Review

Resilience of Tropical Ecosystems to Ocean Deoxygenation

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The impacts of ocean deoxygenation on biodiversity and ecosystem function are well established in temperate regions, and here we illustrate how the study of hypoxia in tropical ecosystems can offer insights of general importance. We first describe how mechanisms of resilience have developed in response to naturally occurring hypoxia across three tropical ecosystems: coral reefs, seagrass beds, and mangrove forests. We then suggest that the vulnerability of these systems to deoxygenation lies in interactions with other stressors that are increasing rapidly in the Anthropocene. Finally, we advocate for the adoption of a broader community- and ecosystem-level perspective that incorporates mutualisms, feedbacks, and mechanisms of self-rescue and recovery to develop a better predictive understanding of the effects of deoxygenation in coastal ecosystems.

Why Study Deoxygenation in Tropical Ecosystems?

Ocean deoxygenation driven by eutrophication and climate change is accelerating worldwide, and is one of the greatest threats to life in the ocean and to humans that depend on healthy seas [1–4]. However, we have a major blind spot in our understanding of ocean deoxygenation: research on hypoxia in tropical coastal ecosystems including coral reefs, seagrass meadows, and mangrove forests has lagged behind temperate systems, despite the large proportion of these systems that are at risk [5,6]. This discrepancy has been documented in meta-analyses [7] and reviews [6] and is evident in publication bias [5]. The few studies that have investigated hypoxia in tropical systems have focused primarily on coral reefs and organismal perspectives [8,9]. However, it is becoming apparent that oxygen limitation (dissolved oxygen concentrations <3 mg/l, but higher for some taxa) is widespread in tropical ecosystems [6] and is emerging as one of the most pressing conservation concerns [10].

Tropical ecosystems differ from temperate regions in several important ways and understanding these differences provides insight on the natural capacity of ecosystems to cope with ocean deoxygenation. Oxygen is more limited in the tropics where warmer temperatures decrease the saturation capacity of dissolved oxygen in seawater, while simultaneously increasing rates of aerobic metabolism that consume and deplete oxygen [1]. Moreover, high biodiversity in the tropics has increased the functional diversity of organisms responding to hypoxia and facilitated the development of mutualisms in which oxygen can be exchanged between partners [3], such as corals and their endosymbionts. Finally, tropical coastal ecosystems are typically more tightly connected to the associated human societies that are dependent on their ecosystem services, and so these coupled human–natural systems are often more vulnerable to human impacts [11]. For example, coastal communities in the tropics are disproportionately dependent on healthy ecosystems needed for fisheries provisions [12], but pollution that fuels deoxygenation via nutrients and organic matter is often less regulated in the tropics [13].

Hypoxia as a Natural Feature of Tropical Ecosystems

There are three main drivers of oxygen depletion in coral reefs, mangrove forests, and seagrass meadows that make them naturally subject to hypoxia at a variety of scales. First, they engineer...
landscape-scale biogenic features such as seagrass pools [14], mangrove ponds and channels [15,16], and coral lagoons and flats [17]. These biogenic features reduce oxygen replenishment by increasing stratification and reducing flushing rates, and these effects may be exacerbated by tides, seasonal cycles, or climate anomalies (Figure 1). Second, the impounded basins and complex habitats formed by mangroves, corals, and seagrass habitats are natural traps for organic matter (e.g., detritus, drift algae) and are themselves sources of copious organic matter, such as mangrove leaves, seagrass blades, and coral spawn [18], which fuel decompositional processes that deplete oxygen. Third, respiratory oxygen consumption by seagrass, corals, and epiphytic algae associated with mangroves at night or in other light-limited conditions, multiplied by their high biomass, can lead to rapid drawdown of dissolved oxygen in the surrounding water column (Figure 1). This respiratory drawdown of oxygen from the water column can be enhanced by the slowing of water flow and dampening of waves by seagrass canopies, coral reefs, and thickets of mangrove stems and roots [19–21]. This regular depletion is evident in diel cycling of oxygen concentrations and offers unique insights into the potential adaptive responses of resident organisms to dynamic oxygen regimes and their broader ecological effects (Box 1).

Anthropogenic deoxygenation is likely to mimic the natural hypoxia regimes of tropical ecosystems. Based on a synthesis of hypoxia observations in temperate coastal ecosystems, Rabalais et al. [22] concluded that human influence on oxygen regimes is most apparent at timescales of hours to weeks and in smaller, semi-enclosed systems such as estuaries, bays, and the inner shelf. These are the same temporal and spatial scales over which tropical marine ecosystems are exposed to naturally hypoxic conditions.

Natural Mechanisms of Resistance to Hypoxia

Corals, mangroves, and seagrasses all possess physiological and structural mechanisms that mediate their oxygen environment and can counteract hypoxia (Figure 1). Mangroves have conspicuous prop roots and pneumatophores that supply atmospheric oxygen to their belowground roots and rhizosphere [23]. Similarly, seagrasses transport oxygen from their blades down to the rhizosphere, creating favorable biogeochemical conditions for nutrient exchange and root health, and release excess photosynthetic oxygen into the canopy [24,25]. Corals capitalize on oxygen produced by their endosymbiotic algae to maintain elevated oxygen concentrations in their tissues and the surrounding water [26]. The photosynthetic production of oxygen by these tropical foundation species, combined with mechanisms that can continue at night, including their ability to utilize oxygen stored in their tissues [27], create oxygenated microhabitats [25,26], absorb atmospheric oxygen [23], and/or redistribute oxygen internally counter to external oxygen gradients [24,28], provide the potential for ‘self-rescue’ not seen in the bivalve reefs or infauna-dominated soft sediments that have been the focus of temperate hypoxia research.

The hypoxia tolerances of marine organisms associated with tropical foundation species are not well established [7], but evidence points towards widespread adaptation to hypoxia across taxonomic groups and habitat types. For example, fish from numerous families exhibit high tolerances to hypoxia in both coral reef [29] and mangrove [30] habitats, whereas other fish overcome low concentrations of dissolved oxygen through surface air gulping [31] or by crawling out of water to breathe air [32]. Ctenophores and cnidarians thrive in hypoxic mangrove ponds just as they do in seasonally hypoxic temperate estuaries [15] and lucinid clams reach their highest abundances in the sulfide-rich hypoxic sediments of seagrass beds [33]. Other species exhibit phenotypic plasticity in response to hypoxia, such as reef-dwelling fireworms that can increase the surface area of their respiratory structures [34]. Despite the handful of studies documenting hypoxia tolerance in tropical species, basic research is needed to elucidate mechanisms of
Figure 1. Interactions of Mangroves, Seagrasses, and Corals with Oxygen Across the Coastal Tropical Seascape. (A) During the day, under high-light conditions, the photosynthetic production of oxygen exceeds respiratory demand, as mangroves, seagrasses, and corals act as net producers of oxygen, which can alleviate hypoxic conditions (indicated in red) in tissues and the surrounding environment. Both mangroves and seagrasses can translocate oxygen to roots and into the rhizosphere, and mangroves have specialized structures, such as the prop roots of red mangroves (2), that possess numerous tiny pores (lenticels) to uptake air for transport to belowground areas (1). (B) At night, respiration continues but photosynthesis ceases, so mangroves (2,3), seagrasses (5), and corals (6) must draw oxygen from their environment, which can locally deplete oxygen. Mangroves (1) continue to supply oxygen to their roots and rhizosphere during darkness, and seagrass does as well (4) provided there is a sufficient supply of oxygen in the water column. Mutualisms between seagrass and lucinid clams, and between the cnidarian host and zooxanthellae of corals, as well as facilitation of propagules by established mangrove trees, play an important role in alleviating both oxygen limitation and associated stressors such as hydrogen sulfide (see Table 1 for details). Mangroves, seagrasses, and corals can also indirectly mediate oxygen concentrations in the adjacent habitat by controlling factors such as water movement and the supply of nutrients and organic matter.
tolerance, the physiological basis for interspecific variation, and the scope for acclimation to near-term deoxygenation trends. For example, recent research in mangrove forests has documented distinct fish and benthic communities in forest interiors where oxygen concentrations are limiting, suggesting that community structure may be influenced by hypoxia [35,36].

The tropics are hyperdiverse and have long been recognized for the ubiquity of mutualisms [37]. This extends to relationships where oxygen serves as a ‘universal currency’ exchanged between partners to facilitate their persistence in oxygen-limiting environments [8]. For example, photosynthetic endosymbionts (Symbiodinium spp.) produce oxygen that is consumed by their coral hosts [38]. Corals also form facultative mutualisms with ‘sleep-swimming’ fish that mitigate nighttime oxygen depletion by ventilating their sleeping crevice with fin movement [39]. Seagrasses can tolerate stressful conditions with the aid of lucinid clams. Seagrasses oxygenate the rhizosphere in exchange for metabolism of toxic sulfides by lucinids, a relationship that is particularly important in the warmer tropics [33]. Mangroves likewise provide oxygen to infauna in sediments around pneumatophores, which is important for microbial biogeochemical cycling [40], and crab burrowing alleviates hypoxic stress in mangrove sediments by enhancing aeration and tidal flushing [41]. These mutualistic interactions are as important for tolerance of deoxygenation at the community level as the physiological mechanisms are at the organismal level. Future research is likely to reveal other mutualisms, particularly between photosynthetic and non-photosynthetic organisms, and relationships involving organisms that oxygenate microhabitats by burrowing or pumping water.

Box 1. The Role of Diel Cycling in Responses to Deoxygenation

Physicochemical properties of seawater fluctuate over predictable temporal scales. In tropical coastal habitats, diel cycling of dissolved oxygen (DO), pH, and temperature (Figure 1A), driven by abiotic conditions (e.g., solar radiation) and the metabolism of tropical foundation species, is one of the clearest examples of this periodicity [86]. Although the scientific capacity to continuously monitor environmental parameters has greatly improved over the past two decades, there remain relatively few time series in tropical habitats that incorporate DO, which limits our understanding of the magnitude of natural DO fluctuations. From a handful of published studies, the average range of DO concentrations over 24 h is roughly equivalent across coral reef and seagrass habitats. The same pattern is amplified in mangroves, where conditions can range from near-anoxic to hyperoxic in just 1 day (Figure 1B). The magnitude of variability in a given environmental parameter, including optima and critical values, often differs spatially within the same habitat type. Fluctuations that exceed projected conditions for the near-future open ocean occur regularly on shallow coral reefs [34,86], seagrass meadows [87], and tropical mangrove ponds [15], and these habitats provide an opportunity to explore the role of contemporary exposure to environmental variability in mediating organismal tolerances to stress. Characterizing variability regimes by habitat and location is an essential first step in providing accurate context to individual organismal tolerances.

Exposure to environmental variability can dramatically alter organismal responses to subsequent stress [88]. Although our limited knowledge of baseline DO variability in the tropics hinders our ability to understand how variability influences response to deoxygenation, prior work with other diel cycling stressors (e.g., temperature, pH) provides a clue that such natural variability could mediate organismal responses to sustained hypoxia. Recent studies have documented both the extent of natural variability in pH and temperature in tropical habitats [85,89–91] and how natural thermal and pH variability can either enhance the resilience or heighten the sensitivity of resident organisms to near-future ocean conditions (i.e., warming, ocean acidification). For example, high variability can increase coral thermal tolerance [92,93] and lower bleaching susceptibility [94,95]. In corals, prior exposure to diel pH cycling has limited effects on responses to sustained pH stress [85,96,97], and in some tropical algae exposure to pH variability can enhance performance [98], increase sensitivity [99], or have no effect during subsequent exposure to low pH [100]. Analogous studies have yet to explore similar relationships with oxygen dynamics in tropical foundation species. We hypothesize that naturally variable oxygen regimes in mangroves, seagrasses, and coral reefs could enhance the resistance or sensitivity of organismal responses to sustained hypoxic stress, although it is also possible that the response to extreme oxygen conditions could be primarily affected by the actual value of the oxygen concentration relative to established critical values rather than prior exposure to variability as has been suggested for temperature stress [51]. Recent evidence from fish that inhabit mangroves suggests that exposure to variable oxygen environments early in life promotes tolerance to hypoxia as adults [101]. These systems should be utilized and closely studied to understand how diel cycling may facilitate resilience of key taxa to anthropogenic deoxygenation.
Adaptations, including metabolic and behavioral traits, mutualisms, and mechanisms of self-rescue, offer protection against deoxygenation. Although hypoxic conditions have been commonly measured in mangrove forests and seagrass beds, there have been no mass mortality events.
attributed solely to naturally occurring hypoxia. Perhaps surprisingly, corals are proving remarkably tolerant to low oxygen, with common Caribbean reef species capable of tolerating near-anoxia for over 1 week (M.D. Johnson, unpublished). Even in extreme hypoxic events associated with mass mortality of some coral species (e.g., *Agaricia lamarcki*), other species persisted (e.g., *Stephanocoena intercepta*) [5], resulting in community assemblage shifts rather than complete loss of corals from the ecosystem. Determining the extent to which these adaptations will translate to tolerance to anthropogenic deoxygenation should be a research priority.

**Multiple Stressors as the Real Culprit**

Are tropical ecosystems immune to the effects of anthropogenic deoxygenation? We suggest the answer is ‘no’, because hypoxia typically co-occurs with other stressors that exacerbate its effects. While some of these stressors co-occur with hypoxia naturally, many are directly intensified by human activity (e.g., ocean acidification, warming, eutrophication) and so they are increasingly likely to be encountered at detrimental levels alongside hypoxia. Multiple stressors commonly have negative synergistic effects from the organismal to ecosystem level [42] and evidence from temperate and pelagic ecosystems suggests that multiple stressor effects involving hypoxia are a general phenomenon and so likely widespread in tropical coastal habitats as well [43–45].

A recent global analysis identified deoxygenation as one of three major stressors of marine systems, along with climate change and ocean acidification, whose causes and consequences are intertwined and increasing in severity at a global scale [2]. Warmer waters increase the likelihood of deoxygenation by increasing rates of microbial oxygen consumption, promoting stratification of the water column, and lowering oxygen solubility [1], while at the same time increasing metabolic demand for oxygen and vulnerability to hypoxia at the organismal scale through a variety of physiological mechanisms [45,46]. Hypoxia and low pH are also likely to co-occur, as the microbial respiration that consumes oxygen produces carbon dioxide [47]. Their co-occurrence is particularly apparent in the shallow impounded habitats formed by tropical foundation species, where solar insolation, atmospheric warming, and aerobic respiration can cause warming, deoxygenation, and acidification that exceed global averages by orders of magnitude (Box 1). The combined effects of multiple stressors, such as low oxygen and acidification, can have synergistic negative effects on the survivorship of corals [48]. Elevated temperatures have also been identified as a contributing factor to hypoxic seagrass mass mortality events [49,50]. Decreased oxygen availability, in turn, is likely to further narrow the thermal tolerance range of tropical species that is already constrained relative to temperate counterparts [51]. Even where temperature and oxygen vary independently of one another spatially, overall warming could increase a system’s vulnerability to hypoxic events, as observed on Panamanian reefs [5]. Based on these observations, we suggest that cases of apparent heat-driven bleaching and mortality of corals and other tropical habitat formers should be re-examined to consider whether hypoxia was an undetected cofactor.

Eutrophication, hydrogen sulfide, and harmful algal blooms (HABs) are three stressors likely to co-occur with deoxygenation since each has biogeochemical linkages to oxygen depletion [22]. Excess nutrients can trigger macroalgae blooms that smother coral reefs, seagrass beds, and mangrove epifaunal communities. Such overgrowth can create microhabitats with low oxygen concentrations by blocking sunlight needed for photosynthesis, restricting water exchange, and fueling microbial respiration [26,52,53] and can push a system from diel cycling of oxygen to persistent hypoxia [54]. As microbial communities shift to anaerobic metabolism, hydrogen sulfide production can lower hypoxia tolerance in corals [48], reduce the seedling growth rates of some mangrove species [40], and cause mass mortality of seagrass [27,55]. HABs have been associated with hypoxia and reef mortality, as well as fish kills in mangrove
lagoons, which is likely to be due to the production of excess organic matter, shading, toxicity, and the smothering of respiratory surfaces that occurs during phytoplankton blooms [56–58].

Additional anthropogenic stressors have the potential to exacerbate the impact of deoxygenation on tropical habitats. Erosional sediments associated with land-use change can blanket nearshore environments, deplete oxygen, and increase sulfide levels, leading to bleaching and death in corals [48] and anoxia in seagrass beds [59,60]. Sediment inputs can also cause high turbidity that may disrupt the photosynthetic self-rescue mechanism for corals and seagrass. Mangroves are susceptible to oil spills that reduce both oxygen concentrations in sediments and oxygen uptake by blocking lenticels [61,62]. Mangroves can also succumb to the combined effects of nutrient limitation and/or sediment starvation that contribute to increasingly hypoxic conditions associated with altered hydrology [63], in what is likely their greatest oxygen-mediated threat that has earned the ominous moniker ‘mangrove heart attack’ [64].

The research capacity of oxygen monitoring programs in tropical marine habitats trails behind that in temperate ecosystems [5], and the addition of dissolved oxygen to the list of commonly measured stressors (e.g., temperature, pH) is needed to elucidate the separate and interactive effects of oxygen limitation on biological communities, to document the global extent of hypoxia, and to determine the drivers of oxygen depletion to aid resource management decisions [65]. Snapshot surveys can detect oxygen gradients across a seascape and identify problematic areas, whereas continuous monitoring programs are logistically more challenging but allow the detection of hypoxic events that may be otherwise difficult to predict. Where monitoring resources are limiting, the choice between the two options will depend on the natural history of the system, existing logistical support, and the reliability of biological indicators of hypoxia.

**Mechanisms of Resilience to Deoxygenation**

Understanding of the mechanisms underlying ecological resilience is critical in predicting the impacts of global change factors, such as deoxygenation, and managing natural systems to maximize ecological function and ecosystem services [66]. We are still in the early stages of exploring how hypoxic stress interacts with tropical coastal ecosystems, but we can piece together a preliminary synthesis of factors determining their resilience from existing empirical observations. In the following sections, we consider resilience through the stages of community response to hypoxic events: onset of hypoxia and the disruption of mutualisms, acceleration of deoxygenation through feedbacks, and community recovery following disturbance. Finally, we consider how these stages that comprise the arc of resilience are likely to vary by ecosystem with scale dependence.

**Mutualism Disruption and Ecological Destabilization**

When mutualisms and their associated feedbacks are overwhelmed by hypoxia and co-occurring stressors, tropical ecosystems may destabilize and become vulnerable to state change [67]. For example, the seagrass and lucinid clam mutualism can break down when seagrass mortality decreases oxygen translocation and elevates sulfide levels, thus leading to mortality of lucinids and further mortality of seagrass [56]. The coral mutualism between cnidarian host and photosynthetic endosymbionts is likewise vulnerable to multiple stressors, with widespread coral bleaching preceding coral mortality during severe hypoxia against a backdrop of elevated temperatures [5]. The mutualism that can occur between mangroves and sponges, in which sponges provide mangroves with nutrients and protection from isopods [69], may be preempted when sponges are killed by episodic stressful abiotic conditions [70], such as hypoxia. Given that oxygen is an indicator of overall ecosystem function in tropical ecosystems [8], excessive respiration and mass mortality associated with hypoxia are signs of destabilization and transition to a new equilibrium (Table 1).
Table 1. Mechanisms of Resilience to Ocean Deoxygenation in Tropical Ecosystems

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Self-rescue ability</th>
<th>Diversity of foundation species</th>
<th>Mutualisms and resilience feedbacks</th>
<th>Deoxygenation feedbacks</th>
<th>Hysteresis potential</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seagrass meadows</td>
<td>Medium</td>
<td>Low</td>
<td>Seagrasses provide oxygen, shelter to lucinids and delibit that fuels production of sulfide consumed by lucinids. Lucinid clams oxidize sulfides that are toxic to seagrass. Seagrass death, organic matter production, hypoxia, sulfide production and intrusion, seagrass death.</td>
<td>Lucinid mutualism breaks down</td>
<td>Low</td>
</tr>
<tr>
<td>Coral reefs</td>
<td>Low</td>
<td>High</td>
<td>Corals provide shelter and resources for zooxanthellae and sleep-swimming fish. Zooxanthellae provide oxygen and sleep swimming fish ventilate crevices with oxygenated water. Coral shelter fish. Fish promote coral by limiting algae. Bleaching and coral respiration, coral death, organic matter production, sulfide production and hypoxia.</td>
<td>Bleaching, Mortality of epibionts, organic matter production, hypoxia.</td>
<td>Medium</td>
</tr>
<tr>
<td>Mangrove forests</td>
<td>High</td>
<td>Low</td>
<td>Sponges provide mangroves with nitrogen and protection against isopods. Mangroves provide sponges with attachment substrate and carbon. Mature mangroves provide propagules with aerated soils with less sulfides. Mortality of epibionts, organic matter production, hypoxia.</td>
<td>Inhibited mangrove recruitment Loss of sponge mutualisms</td>
<td>High</td>
</tr>
</tbody>
</table>

*The dominant foundation species that define tropical coastal ecosystems vary in their resilience to hypoxia in the water column due to a combination of physiological mechanisms, feedbacks, and functional diversity. The result is variation in the potential for initial resistance to hypoxic conditions, hysteresis in shifts of community state, and the overall impact of hypoxia on ecological function. For example, seagrass is resistant to modest hypoxia due to a self-rescue ability through photosynthetic oxygen production and mutualisms with lucinid clams, but once a hypoxia threshold is crossed, the mutualism breaks down and mass mortality occurs due to deoxygenation feedback and synchronized mortality in low-diversity meadows. Corals, by contrast, do not have the same oxygen production capability and the species diversity of the coral community will exhibit wider variation in oxygen tolerances, resulting in onset of mortality at less severe hypoxia and a more graded relationship between oxygen and loss of reef species. Mangroves are relatively unimpacted by low-oxygen conditions because of their high self-rescue potential and minimal dependence on oxygen-mediated mutualisms.*

**Feedbacks and the Acceleration of Deoxygenation**

New feedbacks can emerge with the onset of hypoxia that accelerate and reinforce ecological state change. This is evident where seagrass mortality leads to the accumulation of dead leaves that smother the substrate and fuel microbial respiration, triggering further oxygen depletion, sulfide production, and additional seagrass death [55]. Likewise, the decay of reef organisms that succumb to hypoxia is thought to exacerbate deoxygenation in coral ecosystems [71] and mangrove epifaunal communities [72]. Another feedback can occur where large-scale hypoxia makes reefs more susceptible to disease outbreaks [73] and the disease itself generates microscale hypoxia that accelerates its spread over coral colonies [74]. This cycle plays into the larger dissolved organic carbon, disease, fleshy algae, and microbes (DDAM) feedback model [75] that was expanded to consider how hypoxia not only perpetuates the cycle but can also trigger it [8]. Humans can also play a direct role in hypoxia feedback loops, such as when aquaculture ponds in cleared mangroves become degraded by hypoxia, triggering disease outbreaks, and forcing the abandonment and subsequent clearing of additional ponds [76,77]. Hypoxic conditions in coastal habitats are likely to abate when feedbacks are broken, either by the depletion of organic
matter that fuels microbial respiration, or by reoxygenation through changed oceanographic conditions (e.g., wave mixing, tidal flushing) [22].

Recovery Potential and the Scale Dependence of Resilience

The ability to revert to the previous ecosystem state once hypoxia subsides is likely to vary among tropical foundation species for several reasons (Table 1). First, they differ in the amount of physical structure remaining after mortality that has the potential to promote recovery. Living mangroves and their associated structure are likely to persist through hypoxic events, and when corals die their skeletons function as habitat for recolonization [78]. Seagrass that suffers mortality, however, is rapidly degraded or swept away [49]. Second, recovery of tropical ecosystems is dependent on recolonization and/or regrowth of survivors. Corals that survive hypoxia can serve as the basis for gradual colonial regrowth, whereas seagrass seeds that survive hypoxic seagrass die-offs can generate rapid recolonization, accelerated by vegetative expansion [50,79]. Given that hypoxia is most likely to occur in stagnant areas, local connectivity to source populations in adjacent habitats may foster recovery more than larval resupply from distant sources by ocean currents [80]. Third, community-level interactions will play important roles that differ by habitat, such as on coral reefs where grazers keep dead coral substrate free of algae and available for coral recruitment following hypoxia [81] or in seagrass beds where facilitative successional interactions of rhizohyphic algae modify sediments to promote seagrass regrowth [82,83]. Due to the general lack of long-term datasets incorporating dissolved oxygen observations, there is uncertainty about how these various mechanisms of natural resilience and recovery potential of tropical ecosystems will meet the challenges of the increasing frequency, size, and intensity of hypoxia events occurring with anthropogenic deoxygenation [6].

However, there is accumulating evidence that illustrates how feedback processes and mechanisms of recovery can play out as a function of spatial and temporal scale, particularly when considering instances where the ecosystem recovery timeline can exceed the return time of conditions that trigger hypoxic events (M.D. Johnson, unpublished). This has important implications for the recurrence of hypoxia in systems where the biomass of habitat dominants themselves drives oxygen depletion, such as with seagrass where die-offs have been attributed to high biomass, which increases metabolic demand for oxygen [49,55] and further exacerbates oxygen depletion by slowing water flow [20]. The recovery time for seagrass populations to reestablish high biomass could limit when hypoxia is likely to recur, even if other contributing factors that would otherwise trigger the establishment of hypoxia are in place, in a negative feedback loop. By contrast, mutualisms that normally ameliorate low-oxygen conditions could break down and remain impaired for years following extreme events, as observed when drought diminished the oxygenation of sediments by seagrass, which led to loss of lucinid clams and their potential to ameliorate sulfide stress [68]. Such systems where a key mutualist has been functionally lost are predicted to be less resilient [84] and represent a positive feedback that could leave a system more vulnerable to subsequent hypoxic stress.

Positive and negative feedbacks are not mutually exclusive and may contribute to variable system dynamics by operating at different scales, resulting in spatially patchy mortality and multiyear intervals between die-off events, consistent with seagrass dynamics in Florida Bay, USA [49]. Other systems, such as coral reefs, offer a contrast because hypoxia can develop independent of the living biomass of biogenic habitats, and recovery periods can extend over decades rather than years. Under such circumstances, communities may not have the chance to recover to historic compositions due to the increasing frequency of deoxygenation events and may shift towards more-tolerant species [5] (M.D. Johnson, unpublished). Additional research is needed to fill gaps in our understanding of how disturbance, feedbacks, and mutualisms interact to
determine whether the trend of increasingly frequent hypoxic events is likely to drive a system towards cycles of disturbance and recovery or, rather, towards novel ecosystem states.

Concluding Remarks

We emphasize the importance of incorporating hypoxia in tropical ecosystems into our global understanding of ocean deoxygenation, because these systems offer general lessons about ecological responses and resilience. We suggest that many tropical taxa have developed tolerances in response to naturally occurring hypoxia and that the most severe impacts associated with hypoxia stem from interactions with co-stressors. These impacts follow the breakdown of mutualisms and shifts in feedbacks that push systems past thresholds and reinforce ecosystem state changes. Mass die-offs in tropical ecosystems signal extreme conditions and ecosystem dysfunction and their rarity to date is indicative of the natural resistance of these systems to deoxygenation. However, the increasing occurrence of hypoxic events globally and reoccurrence in some tropical systems is worrisome, particularly given long recovery times [50] (M.D. Johnson, unpublished). Hypoxia is both a cause and a consequence of other, interacting marine stressors (e.g., warming, acidification, eutrophication) and oxygen is the basis for mutualisms and feedbacks that underpin the resilience of these ecosystems. The vital importance of mutualisms to hypoxia resilience and recovery presents rich areas for future research, which is likely to provide additional insights on not only tropical but also temperate ecosystems (see Outstanding Questions).

We advocate that monitoring programs in the tropics include dissolved oxygen and that research on the effects of tropical ocean deoxygenation build on the foundation of organismal studies to include community- and ecosystem-level perspectives across ecosystem types.

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Outstanding Questions

Do the same mechanisms that confer hypoxia tolerance also confer tolerance to other stressors, such as thermal stress and ocean acidification, or are there trade-offs? Answering this question will determine whether there are ‘super-species’ that are generally stress tolerant or whether species physiological tolerances are stressor specific.

Do tropical foundation species fuel or ameliorate hypoxia in the ecosystems they engineer and the adjacent habitats? Given the potential for foundation species to generate photosynthetic oxygen, contribute to organic matter loading, take up nutrients, and restrict water flow, it remains to be determined how these factors contribute to net oxygen concentrations across the seacape.

How does diel oxygen cycling mediate ecological responses to sustained hypoxia? The evidence is mixed on whether cycling of other stressors, such as pH, is as stressful as sustained conditions, and resolving this question for hypoxia will contribute to our basic understanding of stress responses in marine organisms.

Do the communities associated with tropical foundation species differ in their relative tolerance to hypoxia because of differing oxygen regimes? Some ecosystem types or regions may be more likely to persist with the increasing prevalence of hypoxia (see hypotheses outlined in Table 1).

What are community recovery times from hypoxia, and how do they compare to hypoxia return times at the same sites? How is return time changing due to human activities? If it is increasing, a higher frequency of hypoxia could overwhelm the natural resilience capacity of tropical ecosystems.

What is the relative importance of natural factors, local anthropogenic stressors (e.g., eutrophication, sedimentation, habitat conversion), and global anthropogenic stressors (e.g., ocean warming, sea level rise) in driving tropical hypoxia? Sites where local anthropogenic stressors have an outsized role offer an opportunity for local resource management to improve ecosystem resilience.


