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Chapter 5

c0005 # Limited Functional Redundancy and Lack of Resilience in Coral Reefs to Human Stressors

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[AU3] s0010 ## INTRODUCTION

p0010 Coral reefs are some of the most diverse, socioeconomically important, and threatened ecosystems in the world. Worldwide there are $\sim$835 species of reef-building corals (Veron, 1995), which in turn provide habitats for some 1−9 million other species (Reaka-Kudla, 1997). Unfortunately, a combination of co-occurring and interacting human stressors is leading to massive losses of coral reefs worldwide (Hughes, 1994; Knowlton, 2001; Gardner et al., 2003; [AU4] Hughes et al., 2003a; Pandolfi et al., 2003, 2005; Bruno et al. 2007a; Wilkinson, 2008; Burrows et al., 2011). This ongoing decline of coral reefs may not only lead to the loss of species but also impair the capacity of a "multi-resource" ecosystem to deliver goods and services critical for social and economic development in many tropical countries (Moberg et al., 1999; [AU5] Brander et al., 2007). Some 655 million people live within 100 km of coral [AU6] reefs (Donner et al., 2007) and many rely on reefs for the delivery of food, jobs, and revenue (Costanza et al., 1997; Newton et al., 2007; Burke et al., 2011; Graham et al., 2011; Mora et al., 2013; Teh et al., 2013). The modern transformation of coral reefs is worrisome because changes could become difficult (or impossible) and expensive to revert (Knowlton, 2001; Scheffer [AU7] et al., 2001, 2003; Mumby et al., 2007b; Rogers, 2013).

p0015 The role of biodiversity on ecosystem resilience has been at the core of much ecological research (Chapin et al., 1998, 2000; Sala et al., 2000; Loreau et al., 2001; Loreau, 2004; Hooper et al., 2005). Resilience is used here as the capacity of a system to return to its original functionality after being disturbed; the constituent species at the recovery state may or may not be the same.

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Experimental and theoretical studies have demonstrated that the more species in a system, the more resilient the system can be to disturbances (e.g., Chapin et al., 2000; McCann, 2000, 2007; Loreau et al., 2001). This may occur as numerous species are likely to play similar functional roles but have different sensitivities to the stressor; thus the functional role of a lost species could be compensated by that of another (Loreau, 1998; McCann, 2000; Loreau et al., 2001; Bellwood et al., 2004). In practice however, coral reefs worldwide, despite their great diversity, are increasingly failing to recover after human disturbances (Nyström et al., 2000; Hughes et al., 2003a; Bellwood et al., 2004). Ecologists have shifted their views from seeing coral reefs as highly diverse, temporally stable, and robust, instead seeing them as fragile and globally stressed (Mumby et al., 2008). The ability of coral reefs to recover and return to pristine states can no longer be taken for granted (Connell, 1997; Aronson et al., 2004). The standing question is then: why are coral reefs not resilient to stressors despite hosting a great diversity of species? Here I review the possibility that coral reefs, despite being diverse, are not as functionally redundant as one may expect.

[AU8]

s0015 DATA QUALITY

p0020 The ability to predict changes in coral reefs (e.g., an ecosystem's response and recovery to a disturbance) depends on the availability of data, which in the case of coral reefs is limited for various reasons.

p0025 First is the lack of historical baselines; without knowing what pristine coral reefs look like, it is hard to assess the relative change of coral reefs in response to a stressor or whether recovery has truly occurred (Knowlton et al., 2008). This situation is evidenced by a handful of opportunistic studies that have been able to reconstruct the "expected" status of pristine reefs (Jackson et al., 2001; Pandolfi et al., 2003, 2005, 2006; Jackson, 2008; McClenachan et al., 2008, Ward-Paige et al., 2010). In one such study, McClenachan et al. (2008) documented that the energy required to sustain monk seals in Caribbean reefs should require biomass levels of $732-1018$ g m^2 of reef, which is three to five times more than those found nowadays on typical Caribbean coral reefs and more than twice that measured on the most pristine reefs in the world.

[AU9]

[AU10]
[AU11]

p0030 Second, for the most part we lack data at the species level. Inherent in the concept of resilience is the idea that the functional role of one species could be replaced by another, and as such the basic functionality of the ecosystem could be sustained in spite of considerable changes in community structure. In coral reefs, the most available long-term source of data is live coral cover of the overall assemblage, which unfortunately has a high risk of failing to depict changes in community composition (Gardner et al., 2003) and even of delivering a false sense of security, as it may obscure negative change in community structure. For instance, variability in the sensitivity of coral reef species to human stressors is leading to changes in community structure from

branching (highly complex) to massive (not so complex) coral species, which in turn is reducing habitat complexity and the diversity of associated fauna. This change in community structure is occurring in spite of a high live coral cover, which is now dominated by massive less complex corals (e.g., Darling et al., 2010, 2013).

p0035   Third, until very recently there was a strong geographical bias for the long-term study of coral reefs in the Caribbean, which has raised concerns over the

[**AU12**] transferability of theory to other regions (Roff et al., 2012). Roff et al. (2012) elucidated, for instance, that the Caribbean may have lower resilience as macroalgae can growth faster there, the region is prone to iron enrichment from Aeolian dust, it has almost completely lost the Acroporid species, and in addition it has a low abundance of and lacks entire groups of herbivore fishes. While these differences are real, and reefs on other parts of the world do indeed lack long-track research, emerging studies show that coral reefs worldwide are depicting similar declining trends (Connell, 1997; Bruno et al., 2007a).

p0040   Fourth, the patchiness of available data often leads to consolidating data from different places and times (the so-called meta-analyses), often giving rise to inconsistences from one compilation to the next (Hughes et al., 2010). Hughes et al. (2010) noted, for instance, how different meta-analyzes of trends in coral cover for the same region differ by up to 17% in absolute terms for the same years. Due to their integrative nature, meta-analyses often rely on simple metrics such as coral cover, which as noted earlier can also fail to identify underlying community changes (Gardner et al., 2003).

s0020 PATTERN OF CHANGE

p0045 In spite of data limitations, there is large agreement that the world's coral reefs are in decline, moving from a dominance by live corals to a dominance by macroalgae and at times invertebrates such as bivalves, sponges, tunicates, and zoanthids (Schutte et al.,; Hughes, 1994; Gardner et al., 2003; Hughes et al., 2003a; Pandolfi et al., 2003, 2005; Bellwood et al., 2004; Cote et al., 2005; Bruno et al., 2007a, Wilkinson, 2008; Norström et al., 2009; Burrows et al., 2011). This pattern has been coined as the phrases "phase shifts" (Done, 1992; Hughes, 1994), "alternative states" (Knowlton, 1992; Bellwood et al., 2004), "the slippery slope to slime" (Pandolfi et al., 2005), "trophic cascades" (Dulvy et al., 2004; Mumby et al., 2006, 2007a), and "the straw that broke the camel's back" (Knowlton, 2001) (note: Dudgeon et al. (2010) cautions on the need to differentiate terms such as phase shifts and stable states for describing different patterns of ongoing coral reef transformations).

p0050   Perhaps the best documented example of coral reef "transformation" has been reported for coral reefs in the Caribbean. By the end of 1970s, live coral cover in this region was commonly above 75%, with great dominance by highly 3-D complex Acroporid species. During the 1980s, a mixture of

hurricane Allen, lime coral disease, extreme overfishing of herbivorous fishes, and an unfortunate massive die-off of the urchin grazer *Diadema antillarum* reduced coral cover to just ∼5% by the 1990s, and it has remained so ever since (Schutte et al.,; Hughes, 1994; Nyström et al., 2000; Gardner et al., 2003; Mumby et al., 2007b). The mortality of corals has been followed by a demographic dominance of fast-growing algae (Roff et al., 2012) but see Bruno et al. (2009), reductions in coral reef complexity (Alvarez-Filip et al., 2009) and in the diversity and abundance of associated fishes (Paddack et al., 2009). Despite data limitations, similar patterns of coral reef transformation have been documented in other regions (Connell, 1997; Bruno et al., 2007a; Baker et al., 2008).

p0055   With the exception of a few reefs (e.g., Kaneohe Bay–Hawaii (Hunter et al.,
[AU13]   1995)), there have been very few documented examples of significant phase-shift reversal to coral dominance (Nyström et al., 2000; Bellwood et al., 2004). Significant recovery from bleaching events, not necessarily coral mortality or algae domination, has been documented in the Indian Ocean but not on western Atlantic reefs (Baker et al., 2008; Sheppard et al., 2008). No clear trends of recovery are apparent in the eastern Pacific, the central–southern–western Pacific or the Arabian Gulf, where some reefs are recovering while others are not (Connell, 1997; Baker et al., 2008; Roff et al., 2012). These regional differences are commonly associated with spatial variations in the diversity of ecosystems and thus resilience (Bellwood et al., 2004; Roff et al., 2012), although spatial variations in the intensity of human stressors cannot be completely ruled out (i.e., even though resilience or lack thereof may be similar, reefs around the world are located at different stages along the gradients of human disturbance). Reefs in the Caribbean, for instance, have been exposed to a longer history of insults (Jackson, 1997) and are considerably more populated than other reefs around the world (Mora et al., 2011a), which may explain their greater degradation and failure to recover.

p0060   The magnitude of coral reef transformation is clearly indicated by the fact that ∼19% of coral reefs globally are effectively lost, 15% are critically impacted by humans and likely to be lost within 10–20 years (Wilkinson, 2008; Burke et al., 2011), and the remaining reefs distant from direct human stress will become increasingly vulnerable to global changes in temperature (Mora et al., 2013; Van Hooidonk et al., 2013; van Hooidonk et al., 2013) and acidification (Mora et al., 2013; Ricke et al., 2013). Very few reefs in the world, if any, are currently considered to be in a pristine state (Burke et al., 2011), and some 32.8% of coral reef species worldwide are currently facing elevated risk of extinction (Carpenter et al., 2008).

s0025 DRIVERS OF CHANGE

p0065 The causes of coral reef loss are diverse and intricate. First, it needs to be recognized that human activities have been detrimental to coral reefs over

millennia (e.g., several mega-fauna have been already completely extirpated and many ongoing declines may have started before the onset of scientific research (Jackson, 1997; Jackson et al., 2001; Pandolfi et al., 2003)). Historical reconstructions, however, have illustrated the accelerated impact of human activities over the past 50 years (Jackson et al., 2001; Pandolfi et al., 2003; Wilkinson, 2008). Modern human disturbances (not in order of importance to avoid debate over their relative effect and interactive nature) include unprecedented extreme climates, overfishing, pollution, invasive species, habitat loss, destabilized ecological interactions (e.g., trophic cascades and coral−algal and coral−pathogen interactions), increasing spread and susceptibility to diseases, and impaired metapopulation dynamics (Jackson et al., 2001, 2005; Knowlton, 2001; Harvell et al., 2002; Aronson et al., 2003; Bruno et al., 2003, 2007b; Hughes et al., 2003a,b; Bellwood et al., 2004; Pandolfi et al., 2005; Hoegh-Guldberg et al., 2007; Jackson, 2008; Knowlton et al., 2008; Mora, 2008, 2009; Wilkinson, 2008; Sale, 2011; Ateweberhan et al., 2013). These disturbances vary from local to global scales (Knowlton, 2001; Knowlton et al., 2008, Mora, 2008; Mora et al., 2011a), in their effects from additive to syn-

[AU14] ergistic (Knowlton, 2001; Darling et al., 2008, 2010; Knowlton et al., 2008; Ateweberhan et al., 2013), and from having direct to indirect effects over

[AU15] species (Hughes et al., 2003a,b; Bellwood et al., 2004; Cote et al., 2010; Ateweberhan et al., 2013). Stressors also trigger ecological feedbacks, as weakening of corals increases sensitivity to coral diseases, facilitates the breakdown of reef framework by bioeroders, and leads to the loss of critical habitats and food for associated biota.

s0030 ARE CORAL REEFS FUNCTIONALLY REDUNDANT?

p0070 It is intuitive that in a large pool of species, there should be species with redundant functional roles. However, functional redundancy is often questioned, as this could drive species to extinction mediated by competition (Loreau, 2004). One possibility to avoid such a scenario is via spatial and/or temporal segregation, or via niche specialization. For coral reefs, the idea of functional redundancy is supported by the fact that the number of functional

[AU16] groups often saturates as the number of species increases (Halpern et al., 2008; Mora et al., 2011a). These studies, however, are based on gross classifications of functional groups that can overestimate the extent of functional redundancy. For instance, deeper exploration of morphological (Price et al., 2011) and

[AU17] dietary (Robertson et al., 1986) characteristics of species generally classified as herbivorous has revealed the existence of considerable differences among species. Such small differences may result from niche specialization and have nontrivial effects on coral reefs. For instance, variations in the palatability of algae (e.g., Littler et al., 1983; Ledlie et al., 2007) suggest that a broad portfolio of "herbivores" is required to keep algae cover at check. If specialization is dominant on coral reefs, then redundancy is not as extensive as

originally thought, as different species are likely to have different functional roles.

p0075   If specialization is dominant and functional redundancy is limited, this could lead to each species adding rather than subtracting (due to the cost of ecological interactions) to the functioning (productivity) of ecosystems. This should cause exponential/concave-up biodiversity—ecosystem functioning relationships, which have been recently documented for coral reef fishes (Mora et al., 2011a). Concave-up biodiversity—ecosystem functioning relationships are supported by experimental studies showing that the effect of biodiversity on ecosystem functioning increases over time as species "become more functionally unique through time" (Reich et al., 2012). Limited redundancy may also occur if the maintenance of a given function requires the same functional groups but represented by different species at different times and places, and for different environmental conditions (Peterson et al., 1998; Isbell et al., 2011). In other words, apparently redundant species may actually operate at different scales and conditions, supporting the idea of limited functional redundancy and highlighting the high vulnerability of ecosystems to the loss of even a few species.

p0080   A saturating relationship between richness and functional diversity is also deceiving of functional redundancy, as it fails to indicate the distribution of species within functional groups. For instance, exploration of the frequency distribution of species per functional group has revealed strong right-skew frequencies, with few functional groups having numerous species and most being constituted by a handful of and at times a single species (Bellwood et al., 2004). Indeed, key functional groups such as bioeroders in the Indo-Pacific are almost entirely represented by a single species (the giant humphead parrotfish, *Bolbometopon muricatum*), which given its large body size is unfortunately prone to extensive fishing and thus is missing on most reefs near human settlements (Bellwood et al., 2003). Likewise, branching corals in the Caribbean are solely represented by Acroporid species that have undergone extensive mortality by a combination of severe storms and diseases (Nyström et al., 2000; Roff et al., 2012; Rogers, 2013). Further, Mouillot et al. (2013) recently showed how even rare species often lack functional analogs and carry out some key vulnerable functions in ecosystems, suggesting that even the loss of rare species could have severe consequences for coral reef resilience (see also Jain et al., 2014). This pattern of limited redundancy may be common on coral reefs (Micheli et al., 2005).

[**AU18**]

p0085   Inherent in the idea that biodiversity confers higher resilience is also the idea that similar functional species will have differential sensitivity to stressors in order to ensure ecosystem recovery by the more resistant species (Elmqvist et al., 2003). However, high diversity may offer limited resilience, if all species within a functional group respond the same way to the same stressors, which may also be the case on coral reefs (Nyström et al., 2000, 2008; Bellwood et al., 2004). Fishing, for instance, can impose a similar detrimental impact

over most species of predators and herbivores on coral reefs (Nyström et al., 2000; Bellwood et al., 2004; Micheli et al., 2005). Likewise, warming and diseases appear to have similar deterring effects on the branching corals that provide most of the complexity to coral reefs (Darling et al., 2013; Rogers, 2013).

s0035 SOLUTIONS TO ENSURE RESILIENCE

p0090 Clearly, coral reefs are not as functionally redundant as would be expected from their great number of species. This can explain their reduced resilience to human impact and highlights the urgent need for effective conservation actions. Such actions are urgently needed, because the longer coral reefs move along this declining slippery slope, the harder it will be to reverse such movement, and the larger the risk that it cannot be reversed at all. Mumby et al. (2007b) documented, for instance, that reverting coral—algae phase shifts through the restoration of herbivore fishes would require a fourfold increase of herbivores at coral covers of ∼5% but only a twofold increase at coral covers of ∼30%. There are also chances that human stressors could be so extensive as to impose selective pressures, thus inducing genetic loss that will reduce environmental adaptability and increase chances of random genetic drift, the loss of important genes, and inbreeding depression—not to mention Allee effects of increasingly smaller populations. Human impacts pose real risks of irreversibility of phase shifts and even risk of extinction of coral reefs, which in turn could be detrimental to the welfare of millions of people whose livelihoods depend on coral reefs. This stresses the urgent call for effective conservation actions.

p0095 **Are there other solutions available?** There are many proposed solutions to reverse ongoing declines in biodiversity (Butchart et al., 2010), but for coral reefs they are ineffective as clearly demonstrated by the ongoing losses of such

[AU19] reefs (Mora et al., 2011b), and several reasons may explain this. One possibility is that the large scales over which coral reef populations operate, and the global pensiveness of human stressors and their feedback social loops, call for multinational strategies that are largely lacking (Rockstrom et al., 2009). One potential feedback is that stopping fishing could lead to an increasing demand for agriculture or livestock, which in turn could lead to excessive use of fertilizers and pesticides and land conversion, which in turn could impact coral reefs through runoff. Another explanation for the failure to revert biodiversity loss is that most solutions inherently try to restrict different human uses (e.g., by reductions in fishing, CO_2, development, etc.), often causing a disparity in the costs and benefits of solving problems (Nyström et al., 2000; Donner et al., 2007); these conditions cause considerable conflicts and resistance to proposed solutions (West et al., 2006; Mora et al., 2011b). Another explanation is the issue of selfishness. On one hand, if the problem is global and many countries are concerned, there is always a temptation to just get a free ride

(Nyström et al., 2000). On the other hand, for many countries it is beneficial to gain revenues at the expense of polluting the world (Nyström et al., 2000). Finally, it is possible that current conservation strategies have had a very narrow focus on proximal rather than ultimate causes of coral reef damage. Proximal drivers include overfishing, habitat loss, invasive species, the spread of diseases, climate change, pollution, sedimentation, and eutrophication, whereas the ultimate driver is an ever-growing and expanding human population. This narrow focus leads to adaptive strategies that will struggle in a perpetual effort to maintain or restore biodiversity (Mora et al., 2011b).

s0040 CONCLUDING REMARKS

p0100 The capacity of coral reefs to withstand human assaults can no longer be assumed. Over the next 50 years, it is projected that over 80% of countries with coral reefs will double their human populations (Mora et al., 2011a), not to mention that 1 billion to 2 billion people will be added to the total global population. Since virtually all factors associated with the ongoing decline of coral reefs have human origins, it is easy to predict that stressors on coral reefs will continue and likely exacerbate each other, and that in the next century we will likely witness massive transformation of coral reefs. At the same time, if the evidence suggests a linkage between stressors and people, one has to wonder if longer term, more permanent and perhaps cheaper strategies to mitigate stressors on coral reefs should also include humane solutions to avert population growth (e.g., empowering women, sex education, free or affordable family planning, revisiting subsidies that promote natality, and allowing educated choices on whether or when to have children by better divulgation on the different childbearing costs to the environment, climate, state, family, and individuals). Coral reefs have endured the force of time but are succumbing to that of humans. The ongoing decline of coral reefs despite increasing conservation efforts suggests that we need an urgent paradigm shift that puts the focus on the ultimate drivers of environmental damage rather than expecting that this ecosystem will be resilient to our stressors.

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Abstract:

Coral reefs worldwide are failing to cope with the challenges of increasing human pressures and are thus facing shifts from coral dominance to less desirable and less productive states. The incredible diversity of species in coral reefs will intuitively suggest that they will have a great functional redundancy and thus it will be easy for them to cope with human disturbances. But they do not. I suggest that the incredible diversity of species in coral reefs has actually led to a great degree of specialization, making almost every species unique and thus the entire ecosystem vulnerable to the loss of a few species. Coral reefs do not conform to the expectation that their great diversity will confer them with great resilience. Clearly, the capacity of this ecosystem to withstand human assaults can no longer be assumed and thus considerable management interventions are needed to afford this ecosystem some slack.

[**AU1**]

[**AU2**]