-C., Zhai, W., Hollibaugh, J.T., Wang, Y., *et al*. (2011). Acidification of subsurface coastal waters enhanced by eutrophication. Nat. Geosci. *4*, 766–770.

31. Zeng, X., Chen, X., and Zhuang, J. (2015). The positive relationship between ocean acidification and pollution. Mar. Pollut. Bull. *91*, 14–21.

32. Kelly, R.P., Foley, M.M., Fisher, W.S., Feely, R.A., Halpern, B.S., Waldbusser, G.G., and Caldwell, M.R. (2011). Mitigating local causes of ocean acidification with existing laws. Science *332*, 1036–1037.

33. Gobler, C.J., DePasquale, E.L., Griffith, A.W., and Baumann, H. (2014). Hypoxia and acidification have additive and synergistic negative effects on the growth, survival, and metamorphosis of early life stage bivalves. PLoS One *9*, e83648.

34. Silliman, B.R., and Bertness, M.D. (2002). A trophic cascade regulates salt marsh primary production. Proc. Natl. Acad. Sci. USA *99*, 10500–10505.

35. Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L.E., and Mendelssohn, I.A. (2005). Drought, snails, and large-scale die-off of southern US salt marshes. Science *310*, 1803–1806.

36. Kimbro, D.L., White, J.W., Tillotson, H., Cox, N., Christopher, M., Stokes-Cawley, O., Yuan, S., Pusack, T.J., and Stallings, C.D. (2017). Local and regional stressors interact to drive a salinization-induced outbreak of predators on oyster reefs. Ecosphere *8*, e01992.

37. Pascal, P.-Y., Fleeger, J.W., Galvez, F., and Carman, K.R. (2010). The toxicological interaction between ocean acidity and metals in coastal meiobenthic copepods. Mar. Pollut. Bull. *60*, 2201–2208.

38. Cheng, B.S., Bible, J.M., Chang, A.L., Ferner, M.C., Wasson, K., Zabin, C.J., Latta, M., Deck, A., Todgham, A.E., and Grosholz, E.D. (2015). Testing local and global stressor impacts on a coastal foundation species using an ecologically realistic framework. Glob. Chang. Biol. *21*, 2488–2499.

39. Côté, I.M., Darling, E.S., and Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. Lond. B Biol. Sci. *283*, 20152592.

40. Silliman, B.R., McCoy, M.W., Angelini, C., Holt, R.D., Griffin, J.N., and van de Koppel, J. (2013). Consumer fronts, global change, and runaway collapse in ecosystems. Annu. Rev. Ecol. Evol. Syst. *44*, 503–538.

41. Crain, C.M., Kroeker, K., and Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. *11*, 1304–1315.

42. Caraco, N.F., and Cole, J.J. (1999). Human impact on nitrate export: An analysis using major world rivers. Ambio *28*, 167–170.

43. Stankowski, S.J. (1972). Population density as an indirect indicator of urban and suburban land-surface modifications. US Geological Survey Professional Paper *800*, 219–224.

44. Bellwood, D.R., Hoey, A.S., and Hughes, T.P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc. R. Soc. Lond. B Biol. Sci. *279*, 1621–1629.

45. Knowlton, N., and Jackson, J.B.C. (2008). Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. *6*, e54.

46. Chaussard, E., Amelung, F., Abidin, H., and Hong, S.-H. (2013). Sinking cities in Indonesia: ALOS PALSAR detects rapid subsidence due to groundwater and gas extraction. Remote Sens. Environ. *128*, 150–161.

47. Hughes, T.P., Kerry, J.T., Alvarez-Noriega, M., Alvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., *et al*. (2017). Global warming and recurrent mass bleaching of corals. Nature *543*, 373–377.

48. MacNeil, M.A., Mellin, C., Matthews, S., Wolff, N.H., McClanahan, T.R., Devlin, M., Drovandi, C., Mengersen, K., and Graham, N.A.J. (2019). Water quality mediates resilience on the Great Barrier Reef. Nat. Ecol. Evol. *3*, 620–627.

49. Silliman, B.R., and He, Q. (2018). Physical stress, consumer control, and new theory in ecology. Trend. Ecol. Evol. *33*, 492–503.

50. Vinebrooke, R.D., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., Maberly, S.C., and Sommer, U. (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos *104*, 451–457.

51. Frishkoff, L.O., Echeverri, A., Chan, K.M., and Karp, D.S. (2018). Do correlated responses to multiple environmental changes exacerbate or mitigate species loss? Oikos *127*, 1724–1734.

52. Lambert, A.S., Dabrin, A., Morin, S., Gahou, J., Foulquier, A., Coquery, M., and Pesce, S. (2016). Temperature modulates phototrophic periphyton response to chronic copper exposure. Environ. Pollut. *208*, 821–829.

53. Darling, E.S., McClanahan, T.R., and Cote, I.M. (2013). Life histories predict coral community disassembly under multiple stressors. Glob. Chang. Biol. *19*, 1930–1940.

54. Graham, N.A.J., Chabanet, P., Evans, R.D., Jennings, S., Letourneur, Y., MacNeil, M.A., McClanahan, T.R., Ohman, M.C., Polunin, N.V.C., and Wilson, S.K. (2011). Extinction vulnerability of coral reef fishes. Ecol. Lett. *14*, 341–348.

55. Bernhardt, J.R., and Leslie, H.M. (2013). Resilience to climate change in coastal marine ecosystems. Annu. Rev. Mar. Sci. *5*, 371–392.

56. He, Q., Silliman, B.R., Liu, Z., and Cui, B. (2017). Natural enemies govern ecosystem resilience in the face of extreme droughts. Ecol. Lett. *20*, 194–201.

57. Dunne, J.A., Williams, R.J., and Martinez, N.D. (2002). Food-web structure and network theory: The role of connectance and size. Proc. Natl. Acad. Sci. USA *99*, 12917–12922.

58. Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., and Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. *17*, 360–365.

59. Balmford, A., Gravestock, P., Hockley, N., McClean, C.J., and Roberts, C.M. (2004). The worldwide costs of marine protected areas. Proc. Natl. Acad. Sci. USA *101*, 9694–9697.

60. Bayraktarov, E., Saunders, M.I., Abdullah, S., Mills, M., Beher, J., Possingham, H.P., Mumby, P.J., and Lovelock, C.E. (2016). The cost and feasibility of marine coastal restoration. Ecol. Appl. *26*, 1055–1074.

61. Bruno, J.F., Cote, I.M., and Toth, L.T. (2019). Climate change, coral loss, and the curious case of the parrotfish paradigm: why don't marine protected areas improve reef resilience? Annu. Rev. Mar. Sci. *11*, 307–334.

62. Allison, G.W., Lubchenco, J., and Carr, M.H. (1998). Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. *8*, S79–S92.

63. Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Saenz-Arroyo, A., Rashid Sumaila, U., Wilson, R.W., *et al*. (2017). Marine reserves can mitigate and promote adaptation to climate change. Proc. Natl. Acad. Sci. USA *114*, 6167–6175.

64. Ling, S.D., and Johnson, C.R. (2012). Marine reserves reduce risk of climate-driven phase shift by reinstating size- and habitat-specific trophic interactions. Ecol. Appl. *22*, 1232–1245.

65. Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J.A., Rossetto, M., and De Leo, G.A. (2012). Evidence that marine reserves enhance resilience to climatic impacts. PLoS One *7*, e40832.

66. Olds, A.D., Pitt, K.A., Maxwell, P.S., Babcock, R.C., Rissik, D., and Connolly, R.M. (2014). Marine reserves help coastal ecosystems cope with extreme weather. Glob. Chang. Biol. *20*, 3050–3058.

67. Mellin, C., MacNeil, M.A., Cheal, A.J., Emslie, M.J., and Caley, M.J. (2016). Marine protected areas increase resilience among coral reef communities. Ecol. Lett. *19*, 629–637.

68. Mumby, P.J., and Harborne, A.R. (2010). Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS One *5*, e8657.

69. Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., *et al*. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. PLoS One *3*, e1548.

70. Sala, E., and Giakoumi, S. (2018). No-take marine reserves are the most effective protected areas in the ocean. ICES J. Mar. Sci. *75*, 1166–1168.

71. Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., *et al*. (2014). Global conservation outcomes depend on marine protected areas with five key features. Nature *506*, 216–220.

72. Carassou, L., Leopold, M., Guillemot, N., Wantiez, L., and Kulbicki, M. (2013). Does herbivorous fish protection really improve coral reef resilience? A case study from New Caledonia (South Pacific). PLoS One *8*, e60564.

73. Toth, L.T., van Woesik, R., Murdoch, T.J.T., Smith, S.R., Ogden, J.C., Precht, W.F., and Aronson, R.B. (2014). Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. Coral Reefs *33*, 565–577.

74. Hansen, L., Hoffman, J., Drews, C., and Mielbrecht, E. (2010). Designing climate-smart conservation: guidance and case studies. Conserv. Biol. *24*, 63–69.

75. Lefcheck, J.S., Wilcox, D.J., Murphy, R.R., Marion, S.R., and Orth, R.J. (2017). Multiple stressors threaten the imperiled coastal foundation species eelgrass (Zostera marina) in Chesapeake Bay, USA. Glob. Chang. Biol. *23*, 3474–3483.

76. 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., *et al*. (2018). Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. Proc. Natl. Acad. Sci. USA *115*, 3658–3662.

77. Brown, C.J., Saunders, M.I., Possingham, H.P., and Richardson, A.J. (2013). Managing for interactions between local and global stressors of ecosystems. PLoS One *8*, e65765.

78. Brodeur, M.C., Piehler, M.F., and Fodrie, F.J. (2015). Consumers mitigate heat stress and nutrient enrichment effects on eelgrass *Zostera marina* communities at its southern range limit. Mar. Ecol. Progr. Ser. *525*, 53–64.

79. Wooldridge, S.A., and Done, T.J. (2009). Improved water quality can ameliorate effects of climate change on corals. Ecol. Appl. *19*, 1492–1499.

80. Falkenberg, L.J., Connell, S.D., and Russell, B.D. (2013). Disrupting the effects of synergies between stressors: improved water quality dampens the effects of future CO2 on a marine habitat. J. Appl. Ecol. *50*, 51–58.

81. Strain, E.M.A., van Belzen, J., van Dalen, J., Bouma, T.J., and Airoldi, L. (2015). Management of local stressors can improve the resilience of marine canopy algae to global stressors. PLoS One *10*, e0120837.

82. Wilson, K.A., Davis, K.J., Matzek, V., and Kragt, M.E. (2019). Concern about threatened species and ecosystem disservices underpin public willingness to pay for ecological restoration. Restor. Ecol. *27*, 513–519.

83. Harris, J.A., Hobbs, R.J., Higgs, E., and Aronson, J. (2006). Ecological restoration and global climate change. Restor. Ecol. *14*, 170–176.

84. Waldbusser, G.G., Voigt, E.P., Bergschneider, H., Green, M.A., and Newell, R.I.E. (2011). Biocalcification in the eastern oyster (*Crassostrea virginica*) in relation to long-term trends in Chesapeake Bay pH. Estuar. Coast. *34*, 221–231.

85. Biswas, S.R., Khan, M.S.I., and Mallik, A.U. (2012). Invaders' control on post-disturbance succession in coastal mangroves. J. Plant Ecol. *5*, 157–166.

86. Taylor, M.D.R.B., Rangel-Salazar, J.L., and Hernández, B.C.J.J.o.E.P. (2013). Resilience in a Mexican Pacific mangrove after hurricanes: implications for conservation restoration. J. Environ. Prot. *4*, 1383–1391.

87. National Academies of Sciences Engineering and Medicine (2019). A Research Review of Interventions to Increase the Persistence and Resilience of Coral Reefs (Washington, DC: National Academies Press).

88. Silliman, B.R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T., Jacobi, R., Jacobi, M., and van de Koppel, J. (2015). Facilitation shifts paradigms and can amplify coastal restoration efforts. Proc. Natl. Acad. Sci. USA *112*, 14295–14300.

89. Williams, S.L., Ambo-Rappe, R., Sur, C., Abbott, J.M., and Limbong, S.R. (2017). Species richness accelerates marine ecosystem restoration in the Coral Triangle. Proc. Natl. Acad. Sci. USA *114*, 11986–11991.

90. Huxham, M., Kumara, M.P., Jayatissa, L.P., Krauss, K.W., Kairo, J., Langat, J., Mencuccini, M., Skov, M.W., and Kirui, B. (2010). Intra- and interspecific facilitation in mangroves may increase resilience to climate change threats. Philos. Trans. R. Soc. Lond. B Biol. Sci. *365*, 2127–2135.

91. Brown, C.J., Saunders, M.I., Possingham, H.P., and Richardson, A.J. (2014). Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. Divers. Distrib. *20*, 538–546.

92. Williams, D.R., Stewart, W.P., and Kruger, L.E. (2013). The emergence of place-based conservation. In Place-based Conservation: Perspectives from the Social Sciences, W.P. Stewart, D.R. Williams, and L. Kruger, eds. (Dordrecht: Springer), pp. 1–17.

93. Temmerman, S., Meire, P., Bouma, T.J., Herman, P.M.J., Ysebaert, T., and De Vriend, H.J. (2013). Ecosystem-based coastal defence in the face of global change. Nature *504*, 79–83.

94. van Wesenbeeck, B.K., Mulder, J.P.M., Marchand, M., Reed, D.J., de Vries, M.B., de Vriend, H.J., and Herman, P.M.J. (2014). Damming deltas: a practice of the past? Towards nature-based flood defenses. Estuar. Coast. Shelf Sci. *140*, 1–6.

95. Nicholls, R.J., and Cazenave, A. (2010). Sea-level rise and its impact on coastal zones. Science *328*, 1517–1520.

96. Arkema, K.K., Abramson, S.C., and Dewsbury, B.M. (2006). Marine ecosystem-based management: from characterization to implementation. Front. Ecol. Environ. *4*, 525–532.

97. Tomanek, L., and Somero, G.N. (1999). Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: Implications for limits of thermotolerance and biogeography. J. Exp. Biol. *202*, 2925–2936.

98. Marín-Guirao, L., Entrambasaguas, L., Dattolo, E., Ruiz, J.M., and Procaccini, G. (2017). Molecular mechanisms behind the physiological resistance to intense transient warming in an iconic marine plant. Front. Plant Sci. *8*, 1142.

99. Altizer, S., Ostfeld, R.S., Johnson, P.T.J., Kutz, S., and Harvell, C.D. (2013). Climate change and infectious diseases: from evidence to a predictive framework. Science *341*, 514–519.

100. Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M., and Mathes, M.T. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiol. Biochem. Zool. *81*, 697–708.

101. Peck, L.S., Morley, S.A., Richard, J., and Clark, M.S. (2014). Acclimation and thermal tolerance in Antarctic marine ectotherms. J. Exp. Biol. *217*, 16–22.

102. Donnelly, J.P., and Bertness, M.D. (2001). Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. Proc. Natl. Acad. Sci. USA *98*, 14218–14223.

103. Kroeker, K.J., Kordas, R.L., Crim, R.N., and Singh, G.G. (2010). Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol. Lett. *13*, 1419–1434.

104. Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., and Dolgov, A.V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat. Clim. Chang. *5*, 673–677.

105. Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., and Krauss, K.W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob. Chang. Biol. *20*, 147–157.

106. Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E., Heck, K.L., Jr., Booth, D.J., Coleman, M.A., Feary, D.A., *et al*. (2014). The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc. R. Soc. Lond. B Biol. Sci. *281*, 20140846.

107. Muir, P.R., Wallace, C.C., Done, T., and Aguirre, J.D. (2015). Limited scope for latitudinal extension of reef corals. Science *348*, 1135–1138.

108. Sunday, J.M., Bates, A.E., and Dulvy, N.K. (2010). Global analysis of thermal tolerance and latitude in ectotherms. Proc. R. Soc. Lond. B Biol. Sci. *278*, 1823–1830.

109. Sippo, J.Z., Lovelock, C.E., Santos, I.R., Sanders, C.J., and Maher, D.T. (2018). Mangrove mortality in a changing climate: An overview. Estuar. Coast. Shelf Sci. *215*, 241–249.

110. Thomson, J.A., Burkholder, D.A., Heithaus, M.R., Fourqurean, J.W., Fraser, M.W., Statton, J., and Kendrick, G.A. (2015). Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Glob. Chang. Biol. *21*, 1463–1474.

111. Kelleway, J.J., Saintilan, N., Macreadie, P.I., Skilbeck, C.G., Zawadzki, A., and Ralph, P.J. (2016). Seventy years of continuous encroachment substantially increases "blue carbon' capacity as mangroves replace intertidal salt marshes. Glob. Chang. Biol. *22*, 1097–1109.

112. Rogers, K., Kelleway, J.J., Saintilan, N., Megonigal, J.P., Adams, J.B., Holmquist, J.R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., *et al*. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. Nature *567*, 91–95.

113. Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H., and Machmuller, M. (2009). Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Front. Ecol. Environ. *7*, 73–78.

114. Temmerman, S., De Vries, M.B., and Bouma, T.J. (2012). Coastal marsh die-off and reduced attenuation of coastal floods: A model analysis. Glob. Planet. Chang. *92-93*, 267–274.

115. Stiasny, M.H., Mittermayer, F.H., Sswat, M., Voss, R., Jutfelt, F., Chierici, M., Puvanendran, V., Mortensen, A., Reusch, T.B.H., and Clemmesen, C. (2016). Ocean acidification effects on Atlantic cod larval survival and recruitment to the fished population. PLoS One *11*, e0155448.

116. Colt, S.G., and Knapp, G.P. (2016). Economic effects of an ocean acidification catastrophe. Am. Econ. Rev. *106*, 615–619.

117. Halpern, B.S., Selkoe, K.A., Micheli, F., and Kappel, C.V. (2007). Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conserv. Biol. *21*, 1301–1315.

118. Gedan, K.B., Silliman, B.R., and Bertness, M.D. (2009). Centuries of human-driven change in salt marsh ecosystems. Annu. Rev. Mar. Sci. *1*, 117–141.

119. Jennerjahn, T.C., Gilman, E., Krauss, K.W., Lacerda, L., Nordhaus, I., and Wolanski, E. (2017). Mangrove ecosystems under climate change. In Mangrove Ecosystems: A Global Biogeographic Perspective, V.H. Rivera-Monroy, S.Y. Lee, E. Kristensen, and R.R. Twilley, eds. (Switzerland: Springer, Cham), pp. 211–244.

120. Orth, R.J., Carruthers, T.J., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., and Olyarnik, S.J.B. (2006). A global crisis for seagrass ecosystems *56*, 987–996.

121. Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M., and Scapini, F. (2009). Threats to sandy beach ecosystems: a review. Estuar. Coast. Shelf Sci. *81*, 1–12.

122. Crowe, T.P., Thompson, R.C., Bray, S., and Hawkins, S.J. (2000). Impacts of anthropogenic stress on rocky intertidal communities. J. Aquat. Ecosystem Stress Recov. *7*, 273–297.

123. Benedetti-Cecchi, L., and Trussell, G.C. (2014). Intertidal rocky shores. In Marine Community Ecology and Conservation, M.D. Bertness, J.F. Bruno, B.R. Silliman, and J.J. Stachowicz, eds. (Cambridge, MA: Sinauer Associates), pp. 203–225.

124. Wernberg, T., Krumhansl, K., Filbee-Dexter, K., and Pedersen, M.F. (2019). Status and trends for the world's kelp forests. In World Seas: An Environmental Evaluation, C. Sheppard, ed. (Elsevier), pp. 57–78.

125. Kleypas, J.A., and Eakin, C.M. (2007). Scientists' perceptions of threats to coral reefs: results of a survey of coral reef researchers. Bull. Mar. Sci. *80*, 419–436.

126. Hoegh-Guldberg, O., Poloczanska, E.S., Skirving, W., and Dove, S. (2017). Coral reef ecosystems under climate change and ocean acidification. Front. Ecol. Evol. *4*, 158.

127. Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., and Kay, M.C. (2011). Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience *61*, 107–116.

128. Rodriguez, A.B., Fodrie, F.J., Ridge, J.T., Lindquist, N.L., Theuerkauf, E.J., Coleman, S.E., Grabowski, J.H., Brodeur, M.C., Gittman, R.K., and Keller, D.A. (2014). Oyster reefs can outpace sea-level rise. Nat. Clim. Chang. *4*, 493–497.

129. Gobler, C.J., Doherty, O.M., Hattenrath-Lehmann, T.K., Griffith, A.W., Kang, Y., and Litaker, R.W. (2017). Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. Proc. Natl. Acad. Sci. USA *114*, 4975–4980.

130. Micheli, F., Bishop, M.J., Peterson, C.H., and Rivera, J. (2008). Alteration of seagrass species composition and function over two decades. Ecol. Monogr. *78*, 225–244.

131. Talmage, S.C., and Gobler, C.J. (2009). The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and Eastern oysters (*Crassostrea virginica*). Limnol. Oceanogr. *54*, 2072–2080.

132. Whitfield, P.E., Munoz, R.C., Buckel, C.A., Degan, B.P., Freshwater, D.W., and Hare, J.A. (2014). Native fish community structure and Indo-Pacific lionfish Pterois volitans densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. Mar. Ecol. Progr. Ser. *509*, 241–254.

133. Enwright, N.M., Griffith, K.T., and Osland, M.J. (2016). Barriers to and opportunities for landward migration of coastal wetlands with sea-level rise. Front. Ecol. Environ. *14*, 307–316.

134. Kirby, R.R., Beaugrand, G., and Lindley, J.A. (2009). Synergistic effects of climate and fishing in a marine ecosystem. Ecosystems *12*, 548–561.

135. Center for International Earth Science Information Network - Columbia University (2016). Gridded Population of the World, version 4 (GPWV4): Population Density, (NASA Socioeconomic Data and Applications Center (SEDAC) Palisades, NY).

136. McClanahan, T.R., Graham, N.A.J., and Darling, E.S. (2014). Coral reefs in a crystal ball: predicting the future from the vulnerability of corals and reef fishes to multiple stressors. Curr. Opin. Environ. Sustain. *7*, 59–64.

137. Bates, A.E., Barrett, N.S., Stuart-Smith, R.D., Holbrook, N.J., Thompson, P.A., and Edgar, G.J. (2014). Resilience and signatures of tropicalization in protected reef fish communities. Nat. Clim. Chang. *4*, 62–67.

138. Ladd, M.C., Shantz, A.A., Bartels, E., and Burkepile, D.E. (2017). Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored *Acropora cervicornis*. Mar. Ecol. Progr. Ser. *572*, 129–139.