



OPINION PIECE

Why more comparative approaches are required in time-series analyses of coral reef ecosystems

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ABSTRACT: In the Anthropocene, the negative effects of environmental change on coral reefs are outpacing their capacity for continued growth. However, a few reefs have shown resilience to recent disturbances, and here we suggest that more comprehensive attention to comparative approaches could lead to a deeper understanding of the processes causing declining coral cover and impaired ecological resilience. Using sites in Mo'orea, French Polynesia, and Panama, Eastern Tropical Pacific, as examples of resilient reefs that have been studied for over 35 yr, we demonstrate the potential of the comparative approach by exploring different ecological drivers of community resilience at each location. In both cases, coral reef community resilience is associated with strong herbivory, but in Mo'orea, resilience is a product of rapid coral community recovery through sexual recruitment in response to a largely indiscriminate disturbance (crown-of-thorns seastars), while in Panama, resilience appears to be a product of corals acquiring resistance to a repetitive selective disturbance (bleaching). Based on these trends, we propose a hypothesis-driven conceptual framework to test for mechanisms driving community resilience. The recent decade of coral reef degradation has brought time-series analyses to the forefront of research on these systems, where they are detecting disturbances that are unique to modern ecological science. Without explicit comparison among systems, the research potential of these projects will not be fully realized.

KEY WORDS: Mo'orea · Eastern Tropical Pacific · Scleractinia · Coral reef · Resilience

1. INTRODUCTION

The modern coral reef crisis is intensifying (Hughes et al. 2017), and with the combined effects of natural and anthropogenic disturbances, including climate change and ocean acidification (Doney et al. 2009), there is concern that coral reefs could soon

cease to exist (Hoegh-Guldberg et al. 2007). One response to these threats has been an expansion of time-series analyses (e.g. Flower et al. 2017) that provide the primary means of quantifying the extent to which coral reef communities are changing. Time series are also a source of empirical data informing projections of future reef condition (Pandolfi et al.

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2011), and they can support conservation decisions promoting coral reef persistence (Flower et al. 2017). Despite advances in implementing time-series studies, efforts to compare the results they generate have not kept pace with the availability of new data. Using well-studied coral reefs in Mo'orea, French Polynesia, and Panama, Eastern Tropical Pacific (ETP), as examples of reefs that have shown high resilience in the face of recent disturbances, we use this Opinion Piece to advocate for greater use of the comparative approach in coral reef time-series analyses.

2. CORAL REEF RESILIENCE: RESISTANCE AND RECOVERY

Ecosystem resilience has become a central concern in ecology (Scheffer et al. 2001), and this is especially true for coral reefs where large declines in coral cover have occurred since the 1970s (e.g. Woodley et al. 1981, Hughes 1994, Cinner et al. 2016, Hughes et al. 2017). Ecological resilience, classically, is a measure of a system's ability to persist by absorbing disturbance and maintaining ecological relationships (Holling 1973). Contemporary applications of this concept (e.g. Hughes et al. 2010) include 'resistance' (the ability to maintain state), and 'recovery' (the ability to return to an original state). While coral reef literature has been dominated by reefs where coral mortality has occurred without recovery (e.g. Hughes 1994), a small number of reefs have shown resistance to, or recovery from, major stressors (Glynn et al. 2001, Glynn & Fong 2006, Baker et al. 2008, Pratchett et al. 2013, Graham et al. 2015, Adjeroud et al. 2018, Holbrook et al. 2018, Stimson 2018).

Here, we apply a qualitative approach using 37 yr of time-series analyses to compare 2 locations where coral reefs have shown resilience to disturbances. We contrast potential mechanisms leading to resilience and describe opportunities to exploit comparative approaches to further our understanding of future reefs. We focus on Mo'orea and Panama (Fig. 1), because reefs in these locations have been studied for decades, and their communities have recovered or retained high coral cover following sequential disturbances (Glynn et al. 2017a, Holbrook et al. 2018). Moreover, because of the history of process-oriented research in each location, there are opportunities for advances in understanding the mechanisms driving reef resilience. We do not present new data, nor do we claim that comparisons of coral community dynamics among sites are novel (McClanahan et al. 2007). Rather, we draw attention to the underex-

ploited value of the comparative approach in better understanding the trends of changing community structure affecting coral reefs in different locations where they are exposed to different biotic and abiotic conditions. For detailed methods and a summary of the data, see the Supplement at www.int-res.com/articles/suppl/m608p297_supp.pdf.

Mo'orea and Panama provide examples of coral reefs that appear resilient under present-day conditions and which have recovered from recent disturbances that have caused other reefs to lose coral cover in favor of spatial dominance by macroalgae (e.g. Jackson et al. 2014, Hughes et al. 2017). As we hypothesize below, their resilience appears to arise from differential dependence on mechanisms of resistance versus recovery, which effectively form the end points of a gradient along which Mo'orea, Panama, and other resilient reefs (e.g. Graham et al. 2011, 2015, Gilmour et al. 2013) can be arrayed. We use data from Mo'orea and Panama to highlight the similarities (and differences) among reefs in these 2 locations.

2.1. Patterns of disturbance and resilience

Over the last 4 decades, Mo'orea and Panama have been subject to repeated disturbances, but they differ in the disturbance types and the ways in which they have responded (Fig. 2; Table S1 in the Supplement). Mo'orea experienced 2 substantial El Niño–Southern Oscillations (ENSO), 2 cyclones, and 2 outbreaks of the corallivorous crown-of-thorns seastar (COTS) *Acanthaster planci*. Together, these disturbances resulted in 3 cycles of coral decline, with coral mortality on some reefs reaching nearly 100% as recently as 2010. However, each event was followed by rapid coral community recovery (within ~7 yr), driven initially by high densities of sexual recruits of pocilloporids (Adjeroud et al. 2002, Bramanti & Edmunds 2016), followed by slower recovery of other taxa (Adjeroud et al. 2018, Holbrook et al. 2018). Over the same period, the ETP was subject to 3 major ENSOs (Fig. 2; Table S1). In the first event (1982–1983), some Panamanian reefs with 77% coral cover experienced coral mortality close to 100%, and this was followed by slow recovery (<5% coral cover after 12 yr) compared to recent events around Mo'orea. The subsequent strong ENSO in 1997–1998, however, caused little additional coral mortality, and coral cover continued to increase through asexual proliferation (Glynn & Fong 2006, Glynn et al. 2017b). The third major ENSO, in 2015–2016, also appears to have

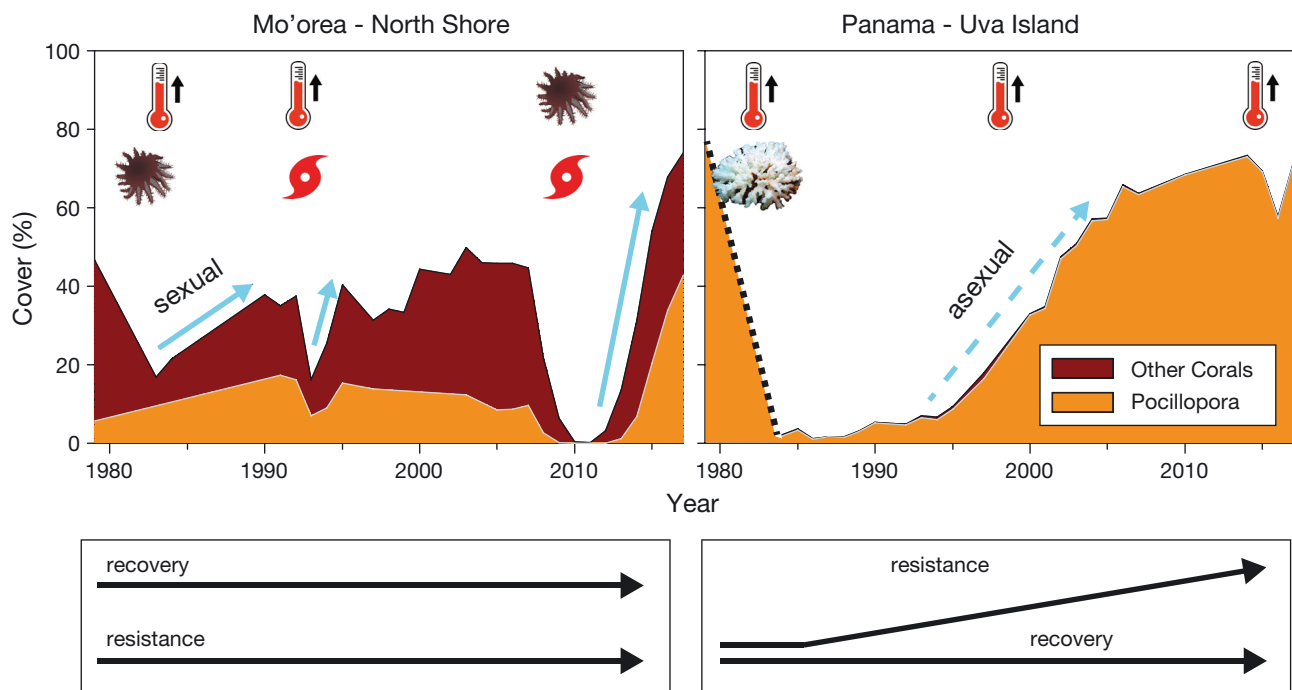
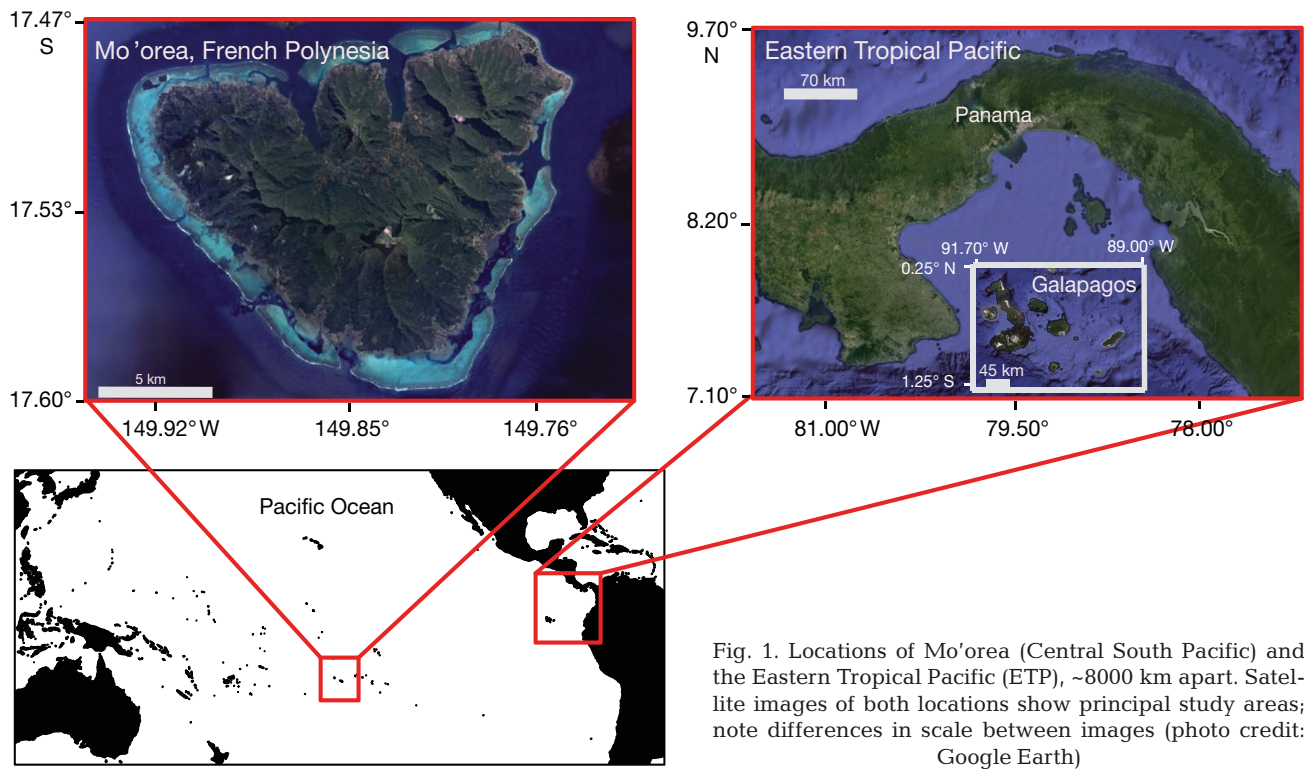


Fig. 2. Percentage cover of stony corals (*Pocillopora* spp. orange; non-*Pocillopora* corals, brown) over 37 yr on the outer reef (10 m depth) of Mo'orea, French Polynesia, and the shallow reeftop of Uva Island, Panama. Coral diversity in Panama is higher in deeper water, though not as high as in Mo'orea. Impacts of major disturbances are shown with icons for hurricanes, crown-of-thorns seastar outbreaks, and coral bleaching. For Panama, coral cover prior to 1982–1983 was estimated at 77 % following Glynn (1976). Blue solid arrows: role of sexual recruitment, blue dashed arrows: role of asexual proliferation. Schematics below illustrate constancy (horizontal) or increasing (upward sloping arrow) community properties. For methods and sources, see the Supplement

caused only minor reductions in coral cover (Fig. 2). Together, these patterns suggest that resilience in Mo'orea is driven by rapid coral recovery, while in Panama it is slower and is driven by increasing resistance to thermal stress.

2.2. Contrasting physical, chemical, and biological contexts in Mo'orea and the ETP

The physical, chemical, and biological environments differ between Mo'orea and the ETP (Table S1). Mo'orean reefs form a cohesive and heavily calcified reef system with a post-glacial/Holocene reef framework that is ~8000 yr old (Montaggioni 1988) and lies within the tropical south Pacific biogeographic region where scleractinian diversity is greater than in the ETP (Glynn & Macintyre 1977, Cortés 1997). In contrast, coral reefs in the ETP are more recent (~5000 yr old) pocilloporid-dominated frameworks that are patchily distributed along the coasts and islands of Central America. Here, they form part of a small and isolated tropical reef fauna and consist of small, weakly calcified reefs that are lower in diversity than those of Mo'orea (Glynn & Macintyre 1977, Cortés 1997). Upwelling in the ETP varies in intensity and duration within the region (Cortés 1997) but generally results in cooler seawater (e.g. in the Galápagos, temperature dips to 18.5°C), with lower aragonite saturation state (Ω_{arag}) and higher nutrients than in Mo'orea (Table S1). While reefs in both locations are frequently affected by disturbance, ENSOs are more extreme in the ETP, while COTS have been more destructive in Mo'orea. Overall, reefs in the ETP occur in an environment that is marginal for reef construction, while in Mo'orea they occur under conditions favorable for reef accretion (Le Campion-Alsumard et al. 1993).

3. COMPARISON UNDERSCORES POTENTIAL DRIVERS OF RESILIENCE

Evidence from the last 37 yr suggests that the mechanisms of coral reef resilience vary between Mo'orea and Panama. While evaluation of the processes underlying these patterns is ongoing, there appear to be at least 4 conditions promoting coral community resilience: (1) reproductive strategies of dominant corals, (2) the dynamics of the corals' algal symbiont communities, (3) abundance and functional diversity of herbivorous fishes, and (4) reef frame-

work persistence. Based on the differences between regions, we propose a conceptual framework to codify and integrate future comparative studies.

3.1. Reproductive strategies of dominant corals

Resilience in Mo'orea is driven by rapid recovery of coral populations through sexual reproduction, while recovery in the ETP is slower, spatially heterogeneous, and largely dependent on asexual proliferation. In Mo'orea, reefs were reduced to near-zero coral cover in 2010 by COTS predation, and most of the coral skeletons were removed by a cyclone in February 2010. Large numbers of sexually produced *Pocillopora* spp. then recruited to the forereef, supplemented by smaller numbers of *Acropora* spp., resulting in rapid reef-wide recovery, and ~70% coral cover on at least 1 forereef site by 2015/16 (Edmunds 2017, Holbrook et al. 2018).

In contrast, asexual reproduction is an important driver of coral recovery in the ETP (Glynn et al. 2017b) and has resulted in the replication of coral host genotypes that have high survivorship under prevailing conditions. After the 1997–1998 ENSO, both massive and branching corals in Panama exhibited re-sheeting of tissue over dead skeletons (Glynn & Fong 2006). Large aggregations of pocilloporid colonies generated through asexual reproduction (Baums et al. 2014) suggest that the dense frameworks of *Pocillopora* in the ETP are products of clonal proliferation (i.e. fission) and subsequent fusion. Moreover, although many corals produce sexual gametes on ETP reefs (e.g. Glynn et al. 1991, 2017b), and sexually derived coral recruits have been commonly found on volcanic outcrops, these recruits are only found at low densities on the shallow reefs of Panama (Glynn et al. 2017b).

3.2. Dynamics of algal symbiont communities in reef corals

Despite the low diversity of corals and their dinoflagellate symbionts in the ETP, thermotolerant *Durussdinium glynnii* (formerly *Symbiodinium* D1, LaJeunesse et al. 2018) is common in pocilloporids. During the 1997–1998 ENSO, Panamanian pocilloporids containing thermally sensitive *Cladocopium* (*Symbiodinium* C1b-c) severely bleached, while colonies containing *Durussdinium* did not (Glynn et al. 2001). However, only ~5% of bleached colonies died, and by 2001, the abundance of *D. glynnii* in

coral hosts increased by ~50% (Baker et al. 2004). These trends suggest that bleached colonies shuffled their symbionts in favor of *D. glynnii* following bleaching, and that this process, possibly combined with differential mortality of corals containing *Cladocopium* (Baker et al. 2004, LaJeunesse et al. 2010) resulted in an increase in thermal tolerance. In contrast, the 1982–1983 ENSO was of similar magnitude to that of 1997–1998 but was characterized by extensive coral bleaching and mortality, suggesting that *D. glynnii* was rare in pocilloporids prior to 1982. Further increases in the dominance of *D. glynnii* in pocilloporids following the 2015–2016 ENSO would enhance support for this hypothesis and indicate that the thermotolerance of these reefs might continue to increase.

In Mo'orea, coral and dinoflagellate symbiont diversity are higher than in the ETP (Table S1). Pocilloporids on the forereef are dominated by members of *Cladocopium*, with *Durusdinium* more common on fringing reefs (Putnam et al. 2012). It is not known whether the moderate bleaching that occurred since the 1980s (Pratchett et al. 2013) shifted dinoflagellate communities to favor *Durusdinium* in the common corals. Since *Durusdinium* is already common in some *Pocillopora* and *Acropora* in Mo'orea (Putnam et al. 2012), further shifts in symbiotic algal commu-

nities to favor these symbionts might occur following future bleaching events, and corals unable to acquire *Durusdinium* may suffer higher mortality. However, the greater diversity of symbionts in Mo'orea versus the ETP suggests that shuffling of other symbionts may also be possible (e.g. Darius et al. 1998, 2000, Putnam et al. 2012, Rouzé et al. 2017).

3.3. Abundance and functional diversity of herbivorous fishes

Herbivorous fishes on the Mo'orea forereef and some reefs of Panama differ in abundance, biomass, functional guild composition, and size-frequency distributions (Fig. 3). However, the intensity of herbivory in both communities appears to be sufficient to suppress dense macroalgal growths, as reefs in Mo'orea and the ETP become dominated by crustose coralline algae and algal turfs instead of macroalgae following disturbances (Smith 2005, Adam et al. 2011, Holbrook et al. 2016). This contrasts with coral reefs in many other locations where fish herbivory is curtailed by overfishing, and disturbances favor rapid transitions to macroalgae (Hughes et al. 2007). Although the abundance of herbivorous fishes is lower in Uva Island, Panama, than on the forereef of

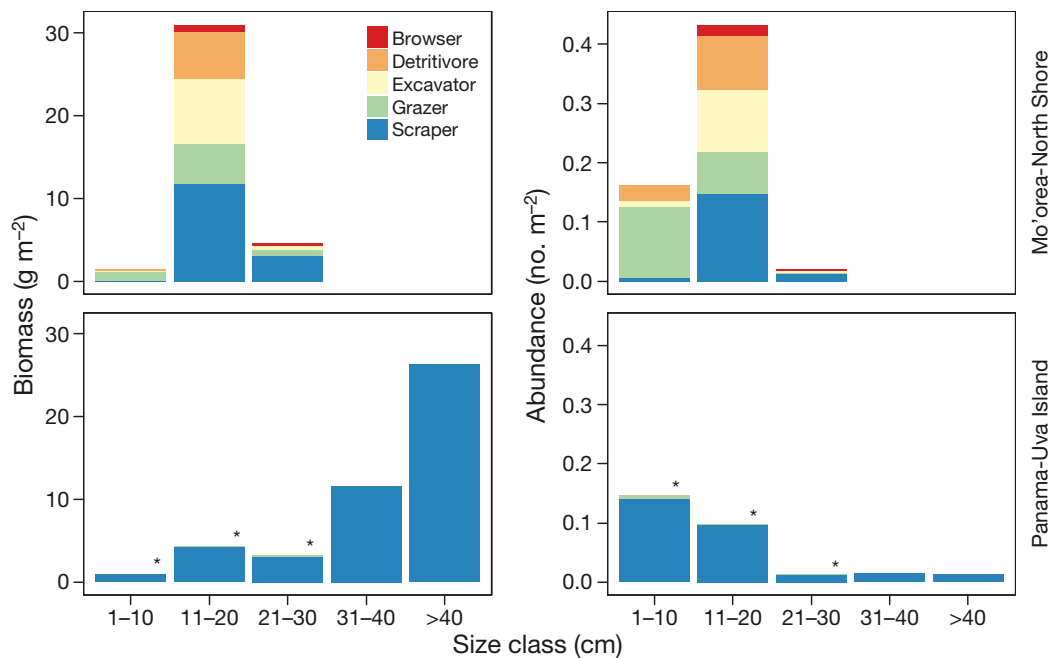


Fig. 3. Mean abundance and biomass of fish herbivores by size classes for the north shore (12 m depth) of Mo'orea from 2010 to 2012, and Uva Island (0–7 m depth), Panama, from 2001–2003, divided by functional feeding group. During this time in Mo'orea, the fish herbivores increased in response to a crown-of-thorns seastar outbreak and a major cyclone. Uva Island has a similar range of functional groups as Mo'orea, but diversity is lower and abundance and biomass are dominated by scraping parrotfishes. Territorial damselfishes have a very different role in influencing algae and are not included. * = low abundances of grazing fishes (thin green block). For methods and sources, see the Supplement

Mo'orea, their collective biomass is similar. Further, the herbivorous fish community on the forereef of Mo'orea is composed of a more functionally diverse assemblage of smaller fishes (<30 cm) while in the ETP the herbivorous fish community is dominated by a single feeding guild of large parrotfishes (Fig. 3). Since reliance on a single fish guild limits functional redundancy and complementarity, which are 2 important components of resilience (Rasher et al. 2013), reefs in the ETP may be more susceptible to increased fishing pressure. However, because herbivore function is size-dependent, the absence of large individuals likely results in the loss of some function on Mo'orean reefs compared to other less-fished locations in the Pacific (Bellwood et al. 2012). This loss could be most important in driving variation in resilience when combined with other stressors, such as increased nutrient supply, that also vary within and between regions.

3.4. Reef framework persistence

The topographically complex calcium carbonate framework created by zooxanthellate scleractinians and other calcifiers is vital to coral reef ecosystem function (Graham & Nash 2013, Ferrari et al. 2018) and is heavily influenced by a diversity of abiotic factors that modify the performance of zooxanthellate corals (e.g. Kleypas et al. 1999). Reef accretion and dissolution are sensitive to seawater chemistry with, for example, high nutrient fluxes and low seawater pH (or aragonite saturation state, Ω_{arag}) negatively impacting the structural integrity of the reef framework and the ability of reefs to persist through periods of declining net calcification (e.g. Manzello et al. 2008, DeCarlo et al. 2015, Silbiger et al. 2018). However, net reef accretion depends on the interplay among many factors, including site-specific physical and biological conditions, and disturbance history (e.g. Manzello et al. 2014, Silbiger et al. 2017).

The seawater in Mo'orea and the ETP differs in Ω_{arag} , nutrients, and salinity (Table S1), all of which affect the persistence of the reef framework. Corals in the ETP have lived for millennia under low and variable seawater pH (and Ω_{arag}) and, in some places, high nutrients, variable salinity, and low temperatures due to upwelling (Manzello et al. 2008). In contrast, seawater chemistry in Mo'orea is more seasonally stable (Carpenter et al. 2018). These differences suggest that corals in the ETP may be more resistant to chronically low pH and reduced temperature compared to those in Mo'orea. Bioerosion, however, is

much higher in some parts of the ETP than Mo'orea (25.4 vs. 2.6 kg m⁻² yr⁻¹, respectively; Chazottes et al. 1995, Reaka-Kudla et al. 1996), and in the ETP, is largely attributable to sea urchins (e.g. Glynn 1988; see Table S1 for abundance on study reefs). Coral reefs in the Galápagos Islands, where upwelling is greatest in the central and southern islands (low Ω_{arag} and high nutrients), transitioned to net erosion after the 1982–1983 ENSO (Glynn 1988) and have not recovered since (Glynn et al. 2017c). Conversely, reefs with lower upwelling intensity in the northern Galápagos (higher Ω_{arag} and lower nutrients) have recovered (Glynn et al. 2015).

4. CONCEPTUAL FRAMEWORK FOR THE COMPARATIVE APPROACH

While the coral reefs of Mo'orea and the ETP are not unique in displaying resilience in recent years (e.g. Gilmour et al. 2013, Graham et al. 2015), our comparison suggests they represent the ends of a gradient of mechanisms promoting ecological resilience (Fig. 4). As Mo'orea and the ETP span a range of environmental conditions (Table S1), comparing them has utility as a space-for-time substitution in understanding the structure and function of coral reefs in the warmer and more acidic seawater of the future. In this section, we describe a conceptual model that codifies and integrates the outcome of a comparison of Mo'orea and the ETP.

Our contrast of Mo'orea and the ETP underscores the diversity of mechanisms promoting reef resilience, and their association with the ecological and environmental history of each reef (Fig. 4). Reef-building corals in the ETP may have acquired resistance to ENSO events through the response of the holobiont to thermal perturbations. These events appear to have functioned as selective agents favoring thermally tolerant algal symbionts (Baker et al. 2004) and host genotypes, thus increasing resistance of the coral community to future increases in temperature (Fig. 4). In the ETP, it is also likely that the dominance of *Pocillopora*, a genus which routinely hosts *Durussdinium glynnii* in the ETP, has contributed to the capacity of these reefs to acquire thermal resistance. The acquisition of thermal tolerance has contributed to coral community recovery in the ETP, but this mechanism contrasts with Mo'orea, where the coral community relies on high rates of sexual recruitment to promote recovery. The proximal causes of these differences are unknown, but it is interesting to speculate that they reflect the young geological

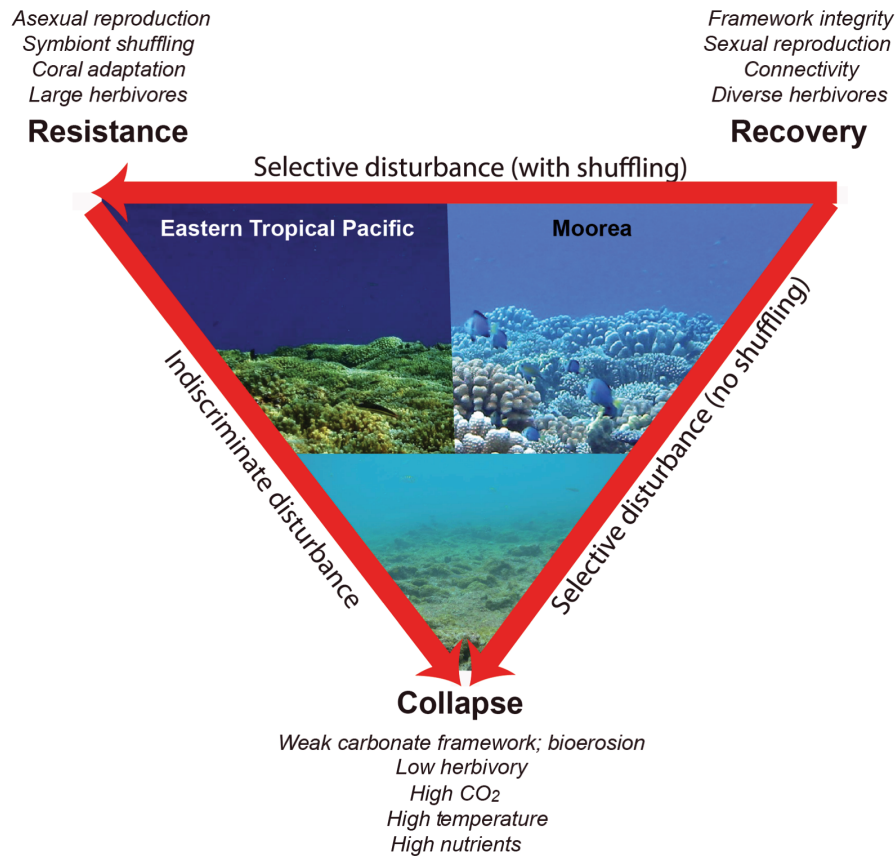


Fig. 4. Conceptual diagram placing reefs in Mo'orea and the Eastern Tropical Pacific (ETP) in a phase shift context where reefs can transition from 'Mo'orea-like' to an 'ETP-like' or to a collapsed state depending on the disturbance regimes. Disturbances with selective effects (e.g. bleaching acting on corals with differing thermal sensitivities) that operate in a system with weak calcification and low topographic relief favor the 'ETP-like' state, whereas exposure to indiscriminate disturbances in a strongly calcified system with high topographic relief favor a 'Mo'orea-like' state. Resilience is context-specific, however, and ecosystem collapse might occur if Mo'orea-like reefs are exposed to selective disturbances for which algal symbiont communities cannot compensate, or if ETP-like reefs are exposed to disturbances that have indiscriminate effects on corals. Ecosystem processes that cause shifts in community function are listed outside the triangle, while disturbance events are listed as axes of the triangle

age of reefs in the ETP relative to Mo'orea and their structurally compromised framework that limits the success of sexual recruitment on unstable surfaces. In the ETP, it is also likely that the ability of coral to acquire thermal resistance was facilitated by a community of large herbivorous fishes that limited transitions to macroalgae during major ENSO disturbances, thus ensuring that the thermal regime remained the strongest selective force acting on the corals. Coral community resilience in the ETP appears to have been mediated by disturbances acting on coral populations under conditions that are marginal for the survival of reef corals.

In contrast, community resilience in Mo'orea has been driven by rapid recovery of coral populations following disturbances (Fig. 4), the most devastating of which (i.e. COTS) have generally indiscriminate

effects by killing corals regardless of their functional identity (i.e. these disturbances have a weak potential as selective agents) (Holbrook et al. 2018). In Mo'orea, the recovery of the coral community appears to have been facilitated by sexual reproduction of reef-building corals, a structurally stable reef framework, and a functionally diverse community of small herbivorous fishes that deterred a phase shift to macroalgae on the forereef (Adam et al. 2011). Coral community resilience in Mo'orea appears to have been mediated by responses to diverse but indiscriminate disturbances operating in a more structurally stable reef environment.

This conceptual framework highlights the kinds of research required to understand the processes underlying decadal-scale changes in the coral community structure (Fig. 2). In particular, it motivates

the predictions that 'Mo'orea-type' reefs could transition to 'ETP-type' reefs should the disturbance regime change to favor a small number of thermally tolerant coral species, such as through an increase in bleaching intensity. Alternatively, reefs might undergo functional collapse if the density of fish herbivores decreases, or if changes in algal symbiont communities do not enhance coral survival (Fig. 4). Likewise, if the disturbance regime in 'ETP-like' reefs were to shift from selective to less discriminating (such as a COTS outbreak), or to another selective disturbance to which these reefs are naïve (such as a disease outbreak), or if key parrotfish populations are lost, these reefs may also undergo functional collapse.

5. CONCLUDING REMARKS

Despite an increasing number of long-term analyses of coral reef communities, it is remarkable how infrequently data from multiple projects are compared. Our qualitative comparisons of resilient reefs in Mo'orea and the ETP highlight fundamentally different mechanisms of resilience operating in these 2 systems. Future qualitative and quantitative comparisons of reef dynamics in different locations could allow for: (1) the development of new conceptual models of reef resilience and (2) the testing of hypotheses addressing the mechanisms thought to promote resilience or the transitions between community types highlighted by the comparative process. The ongoing global declines in coral abundance and diversity, and the dire projections for the future of coral reefs, provide strong incentives to maximize the research potential of ongoing time-series analyses of these communities. Critically, as these projects mature in longevity and sample across multiple disturbance events, the intrinsic values of replicate observations, and their use in a comparative framework, are greatly increased. In the rush to find ways to enhance the persistence of coral reefs in the Anthropocene, it is timely for biologists to revisit the merits of using one of the oldest tools of their trade—the comparative approach—to fully leverage knowledge from the coral reefs that still can advance our understanding of reef resilience.

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