Responses of Coastal Ecosystems to Climate Change: Insights from Long-Term Ecological Research

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Coastal ecosystems play a disproportionately large role in society, and climate change is altering their ecological structure and function, as well as their highly valued goods and services. In the present article, we review the results from decade-scale research on coastal ecosystems shaped by foundation species (e.g., coral reefs, kelp forests, coastal marshes, seagrass meadows, mangrove forests, barrier islands) to show how climate change is altering their ecological attributes and services. We demonstrate the value of site-based, long-term studies for quantifying the resilience of coastal systems to climate forcing, identifying thresholds that cause shifts in ecological state, and investigating the capacity of coastal ecosystems to adapt to climate change and the biological mechanisms that underlie it. We draw extensively from research conducted at coastal ecosystems studied by the US Long Term Ecological Research Network, where long-term, spatially extensive observational data are coupled with shorter-term mechanistic studies to understand the ecological consequences of climate change.
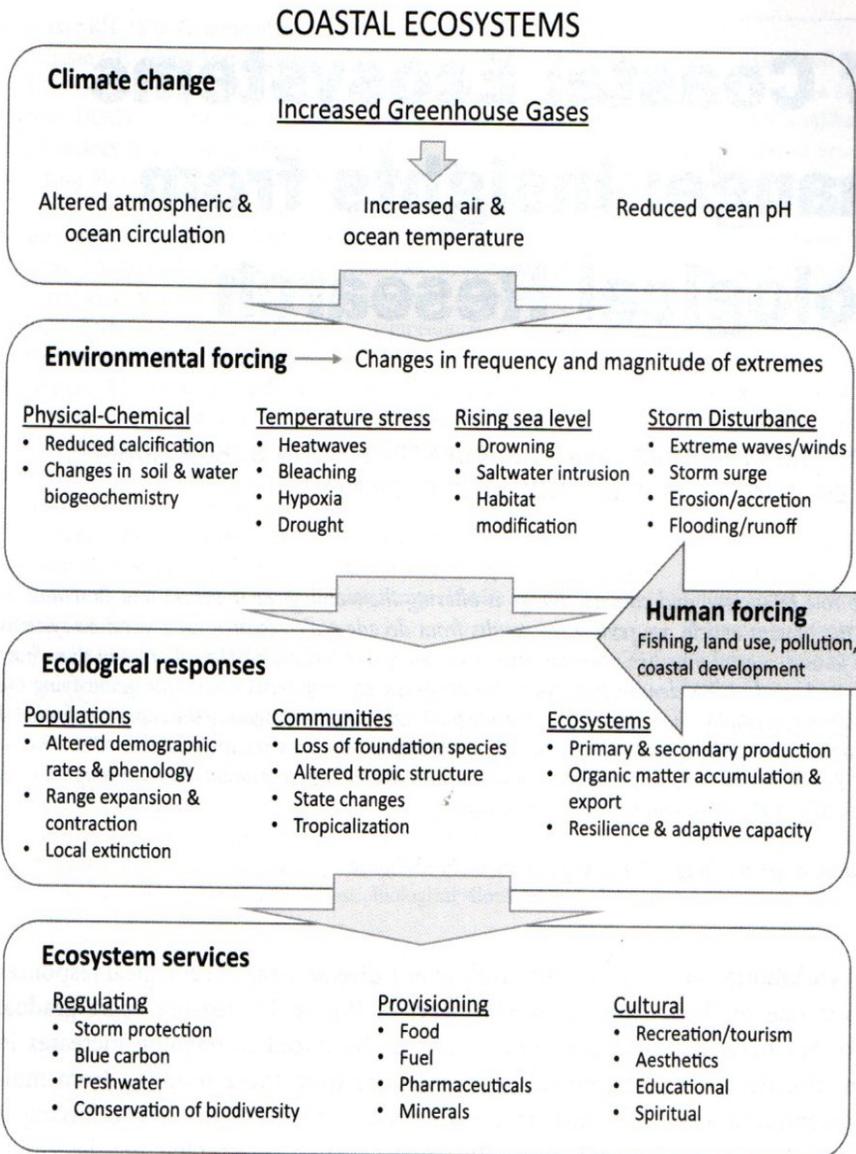
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Understanding the role of climate variability in structuring patterns in nature remains one of the most fundamental topics in ecology. There has been an even greater interest in this topic in recent decades as a consequence of the ongoing increases in greenhouse gas emissions, which are causing global temperatures and sea level to rise and the oceans to become less alkaline (IPCC 2021). These gradual secular trends are being accompanied by more acute increases in the frequency and amplitude of fluctuations around the trending averages in land and ocean temperatures, precipitation, wind and wave energy, ocean pH, and sea level. Such climate-related forcings interact with nonclimate human impacts (e.g., land use, extraction of natural resources, pollution) to influence the structure and function of ecological systems and the goods and services that they provide to society (IPCC 2014).

The ecological consequences of climate change are particularly evident in coastal regions (Bindoff et al. 2019), which host one-third of the world's human population, despite accounting for only 4% of the Earth's total land area (Mehavar et al. 2018). The land–ocean margin that accounts for the high value of the coastal zone exposes coastal ecosystems to a plethora of environmental forcings affected by climate change, as well as nonclimate human drivers, which, in turn, collectively alter a diverse array of ecological responses and ecosystem services (figure 1). Teasing apart gradual secular trends that can be traced to ongoing increases in greenhouse gas emissions from those resulting from multiannual to decade-scale fluctuations in climate forcing is challenging. But such research is essential for determining the natural capacity of coastal ecosystems to resist and adapt to climate change (Harley et al. 2006) and the types of human interventions that effectively mitigate them (Abelson et al. 2020, Gaitan-Espitia and Hobday 2021). This requires a mechanistic understanding of the diverse array of ecological responses to climate change at the population, community, and ecosystem levels, which is best achieved with temporally and spatially extensive research.

Ecological responses to climate change are likely to be greatest when they alter the abundance or performance of one or more species that have a disproportionate role in defining the ecological community in which they live. Such is the case for many coastal ecosystems in which corals, kelps, seagrasses, mangroves, and marsh grasses serve as structure forming foundation species (*sensu* Dayton 1972). Largely through nontrophic interactions, these species act to determine local and regional biodiversity, control ecological dynamics and stability, modulate critical ecosystem processes (e.g., primary production, carbon storage and export,

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COASTAL ECOSYSTEMS

Climate change

Increased Greenhouse Gases

Altered atmospheric &
ocean circulation

Increased air &
ocean temperature

Reduced ocean pH

Environmental forcing ⟶ Changes in frequency and magnitude of extremes

Physical-Chemical
- Reduced calcification
- Changes in soil & water biogeochemistry

Temperature stress
- Heatwaves
- Bleaching
- Hypoxia
- Drought

Rising sea level
- Drowning
- Saltwater intrusion
- Habitat modification

Storm Disturbance
- Extreme waves/winds
- Storm surge
- Erosion/accretion
- Flooding/runoff

Human forcing
Fishing, land use, pollution, coastal development

Ecological responses

Populations
- Altered demographic rates & phenology
- Range expansion & contraction
- Local extinction

Communities
- Loss of foundation species
- Altered tropic structure
- State changes
- Tropicalization

Ecosystems
- Primary & secondary production
- Organic matter accumulation & export
- Resilience & adaptive capacity

Ecosystem services

Regulating
- Storm protection
- Blue carbon
- Freshwater
- Conservation of biodiversity

Provisioning
- Food
- Fuel
- Pharmaceuticals
- Minerals

Cultural
- Recreation/tourism
- Aesthetics
- Educational
- Spiritual

Figure 1. Conceptual diagram depicting how the major aspects of climate change in coastal ecosystems influence different types of environmental forcing to elicit ecological responses at different levels of biological organization, which in turn alter ecosystem goods and services.

and nutrient flux) and provide intrinsic value to society (Angelini et al. 2011, Ellison 2019).

In the present article, we review the importance of long-term, site-based research in elucidating environmental responses to irregular shifts, oscillations, and directional changes in climate (hereafter referred to collectively as *climate change*). We focus on examples from coastal ecosystems defined by structure-forming foundation species to highlight their vulnerability to climate change and to show how this vulnerability can cascade to affect important attributes of the communities and ecosystems that they delineate. Using these examples, we further explore the consequences of climate change within a broader conceptual framework of resilience and adaptive capacity, both in terms of the ecological attributes of coastal ecosystems and of the regulating, provisioning, and cultural services that they provide to society. Our review is purposely not intended to be global in scope. Rather, we draw extensively from research conducted

at a diverse collection of coastal ecosystems (e.g., coral reefs, kelp forests, coastal marshes, seagrass meadows, mangrove forests and barrier islands) studied by the US Long Term Ecological Research (LTER) Network (table 1), where long-term, spatially extensive observational data have been coupled with shorter-term experiments and other types of mechanistic studies to understand the nature and causes of long-term ecological change (Alber et al. 2013). The present article is part of a special issue that marks the 40th anniversary of the National Science Foundation's LTER program. The companion articles in this special issue (Jones and Driscoll 2022, Campbell et al. 2022, Hudson et al. 2022, and Ducklow et al. 2022, all in this issue) address responses of forest, freshwater, dryland, and marine pelagic ecosystems to climate change, highlighting LTER research.

Long-term ecological research and climate change

How climate variation alters coastal ecosystems depends on the temporal and spatial scales over which environmental drivers and the ecological attributes of interest change. For example, seasonal patterns of plant growth and animal activity are predictable because they are directly linked to regular changes in the distribution of solar energy on the Earth's surface that underlie patterns of light and temperature (Nelson et al. 1990, Battey 2000). By contrast, annual fluctuations in these same processes tend to be more erratic as a result of irregular shifts or periodic oscillations in precipitation and temperature (Mackas and Tsuda 1999, Knapp and Smith 2001, Zhang et al. 2016, Uboni et al. 2015). The climatic conditions that result from such erratic fluctuations can be acute and occur abruptly as a result of severe storms and heatwaves or can be more moderate and occur gradually over a long period of time such as global warming, sea-level rise, and ocean acidification caused by anthropogenic increases in atmospheric carbon dioxide (figure 1). As such, the ecological effects of long-term climate change can be manifested as changes in the average conditions, changes in the variability surrounding the average conditions, or a combination of the two.

Determining how climate-induced changes in ecological patterns deviate from the norm is challenging in the absence of contextual information needed for comparison. Therein lies the value of long-term, spatially distributed

Table 1. Ecological responses to major forms of environmental forcing caused by climate change for different coastal habitats studied by the US Long Term Ecological Research (LTER) Network.

Habitat	Environmental forcing caused by climate change	Ecological response to environmental forcing caused by climate change
Coral reef (MCR)	Ocean warming	Coral bleaching
	Reduced pH	Reduced calcification leading to reef erosion
	Increased hurricane frequency or intensity	Increased mortality, change in reef topography
Kelp forest (SBC)	Ocean warming	Altered demographic rates, range shifts, disease outbreaks
	Increased storm frequency or intensity	Decreased NPP, biodiversity and foodweb complexity
Tidal marsh (GCE, PIE, FCE, VCR)	Increased storm frequency or intensity	Erosion, saltwater intrusion, flooding, sediment accretion
	Sea-level rise	Loss of intertidal habitat, saltwater intrusion, altered NPP
	Atmospheric or ocean warming	Shifts in phenology and NPP, range expansion and contraction
Seagrass meadow (FCE, VCR)	Ocean warming	Massive die off, tropicalization
	Increased dissolved carbon dioxide	Enhanced NPP
	Increased hurricane frequency or intensity	Increased mortality
Mangrove forest (FCE)	Ocean warming, fewer freezing events	Range expansions and landward migration
	Sea-level rise and salt water intrusion	Loss of peat soils, conversion to open water
Barrier island (VCR)	Sea-level rise	Erosion or accretion of upland sediments
	Increased storm frequency or intensity	Erosion or accretion of upland sediments
	Warming, fewer freezing events	Seaward expansion of woody plants

Note: A map and additional information on each site can be found in the LTER site profiles (https://lternet.edu/site). *Abbreviations:* FCE, Florida Coastal Everglades LTER; GCE, Georgia Coastal Ecosystems LTER; MCR, Moorea Coral Reef LTER; NPP, net primary production; PIE, Plum Island Ecosystems LTER; SBC, Santa Barbara Coastal LTER; VCR, Virginia Coastal Reserve LTER.

research programs from a diversity of ecosystem types, such as those included in the US LTER Network. Such programs integrate continuous time series observations to document patterns of change in environmental drivers and ecological responses with shorter-term experiments and directed sampling and modeling to establish the causation of ecological responses and their consequences (Magnuson 1990). For instance, a time series collected during the span of a typical 3–5-year research grant may be interpreted as a sharp increase or decline in species abundances that leads to reduced or heightened concerns by resource managers and policymakers. However, when viewed over a longer time frame, such increases and declines may simply reflect fluctuations in population dynamics due to normal cycles of disturbance and recovery. This is the case for the southern wax myrtle *Morella cerifera* on Virginia barrier islands (figure 2a) and the cordgrass *Spartina alterniflora* in Georgia salt marshes (figure 2b). By contrast, gradual increases or declines in species abundance in response to ongoing changes in the environment may be undetectable over the short term, leading to a false conclusion of little or no change, as is evidenced by the threespot dascyllus damselfish (*Dascyllus trimaculatus*) on the reefs of Moorea, French Polynesia (figure 2c), or sawgrass (*Cladium jamaicense*) in marshes of the Florida Everglades (figure 2d). Similarly, a

relatively short time series showing little change may miss abrupt responses to episodic climate events such as the mass mortality of spined sea stars (*Pisaster* spp., a keystone predator; Paine 1966) throughout the Pacific coast of North America following a marine heatwave (figure 2e) or a poleward range expansion of the fiddler crab (*Minuca pugnax*), an ecosystem engineer (*sensu* Jones et al. 1997) in New England salt marshes (figure 2f).

Spatial gradients in the environment add additional complexity to understanding the role of climate variability in modifying ecological patterns and processes in nature (Swanson and Sparks 1990, Metz and Tielborger 2016). Such gradients are particularly prominent in coastal ecosystems in which they occur over relatively short distances, are sensitive to small changes in elevation or depth, and are typically affected by changes in climate that alter environmental drivers on land as well as in the ocean (Cloern et al. 2014, Brown et al. 2019). Not surprisingly, challenges arise when trying to determine the generality of climate-induced changes in ecological patterns from spatially limited data. The ability to generalize local patterns to a broader region can be compromised if a research site resides in an "invisible" place, where the significance of results is unclear (Swanson and Sparks 1990). Attempts to scale up may be justified in cases in which local site dynamics match those of the broader region, as can be seen in herbivorous fishes
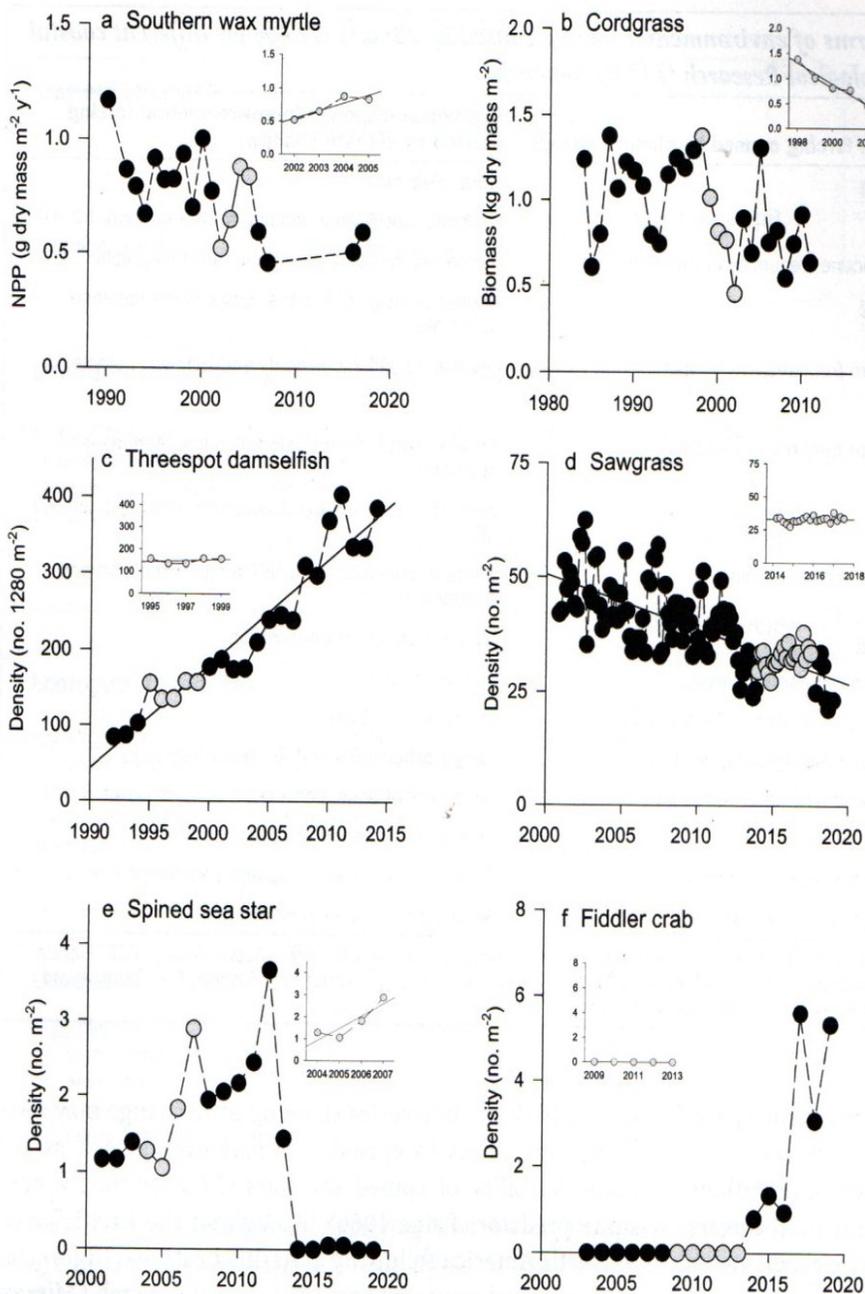
Figure 2. Examples illustrating how short-term data can lead to erroneous conclusions pertaining to longer-term trends in (a) southern wax myrtle, (b) cordgrass, (c) threespot damselfish, (d) sawgrass, (e) spined sea star, and (f) fiddler crab. Short time series is shown as an inset in the long time series. Yellow or lighter colored data points in long time series are the data shown in the short time series. The data sources are provided in supplemental table S1.
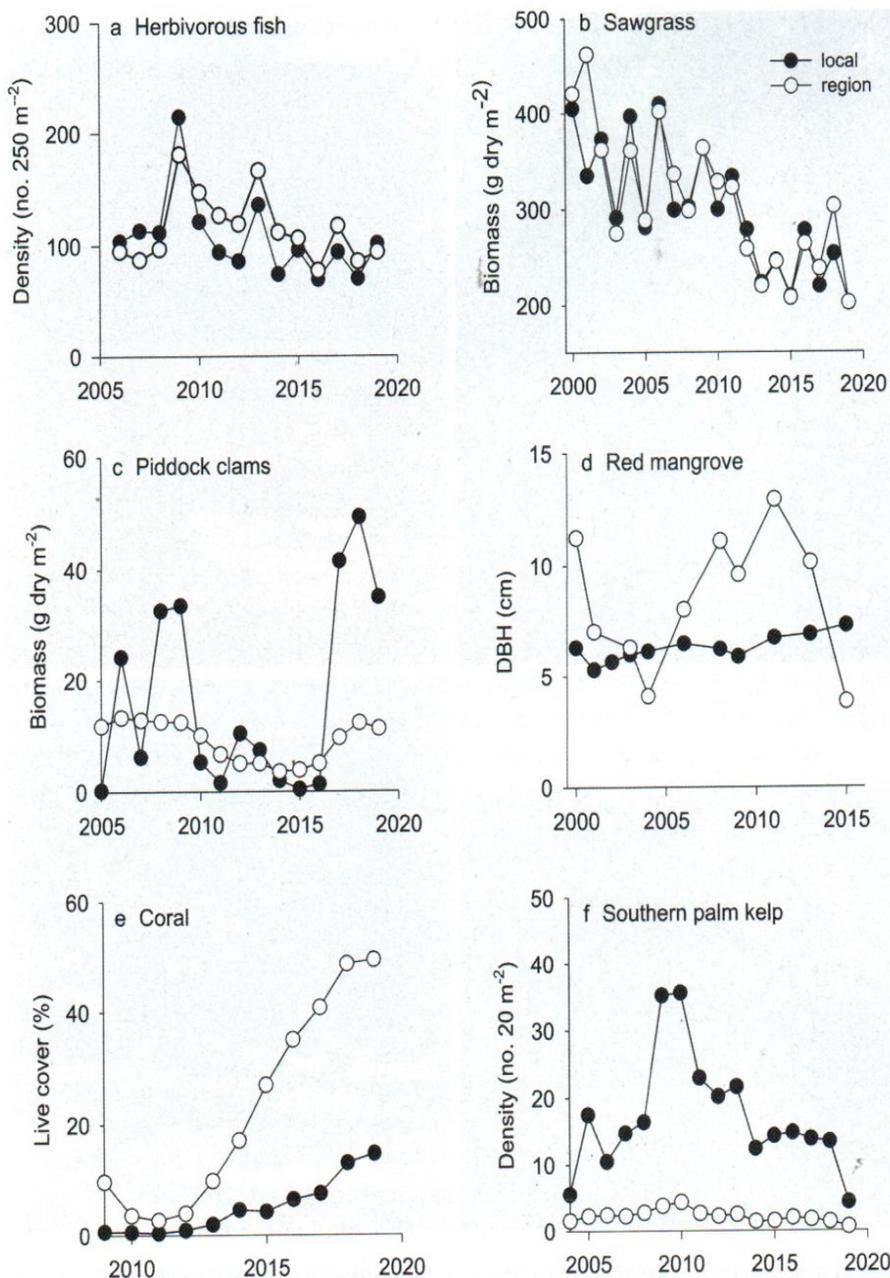
Diverse ecological responses to climate change in coastal ecosystems

Below, we summarize key findings from long-term ecological research in different types of coastal ecosystems to show how varied forms of environmental forcing driven by climate change alter the abundance and performance of structure forming foundation species to influence a variety of community and ecosystem properties.

Coral reefs. In the shallow coastal waters of the tropics, hermatypic corals form the foundation of highly diverse marine communities that are being fundamentally altered by climate change. Stress from marine heatwaves can cause reef-forming corals to expel their algal symbionts resulting in death, a phenomenon known as *coral bleaching*. Long-term records reveal that bleaching events resulting in mass mortality of corals are becoming more common across coral reefs worldwide (Hughes et al. 2017, Sulley et al. 2019). The slowly eroding dead skeletons left behind after a major bleaching event constitute a substantial material legacy of the event akin to the dead tree trunks in a terrestrial ghost forest (Foster et al. 1998). By contrast, physical disturbance from major hurricanes and cyclones can rapidly transform structurally complex assemblages of living coral into scattered piles of calcium carbonate rubble (Harmelin-Vivien 1994). Ocean acidification is also emerging as a major but slowly developing climate-related phenomenon that is threatening coral reefs by making it harder for corals to build their skeletons and by weakening coral skeletons and calcifying coralline algae that cement together the reef framework (Hoegh-Guldberg et al. 2007, Comeau et al. 2019).

Long-term research has shown that different climate-related drivers of coral mortality can have very different effects on habitat structure (figure 4a). For example, severe storms, which reduce the physical structure provided by corals, typically have much larger and more immediate effects on the diversity, abundance, and composition of reef-associated species than bleaching, which can leave the skeletons of dead coral colonies intact for many years before they erode (Graham et al. 2015, Holbrook et al. 2008, Pratchett et al. 2008). These climate-related disturbances can have long-lasting legacies on reefs, often triggering fundamental
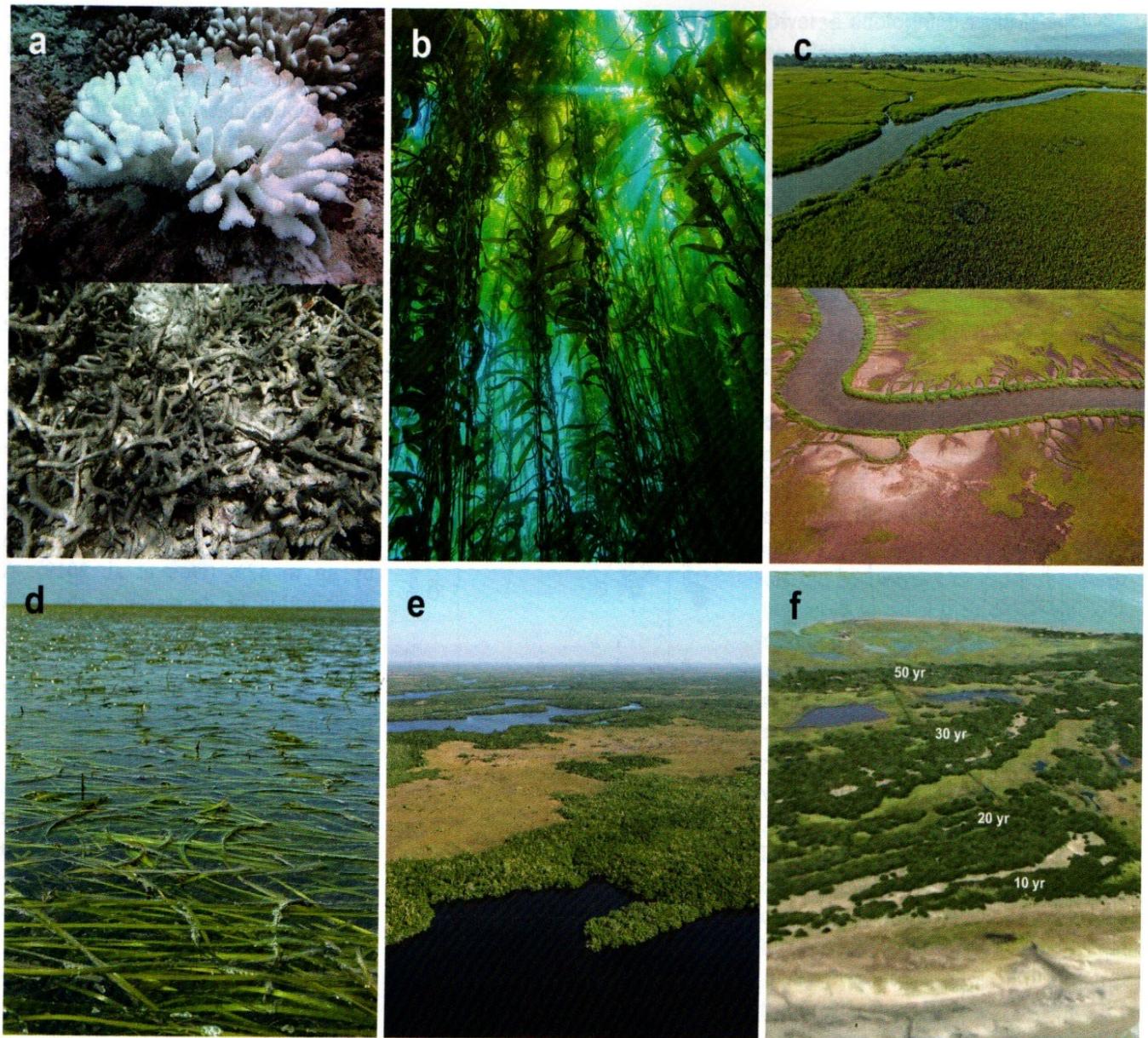
on coral reefs of Moorea (figure 3a) and sawgrass in Shark River Slough in the Everglades (figure 3b). However, this is often not the case as local populations and communities can vary asynchronously over time, causing their dynamics at a single site to differ considerably from the region as a whole, as is evidenced by the abundance of piddock clams in the Santa Barbara Channel (figure 3c) and the size of red mangroves in the Everglades (figure 3d). Alternatively, the ecological dynamics of different sites within a region may vary synchronously over time but differ in the magnitude of fluctuations, causing temporal changes at a particular site to be much smaller (figure 3e) or larger (figure 3f) than that of the entire region.

Figure 3. *Paired comparisons between the local (black circles) and regional (white circles) dynamics of (a) herbivorous fish on coral reefs of Moorea, (b) sawgrass in the Florida Everglades, (c) piddock clams in California kelp forests, (d) red mangroves in the Florida Everglades, (e) hermatypic coral in Moorea, and (f) southern palm kelp in California. The examples illustrate conditions under which local dynamics closely match regional dynamics (a and b), local dynamics differ from regional dynamics (c and d), and the amplitude of local dynamics differs from the amplitude of regional dynamics (e and f). The data sources are provided in supplemental table S2.*

The gradual process of ocean acidification makes quantifying its ecological effects more challenging than measuring abrupt changes in coral populations caused by marine heatwaves and severe storms. Long-term research on changes in the composition of the benthic community (e.g., Holbrook et al. 2018) have informed short-term *in situ* experiments designed to study the effects of increased carbon dioxide on reef functions (i.e., free ocean carbon enrichment experiments, or FOCE). The results from FOCEs in Moorea, French Polynesia showed that future conditions of ocean acidification can reduce the net community production of coral reefs by approximately 25% and daily net community calcification by up to 47% (Doo et al. 2019). A combination of decreases in the rates of calcification by corals and calcifying algae and an increase in overall dissolution rates caused a shift in overall reef function in the community exposed to future conditions of ocean acidification. Furthermore, mesocosm experiments on the Great Barrier Reef suggest that gradual ocean warming and acidification together are likely to cause a greater rate of dissolution of calcium carbonate at night (when there is no active reef building by corals and other calcifiers) than either factor alone (Dove at el. 2020).

Kelp forests. In cooler waters of temperate and polar regions large structure-forming macroalgae known as kelps form underwater forests that are among the most productive ecosystems in the world (Reed and Brzezinski 2009, Krumhansl and Scheibling 2012). These iconic foundation species are increasingly being threatened by rising ocean temperatures associated with climate change (Raybaud et al. 2013, Filbee-Dexter et al. 2016, Wernberg et al. 2019). Observations of range contractions at the equatorward edge, expansions at the poleward edge in many kelp species have been linked to the direct or indirect effects of gradual ocean warming and episodic marine heatwaves worldwide (reviewed in Smale 2020). The results from a short-term experiment involving the fucoid kelp *Scytothalia dorycarpa* in western Australia suggested that local adaptation may cause central and equatorward-edge populations to be equally vulnerable to anomalous warming events (Bennett et al. 2015). However, long-term observations spanning multiple decades showed

shifts in benthic community composition away from coral-dominated systems toward macroalgal dominated systems (Ostrander et al. 2000, Adam et al. 2014, Graham et al. 2015). Time series data have shown that coral-to-macroalgal phase shifts can persist for a decade or more (e.g., Schmitt et al. 2019) and have profound ecological effects on other aspects of the reef community, including biotic interactions, trophic structure, biodiversity, and fisheries production (Schmitt and Holbrook 2007, Lenihan et al. 2011, Ainsworth and Mumby 2015, Leenhardt et al. 2016, Rassweiler et al. 2020).

Figure 4. Impacts of climate change in coastal ecosystems. (a) Coral reefs in Moorea following disturbance from a bleaching event (top) and a cyclone (bottom), (b) large three dimensional structure of giant kelp in southern California makes it disproportionately susceptible to wave disturbance, (c) Aerial view of a heathy Georgia saltmarsh (top) and a Georgia saltmarsh degraded by a large die-off event (bottom), (d) Restored eelgrass meadows in the Virginia Coast Reserve cover 36 square kilometers after 20 years, (e) Fringe riverine mangroves transition to dense stands of sawgrass in ecotonal wetlands of the Florida Everglades, and (f) Chronology of Morella cerifera shrub expansion on North Hog Island, Virginia. Photographs: (a) Russell Schmitt, (b) Douglas Klug, (c) John Schalles (top) and Matthew Ogburn (bottom), (d) Kylor Kerns, (e) John Kominski, (f) Julie Zinnert.

this was not the case for two foundation species of large canopy forming kelps in North America (*Macrocystis pyrifera* and *Nereocystis luetkeana*) whose center range populations showed unremarkable responses to anomalously high temperatures associated with an unprecedented 2-year warming event (Reed et al. 2016, Hamilton et al. 2020). In the case of *M. pyrifera*, resistance to this warming event across 7 degrees of latitude in southern and Baja California was negatively correlated with the mean temperature of the warmest month and uncorrelated with the local temperature anomaly, indicating that canopy loss was more sensitive to exceeding an absolute temperature threshold than to

the magnitude of the anomalous increase in temperature (Cavanaugh et al. 2019a).

Climate change manifested as increases in the frequency of severe storm-related wave disturbance (figure 1) also poses a major threat to kelp forests. This is particularly true for kelp forests defined by large species such as *M. pyrifera* (figure 4b), which extend throughout the water column making them more susceptible to being removed by large waves (Dayton and Tegner 1984, Reed et al. 2008). Long-term observations and experiments in southern California show that reductions in this foundation species due to wave disturbance depresses the biomass, biodiversity and food

web complexity of the kelp forest community (Byrnes et al. 2011, Miller et al. 2018, Castorani et al. 2018) and reduces its temporal stability (Lamy et al. 2020).

Monthly observations spanning two decades in southern California show that rapid growth of a relatively small biomass (approximately 0.4 kilograms dry mass per square meter) that turns over 10–12 times per year is principally responsible for *M. pyrifera*'s high net primary productivity (NPP; Rassweiler et al. 2018). However, interannual variation in *M. pyrifera*'s standing biomass caused by wave disturbance controls year-to-year fluctuations in its NPP (Reed et al. 2011). These results motivated a decade-long experiment that tested the effects of annual *M. pyrifera* removal in winter (to simulate increased frequency of storm disturbance) on the understory algal assemblage. The results from this experiment showed that increased NPP by the understory in response to reduced shading by *M. pyrifera* following its removal was not sufficient to compensate for the decreased NPP by *M. pyrifera*, indicating that a future with more frequent winter wave disturbance, irrespective of ocean warming, will most likely reduce the productivity of these systems (Castorani et al. 2021).

Coastal marshes. Native cordgrasses (*Spartina* spp.) are perennial foundation species that define the structure of salt marshes along the Atlantic and Gulf coasts of North America (Pennings and Bertness 2001). They enhance salt marsh communities in this region by accreting and stabilizing the sediment, ameliorating chemical and physical stress to other plants and animals and providing food, shelter, and foraging habitat for diverse assemblages of consumers. These foundational attributes can be diminished or eliminated by heatwaves, droughts, hurricanes, rising sea level, hypersaline conditions, and other factors that cause sudden die back events (figure 4c), which have been reported for *S. alterniflora* throughout its native range (Alber et al. 2008). Long-term observations coupled with short-term experiments in marshes of Georgia and Louisiana in the United States show that the community response to such diebacks can vary considerably depending on the geological and hydrological setting as well as the disturbance history of a site, demonstrating that the responses are context dependent (McFarlin et al. 2015).

Cordgrasses and other salt marsh vegetation thrive within a narrow tidal range, which makes them particularly vulnerable to drowning from rising sea level if their gains in elevation through accretion are insufficient to compensate for their losses due to sea level rise (Morris 2000, Morris et al. 2002, Crosby et al. 2016). Decades of research at Plum Island, Massachusetts, show that positive anomalies in mean sea level is causing the lower seaward range of *Spartina patens* to contract by 4 millimeters per year, whereas its upper landward range is expanding at only 2 millimeters per year because of accretion (Morris et al. 2013a). By contrast, the vertical range of *S. alterniflora*, which occurs lower in the marsh, has been increasing as it expands into higher elevations. As a result, many of the marshes at Plum Island and elsewhere along the northeast coast of the United States have transitioned from *S. patens*–dominated high marsh to low marsh dominated by *S. alterniflora* (Warren and Niering 1993) with the potential to further transition into unvegetated mudflats as sea level continues to rise.

The biogeochemistry and productivity of salt marsh ecosystems are greatly influenced by both short-term (i.e., intra- and interannual) and long-term (i.e., decadal and longer) changes in temperature, precipitation and relative mean sea level (Short et al. 2016, Tobias and Neubauer 2019). Continuous records at Plum Island since 1999 show that annual NPP of *S. alterniflora* fluctuated by nearly a factor of four in response to changes in the level of mean high water as tidal flushing helps regulate soil salinity as well as hypoxia in marsh porewaters (Morris et al. 2013b). At higher elevations, where *S. patens* dominates, precipitation rather than tidal inundation is the dominant control on soil salinity and the primary factor that accounts for interannual variability in primary production (Forbrich et al. 2018).

Sea-level rise, increased storm surge, and prolonged droughts in coastal areas are expected to increase inundation and saltwater intrusion into many coastal freshwater marshes located landward of salt marshes. Plants in tidal freshwater marshes are particularly vulnerable because they are strongly affected by increased salinity. Saltwater intrusion may be chronic because of rising sea levels or pulsed because of storm surge or reduced river flows. The results from a long-term saltwater addition experiment (SALTEx) near Sapelo Island, Georgia showed that chronic additions of seawater resulted in elevated pore water nutrients and decreased redox potential (Widney et al. 2019), followed by the rapid replacement of plant biomass with benthic microalgae (Craft et al. 2016). This loss of belowground biomass affected the ability of the marsh to maintain elevation and sequester carbon (Solohin et al. 2020). By contrast, pulsed additions of dilute seawater resulted in transient changes in soil biogeochemistry that returned to baseline once dosing ceased (Widney et al. 2019). Collectively, the results from this ongoing research indicate that gradual, persistent sea-level rise will have greater effects on the functioning of coastal freshwater marshes in this region than climate related changes in storm surge and precipitation.

Seagrass meadows. Seagrasses form extensive meadows in shallow coastal waters that serve as important habitat for many species in otherwise featureless soft bottom habitats (Orth et al. 1984). In recent years, rising average ocean temperatures and periodic marine heatwaves have caused massive reductions in seagrass populations in many regions of the world (Thomson et al. 2015, Arias-Ortiz et al. 2018, Berger et al. 2020), especially near the thermal limit of their geographic range (Koch et al. 2013). This is the case for populations of the eelgrass *Zostera marina*, which serves as a foundation species along the mid-Atlantic US coast (Collier et al. 2011, Moore et al. 2012, Berger et al. 2020). Ocean

temperatures that exceed the upper tolerance threshold for periods of days to weeks have led to die offs on scales of square meters to square kilometers (Moore and Jarvis 2008, Aoki et al. 2020a, Berger et al. 2020). Long-term observations of eelgrass populations in Virginia (figure 4d) revealed a tenfold decrease in shoot density following a marine heatwave with populations at cooler intermediate depths being less affected than those in warmer shallower depths (Aoki et al. 2020a). Eelgrass shoot density is positively related to biomass (Berger et al. 2020) and can have a positive feedback on growth because a dense canopy slows water flow, which reduces turbidity and improves light conditions for photosynthesis (Hansen and Reidenbach 2012). Consequently, the massive reduction in shoot density resulting from the heatwave caused a concomitant shift in trophic status from balanced between production and respiration to net heterotrophy. As the meadow recovered this shift was subsequently followed by a transition to net autotrophy within 2 years (Berger et al. 2020).

The poleward range expansion of tropical species in response to warming (i.e., tropicalization) is a consequence of climate change that is transforming the ecological structure and functions of many systems (Osland et al. 2021). Multidecadal studies suggest that temperate seagrass communities may be particularly susceptible to this climate change effect. For example, the replacement of the temperate eelgrass *Z. marina* with the shorter subtropical shoal grass *Halodule wrightii* over a 20-year period led to significant decreases in the abundance and diversity of invertebrates and fishes in seagrass communities of North Carolina (Micheli et al. 2008). Similarly, a 30-year record in seagrass meadows of the northern Gulf of Mexico documented the transition to a fish assemblage dominated by herbivorous subtropical and tropical species (Fodrie et al. 2010). Such tropicalization of temperate seagrass communities is expected to shift the structure of their food webs from detrital based to webs dominated by herbivory with cascading effects on ecosystem functioning (Heck et al. 2015).

Worldwide, seagrass meadows accumulate significant stocks of organic carbon that can remain buried in sediments for decades to millennia (Fourqurean et al. 2012, Orth et al. 2020). When seagrass meadows are lost—for example, because of ocean warming—some or all of the carbon stocks are remineralized, potentially changing these systems from a carbon dioxide sink in the ocean to a source of carbon dioxide to the atmosphere (Macreadie et al. 2019, Pendleton et al. 2016). Such was the case for a 20 square kilometers restored eelgrass meadow in Virginia (figure 4d) that suffered a massive dieback following a marine heatwave. Long-term records of marine sediments in the most heavily affected part of the meadow revealed the entire carbon stock built up over 14 years of restoration was lost within 2 years of the heatwave (Aoki et al. 2021). The recovery of seagrass shoot density and net primary production occurred within 4 years of the dieback (Berger et al. 2020); however, the recovery of sediment carbon stores lagged significantly behind. The loss

of seagrass meadows from temperature stress also resulted in the loss of nitrogen stocks buried in sediments (Aoki et al. 2020b).

Mangrove forests. Mangrove forests are a dominant feature of soft-bottom intertidal and shallow subtidal habitats in tropical and subtropical regions of the world (figure 4e). As foundation species, mangroves not only define the ecological structure and functions of an entire ecosystem, but they are also highly valued for the provisioning (e.g., timber, fuel wood, and charcoal), regulating (e.g., flood, storm and erosion control, prevention of saltwater intrusion), ecological (e.g., biodiversity), and cultural (e.g., recreation, aesthetic, nonuse) services that they provide to society (Brander et al. 2012). Periodic freezing events determine the poleward extent of mangroves and play an important role in regulating their population age structure and dynamics because the resultant defoliation and added mortality alter soil properties and the microclimate (Danielson et al. 2017, Guo et al. 2017, Osland et al. 2017a, 2019), which enhance seedling growth and survival (Ross et al. 2009). In response to warming winter air temperatures, freeze-sensitive mangrove forests are expected to expand at the expense of freeze tolerant salt marshes (Osland et al. 2017b). Long-term records in northeast Florida show that the ecotone between mangrove and salt marsh dominance has shifted multiple times since the late 1700s because of decade-scale fluctuations in the frequency and intensity of extreme cold events (Cavanaugh et al. 2019b). The most recent shift occurred between 1984 and 2011, when the spatial extent of mangroves doubled between 29 degrees and 29.75 degrees north (Cavanaugh et al. 2014). Climate model projections for this region suggest that ongoing warming may push this fluctuating system toward a persistent state of mangrove dominance (Cavanaugh et al. 2019b), which in turn will alter a variety of ecosystem-level attributes and functions (Brander et al. 2012, Guo et al. 2017).

Mangrove forests are also being affected by sea level rise, which has the potential to alter important ecosystem processes. Long-term research has revealed that the high productivity of the peat-dominated mangroves of the Florida Everglades is dependent on a steady supply of the limiting nutrient phosphorus, which is delivered regularly by tides and tropical storms from the Gulf of Mexico and episodically by storm surges (Castañeda-Moya et al. 2013, Rovai et al. 2018, Kominoski et al. 2020). Tidal and storm surge inputs of ocean-derived phosphorus are increasing as sea level rises (Dessu et al. 2018). However, increases in mangrove production resulting from greater access to marine-derived phosphorus are countered by decreases due to higher salinity as every 10–practical salinity unit increase in salinity results in a 5% decline in primary production (Barr et al. 2012, Castañeda-Moya et al. 2013).

The ecological response of mangrove forests to sea level rise can be complex as storm surge and saltwater intrusion (which are expected to increase with sea level rise) can

have opposing effects. For example, research in the Florida Everglades spanning multiple decades revealed that heightened storm surge during several major hurricanes increased sediment deposition and soil elevation, which in turn increased primary production and the amount of organic carbon accumulated in the soils (Smith et al. 2009, Smoak et al. 2013). By contrast, historical records and observational data collected during the past half century coupled with recent shorter-term experiments have shown that saltwater intrusion into more landward freshwater marshes tends to collapse peat soils, causing a reduction in soil elevation and eventual habitat conversion to open water (DeLaune et al. 1994, Charles et al. 2019).

Barrier islands. Barrier islands, consisting of dynamic dune systems formed by waves and tides, occur parallel to approximately 10% of the world's continental shorelines (Stutz and Pilkey 2011). Their geomorphology is principally determined by the transport, deposition, and erosion of sediments, which is largely controlled by climate and a suite of complex interactions involving waves, storms, and fluctuations in sea level (Milliman and Meade 1983, Hayden et al. 1991, Smith et al. 2010). The dominant vegetation on islands interacts with these environmental forcings to influence island dynamics by stabilizing sediments and suppressing erosion (Zinnert et al. 2017).

Recent macroclimate warming and microclimate modification is facilitating range expansion of coastal woody vegetation across the globe in a wide diversity of habitats (Osland et al. 2016, Devaney et al. 2017, Huang et al. 2018). On barrier islands along the Atlantic and Gulf coasts of the United States, long-term research has revealed that increasing temperatures and reductions in extreme freezing events have led to the seaward expansion of woody shrubs into swale grasslands and salt marshes dominated by *S. patens* (Battaglia et al. 2007, Young et al. 2007, Thompson et al. 2017, Huang et al. 2018). In the last century, the nitrogen-fixing evergreen shrub *M. cerifera* has encroached into grassland swales of barrier islands along the Virginia coast of the eastern United States (figure 4f), forming dense 6-meter-tall thickets that have reduced the abundance and diversity of upland grasses and forbs (Young et al. 1995, Huang et al. 2018, Zinnert et al. 2019). Mechanistic studies have shown that underneath the thicket canopy light is reduced by as much as 99% (Brantley and Young 2007), and temperatures are warmer in winter and cooler in summer, creating a positive feedback that further enhances *M. cerifera* growth (Wood et al. 2020). Such changes in vegetation structure and composition induced by warming can have geomorphic consequences that threaten the stability of barrier islands by reducing their resilience to disturbance from sea-level rise and extreme storm events (Irish et al. 2010, Zinnert et al. 2016, Entwistle et al. 2018). For example, shrub expansion increases shoreline erosion with rising seas by restricting sediment movement into the back barrier marsh, altering the long-term resilience of the barrier system (Zinnert et al. 2019).

Climate-driven shifts in coastal vegetation that lead to the establishment of different foundation species can alter a variety of ecosystem processes (Osland et al. 2016). On barrier islands of Virginia, the transition from grassland swales to shrub thickets caused by gradual warming led to an increase in primary production as aboveground NPP in newly established thickets of *M. cerifera* was four times higher than the *Spartina patens* dominated grasslands that they replaced (Knapp et al. 2008). This large increase in NPP led to corresponding changes in soil biogeochemistry because leaf nitrogen resorption efficiency of *M. cerifera* is low relative to *S. patens*, leading to increased nitrogen input with litterfall in an otherwise low nutrient system (Brantley and Young 2008). As the thickets aged, standing stocks of carbon increased by 3–10 times more than those in adjacent grassland (Brantley and Young 2010). The fate of nitrogen and carbon pools in the soil and groundwater of this system is likely to be ephemeral as islands erode and migrate landward with sea-level rise and storms (Zinnert et al. 2019). The process of climate induced shrub expansion and its ecological consequences seen at Virginia islands are occurring at barrier islands and other tidal and nontidal coastal systems elsewhere in the world (e.g., Battaglia et al. 2007, Isermann 2008, Lucas and Carter 2010, Vallés et al. 2011).

Resilience of coastal ecosystems to climate change

Resilience broadly refers to the capacity of an ecosystem configuration (i.e., a state) to maintain its structure and functions in the face of disturbances (Gunderson 2000). The resilience properties of coastal ecosystems are shaped disproportionately by the response of foundation species to perturbations (Osland et al. 2016). Time series observations have revealed that coastal ecosystems can be relatively insensitive to variation in a stressor or environmental driver up to a point, beyond which the system abruptly switches to a completely different state. As was noted earlier, forests of giant kelp along the west coast of North America were insensitive to a prolonged period of elevated sea surface temperatures except where an absolute temperate threshold was exceeded and kelp biomass collapsed (figure 5a). In addition to sea level rise, tidal wetlands are vulnerable to threshold responses to changes in temperature and rainfall because of their profound influence on the dynamics and performance of the foundation species of wetland plants (Osland et al. 2016). Subtropical wetlands, for example, tend to be dominated by mangrove forests in which minimum winter air temperatures remain above −6 degrees Celsius, whereas there is an abrupt transition to dominance by salt marsh plants when the minimum temperature falls just below this value (Osland et al. 2013, 2016). For coral reefs, threshold relationships have often been observed between herbivory and the proliferation of macroalgae that outcompete coral (figure 5b). Because local economies and quality of life are often linked to the vitality of coastal ecosystems, changes in climate that cause ecological thresholds to be exceeded can in turn cause negative socioeconomic

a

b
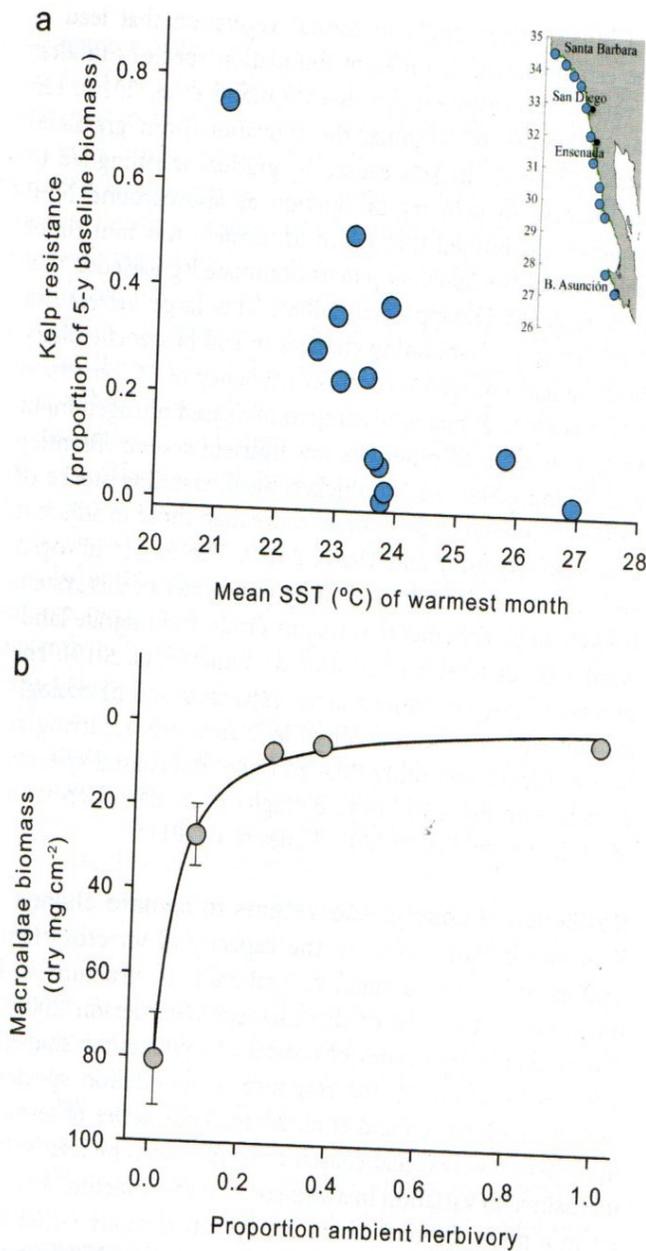
Figure 5. (a) Threshold response in the resistance of giant kelp (Macrocystis pyrifera) to a severe marine heatwave along a 1600 km stretch of the west coast of North America (inset). Shown for each locality is the proportion of canopy biomass remaining after the heatwave relative to the time-average biomass of the previous 5 years versus the absolute sea surface temperature (SST) of the single warmest month during the heatwave (from Cavanaugh et al. 2019a). (b) Results from a field experiment showing the nonlinear response of macroalgal biomass on coral reefs of Moorea to different levels of fishing pressure on herbivorous fishes. Fishing pressure was simulated by experimentally reducing ambient densities of herbivorous fish. The error bars represent the standard error. Source: Adapted from Holbrook and colleagues (2016).

impacts, as was shown for wetlands and sandy beaches in southern California (Barnard et al. 2021). Indeed, threshold responses to climate change have been reported for all six of the coastal ecosystems considered in the present article

(e.g., coral reefs: Holbrook et al. 2008, 2016, Schmitt et al. 2019, 2021; kelp forests: Rassweiler et al. 2010, Bestelmeyer et al. 2011, Cavanaugh et al. 2019a, Detmer et al. 2021; sea grass meadows: Carr et al. 2010, McGlathery et al. 2013, Aoki et al. 2020a; coastal marshes: Fagherazzi et al. 2006, McGlathery et al. 2013, Osland et al. 2013, 2016, Barnard et al. 2021; mangrove forests: Osland et al. 2013, 2016; and barrier islands: Huang et al. 2018). The prevalence of thresholds observed in these studies underscores the importance of detecting when a system is approaching a tipping point to a different state.

Abrupt shifts in community state can be challenging to anticipate (Biggs et al. 2009, Carpenter et al. 2011). One method has been to mine time series data of ecological responses for characteristic statistical signals (early warning indicators) that foretell of an approach to a tipping point (Biggs et al. 2009). This framework has been applied to inundation stress in tidal marshes (Van Belzen et al. 2017) and wave stress on benthic space holders in kelp forests (Bestelmeyer et al. 2011). However, it is best suited for fast-responding variables (e.g., abundance of short-lived phytoplankton) where temporally dense time series data are available (Bestelmeyer et al. 2011, Burthe et al. 2016). Structurally important foundation species often are slow responders, which constrains the utility of this method (Bestelmeyer et al. 2011, Burthe et al. 2016). For such slow responders, long-term experiments coupled with observational data can reveal whether the system is approaching a tipping point (Holbrook et al. 2008, Carpenter et al. 2011, Pace et al. 2013, Sirota et al. 2013). For example, this approach was used to gauge whether ambient levels of herbivory were sufficient to prevent macroalgae from overgrowing coral reefs (Holbrook et al. 2016, Schmitt et al. 2019, 2021), which is important for local management because herbivores often form the bulk of the reef fishery (Rassweiler et al. 2020), and fishing and fisher behavior can greatly affect coral-to-macroalgae state shifts (Rassweiler et al. 2021).

Long-term data in coastal ecosystems also have yielded valuable insight into factors that influence the speed at which a system can rebound from a disturbance. One important factor is the intrinsic characteristics of the ecological response variables. For instance, biogeochemical variables in a coastal river–estuary complex in the western Gulf of Mexico rebounded much faster than population and community variables following a strong hurricane (Patrick et al. 2020). The return time for a given ecological attribute often depends on the degree of change caused by the disturbance, such as for coastal mangrove forests in South Florida, where the rate of recovery of wind-stripped mangrove canopies from a hurricane was inversely related to disturbance intensity as measured by the degree of defoliation (Danielson et al. 2017). Many factors can obscure a simple relationship between disturbance intensity and return rate, including the extent to which recovery dynamics are influenced by external subsidies. For instance, variation in the time it took corals on reefs around Moorea to

rebound from a major disturbance was positively related to the recruitment rate of young coral produced elsewhere (Holbrook et al. 2018, Kayal et al. 2018). For spatially discrete forests of giant kelp in southern California, local populations that were more highly connected demographically to other regional reefs were more likely to persist, which lowered local extinction and enhanced recolonization probabilities (Castorani et al. 2015, 2017). In addition to demographic connectivity, material subsidies from an adjacent ecosystem also can influence recovery times, such as the effect the presence of a seagrass meadow can have on diminishing the export of sediments needed for renourishment of storm-eroded tidal salt marsh platforms (McGlathery et al. 2013).

Not all perturbed systems rebound to their former state. If an abrupt state shift was caused by a small change in a driver that pushed the system over a tolerance threshold, the system can revert back with a small relaxation of the driver (Lam et al. 2020). However, reversal of a state shift is greatly impeded if the relationship between a driver and response itself changes after the shift, creating a situation in which the new, potentially undesirable state can be highly resilient (Scheffer and Carpenter 2003). Such alternative stable states are especially worrisome because reversing a state shift requires a much greater relaxation of the driver, far past the original tipping point. Although alternative stable states are considerably easier to study in theory than in nature, much of the pioneering empirical work has been done in coastal marine ecosystems (Petraitis 2013).

Long-term ecological research in coastal ecosystems has addressed the challenge of identifying and characterizing alternative stable states through three complementary approaches. The first has been to use long-term observational data to determine whether a driver–response relationship changed from before to after an abrupt state change. An example of this is found in the shallow waters of Hog Island Bay, Virginia, where a changing driver–response relationship influenced the resilience of eelgrass meadows (Aoki et al. 2020a). Eelgrass growth diminishes with increasing bottom depth because of attenuation of light needed for photosynthesis, but high densities of eelgrass keep the water clear by dampening water currents that stir up sediments (Hansen and Reidenbach 2012). A marine heatwave resulted in a massive dieback of eelgrass, but only in shallow water where its thermal tolerance was exceeded (figure 6). The persistent failure of eelgrass to recover to its former high density in shallow water is consistent with a change in the depth–plant density relationship from before to after the heatwave (figure 6). It appears that the heatwave flipped shallow eelgrass meadows from a high to a very low shoot density state, where it remained trapped because of the breakdown of the positive feedback of eelgrass density on the local light environment (McGlathery et al. 2013, Aoki et al. 2020a).

A less common approach to exploring alternative stable states in nature has been to use long-term experiments to directly test whether the driver–response relationship differs from before to after a shift. This approach was first applied for a coral reef in Moorea, which revealed that greater herbivory was required to remove well established macroalgae than to prevent them from colonizing a disturbed reef (Schmitt et al. 2019). Confirming long-term field experiments provided additional evidence that macroalgae-dominated and coral-dominated benthic communities can represent alternative stable states under the same conditions on a reef (Schmitt et al. 2019, 2021).

The third approach used to identify and characterize alternative stable states, which is more common, has been to develop models parametrized by data from time series observations and mechanistic studies to explore system dynamics (Mumby et al. 2007, Carr et al. 2010, McGlathery et al. 2013, Muthukrishnan et al. 2016, Briggs et al. 2018). This has produced compelling evidence, for example, that adjacent tidal mudflats and salt marshes may represent alternative stable states (Fagherazzi et al. 2006, McGlathery et al. 2013), as might eelgrass meadows and unvegetated soft bottom habitats (Carr et al. 2012, McGlathery et al. 2012, 2013), kelp forested and deforested reefs (Ling et al. 2015), and coastal grasslands and shrublands (Huang et al. 2018, Huang et al. 2021).

Implications of climate change for key ecosystem services and prospects for adaptive capacity. Coastal ecosystems provide a wide array of critical regulating, provisioning, and cultural services to society (figure 1). The extent to which climate change will degrade these services depends in large part on an ecosystem's ability to adjust its resilience to climate change (i.e., its adaptive capacity; Angeler et al. 2019), as well as adaptive management actions imposed on the system by humans (Barnard et al. 2021). Unfortunately, our understanding of the intrinsic adaptive capacity of coastal ecosystems to our changing climate is quite limited (Harley et al. 2006).

Of great societal concern is the loss of shoreline protection against coastal erosion and storm surge provided by coastal ecosystems. In some instances, there is little adaptive potential without direct human intervention, such as for many tidal wetlands, barrier islands, and sandy beaches under intense threat of drowning because sediment accretion cannot keep pace with sea-level rise (Kirwan and Megonigal 2013, McGlathery et al. 2013, Mariotti and Carr 2014, Zinnert et al. 2017, Hopkinson et al. 2018, Myers et al. 2019). There already has been considerable effort to restore tidal wetlands using native vegetation as a living shoreline to guard against erosion and storm surge (Gitman et al. 2016, Currin 2019). In addition to active restoration, additional mitigation efforts will likely be needed to prevent marsh drowning to counteract the decades-long reduction in the delivery of terrestrially derived sediments caused by human development upstream (Weston 2013, Watson et al. 2017, Hopkinson et al. 2018). Even so, migration of tidal marshes and beaches up the shore with rising ocean waters often
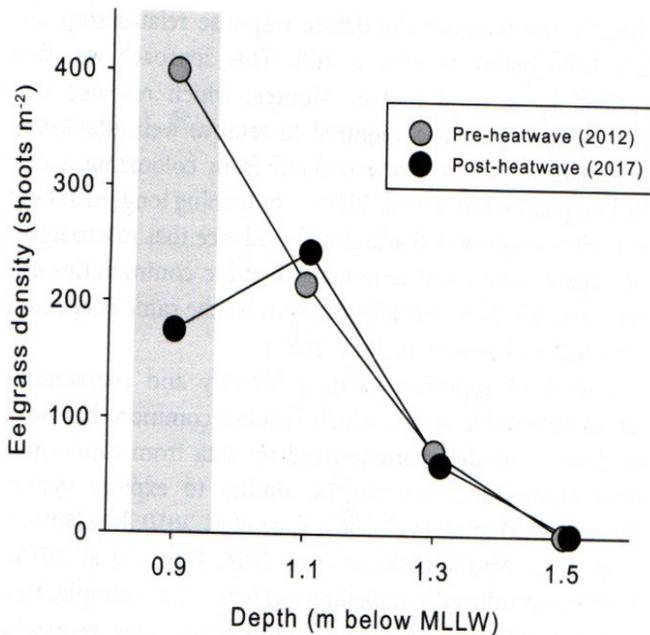
Figure 6. An example of potential alternative stable states in the average shoot density of eelgrass as a function of water depth for 58 restored eelgrass meadows in Hog Island Bay, Virginia. Data are from two time periods in a long time series immediately before an extreme, but brief, marine heatwave event in July 2012 (the blue or lighter colored circle) and after 5 years of recovery from the heatwave (the black circles) Source: Adapted from Aoki and colleagues (2020a).

will be limited by fixed hardscape and other infrastructure (Doody 2004, Arkema et al. 2013, Dugan et al. 2018). Similarly, shoreline protection provided by coral barrier reefs is at high risk to climate change because a warming, acidifying ocean reduces the ability of coral to calcify and increases the dissolution rate of the reef's carbonate framework (Dove et al. 2020). The weakened reef framework is expected to be more prone to storm damage (Madin et al. 2012) and less able to grow upward fast enough to keep pace with sea level rise (Dove et al. 2020).

With respect to provisioning services, coral reefs provide the bulk of the protein consumed by people in coastal tropical regions. Long-term ecological and sociological data from Moorea reveal that the small-scale coral reef fisheries can buffer a considerable amount of environmental perturbation. The total biomass of the targeted fishes changed little over the decade following a massive coral mortality event and coral-to-macroalgae state shifts on many reef tracts around Moorea (Adam et al. 2014, Rassweiler et al. 2020). The high resistance of fishable biomass resulted from population declines of some species that were offset by gains in other fish groups (Adam et al. 2014, Han et al. 2016, Rassweiler et al. 2020). As a consequence, the disturbance-induced change on the reef was mirrored by similar changes in the composition of the catch because fishers maintained their practice of capturing targeted species in proportion to their availability (Rassweiler et al. 2020). As a result, there was little consequence to relative market prices (Nassiri et al. 2021).

Long-term ecological research is revealing insight into possible adaptive strategies to maintain the role of foundation species in shaping biodiversity of coastal ecosystems. For instance, the loss of giant kelp on temperate reefs has profound implications for higher trophic levels (Schmitt and Holbrook 1990, Okamoto et al. 2012, Miller et al. 2018, Castorani et al. 2018, Detmer et al. 2021). Increasing the number of kelp forests in a region that are fully protected by a network of marine reserves could lower extinction and increase recolonization rates of giant kelp by helping to increase demographic connectivity among regional reefs (Castorani et al. 2015, 2017, Arafeh-Dalmau et al. 2021). For coral reefs, the extent to which fish biodiversity declined with a loss of coral biodiversity was greatest on reefs where the highest proportion of fishes were coral habitat specialists because they are more vulnerable to the loss of coral diversity than species that are habitat generalists (Holbrook et al. 2015). However, when coral cover is very low, a small increase in cover from restoration efforts can have a disproportionately large effect on restoring fish biodiversity (Holbrook et al. 2008).

Finally, the biological mechanisms underlying rapid adjustments of organisms to climate drivers are an area of active research. Those being explored include processes that promote rapid evolution (i.e., a change in allele frequencies in a population between generations) and those that result in heritable phenotypic plasticity (i.e., transgenerational plasticity). For example, multigenerational adaptive responses could reflect changes in parental provisioning to their offspring, epigenetic responses (i.e., heritable change in gene expression without alteration of DNA sequences) or genetic mechanisms that involve associated microorganisms (Torda et al. 2017, Duarte et al. 2018, Wong et al. 2018, 2019, Putnam 2021). Although the evidence is sparse, some species in coastal ecosystems have shown the capacity for rapid adaptive responses to changing climate drivers (Reusch 2013, Torda et al. 2017), such as increases in thermal tolerances following a moderate heatwave in corals (Maynard et al. 2008) or when seagrasses expand their geographic range (Wesselmann et al. 2020).

Conclusions

Coastal ecosystems have tremendous ecological, cultural, and economic value, and preserving their critical social-economic services is viewed as a high priority throughout the world (Millennium Ecosystem Assessment 2005, Carpenter et al. 2009, Mehvar et al. 2018). Long-term, site-based research programs distributed across the globe (Muelbert et al. 2019) provide ideal research platforms for addressing critical information gaps in ecological responses to climate and human forcings, and the resilience and adaptive capacity of coastal ecosystems to withstand them (Cowles et al. 2021). As is detailed in the present article, such research platforms in coastal ecosystems have been instrumental in revealing the factors that influence trajectories and time scales of recovery following extreme

climate events (e.g., heatwaves, freezes, large wave events) and in identifying the critical thresholds or tipping points beyond which a coastal system switches to a different state. Long-term ecological research has also contributed disproportionately to advancing our understanding of the capacity of ecosystems to adapt to climate change, whereas shorter-term experiments motivated by longer-term observations are providing novel insight into the biological mechanisms that underlie this adaptive capacity. Such information is critically important to human systems interested in implementing best practices for preserving the many goods and services provided by coastal ecosystems. Emerging research in evolution, genetics, and epigenetics informed by long-term ecological research offers potentially innovative solutions to mitigating the ecological impacts of climate change (Gaitan-Espitia and Hobday 2021, Coleman and Wernberg 2021). The successful implementation of these and other forms of mitigation that increase the capacity of coastal systems to adapt to future change is sure to benefit from a long-term, spatially expansive perspective.

Supplemental material
Supplemental data are available at *BIOSCI* online.

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