

## Review Article

# Coral Reef Resilience through Biodiversity

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Irrefutable evidence of coral reef degradation worldwide and increasing pressure from rising seawater temperatures and ocean acidification associated with climate change have led to a focus on reef resilience and a call to “manage” coral reefs for resilience. Ideally, global action to reduce emission of carbon dioxide and other greenhouse gases will be accompanied by local action. Effective management requires reduction of local stressors, identification of the characteristics of resilient reefs, and design of marine protected area networks that include potentially resilient reefs. Future research is needed on how stressors interact, on how climate change will affect corals, fish, and other reef organisms as well as overall biodiversity, and on basic ecological processes such as connectivity. Not all reef species and reefs will respond similarly to local and global stressors. Because reef-building corals and other organisms have some potential to adapt to environmental changes, coral reefs will likely persist in spite of the unprecedented combination of stressors currently affecting them. The biodiversity of coral reefs is the basis for their remarkable beauty and for the benefits they provide to society. The extraordinary complexity of these ecosystems makes it both more difficult to predict their future and more likely they will have a future.

## 1. Introduction

Increasing concern over worldwide deterioration of coral reefs and the likelihood that global climate change will cause further degradation has led to a focus on the concept of reef resilience. Local, regional, and global stressors have the potential to cause irreversible losses of biodiversity in some reefs and consequently of the ecosystem services they provide [1–9]. Even the physical structure of some coral reefs may be in jeopardy. Can these reefs recover and persist? Can they be managed for resilience? The future of many reefs will depend on whether fundamental processes like photosynthesis, calcification, and recruitment can continue in the face of a multitude of local and global stressors. Reefs that previously could recover after a disturbance may not be able to survive the assaults of global climate change, especially when combined with local pressures.

The limits of our current knowledge of the biodiversity of coral reefs, of the potential for corals and other reef species to adapt to climate change, and of the effects of increasing sea water temperatures, ocean acidification, and other components of climate change on reef organisms make it challenging to predict what the future holds for coral reefs.

As Vitousek et al. [10, page 498] observed, “we are changing Earth more rapidly than we are understanding it.” Ten years ago, Walther et al. [11] noted that marine and terrestrial ecosystems were already being affected by human-driven changes in the climate.

This paper reviews and synthesizes scientific literature that provides insights into the future for coral reefs in the face of climate change and explores the concept that biodiversity could help confer resilience. It evaluates the potential for management to reverse degradation, identifies some key research priorities, and explores the possibility that coral reefs will prove to be resilient primarily because of their inherent complexity and biodiversity.

## 2. What Is Resilience?

Resilience is not a new concept. In 1973, Holling [12, page 14] defined it as “a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables.” He differentiated it from stability which he defined as “the ability of a system to return to an equilibrium state

after a temporary disturbance—the more rapidly it returns and the less it fluctuates, the more stable it would be.” Holling noted that the spruce budworm forest community in eastern Canada, which experiences budworm outbreaks and shifts in dominance of different tree species, is highly unstable but the instability confers high resilience. Holling did not discuss any marine examples. It is possible that coral reefs are relatively stable ecological systems which are less likely to be resilient than other ecosystems when disturbed. Reef scientists still debate the relative stability of coral reefs with some suggesting that some reefs are stable while others are not [13–15]. At least some of the disagreement comes from the consideration and interpretation of reef response over different spatial and temporal scales (see [16]). For example, some might conclude that a reef that recovered to its initial coral cover 100 years after a major disturbance was stable while others would disagree.

Although the word resilience is sometimes used to encompass resistance, greater clarity is achieved by making a distinction between the two [14, 17]. Resilience commonly refers to the ability to rebound, while resistance refers to the quality of opposing or withstanding. When applied to coral reefs, resistance can refer to the ability of the entire reef or of individual corals and other organisms to remain unaffected by a stress. For example, fragile, branching corals are more likely to be damaged by storm waves than massive corals which could be thought of as more resistant.

In essence, coral reef resilience can be thought of as the capacity for the reef to recover after disturbance or stress. The term recovery has been used in many ways. In his review of 65 quantitative studies of coral abundance worldwide, Connell [18] defined recovery as an increase in coral abundance (cover) but he noted that such recovery did not necessarily imply a return to the reef’s former structure and function, including colony size structure, species composition, and diversity of functional aspects such as growth and reproduction. However, as Done [19, p. 128] noted, the most stringent definition of the point in time when recovery can be considered complete, in ecological and geological terms, “would be the restitution of prior diversity, mix of colony growth forms (if not species), colony size, frequency distributions, and structural extent and complexity of reef framework (after Johannes [20]).” Although the concept of resilience is based on the capacity to recover, it broadens the perspective to include the consideration of factors (such as connectivity) that contribute to resilience beyond the boundaries of the specific disturbed location (see [21]).

### 3. Signs of Coral Reef Stress

The most recent International Coral Reef Symposium (July 2012) produced a Consensus Statement that was signed by hundreds of scientists and managers recognizing the severity of climate change and calling for global action to reduce emission of carbon dioxide and other greenhouse gases. The previous symposium, in 2008, issued a Call to Action, noting that coral reefs are on the brink of collapse, primarily because of the actions of humans. Major concerns include

increasing levels of carbon dioxide, overfishing, and coastal development ([22–24]).

Disturbances (also referred to as stressors or stresses) can vary greatly. Lugo and Snedaker [25, page 56] state “The term *stress* is used—to describe any action or influence which retards or restricts the normal functioning or development of living biological units (species, populations, communities, or whole systems). Stress can be construed as a drain of potential energy that would otherwise be available for other ecological purposes.”

Stressors can be acute or chronic, natural or anthropogenic, direct or indirect. Some are far harder to evaluate and manage than others. Damage from anchors is easier to understand than the effects of overfishing, and the effects of greenhouse gas emissions and ocean acidification are particularly difficult to comprehend and address [2, 26, 27]. Some stressors, like hurricanes, are clearly natural and impossible to control and some, like sewage input, are clearly associated with human actions and therefore possible to manage. Diseases of corals and other reef organisms, which are becoming of increasing concern, are poorly understood, and currently not possible to classify exclusively as natural or anthropogenic.

Some reefs have changed so much in terms of their dominant organisms that they have been described as undergoing a phase shift, usually involving the replacement of corals with macroalgae as the dominant benthic component. There has not been consensus on what constitutes dominance by corals, meaning that it is not possible to state just when major shifts have occurred [28, 29]. Although there is discussion of communities shifting from dominance by corals to dominance by macroalgae above a certain threshold, that threshold has not been rigorously or consistently defined. Furthermore, there has been insufficient discussion of the temporal aspect of phase shifts—in other words, how long must the change persist to be considered a shift? Another complicating factor is that macroalgal abundance varies greatly, and single values for macroalgal cover recorded during annual surveys may or may not accurately reflect the influence of macroalgae on the reef for the entire year. After an extensive analysis of reef studies from 1996 to 2006, Bruno et al. [29] concluded that the replacement of corals by macroalgae as a dominant benthic component has been less extensive and common than many have assumed. Phase shifts were less common in the Indo-Pacific than in the Caribbean (see also [30]). They acknowledge that major shifts may have occurred before most reef surveys began.

In many cases, there have been significant losses of living coral and increases in algae (e.g., [19, 31–33]). In one of the best examples, Jamaican reef zones over a depth range of 7 m to 35 m exhibited a phase shift (by any definition) from a combination of natural and human stressors with significant declines in coral cover (from over 50% down to less than 5%) and increases in macroalgal cover to over 90% [33]. A loss of herbivorous fish and urchins decreased the resilience of these reefs, and little recovery has occurred [21].

Some argue that phase shifts are reversible while alternate stable states are not, and they conclude that coral reefs for the most part have exhibited reversible phase shifts, leading to the



FIGURE 1: Coral bleaching in the Keppel Islands, Australia, 2006. (photo by R. Berkelmans).

hope that the degradation can be reversed [34]. Several recent papers have debated the applicability of the terms phase shift and alternate stable states/regime shifts [28, 34, 35].

Regardless of the terms used to characterize changes on reefs, and whether or not all would agree that shifts have occurred, the focus needs to be on whether or not the coral reef can recover to its former condition and composition following disturbance, in particular anthropogenic disturbance. Decreases in coral cover may be large enough to warrant concern and action even in cases where no shifts are apparent.

**3.1. Global Stressors.** Recently global climate change (GCC) has been described as the single greatest threat to coral reefs (e.g., [23, 36]). However, it is important to keep in mind that GCC is not a single threat. It encompasses higher temperatures, sea level rise, ocean acidification, and changes in major storm patterns (e.g., [27, 37, 38]). The various, inherently different components of GCC need to be differentiated as they will have varying effects on reefs and closely linked ecosystems such as seagrass beds and mangroves, which have received much less attention than reefs. This review focuses particularly on warming and acidification because they are potentially the most damaging.

It is now clear that human actions are affecting the earth's atmosphere and that  $\text{CO}_2$  and other gases will increase within the next 50 years [27, 39–42]. In less than four decades, by the middle of this century, mean atmospheric  $\text{CO}_2$  over 500 ppm is expected, along with an increase of  $2^\circ\text{C}$  or more in mean global temperature and an increase in mean overall acidity of over 60% ([43, 44]). There are constraints on our ability to predict how this changing climate will affect coral reefs, particularly how they will respond to warmer, more acidic oceans [27, 37, 45, 46]. The most conspicuous effects of climate-driven change on reefs are the bleaching episodes that have been increasing in frequency in association with higher seawater temperatures [47–50], (Figure 1).

Bleaching reflects the loss of zooxanthellae pigments after disintegration and expulsion of zooxanthellae [51, 52]. Both the visible and ultraviolet components of solar radiation can act alone or together to increase the likelihood of bleaching

by decreasing the temperature threshold above which it occurs [51, 53–55]. The host coral and zooxanthellae are both affected by the production of reactive oxygen species associated with thermal stress [51]. High seawater temperatures do not always result in extensive bleaching of corals and other reef organisms, as rainfall and overcast conditions (not currently accounted for in most climate models) can reduce the stress contributed by concomitant high irradiance [56, 57]. Sometimes bleaching is very widespread as in 1998 when reefs were affected globally, but it can be regional as in the Caribbean in 2005 or very localized, as local current patterns can reduce the stress from high temperatures [58].

Global climate change, according to a model developed by Bender et al. [59], is expected to decrease the overall frequency of tropical cyclones but double the frequency of the most powerful storms (categories 4 and 5) by the end of this century. Hurricanes can be very destructive (e.g., [60, 61]), however reef damage is often patchy, varying from zone to zone, over a gradient of depths, and even within zones [62]. Swells from huge storms can alter light and current patterns by rearranging the physical structure and local topography [61]. Predicted decreases in the aragonite saturation state of reef waters from GCC could make corals more fragile and vulnerable to storms [19]. In addition, physical damage might lead to more coral disease [63, 64]. A decrease in the structural complexity of reefs could affect fish recruitment and survival [65]. However, these intense storms also can have positive effects—they can move sediments off of reefs into deeper water [62] and lower water temperature, decreasing the likelihood of coral bleaching events [66]. Florida reefs had less bleaching in 2005 than reefs in the northeastern Caribbean, partly because several hurricanes tracked over or close to the reefs in Florida but not those in Puerto Rico and the US Virgin Islands.

Calcification is obviously fundamental to the development and survival of coral reefs. Erez et al. [67] noted “the existence of these wave resistant structures in spite of chemical, biological, and physical erosion depends on their exceedingly high rates of calcification.” Ocean acidification associated with elevated  $\text{CO}_2$  (and lower pH levels) could have particularly severe consequences for coral reefs because of its effects on calcification, the process responsible for overall reef architecture [27, 67–71]. Reefs may collapse into rubble and dissolve, possibly as early as 2050 when  $\text{CO}_2$  concentrations reach 560 ppm [67, 72, 73]. However, Pandolfi et al. [46] suggest that these predictions are too dire. Although some scientists have suggested that corals could move poleward to escape warming temperatures, other constraints such as lower light regimes and reduced aragonite saturation could prevent reefs from forming in these higher latitudes [45, 74].

We need to know more about the links among different stressors, for example among high seawater temperatures, bleaching, and coral disease [75–81]. (Bleaching is a disease but it is differentiated here from diseases associated with initial tissue loss (see [82]).) Disease prevalence often is correlated with higher seawater temperatures [83]. It seems logical that thermally stressed corals would be more likely to become diseased [84], but not many studies conclusively

demonstrate this connection. In one of the few studies of multiple diseases over a wide geographic area, Cróquer and Weil [78, 79] explored the link between bleaching severity in 2005 and disease prevalence a year later on reefs from Bermuda, Puerto Rico, Grand Cayman, Panama, Curacao, and Grenada. Although they found a significant correlation between the percent of bleached corals and disease prevalence, some sites with intense bleaching did not have increase in disease. Based on six years of data from 48 sites on the Great Barrier Reef, Selig et al. [75] and Bruno et al. [76] found a high correlation between high temperatures and disease. However thermal stress was not correlated with the severity of bleaching [85].

Bleaching is sometimes, although not always, followed by an outbreak of coral disease involving tissue loss (mortality), and disease outbreaks are not always preceded by bleaching [76, 80, 86–88]. Diseased corals can be more susceptible to bleaching [77]. We also need to determine the relationship between diseases and excessive nutrients or other effects of human mismanagement [89–91].

Interestingly, two comprehensive review papers [49, 74] barely mention coral diseases, perhaps because many reports of significant outbreaks and of new diseases have been quite recent, since these reviews were published. Several recent papers on reef resilience have failed to even mention coral diseases or have not addressed them sufficiently. Coral diseases have caused significant levels of mortality in the Caribbean [87, 92, 93], and they are of increasing concern in the Indian and Pacific Oceans (e.g., [76, 94, 95]). It is possible that in some studies based on insufficiently frequent monitoring at least some coral mortality attributed to bleaching was actually from disease. Coral diseases are complex, involving corals, the environment, and associated microbial communities [96–98]. New research approaches using genetics and molecular biology could help demonstrate the shifts in the microbiota that occur when a coral becomes diseased and help reveal how the coral holobiont responds to particular stresses [99, 100].

#### 4. Where, in the World, Have Reefs Recovered?

An examination of reefs that have recovered or are recovering would help identify the characteristics that confer resistance and resilience. Unfortunately, there are remarkably few examples of reefs recovering significantly after disturbances, and even fewer after the removal of anthropogenic stressors. Most reports of recovery have been for relatively short periods of time and over small spatial scales (in the Caribbean: [101–104]; in the Eastern Pacific: [105]; in the Great Barrier Reef, Australia, [106], but see [107]). In Kaneohe Bay, Hawaii, diversion of sewage resulted in an increase in coral cover [108, 109], although cover by the invasive algae increased a few years later and then decreased once again [110].

To date no one has documented a persistent reversal of a phase shift (or a severely degraded reef) back to initial coral cover and coral community composition over a large spatial scale on a Caribbean reef [28]. Increases in the density of the grazing sea urchin *Diadema antillarum*, following

its epidemic die-off in the 1980s, have been associated with greater coral recruitment in Jamaica [111, 112]. After mortality from bleaching in 2005 reversed some of these gains [104, 113], coral cover is once again increasing [104].

Pacific reefs may recover more easily than Caribbean reefs [18, 114], but there are too few examples of significant reef recovery to allow a rigorous evaluation of this concept. Fifteen years ago, Connell [18] reviewed studies that had been conducted for a minimum of four years and found declines in coral cover without significant recovery in 57% of the sites from the Western Atlantic and only 29% of sites in the Indo-Pacific. All sites that recovered in terms of coral cover (29% of the total) were in the Indo-Pacific. He attributed the greater likelihood of recovery in the Indo-Pacific to the greater frequency of acute disturbances (e.g., *Acanthaster* predation, hurricanes) in the Indo-Pacific and chronic disturbances in the Western Atlantic (e.g., overfishing, decreases in herbivory, coastal construction). Halford et al. [107] found complete recovery of corals and nearly total recovery of fish assemblages over 80 km of the Great Barrier Reef about a decade after major storm damage. Monitoring of sites across 1300 km of the Great Barrier Reef (1995 to 2009) indicated increases in coral cover for some reefs but decreases for others [115]. Recently, De'ath et al. [9] reported a loss of over 50% coral cover along the Great Barrier Reef from 1985 to 2012 based on surveys of 214 reefs, attributing the decline to cyclones (48%), Crown-of Thorns starfish (42%), and bleaching (10%).

Roff and Mumby [30] identify a number of factors that could result in Caribbean reefs potentially having less resilience than reefs in the Indo-Pacific, including lower biomass and diversity of herbivores, lack of acroporid corals, and faster rates of macroalgal growth. They note the significant role that disease has played, particularly in causing the loss of acroporid populations in the Caribbean. The higher levels of disease in the Caribbean, affecting almost all of the coral species, not just *Acropora palmata* and *A. cervicornis*, should also be considered [93].

Some examples of reef resistance to, or resilience after, bleaching can be found. Diaz-Pulido et al. [106] noted rapid recovery of *Acropora* spp. colonies on reefs in the Great Barrier Reef that had been almost completely killed by bleaching and subsequent colonization by macroalgae. Coral recruitment, regrowth of corals, and seasonal die-off of the algae contributed to the increased coral cover within just one year of the disturbances. In Moorea, the abundance of butterflyfishes and corals returned to former levels after an outbreak of the crown-of-thorns starfish, bleaching, and hurricanes, but the species composition of the corals and fish differed greatly [116].

In Jamaica, bleaching in 2005 led to a decrease in the size classes of most of the coral species at fringing reef study sites with some but not all species showing an increase in mean size class by 2008 [104]. Colonies of all species increased in abundance by 2008. However, in the US Virgin Islands, widespread bleaching in 2005 was followed by a disease outbreak that led to an average decrease in coral cover of c. 60% [87], and little increase in coral cover has been observed

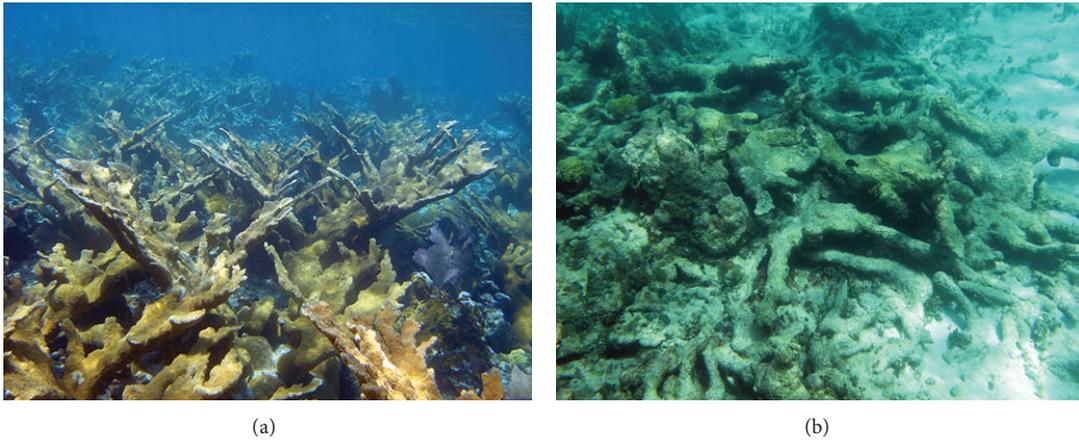


FIGURE 2: Some *Acropora palmata* zones in the Caribbean have recovered while others have not. Photos from St. John, US Virgin Islands. (photos by C. Rogers).

since then (J. Miller, National Park Service (NPS), unpublished data). In the summer/fall of 2010, moderate to severe bleaching occurred again on these reefs, but diseases caused less mortality (J. Miller, NPS, unpublished data.). The less severe bleaching in 2010 does not necessarily demonstrate increased resistance of the corals that survived the 2005 episode to bleaching as the temperature patterns preceding each of the two events differed in terms of number of days above a threshold of  $29.5^{\circ}\text{C}$  and the rates of temperature increase in the preceding spring and summer (J. Miller, pers. obs., NPS and C. Rogers, US Geological Survey (USGS), unpublished data).

In the Caribbean both *Acropora palmata* and *A. cervicornis* declined significantly beginning in the late 1970s [13, 117, 118]. A few studies document some recovery of these species (listed as threatened under the US Endangered Species Act in 2006), but there are currently insufficient data to know if they will ever return to their former abundance and size frequency distributions, (Figure 2).

Recently, Graham et al. [119] used a meta-analysis to explore reef recovery based on 22 publications with data from a total of 48 sites in the Pacific and Atlantic. They included only studies where there had been a decrease of at least 10% in coral cover after a pulse disturbance—most after bleaching. They considered recovery any increase in coral cover after disturbance, no matter how small. It is not clear if any of the reef areas returned to the initial level of coral cover present before the disturbance. Graham et al. [119] noted that none of the studies included sufficient information on ecological characteristics that could potentially play a role in promoting recovery such as structural complexity, fish diversity, and algal cover. Only two were found from the Caribbean (in Belize and St. John, US Virgin Islands). However, the report from St. John [120] was from a reef where coral cover later declined dramatically [87]. Miller et al. [87] reported an increase in coral cover at two out of four long-term monitoring sites in St. John and St. Croix from 2000 to 2004 but then, as noted above, quantified an average decline of about 60% of coral cover following bleaching and disease in 2005/2006.

More research is needed to identify the characteristics of resistant and resilient reefs in the face of all components of global climate change. Resilience will vary depending on the stressor. To date, most of the focus has been on increasing seawater temperatures. Limited evidence suggests that reefs are more likely to resist or to recover from thermal stress if they have experienced high temperature variability over prolonged periods, have corals with thermally tolerant symbionts, are protected from high irradiance, are found where currents are strong (and perhaps where upwelling occurs), have high abundance of herbivorous fishes, and are connected to sources of larvae to replenish degraded populations.

## 5. Management of Coral Reefs under a Changing Climate

The year 2010 was the International Year of Biodiversity. A recent assessment shows that the 1992 Convention on Biological Diversity failed to meet its goal of substantially reducing the loss of global biodiversity by 2010 [121]. In addition, the IUCN Red List Index for corals declined dramatically indicating increased risk of extinction for corals (see also [122]). Only about 0.5% of the ocean is currently protected [121]. Coral reefs comprise less than 0.1% of the ocean, and only about 4.9% of them are inside no-take areas (less than 1% outside of Australia). Only 6% of the total tropical coral reef area (estimated as 250,000 sq km) is in marine protected areas (MPAs) that are considered effective, with 13% partially effective [23].

Besides reducing the loss of biodiversity and maintaining ecosystem services, scientists have stated other goals for coral reefs, including preventing or reversing phase shifts, and “managing coral reefs for resilience” [35, 123]. Does it matter what the goal is? Would management be different for biodiversity conservation than for resistance to bleaching or to conserve areas that can seed “down current” areas?

Although management priorities can sometimes be contradictory, most would agree that the overall goal is to

maintain biodiversity and ecosystem services, and that there are limited management options beyond control of local stressors associated with human actions, such as coastal development (e.g., [17]), establishment of effective networks of marine reserves [58, 124], and increasing protection of reefs that are likely to be more resistant and resilient [125–127].

Managing a coral reef means to do whatever feasible to reduce the stressors affecting the reef. Reef managers can only attempt to control what humans are doing on a local basis—they cannot lower seawater temperature and stop bleaching from occurring. The goal is not to manage for reefs with fewer species that may be better able to cope with storms or thermal stress associated with GCC but rather to attempt to manage whatever stressors we can control in order to reverse the degradation ultimately leading back to original reef structure and function.

Côté and Darling [128] state that “management that controls local stressors to reverse degradation and recover original species assemblages will actually increase the proportion of sensitive taxa within the assemblage and may effectively decrease ecosystem resilience to climate change.” However, many scientists would agree that the goal is not maintenance of a resilient reef of low biodiversity but rather the recovery of a reef with the highest biodiversity and coral cover possible for the given location. The concept of sensitive taxa is misleading, as shifts in relative abundance of coral species are much more likely than elimination of coral species. In the US Virgin Islands, after severe bleaching and disease in 2005/2006, species in the *Montastraea annularis* complex declined significantly but remained the most abundant. Almost all species were affected, and even the most sensitive (*Agaricia agaricites*) survived [87]. Côté and Darling [128] seem to assume that species will respond the same way each time they are stressed, for example during a bleaching event. However, this is not the case (e.g., [129]). We know that species vary in their responses to these events and that individual coral colonies within a species can show a variety of responses ranging from complete recovery to total mortality (e.g., [130]). Species that are very susceptible to increased temperatures in one location may bleach less in another [129]. In addition, coral species may be more susceptible to some disturbances, including different aspects of climate change, than others. For example, the Caribbean branching species *Acropora cervicornis* is more vulnerable to storm damage than massive coral species but less likely to be affected by increases in sedimentation [60, 131].

In contrast to the recommendation by Côté and Darling [128] that more protection be given to less diverse reefs with more resistant coral species, the models developed by Baskett et al. [125] indicate that “protecting diverse coral communities is critical, and protecting communities with higher abundances of more thermally tolerant coral species and symbiont types secondary, to the long-term maintenance of coral cover.” We need to conserve species (and their interactions) because we do not know which ones are most critical to ecosystem functioning and which ones might provide resilience [132]. Neither Côté and Darling [128] nor Baskett et al. [125] explicitly address coral mortality

from storms, and increased storm frequency and intensity is predicted with GCC.

Some studies have attempted to identify reefs that have the highest likelihood of persisting under climate change, using both empirical data and models [126, 127]. McClanahan et al. [126, 127] sought to identify reefs that were likely to be resilient and which also had moderate to high diversity and low to moderate exposure to high temperatures and other factors associated with climate change. They found some potential refugia within the West Indian Ocean but acknowledged it was difficult to clearly identify locations that would meet all the necessary criteria. Berkelmans [133] examined the history of bleaching at several reefs on the Great Barrier Reef (Australia) and suggested that corals on some of the reefs had become acclimatized to high seawater temperature, perhaps through zooxanthellae shuffling [134–136] or selection of more resistant holobionts, leading to an increase in bleaching thresholds.

It only makes sense to control local stressors to increase the chances that reefs can withstand the onslaught of global climate change. Different human-related stressors differentially affect processes like coral growth, recruitment, mortality, and competition with macroalgae, and therefore, possible responses to and recovery after thermal stress or other disturbances. Consequently, local management priorities could change given specific, local conditions [125, 130]. Wooldridge and Done [137] showed that improving water quality at Great Barrier Reef sites, specifically reducing excess nutrients, could effectively increase the upper thermal threshold for coral bleaching—providing a concrete example of how control of local stressors could increase reef resistance. Carilli et al. [138] examined cores of *Montastraea faveolata* from four sites off Belize, and found that the 1998 bleaching event reduced extension (growth) rates at all locations. The growth rates of corals from sites stressed by sedimentation, nutrients, high human population, and fishing pressure had not recovered eight years later, but growth rates of corals from less stressed sites were back to prebleaching rates in three years.

Entire reef zones could respond differently to management actions. Mumby and Hastings [139] used a model based on empirical data to explore the consequences of increased grazing by parrotfish and found that the higher grazing pressure would lead to greater coral recovery on deeper zones (7–15 m) than on shallow zones (3–6 m deep). Although the increase in grazing was higher in the shallower reefs, the effects on coral were negligible because grazing intensity was already high enough to move the modeled reefs towards a coral rather than a macroalgal state.

*5.1. Marine Reserves: One of the Most Promising Tools.* Establishment of marine protected areas (MPAs), specifically marine reserves, is one of the most promising tools for reef conservation [140]. Marine reserves are defined here as “no take zones” where fishing and most or all other extractive activities are prohibited. Marine reserves can be very effective in reversing the effects of overfishing (e.g., [141]), but it is not clear if reefs within marine reserves would be better

able to cope with the disturbances associated with climate change. Although we might intuitively think that reefs within marine reserves would be more resistant to disturbance or resilient after disturbance, there is much uncertainty and little evidence to date. Establishment of marine reserves often leads to an increase in formerly harvested species and could result in increases in coral cover if the intensity of grazing increases, allowing more coral recruitment [142]. In an experimental study that confirms the role of herbivory in reef resilience, Hughes et al. [143] used exclusion cages to manipulate the density of herbivorous fishes on reef areas that bleached in 1998. They found that coral cover increased in control areas but not in caged areas where macroalgae increased.

McCook et al. [144] point out that the potential benefits for reef-building corals are even more important than those documented for fishes, because the whole ecosystem depends on these corals. The marine reserves they examined on the Great Barrier Reef had fewer outbreaks of the starfish *Acanthaster planci* and, consequently, higher coral cover. However, they acknowledge that our understanding of how reserves can benefit corals is still limited. Mumby and Harborne [145] found increased coral cover within reserves in the Bahamas attributable to higher grazing by parrotfishes. Kramer and Heck [146] compared herbivorous fishes, coral cover, and species richness between small marine reserves (called Special Protected Areas, or SPAs) and nearby unprotected areas in the Florida Keys Marine Sanctuary. Outside the reserves, they found higher coral cover and number of coral species and a lower abundance of the larger herbivorous fish species. However, they did not examine trends over time in these parameters from the establishment of the SPAs several years before their study began, and no data are available for initial coral cover. No difference in coral or macroalgal cover was detected after 10 years of protection (no-take) at Glover's Reef, Belize [147]. It is not surprising that some papers have reported no difference for reefs inside and outside MPAs, given that these studies were not restricted to areas that were marine reserves with effective enforcement (see [148]).

Some studies have shown significant coral declines even within no-take zones, attributable to bleaching [149]. The 2005 bleaching episode in the Caribbean, which was at least partly associated with climate change [40], was followed by a disease outbreak which led to substantial losses in coral cover within and outside of a marine protected area [87].

In the Philippines, Raymundo et al. [150] found lower coral disease prevalence inside MPAs (no-take) with more diverse reef-fish communities than in unprotected areas. The density of coral-feeding butterflyfishes (Chaetodontidae) was significantly related to the prevalence of disease for sites with  $\geq 50\%$  coral cover. They hypothesized that these fishes are vectors of disease and more abundant outside reserves because fishing removes their predators. This would not necessarily be true in the Caribbean, where there are fewer Chaetodontid species feeding directly on corals and coral cover is typically less than 50%.

Large declines in coral cover from bleaching, sedimentation, and Crown-of-Thorns starfish in both marine reserves

and unprotected areas in Papua New Guinea resulted in a surprising decrease in abundance of over 75% of reef fish species including many that are not obligate associates of living coral [151]. Species that depended on living coral for juvenile recruitment were the most affected. This study showed a close link between fish biodiversity and the condition of the coral habitat.

In general, Caribbean coral reefs have not only lost coral cover but have become structurally less complex over the last several decades primarily because of coral diseases and hurricanes [152]. Further research is needed on how reef structure is related to biodiversity. Preliminary studies of reefs in three marine parks (Bonaire, Puerto Rico, and St. Vincent and the Grenadines) revealed that overall species richness (including not only corals, but also fish and many other groups) was highest on reefs with the highest topographical (structural) complexity at Bonaire and Puerto Rico [153]. Coral cover and complexity tended to be correlated, but highest coral species richness was not always associated with the highest topographical complexity.

McClanahan et al. [126] noted a possible surprising disadvantage to the creation of marine reserves in the West Indian Ocean, the promotion of faster-growing but more bleaching-susceptible coral species. In this case, a management strategy could lead to differential coral mortality. However, it is not clear that such protected areas (fisheries closures) would lead to more coral species that are more susceptible to thermal stress in other geographic areas. Bleaching susceptibility among Caribbean corals is not always quantifiable or consistent.

Models can help to identify the best locations for establishing MPAs or a network of MPAs to provide protection to reefs from climate change. For example, Mumby et al. [58] used a model to suggest placement of protected areas where thermal stress has been relatively low. They note that integrating connectivity into the design of marine reserves is challenging partly because of the "bewildering number of connections within the system." Ideally, MPAs would be a source of larvae to replenish degraded, unprotected areas. Baskett et al. [125] used models to show that corals on reefs linked to reefs with lower seawater temperatures, and less thermal stress, could more effectively withstand climate change. However, reefs are subject to many stressors and it is unlikely that they can be protected from all aspects of climate change. In addition, hurricanes, expected to increase in frequency, can actually benefit reefs by lowering seawater temperatures. In 2005, reefs in Florida suffered more physical damage from storms than those in the USVI and Puerto Rico, but they did not experience such severe bleaching or subsequent disease outbreaks [87, 154].

In designing reserves and networks of reserves, it is important to identify sinks and sources of marine larvae ([155, 156]) and to consider the entire, integrated seascape of habitats, particularly mangroves, seagrass beds, and coral reefs [157]. However, even the best-designed networks of marine protected areas could be ineffective if global warming changes the characteristics of connectivity [158]. Ideally, connectivity should be included in the design of these networks.

## 6. Connectivity: A Prerequisite for Resilience

Recovery of degraded coral reefs depends to a large extent on connectivity with sources of larvae of corals, fish, and other reef organisms and on their successful settlement and growth ([159, 160]). Climate change is likely to change existing connectivity dynamics [158]. Much more information is needed on localized current patterns and duration of larval viability. We also need to understand how climate change will affect coral reefs, mangroves, and seagrass beds, and the biological and physical connections among these ecosystems. They are linked because of the movement of fishes at all life stages and the transport of nutrients ([157, 160, 161]). Seagrass beds and mangroves are critical nurseries, providing food and shelter, for larvae of fish and invertebrates that later move to coral reefs. Reefs buffer shoreward seagrass beds and mangroves from destructive ocean waves, and seagrass beds and mangroves reduce harmful runoff of freshwater and sediments from land that could affect reefs.

Recovery of reefs requires larvae to replenish depleted populations of corals, fish, and other organisms. Complex water current patterns combine with the life histories of key organisms to determine if larvae will be available to help reefs recover. Global warming could affect current patterns with consequences for larval transport; higher water temperatures could shorten pelagic fish larval duration effectively reducing the spatial scale of connectivity [158]. Models are not only helpful but essential in showing connections among coral reefs (inside and outside marine reserves) as well as among reefs, seagrass beds, and mangroves. In some locations, these ecosystems are closely linked; if reefs collapse, seagrass beds and mangroves could also collapse. Reefs that are closely connected to mangroves and seagrass beds might be more resilient, less vulnerable to climate change, than those that are not, or those that are remote [162]. For example, although more research is needed, it is possible that mangroves and seagrass beds would be a source of herbivorous fishes that would influence grazing pressure on reefs affected by bleaching, keeping algae in check while corals recover. Many fish depend on two or more of these habitats for daily movements to find shelter and food or at different stages of their development. In a study in Puerto Rico, the highest mean number of species and density for fishes in mangroves were found where the surrounding seascape (within 100 m of mangroves) was most heterogeneous and provided shelter and settlement sites—with high cover of seagrasses, proximity to coral reefs, and deeper water [157]. Because juveniles of many fish species use shallow seagrass, coral reef, and mangrove habitats, if one habitat declines, others might remain available [157, 163].

Mumby and Hastings [139] used models of Caribbean reefs to show that deeper reefs (7–15 m) near mangroves were better able to recover from intense storms than those that were not linked to mangroves because the mangroves supported a high abundance of parrotfish that reduced cover of macroalgae that compete with corals. Mangroves have suffered even greater degradation and destruction than coral reefs [164].

Reefs, mangroves, and seagrass beds will vary in their response to individual components of climate change—for example, in general mangroves are less likely to be affected by GCC, but rising sea level has been identified as possibly the greatest threat to these systems (e.g., [165]). In contrast, rising sea level could benefit some reef zones and would probably not affect seagrass beds significantly. Growth of seagrasses (and other noncalcifying organisms) could actually increase [166]. All of these tropical ecosystems have already been affected greatly by human activities [167].

## 7. Biodiversity and Resilience

We currently lack some very basic information, particularly on the biodiversity of coral reefs. It is likely that over 90% of the estimated number of coral reef species in the world (estimates range from one to two million) have not even been discovered yet [169–171]. We are no doubt losing species that we have not even identified. The 2010 Census of Marine Life [171] reports discovery of at least 6,000 new species, some associated with coral reefs. As Knowlton [3] points out, we know very little about how human activities affect coral reef biodiversity. For many species we even lack sufficient information on ecological functions and life histories, and on distribution of their habitats [15, 167]. We also do not fully understand how species richness affects ecosystem processes and how biodiversity affects ecosystem function and services [5, 7, 132, 172].

Willis and Bhagwat [173] examined models that predict how climate change will affect terrestrial biodiversity. They showed that more refined models that considered local topography and what they termed “microclimate buffering” predicted different (usually lower) rates of extinction for many systems. It is likely that their cautionary comments would apply to models for coral reefs and climate change as well.

Further research on how different reef species will respond to global stressors (combined with local ones) is of the highest priority [65, 158]. Little is known of how different species are reacting to the various stressors and how they will react to the increasing effects of climate change [27, 174]. Coral species vary in their susceptibility to bleaching [175, 176], (Figure 3).

We need to have a better understanding of the molecular and physiological mechanisms that determine the tolerance of coral hosts and zooxanthellae to different stressors [99, 177]. Although some corals may be able to adapt to higher seawater temperatures (see [178, 179]), we do not know how much or how quickly. Recent studies of corals in the shallow lagoon in Ofu Island (American Samoa) show that corals that were exposed to more variable temperatures were more tolerant to high temperatures under experimental conditions [81]. Likewise, the high diversity and abundance of corals found in shallow mangrove areas in St. John, US Virgin Islands, may persist in spite of high temperatures because of a combination of acclimatization to variable temperatures and shading by mangrove trees [168]. Van Woesik et al. [180] observed that corals growing in more



FIGURE 3: A bleached colony of *Diploria labyrinthiformis*, near unbleached colonies of *Colpophyllia natans*, *Porites porites*, *Porites astreoides*, and *Millepora alcicornis*, St. John, US Virgin Islands (from [168]).

turbid waters in Palau bleached less in 2010 than those in clearer, offshore waters, although they experienced the highest temperatures. In Southeast Asia, reefs that bleached in 1998 and had higher temperature variability bleached less in 2010, showing the role that thermal history can play [129]. Grotto et al. [181] found that experimentally bleached colonies of *Montipora capitata* were able to replenish their energy reserves and biomass by increasing their feeding rates on zooplankton, while colonies of *Porites compressa* and *Porites lobata* were not. They suggest that corals with the ability to increase heterotrophy will have a better chance to survive prolonged bleaching events. Experiments involving feeding of two species of corals under elevated temperatures indicated that heterotrophy decreased their susceptibility to bleaching [182].

Even different populations within the same coral species may react differently to climate change [67, 174, 183]. Further information is needed on the ability of different corals within a population to resist stressors and/or recover following stress. Vollmer and Kline [184] showed that 3 out of 69 colonies of *Acropora cervicornis* were naturally resistant to white band disease suggesting that different genotypes might have more resistance to disease—a promising area for future research. Coral colonies with more photoprotective fluorescent pigments will be less susceptible to bleaching than others of the same or different species [185]. If major reef-builders (here defined as corals that reach a larger size and contribute more to the overall framework of reefs) adapt but other coral species do not, the coral diversity would decrease but the reef could persist. The diversity of the fish and other organisms also might decrease. For corals, fish, and other reef organisms, rates of recovery could differ depending on the type of disturbance, notably those that affect coral cover and those that reduce structural complexity. Coral species richness and architectural complexity will not always be correlated because some species, such as *A. palmata* and *M. annularis* in the Caribbean, contribute far more to the complexity than others and can be dominant. The loss of some coral species will be more disruptive than the loss

of others. The declines in *Acropora palmata* from disease and hurricanes in the 1980s and 1990s changed the shallow seascape in the Caribbean. The full ramifications of losing this species, (for which there is no ecological equivalent), including the effects on fish and other reef organisms, were not well documented.

We focus on corals as the architects of the reef, but we need more information on how fish and other reef organisms will be affected by climate change, and we need to learn more about the functional role of different organisms and their ecological equivalency [36, 65, 186–188]. Many studies of resilience emphasize the role of herbivory in reef recovery following disturbances. It is becoming clear that different herbivorous fish species (e.g., Scaridae and Acanthuridae) can vary in their ability to control algal cover and open up new space for coral recruitment [189, 190]. We need to know which fish species are indicators of reef regeneration and which other groups besides herbivores can play a role in making reefs more resilient [65].

Several studies show that bleaching, particularly when followed by mortality and/or subsequent loss of reef structure when corals collapse, can lead to changes in fish assemblages [188, 191–193]. At One Tree Island, Great Barrier Reef, major bleaching led to a decrease in fish recruitment [194]. Loss of corals, both cover and physical structure, can lead to declines in abundance and/or diversity of fish [151, 193]. Extensive mortality following the 1998 bleaching of Chagos Reefs (Indian Ocean) led to severe erosion, with decreases in abundance and diversity of fish that depend on corals [191].

Few studies of the effects of elevated CO<sub>2</sub> on coral reef organisms are available [195]. De'ath et al. [196] examined colonies of *Porites* from 69 reefs along the Great Barrier Reef and detected declines in linear growth (13.3%) and calcification (14.2%) since 1990. Bak et al. [197] suggested that a decrease in *Acropora palmata* growth rates in Curacao over 30 years might be related to a decrease in pH. Both growth and recruitment of crustose coralline algae, important for coral recruitment and for cementing reef framework, were reduced by elevated seawater carbon dioxide concentrations in experimental mesocosms [69]. In other experiments in which carbon dioxide levels were increased, the calcification rates of crustose coralline algae were more sensitive than those of corals [198].

Corals and other reef species also vary in their response to acidification [46]. Key species and functional groups (e.g., urchin and fish grazers, bioeroding sponges) could be affected very differently by changes in seawater chemistry, thereby affecting critical reef processes. Some noncalcifying organisms could actually benefit. For example, growth of seagrasses could increase [166]. Kleypas and Yates [195] also point out that algae that bore into coral skeletons dissolve more calcium carbonate at higher CO<sub>2</sub> concentrations [199], possibly tipping the balance from reef accretion to reef dissolution. The threshold above which reefs shift from net accretion to net dissolution will vary substantially on different reefs, reflecting differences in community composition, geographic location, mixing rates of water masses, and other factors [195].

Biodiversity resides not only within coral reefs at the scale of individual reefs, but also within individual coral colonies that contain zooxanthellae as well as a diverse array of other organisms such as bacteria, fungi, and Archaea ([200–202]). There is limited knowledge not only about zooxanthellae but also about these other members of the diverse microbial communities within corals themselves and the degree to which they might be able to adapt to ocean acidification (e.g., [70, 200, 201]). The diversity of these different microorganisms, which interact in complex ways with the coral host [201], could confer resilience to some coral species.

Corals may be able to acclimatize or eventually adapt to warmer temperatures because of the diversity of their symbiotic dinoflagellates (zooxanthellae) and a variety of physiological mechanisms [136, 203–206]. Some symbionts appear to confer resistance to thermal stress [207]. In addition, experiments have shown that some bleached corals can acquire new zooxanthellae from the water column to replace suboptimal ones [178, 179]. Baird et al. [208] argue that research should focus on the holobiont—not just on the zooxanthellae but also on the coral host and its potential to adapt to increasing temperatures (see also [47]). Coral species with the same symbiotic microalgae clades respond differently to thermal stress. Sammarco and Strychar [209] point out our lack of understanding of how corals and their symbionts respond to stressors other than increasing seawater temperatures. Van Oppen and Gates [99] note that hybridization of coral species, while evidently rare, could, over evolutionary time scales, make corals more capable of responding to environmental changes “providing the potential for adaptive evolution.”

It is not just different reef species that will respond differently. Reef zones may respond dissimilarly to the variety of stressors. Although disease appears to have been the cause of much of the mortality of *Acropora palmata* (typically less than 5 m deep) and *A. cervicornis* in the late 1970s and 1980s [117, 210], and of the die-off of the important sea urchin grazer *Diadema antillarum* [211], at least some of the shallow reef zones with these coral species have not been carpeted with macroscopic algae that can radically reduce recruitment [212, 213]. Perhaps there has not been a shift to macroalgal dominance in some of these locations because grazing is more intense in shallow water or heavy wave action periodically removes the macroalgae from the reef.

Deep reefs, farther from the influence of humans, have been considered as possible refugia for organisms that could become sources of larvae that could replenish degraded reefs closer to shore. However, some deep reefs have had extensive coral mortality and increases in algal cover from undetermined causes [214–216]. The severe mass bleaching in 1997–1998 affected corals at depths over 30 m [217]. In addition, although few studies exist, corals growing in deeper water may not be as fecund as those in shallower water [218], and not all coral species inhabit deep reefs.

## 8. Conclusion

At a conference in 1993, participants concluded that the most serious threats to reefs were associated with human activities: shoreline development, overfishing, degraded water quality from sediments and sewage [219]. Then, with severe bleaching episodes beginning in 1998, the focus shifted more to global stressors and climate change [74]. In some ways we are back to where we started with an emphasis on managing human activities at a local level while still hoping that international efforts to control greenhouse emissions will become more effective [4, 23, 38, 142, 220, 221]. Managing local stressors is far more feasible than trying to control global stressors, but even this has not proven to be easy. In spite of all of the uncertainties, it only makes sense to move forward with controlling those stressors that we can control [23, 71]. Where it is feasible to design networks of marine reserves, every effort should be made to protect areas that are likely to survive future climate-driven changes, although this is very challenging [23].

Coral reefs are at a crossroads, and the situation is urgent [23, 71]. Humans are clearly reducing the resilience of reefs [21]. Over 15 years ago, Walker [186] noted “the loss of species and ecosystems is proceeding faster than research aimed at identifying priorities.” Soon after, Vitousek et al. [10] stated “we can accelerate our efforts to understand Earth’s ecosystems and how they interact with the numerous components of human-caused global change.”

The biodiversity of these complex ecosystems, one of their defining characteristics, offers some hope that they will have a future. Conserving biodiversity increases the chance that marine ecosystems, including reefs, can adapt or recover after disturbances [7]. A loss of biodiversity could reduce resilience [6, 132], but we still have most of the “pieces.” Carpenter et al. [122] highlighted an elevated risk of extinction for reef corals in just 10 years (1998 to 2008) from local and global stressors. However, to date, the observed changes on coral reefs reflect shifts in relative abundance of corals rather than losses of species. To date, no coral species has become extinct throughout its range [50]. However, many are at risk [122], and Knowlton [3] noted that some of the most important framework-building corals, on which so many other species depend, have declined the most. In addition, some models predict that because of a delayed response, even species that are the best competitors can become extinct long after habitat fragmentation and degradation [222]. Hoegh-Guldberg [71] notes little evidence that corals will be able to adapt to all of the changes and concludes that reefs could become rare globally by the middle of this century.

There are some encouraging signs. Even threatened species, such as the Caribbean acroporids, that declined significantly from disease and hurricanes, have persisted and are increasing in some locations [142]. Likewise, the herbivorous sea urchin *Diadema antillarum* is becoming more abundant in some places in the Caribbean [223]. Corals in some areas show evidence of acclimatizing to warmer sea water temperatures [129, 174]. Some reefs have recovered well after major bleaching episodes. Although there have been few success stories [123], and restoration efforts will at best

have very localized benefits, the future does not look entirely bleak.

The high biodiversity of coral reefs means that a high diversity of responses to local and global stressors (including increasing temperatures) is anticipated. Coral species and other reef organisms will differ in their ability to deal with local stresses and the different aspects of climate change (e.g., [224]). Responses will vary even within populations [174]. Some coral species that are more susceptible to bleaching may recover faster and evolve faster than less vulnerable species [46]. In addition, the effects of local and global stressors will vary substantially within different regions [11, 137, 138, 225], and on different reefs and even within different reef zones—not all will suffer equally from high temps, ocean acidification, and increasingly powerful storms. To add to the complexity, many of the possible changes to environmental factors, such as ocean currents, are unpredictable [158].

None of us can predict what reefs will look like in 100 years, or even two decades from now. Ocean acidification and temperature increases are occurring along with changes in other global and local stressors [4, 11, 46]. Changes in climate can push already stressed ecosystems beyond their limits for recovery, but many reefs could have the ability to resist and/or recover after disturbance. Walther et al. [11] point out that linking oceanic and atmospheric processes to the responses of communities and populations is complex. The fossil record provides evidence that at least some coral reefs may be able to persist in spite of global climate change [46].

Additional research and long-term monitoring are essential to improve our predictions of the future for coral reefs and to guide management of reefs and associated ecosystems. Models can be helpful, partly by illustrating areas we need to know more about, or by indicating the best placement for marine reserves. However, by necessity, models are oversimplified. Recent models have not adequately taken coral diseases into consideration, and disease outbreaks not only have already caused severe and widespread mortality of corals but also may well increase in the future.

Many have noted the urgent need for international cooperation to reduce atmospheric concentrations of greenhouse gases [23, 226]. Given the challenges of curbing emissions on a global scale, local efforts to reduce the more tractable stresses to coral reefs and to protect marine areas that show signs of greater resistance and resilience should be emphasized [23]. Rau et al. [227] suggest that more proactive options should be considered—for example, selective breeding of more resilient species, artificial shading of some portions of reefs during thermal stress, and artificial upwelling.

There is no simple answer to the question of how climate change will affect tropical ecosystems, and the connections among them, because of the complexity and unpredictability of the stressors associated with climate change. Reefs that are linked to mangroves and seagrass beds might be more resilient than those that are not or those that are remote. Connectivity to sources of larvae is the basis for resilience. High levels of herbivory, high structural complexity, and presence of fast-growing, resistant corals will contribute to reef resilience.

The remarkable complexity of coral reefs, one of their essential core characteristics, makes it both more difficult to predict their future and more likely that they will have a future. Managers may be able to increase the chances that reefs will persist but the greatest hope may reside in the reefs themselves in the form of biodiversity at all scales.

Over the spatial scale from coral colonies, with their microbial communities, to coral species to reefs across the globe, essentially from genetic diversity within populations to the diversity of ecosystems across the seascape, the different response to the array of stressors makes it likely that at least some reefs will prove to be resilient and persist in spite of local and global pressures. Although there is a great deal of uncertainty as to how the environment will change, there is certainty that large changes will occur.

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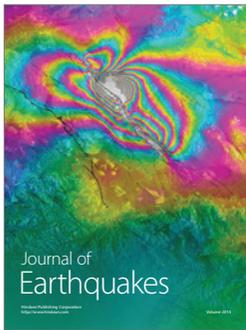
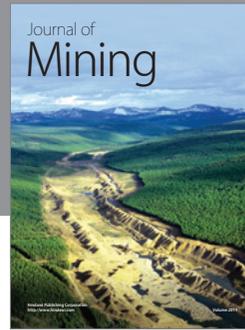
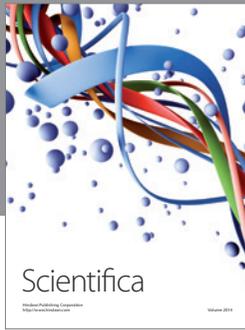
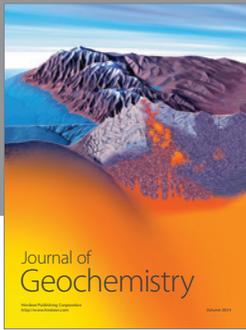
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