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http://hdl.handle.net/10026.1/18931

10.1111/gcb.16034
Global Change Biology
Wiley

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Received: 20 July 2021 | Revised: 4 December 2021 | Accepted: 7 December 2021

DOI: 10.1111/gcb.16034

Global Change Biology WILEY

REVIEW

Coral reef benthic community changes in the Anthropocene: Biogeographic heterogeneity, overlooked configurations, and methodology

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Abstract

Non-random community changes are becoming more frequent in many ecosystems. In coral reefs, changes towards communities dominated by other than hard corals are increasing in frequency, with severe impacts on ecosystem functioning and provision of ecosystem services. Although new research suggests that a variety of alternative communities (i.e. not dominated by hard corals) exist, knowledge on the global diversity and functioning of alternative coral reef benthic communities, especially those not dominated by algae, remains scattered. In this systematic review and meta-analysis of 523 articles, we analyse the different coral reef benthic community changes reported to date and discuss the advantages and limitations of the methods used to study these changes. Furthermore, we used field cover data (1116 reefs from the ReefCheck database) to explore the biogeographic and latitudinal patterns in dominant benthic organisms. We found a mismatch between literature focus on coral-algal changes (over half of the studies analysed) and observed global natural patterns. We identified strong biogeographic patterns, with the largest and most biodiverse biogeographic regions (Western and Central Indo-Pacific) presenting previously overlooked soft-coral-dominated communities as the most abundant alternative community. Finally, we discuss the potential biases associated with methods that overlook ecologically important cryptobenthic communities and the potential of new technological advances in improving monitoring efforts. As coral reef communities inevitably and swiftly change under changing ocean conditions, there is an urgent need to better understand the distribution, dynamics as well as the ecological and societal impacts of these new communities.

KEYWORDS
Anthropocene, benthic organisms, community turnover, coral reefs, reef changes, reef monitoring

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1 | INTRODUCTION

Growing anthropogenic and climate stressors are driving ecological changes with profound global consequences (Cardinale et al., 2012; Johnson et al., 2017; Malhi et al., 2020). As highlighted by recent events, biodiversity losses are not only an environmental emergency, but can have widespread effects by contributing to disease outbreaks (Roe, 2019), and to the collapse of entire ecosystems and the services provided (Asch et al., 2018; IPBES, 2019). Tropical areas, which simultaneously exhibit low resistance/resilience to climate change, and mounting pressures on natural resources linked to their rapid economic and demographic growth, are especially vulnerable to ecological changes (Barlow et al., 2018; Cinner et al., 2018). As such, prevention of biodiversity collapse and ecological shifts is paramount, however, addressing key knowledge shortfalls is required to design effective conservation approaches (Barlow et al., 2018).

Increasing environmental degradation (e.g. eutrophication, pollution) and variability (i.e. related to climate change) are driving non-random community changes in many ecosystems (Cloern et al., 2016; Neumann et al., 2017; Plass-Johnson et al., 2016). Changing environmental conditions not only push some species towards and beyond their physiological limits, but also modify the network of interactions (Diamond et al., 2012; Gilman et al., 2010). Since species are highly interconnected, both phenomena can trigger cascade effects and drive large community changes (Gilman et al., 2010). Ecological changes can be slow and gradual (i.e. changing linearly as a response to continued disturbances), or abrupt and sudden (Cooper et al., 2020; Wernberg et al., 2016). Abrupt community changes, often defined as regime or phase shifts, are thought to occur when an ecological threshold or tipping point has been reached, in which a small cumulative increase of a stressor drives a much larger ecological change than expected from linear effects, and results in a functionally different stable system (Biggs et al., 2009; Connell et al., 2017). Some shifts can be reversed in relatively short periods of time (<50 years) if the drivers and disturbances are eliminated and the pre-shift conditions are re-established (Bestelmeyer et al., 2011). However, in other cases even if the initial conditions are restored, the system might remain in the alternate state (or 'basin of attraction'), through a phenomena known as hysteresis (i.e. the pathway and rate of recovery differs from those of degradation; Beisner et al., 2003). Alternate stable states are often a consequence of the establishment of feedback mechanisms between state variables and drivers that reinforce the alternate state and its persistence (Schmitt et al., 2019; Schröder et al., 2005).

Both abrupt and gradual community changes often lead to functionally impoverished communities with profound socio-ecological implications (Conversi et al., 2015; Cooper et al., 2020; Scheffer & Carpenter, 2003). The high complexity and heterogeneity of these changes or shifts have resulted in a lack of agreement on criteria to identify and analyse community changes and have led to the development of overlapping theories and terminologies across disciplines, which further hampers their detection and global understanding (Bestelmeyer et al., 2011; Hughes et al., 2013; Pulsford et al., 2016). Whilst several frameworks have been proposed that intend to facilitate the transition between theory and field observations (e.g. Bestelmeyer et al., 2011) and standardize the study of regime shifts (e.g. the Regime Shift Database, Biggs et al., 2018), the identification of community changes and especially the mechanisms causing them remains difficult.

Increasing evidence suggests that most coral reefs will undergo compositional, structural and functional changes as ecosystem resilience erodes in response to local stressors, including overfishing, eutrophication, acidification and increasingly frequent marine heatwaves and storms (Hughes et al., 2017a; Woodhead et al., 2019). In coral reefs, abrupt community changes (i.e. regime shifts) were initially described on Jamaican reefs in the 1980s (Hatcher, 1984; Hughes et al., 1987). After years of experiencing resilience erosion through overfishing and eutrophication, the damage caused by a major hurricane together with the massive mortality of the grazer urchin *Diadema antillarum* led to a transition from a coral- to an algae-dominated community on these reefs (Hughes, 1994; Hughes et al., 1987). Since then, coral-algal shifts have been increasingly reported and studied, with a large body of literature investigating the drivers and feedback mechanisms that lead to, support, and reinforce such community changes (Bellwood et al., 2006a; Dinsdale & Rohwer, 2011; Dixson et al., 2014; de Goeij et al., 2017; Haas et al., 2016; Hoey & Bellwood, 2011). However, the high controversy regarding what constitutes a coral reef regime shift (e.g. extend and timescale of the changes to be considered a regime shift), as well as the presence/absence of hysteresis mechanisms leading to alternate states (e.g. Dudgeon et al., 2010; Mumby et al., 2013; Schmitt et al., 2019; van de Leemput et al., 2016), have been a limiting factor in defining, recognizing and understanding coral reef regime shifts, especially towards non-algal-dominated states. This has been partially due to the fact that the hypothesis of alternative states suggests that more than one stable state (i.e. community configuration) can occur in the same place under the same exact environmental conditions, which is extremely challenging to prove experimentally in ecosystems with relatively slow benthic biomass dynamics, such as coral reefs (Dudgeon et al., 2010; Knowlton, 2004; Mumby et al., 2013). In previous reviews, community shifts were generally defined as extensive relative decreases in projected (i.e. 2D) reef substrate cover of hard corals (i.e. reef-building corals including both scleractinian corals and hydrocorals) in combination with a relative increase in cover of other benthic reef organisms that persisted at least 5 years (Norström et al., 2009). However, in many remote locations, long-term monitoring programs are either not established or not linked to research programmes, which results in a failure to detect community shifts and evaluate the persistence of non-hard-coral-dominated habitats (Obura et al., 2017). For example, reports of reef habitats dominated by organisms other than hard corals, such as soft corals or zoanthids, are not rare, but since many of these observations are sporadic, few of these studies discuss possible community shifts (e.g. Baum et al., 2016; Lin & Denis, 2019; Wee et al., 2017).

In fact, recent research suggests that coral reefs dominated by invertebrates other than hard corals, such as sponges and soft

corals, might be becoming more frequent as a result of global change (Bell et al., 2018; Chaves-Fonnegra et al., 2018; Inoue et al., 2013; Lesser & Slattery, 2020). Yet, information regarding changes to such alternative communities remain highly scattered and the drivers and mechanisms behind the proliferation of these alternative organisms remain largely unknown (Norström et al., 2009; Reverter et al., 2021). For example, whereas some changes have been observed after specific pulse disturbances, such as bleaching events (Chaves-Fonnegra et al., 2018) or ocean acidification (Inoue et al., 2013), their frequency, distribution and implications for ecosystem functioning remain unexplored.

Here, we systematically review the literature on different tropical coral reef benthic community changes in order to identify important research gaps. The aim was to perform a broad review, including gradual and abrupt changes with or without hysteresis mechanisms, to provide a global understanding of the benthic community changes that coral reefs are facing, including all studies addressing coral reef community shifts irrespective of postulated theories and used terminologies. To accomplish that, from here on, the coral reef benthic communities dominated by organisms other than hard corals (i.e. alternative organisms) are defined as alternative communities for simplicity. However, to avoid new controversy, we stress out that this terminology is not related to the 'alternate state' theory (Beisner et al., 2003; Mumby et al., 2013), and, therefore, does not imply the presence or absence of hysteresis mechanisms, which was not possible to evaluate from the data collected. In addition, we collected benthic data on 1116 reefs from the ReefCheck database and used different meta-analytic tools to explore biogeographic and latitudinal patterns in dominant benthic organisms, in order to evaluate whether the scientific literature reflects field benthic patterns. Finally, we discuss the advantages, limitations and challenges of the methods currently used to detect and study such community changes.

2 | DATA COLLECTION AND ANALYSIS

2.1 | Systematic literature review

We systematically searched all peer-reviewed journals and PhD theses in Web of Science (up to 15 December 2020) that investigated coral reef community changes or shifts. We performed our research following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Moher et al., 2009). The following keywords were used: (phase OR alternate OR abrupt) AND (change OR shifts OR regime OR state) AND (coral reefs). This yielded 1724 articles, of which 769 were selected for further screening after the title and abstract analysis. Full-text of the retained articles were then reviewed to determine whether they met at least one of the following criteria: (1) they directly studied or reviewed tropical coral reef benthic community changes, (2) they examined coral reef communities, in which at least the cover of two response variables (i.e. benthic organisms) was reported, (3) they explored drivers and triggers driving changes in response variables, (4) they investigated biotic mechanisms that could alter response variables or (5) they studied direct or indirect implications of changes in response variables to ecosystem functioning or ecosystem services. Articles assessing any of these five criteria were included in the systematic literature review resulting in 523 analysed publications (Data S1). The following information was extracted from each of the retained articles: year of publication, type of benthic organisms studied, geographic region and methods used. The type of examined benthic organisms was intended to provide information about the kind of benthic community changes studied and included the following categories: benthic algae (e.g. containing both macro- and turf algae), hard corals (when different coral genera or species were comparatively investigated, including both scleractinian and hydrocorals), cyanobacteria, sponges, soft corals, zoanthids, ascidians, corallimorpharians, and 'mixed' benthos (for studies that assessed more than three of the previous categories). The geographic regions were classified into the main tropical geographic realms (Tropical Atlantic, Western Indo-Pacific, Central Indo-Pacific realm, Eastern Indo-Pacific and Tropical Eastern Pacific) and provinces (Caribbean, South West Atlantic, North Western Indian (combining Red Sea and Persian Gulf), Western Indian, Central Indo-Pacific province, Central Pacific, South West Pacific, Polynesian and Hawaiian) following previous works (Cowan, 2014; Kulbicki et al., 2013; Spalding et al., 2007). The methods were classified into surveys, long-term monitoring (surveys during ≥5 years), modelling, aquaria experiments, field experiments, benthic sample analyses and literature review. We distinguished between experiments (aquaria or field) where only observational data were collected (e.g. abundance of biological variables or the outcome of an interaction) and experiments where further sample analysis of benthic organisms was undertaken to study more detailed mechanisms or processes (e.g. nutrient cycling, microbial communities or chemical cues). The latter were first classified as aquaria or field experiments and further classified as benthic sample analyses. When a study included more than one methodology, for example, field experiments and benthic sample analysis, all methods were considered in the numerical analyses.

2.2 | Meta-analysis from benthic cover data from ReefCheck Database

We additionally collected benthic cover data from 1116 tropical coral reefs from the ReefCheck database (http://data.reefcheck.us/). Data were only collected for shallow reefs (≤15 m) that had been monitored between 2009 and 2019. For each site, we collected the following information: site name, latitude, longitude, biogeographic region, biogeographic realm, survey date(s), survey depth, and (relative projected) cover (%) of hard corals (including both scleractinian and hydrocorals as these are often grouped as one category in ReefCheck), algae, soft corals, sponges and other benthic organisms. We then calculated the most abundant biotic group, which was defined as the group displaying the largest

relative benthic cover. The log response ratio (LnRR) was calculated between alternative organisms (algae, soft corals and sponges) and hard corals at each of the biogeographic provinces using the escalc function from the R package 'metafor' (Viechtbauer, 2010). Nested linear regression and linear mixed models were constructed to examine the relationship between the LnRR (alternative organisms/hard corals) and latitude using the lme4 package for R (Bates et al., 2015). Absolute latitude (i.e. degrees from the equator) and survey depth were included as fixed effects, whilst nested biogeographic information (province/realm) was included as a random effect. Akaike's information criterion for smaller sample sizes (AICc) was used to assess the explanatory value and parsimony of each model. Akaike weights (wi) were used to select the model with the best fit (model with the highest weight; Arnold, 2010). The R package bootpredictlme4 (Duursma, 2017) was used to predict LnRR values and their standard errors from the chosen model using 500 bootstraps, and the R package visreg (Breheny & Burchett, 2017) was used for visualization.

3 | TYPES OF COMMUNITY CHANGES AND BIOGEOGRAPHIC HETEROGENEITY

Despite coral reef benthic community changes being initially reported during the 1980s, the scientific interest has grown exponentially during the last decade, with nearly half of the articles on the topic being published within the last five years, between 2015 and 2020 (Figure 1a). We identified eight different alternative organisms that can lead to non-hard-coral-dominated communities: algae, sponges, soft corals, zoanthids, cyanobacteria, ascidians, anemones, and corallimorpharians (e.g., Baum et al., 2016; Biggerstaff, Jompa, et al., 2017; Cruz et al., 2016; Fong et al., 2020; Ford et al., 2017; Tebbett et al., 2019; Tkachenko et al., 2017; Work et al., 2008). Changes towards alternative benthic communities can result from competitive replacement when a modification in environmental conditions changes the outcome of competitive interactions in favour of the alternative organism. For example, sponges have been observed to outcompete corals and dominate benthic assemblages at some Indonesian sites with turbid waters (Biggerstaff et al., 2015, Biggerstaff, Jompa, et al., 2017, Biggerstaff, Smith et al., 2017). Similarly, a loss of top-down (i.e. loss of predators) or bottom-up (i.e. increase in the nutrient) control due to anthropogenic activities, such as overfishing and coastal pollution/eutrophication, is also known to promote proliferation of algae and lead to coral-algal shifts (Cheal et al., 2010; Fong et al., 2020; McManus et al., 2000; Smith et al., 2010). Changes in benthic dominance can also be a result of vacant substrate recolonization after large disturbances that induced widespread mortalities, such as mass bleaching events, storms or diseases outbreaks (Cerutti et al., 2020; Doropoulos et al., 2014; Hughes et al., 1987; Roff et al., 2015).

We also identified two types of compositional changes within hard coral communities: (1) a shift towards reefs dominated by fast-growing hydrocorals, such as *Heliopora* or *Millepora*, and (2) a turnover between branching hard-coral communities (e.g. Acroporidae) towards communities dominated by massive and encrusting species (e.g. Poritidae, Agaricidae, Faviidae), which were mostly related to their different sensitivities to disturbances and recovery potential (Adjeroud et al., 2018; Darling et al., 2019; González-Barrios et al., 2021; Harii et al., 2014; Toth et al., 2019). Acroporidae are amongst the most susceptible corals to thermal stress, with acroporids showing higher bleaching and mortalities after thermal stress than massive corals such as *Porites*, *Dipsastrea* and *Goniastrea* (Schoepf et al., 2015; Thinesh et al., 2019). *Porites* corals have also been shown to be less susceptible and have a higher recovery potential after allelopathic damage by algae whereas corals of the genus *Acropora* and *Pocillopora* showed no signs of recovery after the removal of aggressive algal competitors (Bonaldo & Hay, 2014; Rasher et al., 2011). In contrast, increased abundance of hydrocorals, such as *Heliopora coerulea*, has been attributed to enhanced growth performance under warmer temperatures, which allows them to colonize new substrate and overgrow slower-growing scleractinian corals (Guzman et al., 2019).

Overall, the literature analysis shows that over half of the studies are focused on coral-algal changes (Figure 1b). However, the relative number of benthic-community-change studies towards non-algal organisms has increased over time from only 25% between 1980 and 2000 to nearly half of the studies (47%) between 2015 and 2020 (Figure 1a). This raises two questions: (1) Whether these results reflect natural patterns and new communities are indeed emerging as a result of global change and more frequent pulse disturbances (e.g. mass bleaching events), or other anthropogenic disturbances (e.g. eutrophication, pollution, overfishing)? (2) Whether non-algal community changes might have been overlooked in the past?

3.1 | Biogeographic patterns

In order to bring some insights into whether non-algal-dominated reefs might have been overlooked in the literature and to compare field data with the found literature trends, we collected data on the relative benthic cover of 1116 reefs using the ReefCheck database. Our results showed marked biogeographic differences in the relative abundance and type of dominant benthic organisms (Figure 2a). For example, the Tropical Atlantic (Caribbean and SW Atlantic provinces), which is the most-studied realm according to our literature analysis (Figure 1c), was the only region where alternative communities were more abundant than hard coral-dominated reefs (Figure 2a). In fact, the Caribbean was the only province where the LnRR between algae and hard coral cover was significantly higher than 0, which indicated that Caribbean reefs presented higher covers of algae than hard corals (Figure 3a). Caribbean reefs also displayed the highest sponge/hard coral LnRR, whereas SW Atlantic reefs presented the highest soft coral/hard coral LnRR (Figure 3a). These results highlight a higher relative cover in alternative organisms in these regions, which might be linked to a higher susceptibility to changes towards non-hard coral-dominated communities.

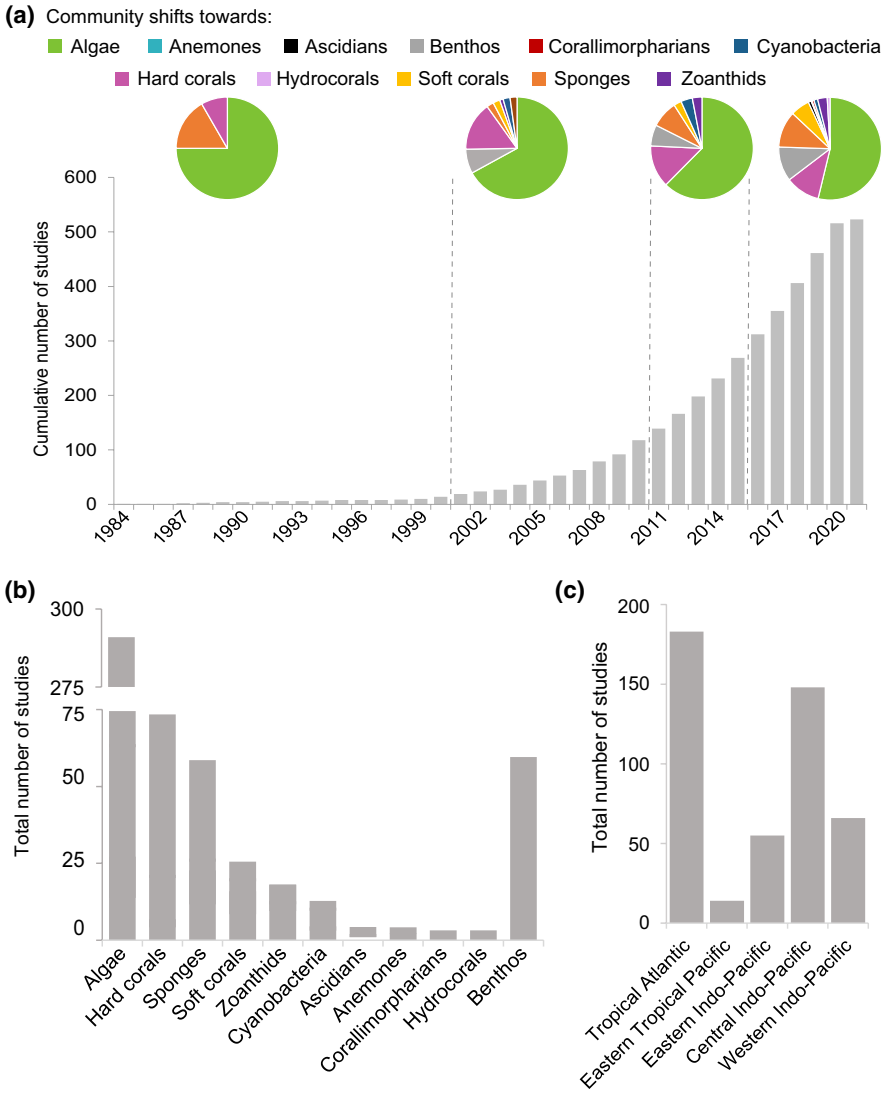

FIGURE 1 Trends in the research literature on tropical coral reef community shifts. (a) Annual number of studies published and relative abundance of articles on the different benthic organisms. (b) Total number of community shift studies on each of the alternative benthic organisms. (c) Total number of community shift studies in each biogeographic region

Reefs from the Eastern Pacific realm (Polynesian and Hawaiian province) also presented an important proportion (30%) of algal-dominated reefs, which were the most abundant alternative community in these regions (Figure 2a). After the Tropical Atlantic reefs, Eastern Indo-Pacific reefs presented the largest LnRR algae/hard coral values (Figure 3a). These results are in agreement with the previous works suggesting that regions with poor coral richness and limited coral functional redundancy (e.g. Tropical Atlantic, Eastern Indo-Pacific) might display lower reef resilience to external stressors (McWilliam et al., 2018) and therefore a higher tendency towards community changes. However, the results from the Eastern Pacific need to be examined carefully due to the low survey numbers (Figure 2a). More research needs to investigate reef resilience and community benthic changes in the Eastern Indo-Pacific, where previous research suggests that at least some reefs in that region (e.g. Moorea in French Polynesia) have repeatedly recovered from disturbances and algal shifts (Adjeroud et al., 2018; Done et al., 1991; Mumby et al., 2016).

Hard corals dominated over 80% of the Western and Central Indo-Pacific reefs (Figure 2a). However, interestingly, in the NW Indian and the Central Indo-Pacific provinces, which includes the Coral Triangle, the most abundant alternative communities were soft-coral-dominated reefs, with the LnRR value soft coral/hard coral in the Central Indo-Pacific province being significantly higher than the LnRR algae/soft coral value (Figures 2a and 3a). These results at the hotspot of marine biodiversity contrast with the common assumption that algal reefs are the most common alternative community worldwide and urge to better understand how changes from hard to soft-coral-dominated communities might affect ecosystem functioning and services.

Overall, our results suggest that the focus on the Tropical Atlantic has directed the scientific research towards studies on coral-algal and coral-sponge community changes (Figures 1b,c and 2). However, coral reef dynamics remain severely understudied in other biogeographic regions, such as the Central and Western Indo-Pacific (Figures 1c and 2a), in which a different community composition combined with specific local and regional drivers might result in different ecosystem functioning. Blast fishing, for example, is one of the main causes for coral reef degradation and community changes in the Indo-Pacific, especially in Southeast Asia (Burke et al.,

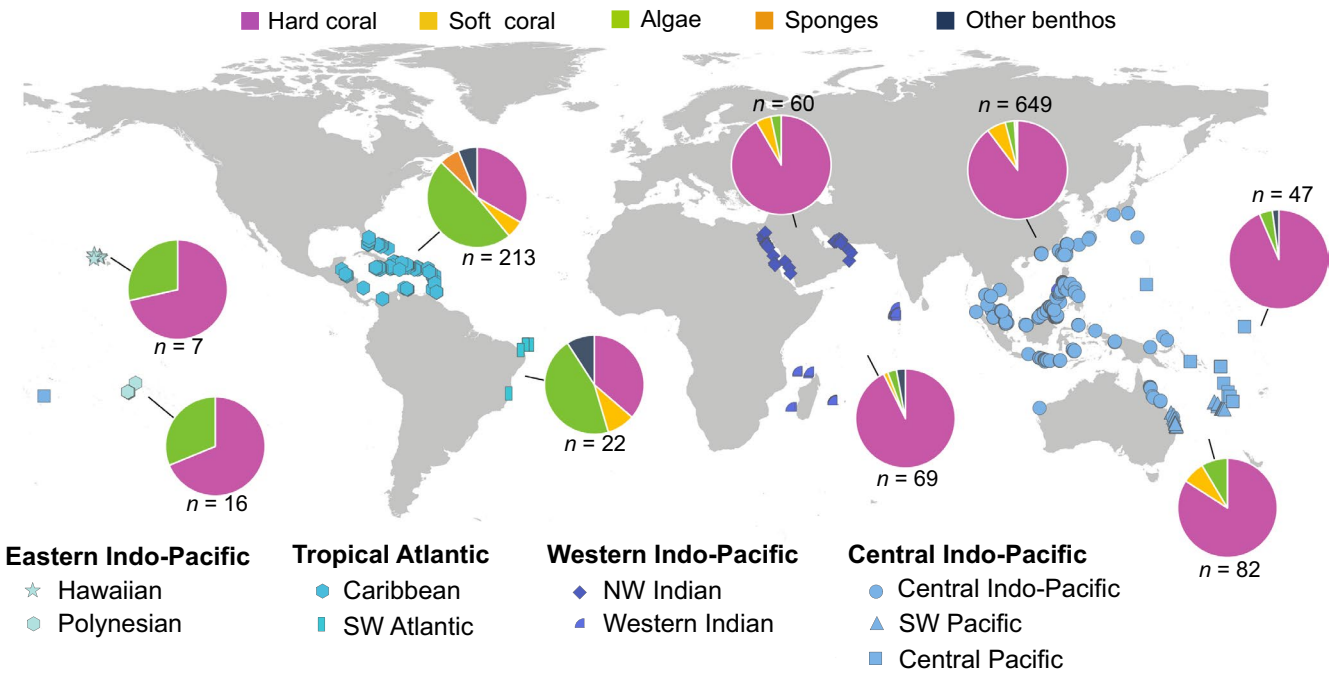

FIGURE 2 Sites from which reef benthic cover was collected from ReefCheck database, with a relative abundance of reefs dominated by the different benthic groups at each biogeographic province and the number of reefs (*n*) studied

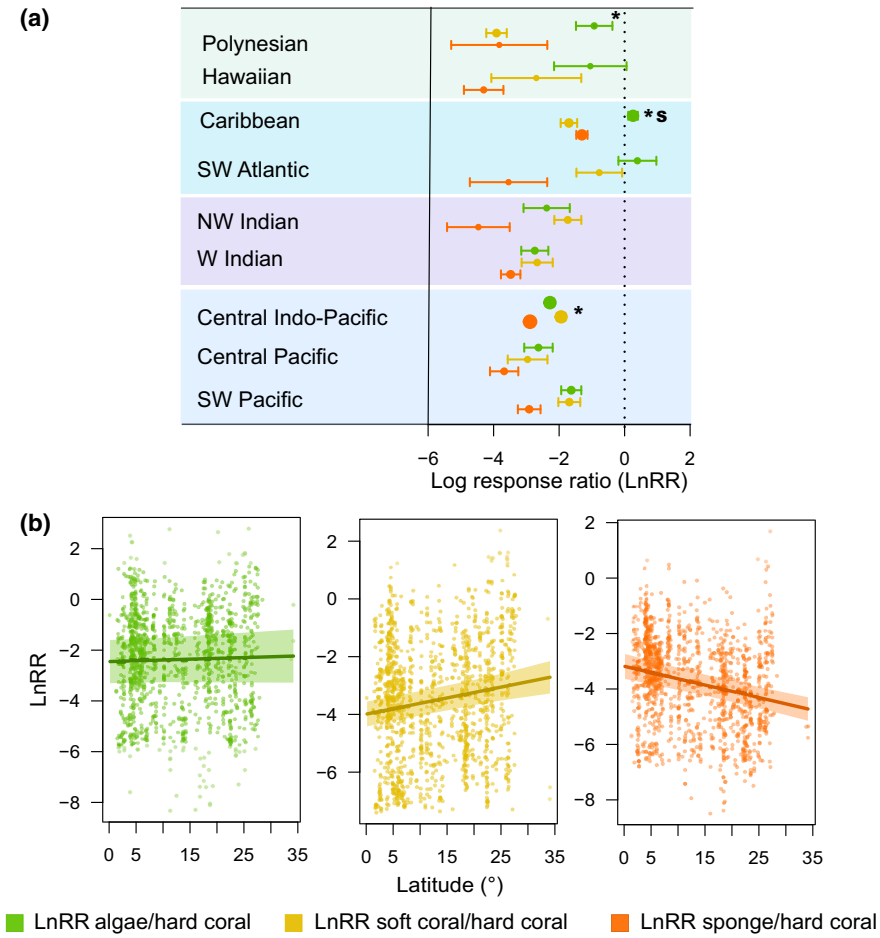

FIGURE 3 (a) Log response ratio (LnRR) between alternative organisms (algae, soft coral, sponges) and hard coral cover for each of the biogeographic provinces. * indicates LnRR values that are significantly different (*p*-value <.05) from the other LnRR values for that province. (b) Predicted changes in LnRR between alternative organisms and hard coral in response to absolute latitude (°). Dots represent the raw data and the lines of the linear mixed model output with SE

2011; Chan & Hodgson, 2017) and East Africa (Braulik et al., 2017). Blast fishing creates vast unstable rubble fields that are unsuitable for coral settlement and thus inhibit the re-establishment of hard coral communities for centuries (Fox et al., 2019; Sawall et al., 2013). These rubble fields were observed to especially favour the proliferation of soft corals (e.g. Xeniidae) and to a lesser extent the settlement of sponges in sites with high currents as well as corallimorpharians in shallower depths (up to 6 m; Fox et al., 2003, 2005). It is well known that the socio-environmental context (e.g. research possibilities and site accessibility) has historically driven uneven geographical focus in ecological research, especially in the tropics (Stocks et al., 2008). Acknowledging such differential focus and the possible associated biases is extremely important to understand differences in ecosystem dynamics and to define appropriate global and local conservation strategies.

A disparity in the resilience between Caribbean and Indo-Pacific reefs was previously hypothesized by Roff and Mumby (2012), who related it to specific biogeochemical differences between both basins. For example, the Caribbean region is exposed to high aeolian dust from the Sahara Desert, that could cause basin-wide iron-enrichment promoting macroalgal growth, which combined with a lack of fast-growing acroporid corals and lower herbivore biomass and diversity, may result in much lower reef resilience and hence a higher number of alternative reefs (Roff & Mumby, 2012). More recent works have shown that species-poor biogeographic provinces (such as the Caribbean, SW Atlantic and Hawaii) have much lower coral (and probably benthic) trait diversity and redundancy, which in turn may translate to lower resilience (McWilliam et al., 2018, 2020). For example, McWilliam et al. (2020) showed that the site with the lowest functional diversity (i.e. Jamaica vs. Great Barrier Reef) experienced the highest trait diversity loss following disturbance. A disparity in resilience between biogeographic regions and thus their susceptibility to benthic changes is related to multiple factors including their socio-environmental context, biogeochemical setting and the ecological functions of the different benthic organisms. Therefore, as previously highlighted by other authors (Bruno et al., 2009; Roff & Mumby, 2012), the dominance of Caribbean literature on coral reef community changes, combined with the specific processes from this region that are not globally transferable, might have introduced a biased perception of global coral reef community changes. Our results not only confirm this, but also identify novel alternative communities (i.e. soft-coral-dominated communities) at the hotspot of marine biodiversity.

3.2 | Latitudinal patterns

High-latitude reefs have been considered as a potential refuge for corals in the light of climate change (Beger et al., 2014; Yu et al., 2019). However, recent works suggest that whilst these reefs might be more resilient to some environmental impacts (e.g. temperature changes), they could be strongly affected by anthropogenic local stressors (e.g. overfishing, eutrophication), and thus be at risk of benthic community changes (Cruz et al., 2018; de Bose et al., 2013; de Oliveira Soares, 2020). For example, Cruz et al. (2018) showed that high-latitude reefs in the SW Atlantic province presented a high susceptibility of shifting towards zoanthid and macroalgal-dominated communities, which was strongly related to local human impacts, such as proximity to human population and dredged ports.

In order to explore whether latitude might explain some of the previously observed biogeographic heterogeneity in the cover of benthic reef organisms, we analysed the relationships between the LnRR (between alternative organisms and hard corals) and latitude using nested linear mixed models (Data S2: Tables S1–S4). Our results showed that algae/hard coral LnRR do not significantly change with reef latitude (Figure 3b). However, soft coral/hard coral LnRR significantly increased with latitude, suggesting that at high latitudes reefs display higher relative covers of soft corals (Figure 3b). In contrast, a significant negative relationship was found between sponge/hard coral LnRR and latitude (Figure 3b).

Although not many studies have explored how latitude affects coral reef benthic communities over large scales, previous works showed latitude as a strong determinant of coral reef benthic structure in the Western and Central Indo-Pacific realms (Bennett & Bellwood, 2011; McClanahan et al., 2014; Porter et al., 2013). Schleyer and Porter (2018) observed higher absolute abundances of soft corals (especially *Sinularia* sp.) in high-latitude South African reefs, which was corroborated by our results confirming that this trend transcended the Western Indian Province. Overall, these results show interesting previously unexplored patterns of coral reef benthic structuring related to latitude and highlight the need forx more research focused on unravelling how differential benthic compositions across latitudes might affect the dynamics and benthic community changes of coral reefs. However, we want to highlight that our models do not incorporate time as a variable. Therefore, whether temporal changes towards certain alternative organisms are more likely at higher/lower latitudes remains unknown.

4 | METHODS: STATE OF THE ART, LIMITATIONS AND PERSPECTIVES

4.1 | Analysis of methods used in the literature

In order to better understand how coral reef benthic community changes are detected/studied and to identify possible research gaps, we analysed the methodology used in the scanned studies (i.e. excluding reviews). We classified the methods from descriptive (i.e. quantitative methods, such as surveys that provide an indication of the coral reefs status) to mechanistic (i.e. methods that explore the underlying mechanisms driving the changes, such as modelling and experimental set-ups).

The majority of studies used descriptive methods reporting the abundance of the biological responses, with 36% of the studies using sporadic surveys and 21% surveying reefs at least for 5 years (long-term monitoring; Figure 4). Of these monitoring studies (both short

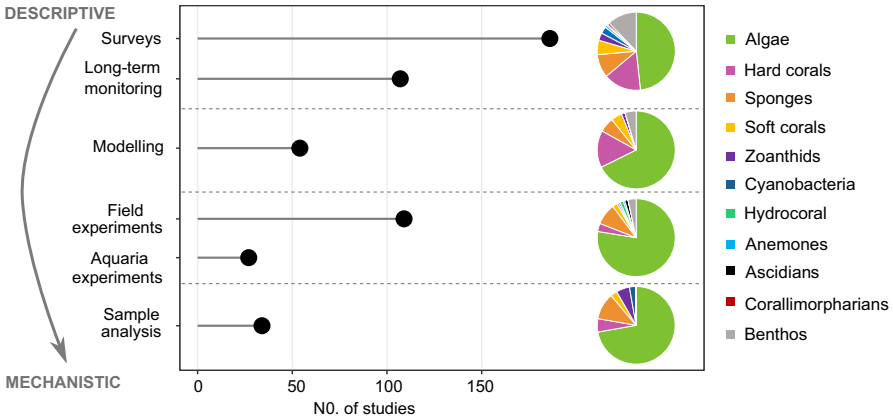

FIGURE 4 Number of studies using the different methodologies identified, with the relative proportion investigating the distinct benthic organisms. Long-term monitoring was considered when surveys of a site were done for at least 5 years. The category sample analysis represents studies where samples from benthic organisms (e.g. in field or aquaria experiments) were taken and further processed to study underlying processes (e.g. microbial communities, chemical cues, nutrient cycling)

and long-term), only 12% considered more than three alternative organism categories simultaneously (displayed in Figure 4 as benthos category), 47% of the studies focused on changes in hard coral and algal cover, 15% on changes within hard coral morphologies or genus, and only 6% and 9% on changes in soft coral and sponge cover, respectively. Changes in zoanthids, cyanobacteria, hydrocorals, anemones, ascidians and corallimorpharians were investigated in less than 5% of studies (Figure 4). Overall, these proportions were highly similar for both surveys (<5 years) and long-term monitoring studies (>5 years; Figure 4).

Less used were methodologies that examine processes/mechanisms leading to changes in benthic communities. Field and aquaria experiments (26% in total) were mostly used to investigate the role of specific drivers in species succession or to investigate changes in biological variables under specific conditions, whereas modelling (10%) was used to predict biological responses under different contexts (e.g. drivers or triggers, species configurations). Finally, 7% of the studies investigated specific response and feedback mechanisms through coupling experiments with the collection and analysis of benthic samples (e.g. implications on nutrient cycling, role of microbial communities or chemical cues in competition success).

Overall, studies investigating non-algal changes were mostly descriptive, highlighting an important gap in mechanistic studies (e.g. modelling, experiments, and sample analysis). For example, 75% of the experimental studies investigated coral-algal changes, but only 2% examined processes that potentially lead to soft-coral changes (Figure 4). Such studies are vital to shed light on the drivers of these changes, their implications on coral reef functioning and whether recovery might be possible. For example, recovery from algal phase shifts by restoring top-down and bottom-up control processes has been discussed (Hughes et al., 2010; Idjadi et al., 2010; McClanahan et al., 2011). However, although, such recovery has been observed in some instances (Idjadi et al., 2010), many studies have identified feedback mechanisms that reinforce algal dominance and prevent shift reversal towards coral-dominated communities (Johns et al., 2018). Higher algal densities not only display direct negative effects on corals through more frequent interactions—which can lead to coral disease (Nugues et al., 2004) and tissue damage through allelopathy and microbial mechanisms (Barott et al., 2012; Rasher & Hay, 2010; Roach et al., 2020)—but can also disrupt several ecosystem-scale processes. For example, high algal densities can inhibit coral settlement (Chong-Seng et al., 2014; Webster et al., 2015), promote environmental heterotrophic bacteria (Haas et al., 2016) and suppress herbivory processes (Dell et al., 2016; Hoey & Bellwood, 2011), all of which reinforce algal dominance and prevent coral reef recovery. Some preliminary studies suggest other alternative organisms, such as cyanobacteria or soft corals, might also establish reinforcing mechanisms like coral settlement inhibition (Kuffner & Paul, 2004; Maida et al., 1995). However, these feedback mechanisms remain highly unexplored, severely limiting our understanding of the persistence of these alternative communities.

4.2 | Limitations and perspectives in studying coral reef benthic communities

Although surveys are key in identifying community changes, the use of different metrics and approaches to quantify communities can introduce essential biases in identifying and thus understanding shifts towards certain alternative organisms. Traditionally, two-dimensional (2D) relative cover assessments have been mostly used to monitor coral reef status and changes in benthic communities. However, although these techniques have the advantage to be easily implemented, they have been criticized for their oversimplification of structurally complex reefs, leading to biased quantification of benthic groups (Brito-Millán et al., 2019; Kornder et al., 2021). For example, a recent study on the island of Curaçao (Tropical Atlantic) showed that using 'traditional' 2D relative cover assessments, reefs were dominated by non-calcifying phototrophs (i.e. macro- and turf algae, benthic cyanobacterial mats; 52%) and scleractinian corals (32%), with relatively low cover of sponges (1.6%). But a 3D estimate of these reef surfaces, including the concealed 'cryptic' surfaces

(e.g. overhangs, crevices, cavities), which comprised approximately half of the total reef surface, decreased the relative dominance of non-calcifying phototrophs and corals to 25% and 11% respectively, and now showed a dominance of sponges (20%) and calcifying algae (19%; Kornder et al., 2021). Moreover, the largest difference compared with traditional 2D cover surveys was observed in biomass (e.g. ash-free dry weight or organic carbon content) estimates: reefs were then dominated by sponges (52%) and scleractinian corals (27%), with only 3% of non-calcifying phototrophs (Kornder et al., 2021).

Concealed cavity dwelling organisms or 'coelobites' (Choi & Ginsburg, 1983; e.g. calcifying algae, (excavating) sponges, tunicates, polychaetes) are tremendously underestimated in coral reef community surveys, as was also found for Red-Sea reefs (Richter et al., 2001; Wunsch et al., 2000). In addition, the relative contribution of erect organisms to total reef benthos, such as massive sponges and soft corals are undervalued in projected surface cover estimates. The importance of cryptic communities has also been recognized within the global ARMS project (www.oceanarms.org), where standardized three-dimensional collectors are used to attract both encrusting species (corals, algae, etc.) and motile organisms. This approach revealed that organismal groups underrepresented in common surveys (i.e. Porifera, Arthropoda, Annelida) dominate coral reef communities across the globe (Pearman et al., 2018; Vicente et al., 2021). Studies exploring community changes towards many of these organisms are in most cases non-existent or severely inaccurate since baseline studies on the contribution of these organisms to the total reef community are largely lacking. Cryptic communities are found to be important in the cycling of resources on coral reefs, for example, the cycling of dissolved organic matter (DOM) through the sponge loop (de Goeij & van Duyl, 2007; de Goeij et al., 2013), and the regeneration of inorganic nutrients (DiSalvo, 1974; Tribble et al., 1988). Cryptic habitats could also serve as a refuge for non-coral invertebrates, which can become dominant on the reef following natural or anthropogenic disturbances (e.g. increase in cover of the sponge *Mycale laevis* following the reduction in sponge predators, Loh & Pawlik, 2009; Loh et al., 2015), eventually leading to alternative communities. However, the reported 'flattening' of reefs (Alvarez-Filip et al., 2009; Magel et al., 2019) due to a loss of structurally complex organisms (e.g. branching corals or algae), can also lead to a loss of ecological function attributed to cryptic organisms (Kornder et al., 2021; Newman et al., 2015). Therefore, it is pivotal to include cryptic communities in general benthic surveys to understand how reefs will develop in the future.

Emerging new technological advances have the potential to facilitate and increase the repeatability of coral reef monitoring efforts, but also to assess some of the aforementioned survey limitations (reviewed in Madin et al., 2019 and Obura et al., 2019). Automated survey platforms (e.g. Autonomous Underwater Vehicle [AUVs], Unmanned Airborne Vehicles [UAVs], satellite imaging) allow to expand the spatial and depth range coverage of coral reefs surveyed. However, the precision of these methods, although continuously improving, does not yet allow the identification of benthic organisms up to the family level (Allen Coral Atlas, 2020; Madin et al., 2019; Murfit et al., 2017). In contrast, the combination of diving/snorkelling surveys using Structure from Motion (SfM) photogrammetry and underwater hyperspectral imagery allow for fine-scale (≤1 mm to 1–2 cm resolution) three-dimensional (3D) investigation of benthic reef communities, including previously overlooked benthic organisms (Chennu et al., 2017; d'Urban Jackson et al., 2020; Kornder et al., 2021; Rossi et al., 2020). The creation of 3D visualization models via SfM enables detailed analyses of benthic reef community dynamics, such as changes in growth rates and the outcome of species competition over larger spatial scales than possible by traditional monitoring methods (Lange & Perry, 2020; Olinger et al., 2021). Another example of new imagery technology is the so-called HyperDiver system that is able to gather information-rich observations of benthic communities by recording visual and hyperspectral imagery and collecting data on seawater chemistry, photosynthetic irradiance and estimations about the abundance of photopigments, which can provide important information on reef health (Chennu et al., 2017). However, the accessibility to new technologies in low- and middle-income countries as well as the further development of automated imaging processing tools will be critical to standardize reef monitoring methods, to include cryptic organisms, and to support faster analyses of the vast amount of generated survey data (Madin et al., 2019).

In order to understand the effects of external drivers on the resilience of coral reefs and their sensitivity to community changes, monitoring of coral reef benthos alone is, however, not enough. To unravel the drivers and feedback mechanisms behind benthic community changes, long-term reef observations need to be coupled with monitoring environmental parameters (e.g. temperature, turbidity, nutrients) and mechanistic studies (e.g. modelling, experiments). The Moorea Coral Reef Long-Term Ecological Research (MCR LTER, http://mcr.lternet.edu), which was established in 2004 to study the key mechanisms that modulate ecosystem processes and structure, is a successful example of a program to advance the knowledge of coral benthic community changes (Adam et al., 2021). The MCR LTER combines long-term monitoring of coral reefs around the island of Moorea (French Polynesia, Eastern Indo-Pacific) with modelling and experiments (both in the field and in aquaria) with the aim to investigate coral reef community changes in relation to different global (e.g. climate change) and local (e.g. nutrient enrichment) disturbances (Donovan et al., 2020; Edmunds et al., 2020). However, as highlighted previously, coral reefs display high heterogeneity, and the mechanisms identified in the Eastern Indo-Pacific with its lower coral richness and coral functional redundancy might not be transferable to other regions. Therefore, more comprehensive programs such as the MCR LTER are urgently needed in other biogeographic regions, but establishing such a set-up requires vast resources, which might not be available in most low and Middle-Income countries where most coral reefs are located. This could be, however, achieved by expanding large coral reef monitoring efforts, such as the Global Coral Reef Monitoring Network (GCRMN, https://gcrmn.net/) or the MERMAID Global Database (https://datamermaid.org/)

to incorporate more mechanistic evaluation of the reefs studied. One approach could be collaborations of local scientists teaming up with designated expert panels and institutions strong in financial and human resources. Ideally, such initiatives should be established in the major tropical geographic realms (Tropical Atlantic, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific and Tropical Eastern Pacific) in order to evaluate coral reef benthic community changes on a global scale.

5 | CONCLUSIONS AND FUTURE DIRECTIONS

As the restructuring of tropical coral reef communities towards different and perhaps emergent non-hard-coral-dominated communities becomes inevitable at many locations, there is an urgent need to better understand the dynamics, ecological functions and societal impacts of these new communities. The dynamics and fate of Anthropocene reefs are increasingly driven by the socioeconomic context, which interacts with the natural biophysical setting (Williams & Graham, 2019; Williams et al., 2019), resulting in multiple community types, with different functional implications. Most of the coral reef community shift research to date has focused on the study of coral-algal community changes, which have been popularly considered as the golden standard of a reef's 'degraded state'. Here, we argue that the higher number of studies on the Tropical Atlantic has likely directed scientific research towards the study of coral-algal shifts, whilst overlooking other alternative communities. Furthermore, we show for the first time that soft-coral dominated reefs were the most abundant alternative community in different biogeographic regions, including the hotspot of marine biodiversity (Central Indo-Pacific province). This finding is particularly important, since knowledge on how soft-coral dominated reefs function and what services they provide is extremely limited, and local communities in many of these areas are amongst the most dependent on coral reef ecosystem services such as coral reef fisheries (Eddy et al., 2021).

As previously highlighted by Bruno et al. (2009), most of the management activities to prevent and reverse coral reef benthic changes have been focusing on conserving or restoring top-down and bottom-up processes (i.e. protecting fish and especially herbivore stocks and preventing nutrient enrichment). Whilst these initiatives are very important and may enable protecting key functional species (e.g. species that might limit algal proliferation; Bellwood et al., 2006b; Burkepile & Hay, 2011; Dang et al., 2020; Kuempel & Altieri, 2017), there is still an extremely poor understanding on the mechanisms that drive and reinforce non-algal alternative communities (González-Rivero et al., 2012). Therefore, a better understanding of the drivers, reinforcing mechanisms and the persistence of non-algal alternative communities is urgently required to design appropriate conservation approaches. Mechanistic studies using models and experiments need to be expanded (from the classical triangle 'coral-algae-fish') to incorporate other biological organisms (e.g. sponges and soft corals) and their interactions. Only by understanding the highly multifaceted interactions amongst the different coral reef organisms, we will gain insights on how, where and why coral reefs are changing.

In order to better identify and detect the aforementioned alternative communities, benthic monitoring also needs to move forward in adopting new technologies and techniques. The most commonly used 2D surveys, which only consider projected percentage cover, overlooking cryptobenthic and underestimating erect communities, has important limitations and potential bias on identifying and understanding coral reef benthic changes. This is a limitation often encountered when studying structurally complex ecosystems (i.e. coral reefs, terrestrial forests), and on which researchers are currently working to propose alternative methods that can be widely employed and standardized to provide much more accurate community metrics (Ransome et al., 2017; Rossi et al., 2021). Furthermore, the determination of the sizes or standing stocks of coral reef organisms is only a part of the puzzle to understand how coral reefs function. Understanding the biogeochemical cycling of resources (e.g. fluxes of carbon, nitrogen, phosphorus or certain (in)organic substances) through the ecosystem is also vital. Thereto, assessing the biomass of reef organisms and communities is more important than the relative cover. However, the relatively easy, fast and cost-effective traditional 2D surveys do still provide important information on the 'health' state of reefs (e.g. the relative hard coral to algae or other alternative organisms cover). The inclusion of so far largely ignored hidden or cryptic communities is also highly recommended in future studies, as these communities are markedly different (hence, likely have very different ecological functions) than visible or exposed reef communities (de Goeij et al., 2013; Kornder et al., 2021). The current 'flattening' of reefs will have, at present largely unknown, ecological consequences as cryptic communities, with largely understudied ecological functions, may disappear accordingly. Studies assessing coral reef trajectories and recovery after disturbances should incorporate a functional assessment of the communities as recent studies have shown that cover estimates or alpha diversity measures can mask important changes (McWilliam et al., 2020; Reverter et al., 2021; Richardson et al., 2018). Furthermore, novel threats, such as the increase of pathogens linked to climate change or anthropogenic substances (e.g. emerging persistent organic pollutants, microplastics) and their interactions need to be considered as they might also play a role in benthic community changes (Lamb et al., 2018; Maynard et al., 2015; Reichert et al., 2021).

Finally, it is not only vital to identify different alternative communities and mechanisms that lead to alternative communities, but to understand how these new configurations will affect reef functioning and services. For example, how sessile benthic changes will affect mobile organisms' communities (e.g. vagile invertebrates or fish) and key processes such as larval recruitment, survival and replenishment, which affect simultaneously reef functions, reef resilience and the ecosystem services provided. Whilst these aspects have been widely studied on coral-algal shifts (Ainsworth & Mumby, 2015; Hempson et al., 2018; Pisapia et al., 2019; Robinson et al.,

2019), very few studies have tackled these questions in non-algal alternative communities (Cruz et al., 2015).

ACKNOWLEDGEMENTS

This research was funded by an Alexander von Humboldt postdoctoral fellowship to M.R. Open access funding enabled and organized by ProjektDEAL.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Miriam Reverter and Peter J. Schupp conceived the initial idea. Miriam Reverter collected, analysed the data and wrote the first draft. All authors (Miriam Reverter, Stephanie B. Helber, Sven Rohde, Jasper M. de Goeij and Peter J. Schupp) contributed to the ideas and the writing of the manuscript.

DATA AVAILABILITY STATEMENT

The data used in this work is openly available at https://doi.org/10.6084/m9.figshare.15022800.

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REFERENCES

Adam, T. C., Burkepile, D. E., Holbrook, S. J., Carpenter, R. C., Claudet, J., Loiseau, C., Thiault, L., Brooks, A. J., Washburn, L., & Schmitt, R. J. (2021). Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: Implications for coral to algae phase shifts. *Ecological Applications*, *31*(1), e2227. https://doi.org/10.1002/eap.2227

Adjeroud, M., Kayal, M., Iborra-Cantonnet, C., Vercelloni, J., Bosserelle, P., Liao, V., Chancerelle, Y., Claudet, J., & Penin, L. (2018). Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Scientific Reports*, *8*(1), 9680. https://doi.org/10.1038/s41598-018-27891-3

Ainsworth, C. H., & Mumby, P. J. (2015). Coral–algal phase shifts alter fish communities and reduce fisheries production. *Global Change Biology*, *21*(1), 165–172. https://doi.org/10.1111/gcb.12667

Allen Coral Atlas. (2020). Imagery, maps and monitoring of the world's tropical coral reefs. https://doi.org/10.5281/zenodo.3833242

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3019–3025. https://doi.org/10.1098/rspb.2009.0339

Arnold, T. W. (2010). Uninformative parameters and using Akaike's Information Criterion. *Journal of Wildlife Management*, *74*, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Asch, R. G., Cheung, W. W. L., & Reygondeau, G. (2018). Future marine ecosystem drivers, biodiversity, and fisheries maximum catch potential in Pacific Island countries and territories under climate change. *Marine Policy*, *88*, 285–294. https://doi.org/10.1016/j.marpol.2017.08.015

Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J., & Graham, N. A. J. (2018). The future of hyperdiverse tropical ecosystems. *Nature*, *559*(7715), 517–526. https://doi.org/10.1038/s41586-018-0301-1

Barott, K. L., Rodriguez-Mueller, B., Youle, M., Marhaver, K. L., Vermeij, M. J. A., Smith, J. E., & Rohwer, F. L. (2012). Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1655–1664. https://doi.org/10.1098/rspb.2011.2155

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Baum, G., Januar, I., Ferse, S. C. A., Wild, C., & Kunzmann, A. (2016). Abundance and physiology of dominant soft corals linked to water quality in Jakarta Bay, Indonesia. *PeerJ*, *4*, e2625. https://doi.org/10.7717/peerj.2625

Beger, M., Sommer, B., Harrisson, P. L., Smith, S. D. A., & Pandolfi, J. M. (2014). Conserving potential coral reef refuges at high latitudes. *Diversisty and Distributions*, *20*, 245–257. https://doi.org/10.1111/ddi.12140

Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, *1*(7), 376–382.

Bell, J. J., Rovellini, A., Davy, S. K., Taylor, M. W., Fulton, E. A., Dunn, M. R., Bennett, H. M., Kandler, N. M., Luter, H. M., & Webster, N. S. (2018). Climate change alterations to ecosystem dominance: How might sponge-dominated reefs function. *Ecology*, *99*, 1920–1931. https://doi.org/10.1002/ecy.2446

Bellwood, D. R., Hoey, A. S., Ackermann, J. L., & Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, *12*(9), 1587–1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bellwood, D. R., Hughes, T. P., & Hoey, A. S. (2006). Sleeping functional group drives coral-reef recovery. *Current Biology*, *16*(24), 2434–2439. https://doi.org/10.1016/j.cub.2006.10.030

Bennett, S., & Bellwood, D. R. (2011). Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series*, *426*, 241–252. https://doi.org/10.3354/meps09016

Bestelmeyer, B. T., Ellison, A. M., Fraser, W. R., Gorman, K. B., Holbrook, S. J., Laney, C. M., Ohman, M. D., Peters, D. P. C., Pillsbury, F. C., Rassweiler, A., Schmitt, R. J., & Sharma, S. (2011). Analysis of abrupt transitions in ecological systems. *Ecosphere*, *2*(12), art129. https://doi.org/10.1890/ES11-00216.1

Biggerstaff, A., Jompa, J., & Bell, J. J. (2017). Increasing benthic dominance of the phototrophic sponge *Lamellodysidea herbacea* on a sedimented reef within the Coral Triangle. *Marine Biology*, *164*(12), 220. https://doi.org/10.1007/s00227-017-3253-3

Biggerstaff, A., Smith, D. J., Jompa, J., & Bell, J. J. (2015). Photoacclimation supports environmental tolerance of a sponge to turbid low-light conditions. *Coral Reefs*, *34*(4), 1049–1061. https://doi.org/10.1007/s00338-015-1340-9

Biggerstaff, A., Smith, D. J., Jompa, J., & Bell, J. J. (2017). Metabolic responses of a phototrophic sponge to sedimentation supports transitions to sponge-dominated reefs. *Scientific Reports*, *7*(1), 2725. https://doi.org/10.1038/s41598-017-03018-y

Biggs, R., Carpenter, S. R., & Brock, W. A. (2009). Turning back from the brink: Detecting and impending regime shift in time to avert it. *Proceedings of the National Academy of Science of the United States of America*, *106*, 826–831. https://doi.org/10.1073/pnas.0811729106

Biggs, R., Peterson, G. D., & Rocha, J. C. (2018). The Regime Shifts Database: A framework for analyzing regime shifts in

social-ecological systems. *Ecology and Society*, *23*(3). https://doi.org/10.5751/ES-10264-230309

Bonaldo, R. M., & Hay, M. E. (2014). Seaweed-coral interactions: Variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PlosOne*, *9*(1), e85786. https://doi.org/10.1371/journal.pone.0085786

Braulik, G., Wittich, A., Macaulay, J., Kasuga, M., Gordon, J., Davenport, T. R. B., & Gillespie, D. (2017). Acoustic monitoring to document the spatial distribution and hotspots of blast fishing in Tanzania. *Marine Pollution Bulletin*, *125*, 360–366. https://doi.org/10.1016/j.marpolbul.2017.09.036

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*, *9*(2), 56–71. https://doi.org/10.32614/RJ-2017-046

Brito-Millán, M., Vermeij, M. J. A., Alcantar, E. A., & Sandin, S. A. (2019). Coral reef assessments based on cover alone mask active dynamics of coral communities. *Marine Ecology Progress Series*, *630*, 55–68. https://doi.org/10.3354/meps13128

Bruno, J. F., Sweatman, H., Precht, W. F., Selig, E. R., & Schutte, V. G. W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance. *Ecology*, *90*, 1478–1484. https://doi.org/10.1890/08-1781.1

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2011). *Reefs at risk*. Revisited. World Resources Institute, The Nature Conservancy, WorldFish Center, International Coral Reef Action Network, UNEP World Conservation Monitoring Centre and Global Coral Reef Monitoring Network.

Burkepile, D. E., & Hay, M. E. (2011). Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs*, *30*(2), 351–362. https://doi.org/10.1007/s00338-011-0726-6

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Cerutti, J. M. B., Burt, A. J., Haupt, P., Bunbury, N., Mumby, P. J., & Shcaepman-Strub, D. (2020). Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. *Coral Reefs*, *39*, 15–26. https://doi.org/10.1007/s00338-019-01853-1

Chan, A., & Hodgson, P. A. (2017). A systematic analysis of blast fishing in South-East Asia and possible solutions. *IEEE Underwater Technology*, *2017*, 1–6. https://doi.org/10.1109/UT.2017.7890330

Chaves-Fonnegra, A., Riegl, B., Zea, S., Lopez, J. V., Smith, T., Brandt, M., & Gilliam, D. S. (2018). Bleaching events regulate shifts from corals to excavating sponges in algae-dominated reefs. *Global Change Biology*, *24*(2), 773–785. https://doi.org/10.1111/gcb.13962

Cheal, A. J., MacNeil, M. A., Cripps, E., Emslie, M. J., Jonker, M., Schaffelke, B., & Sweatman, H. (2010). Coral–macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs*, *29*(4), 1005–1015. https://doi.org/10.1007/s00338-010-0661-y

Chennu, A., Färber, P., De'ath, G., de Beer, D., & Fabricius, K. E. (2017). A diver-operated hyperspectral imaging and topographic surveying system for automated mapping of benthic habitats. *Scientific Reports*, *7*, 7122. https://doi.org/10.1038/s41598-017-07337-y

Choi, D. R., & Ginsburg, R. N. (1983). Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida Reef Tract. *Coral Reefs*, *2*(3), 165–172. https://doi.org/10.1007/BF00336723

Chong-Seng, K. M., Graham, N. A. J., & Pratchett, M. S. (2014). Bottlenecks to coral recovery in the Seychelles. *Coral Reefs*, *33*, 449–461. https://doi.org/10.1007/s00338-014-1137-2

Cinner, J. E., Adger, W. N., Allison, E. H., Barnes, M. L., Brown, K., Cohen, P. J., Gelcich, S., Hicks, C. C., Hughes, T. P., Lau, J., Marshall, N. A., & Morrison, T. H. (2018). Building adaptive capacity to climate change in tropical coastal communities. *Nature Climate Change*, *8*(2), 117–123. https://doi.org/10.1038/s41558-017-0065-x

Cloern, J. E., Abreu, P. C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J. O. R., Kahru, M., Sherwood, E. T., Xu, J., & Yin, K. (2016). Human activities and climate variability drive fast-paced change across the world's estuarine–coastal ecosystems. *Global Change Biology*, *22*(2), 513–529. https://doi.org/10.1111/gcb.13059

Connell, S. D., Fernandes, M., Burnell, O. W., Doubleday, Z. A., Griffin, K. J., Irving, A. D., Leung, J. Y. S., Owen, S., Russell, B. D., & Falkenberg, L. J. (2017). Testing for thresholds of ecosystem collapse in seagrass meadows. *Conservation Biology*, *31*(5), 1196–1201. https://doi.org/10.1111/cobi.12951

Conversi, A., Dakos, V., Gårdmark, A., Ling, S., Folke, C., Mumby, P. J., Greene, C., Edwards, M., Blenckner, T., Casini, M., Pershing, A., & Möllmann, C. (2015). A holistic view of marine regime shifts. *Philosophical Transactions of the Royal Society B Biological Sciences*, *370*(1659), 20130279. https://doi.org/10.1098/rstb.2013.0279

Cooper, G. S., Willcock, S., & Dearing, J. A. (2020). Regime shifts occur disproportionately faster in larger ecosystems. *Nature Communications*, *11*(1), 1175. https://doi.org/10.1038/s41467-020-15029-x

Cowan, P. F. (2014). Historical factors that have shaped the evolution of tropical reef fishes: A review of phylogenies, biogeography and remaining questions. *Frontiers in Genetics*, *5*, 394. https://doi.org/10.3389/fgene.2014.00394

Cruz, I. C. S., Loiola, M., Albuquerque, T., Reis, R., de Anchieta C. C. Nunes, J., Reimer, J. D., Mizuyama, M., Kikuchi, R. K. P., & Creed, J. C. (2015). Effect of phase shift from corals to zoantharia on reef fish assemblages. *PLoS One*, *10*(1), e0116944. https://doi.org/10.1371/journal.pone.0116944

Cruz, I. C. S., Meira, V. H., de Kikuchi, R. K. P., & Creed, J. C. (2016). The role of competition in the phase shift to dominance of the zoanthid *Palythoa cf. variabilis* on coral reefs. *Marine Environmental Research*, *115*, 28–35. https://doi.org/10.1016/j.marenvres.2016.01.008

Cruz, I. C. S., Waters, L. G., Kikuchi, R. K. P., Leão, Z. M. A. N., & Turra, A. (2018). Marginal coral reefs show high susceptibility to phase shift. *Marine Pollution Bulletin*, *135*, 551–561. https://doi.org/10.1016/j.marpolbul.2018.07.043

d'Urban Jackson, T., Williams, G. J., Walker-Springett, G., & Davies, A. J. (2020). Three-dimensional digital mapping of ecosystems: A new era in spatial ecology. *Proceedings in the Royal Society B: Biological Sciences*, *287*, 20192383. https://doi.org/10.1098/rspb.2019.2383

Dang, V. D. H., Cheung, P.-Y., Fong, C.-L., Mulla, A. J., Shiu, J.-H., Lin, C.-H., & Nozawa, Y. (2020). Sea urchins play an increasingly important role for coral resilience across reefs in Taiwan. *Frontiers in Marine Science*, *7*(1025). https://doi.org/10.3389/fmars.2020.581945

Darling, E. S., McClanahan, T. R., Maina, J., Gurney, G. G., Graham, N. A. J., Januchowski-Hartley, F., Cinner, J. E., Mora, C., Hicks, C. C., Maire, E., Puotinen, M., Skirving, W. J., Adjeroud, M., Ahmadia, G., Arthur, R., Bauman, A. G., Beger, M., Berumen, M. L., Bigot, L., … Mouillot, D. (2019). Social environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nature Ecology and Evolution*, *3*, 1341–1350. https://doi.org/10.1038/s41559-019-0953-8

de Bose, J. L., Nuttal, M. F., Hickerson, E. L., & Schmahl, G. P. (2013). A high-latitude coral community with an uncertain future: Stetson Bank, northwestern Gulf of Mexico. *Coral Reefs*, *32*, 255–267. https://doi.org/10.1007/s00338-012-0971-3

de Goeij, J. M., Lesser, M. P., & Pawlik, J. R. (2017). Nutrient fluxes and ecological functions of coral reef sponges in a changing ocean. In J. Carballo & J. Bell (Eds.), *Climate change, ocean acidification and sponges* (pp. 373–410). Springer.

de Goeij, J. M., & van Duyl, F. C. (2007). Coral cavities are sinks of dissolved organic carbon (DOC). *Limnology and Oceanography*, *52*, 2608–2617. https://doi.org/10.4319/lo.2007.52.6.2608

de Goeij, J. M., van Oevelen, D., Vermeij, M. J. A., Osinga, R., Middelburg, J. J., de Goeij, A. F. P. M., & Admiraal, W. (2013). Surviving in a marine desert: The sponge loop retains resources within coral reefs. *Science*, *342*(6154), 108–110. https://doi.org/10.1126/science.1241981

de Oliveira Soares, M. (2020). Marginal reef paradox: A possible refuge from environmental changes? *Ocean and Coast Management*, *185*, 105063. https://doi.org/10.1016/j.ocecoaman.2019.105063

Dell, C. L. A., Longo, G. O., & Hay, M. E. (2016). Positive feedbacks enhance macroalgal resilience on degraded coral reefs. *PLoS One*, *11*, e0155049. https://doi.org/10.1371/journal.pone.0155049

Diamond, S. E., Nichols, L. M., McCoy, N., Hirsch, C., Pelini, S. L., Sanders, N. J., Ellison, A. M., Gotelli, N. J., & Dunn, R. R. (2012). A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology*, *93*(11), 2305–2312. https://doi.org/10.1890/11-2296.1

Dinsdale, E. A., & Rohwer, F. (2011). Fish or germs? Microbial dynamics associated with changing trophic structures on coral reefs. In Z. Dubinsky & N. Stambler (Eds.), *Coral reefs: An ecosystem in transition* (pp. 231–240). Springer. https://doi.org/10.1007/978-94-007-0114-4_16

DiSalvo, L. H. (1974). Soluble phosphorus and amino-nitrogen release to the sea water during recoveries of coral reefs regenerative sediments. In A. M. Cameron & B. M. Campbell (Eds.), *Proceedings of the 2nd International Coral Reef Symposium* (pp. 11–19).

Dixson, D. L., Abrego, D., & Hay, M. E. (2014). Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery. *Science*, *345*(6199), 892–897. https://doi.org/10.1126/science.1255057

Done, T. J., Dayton, P. K., Dayton, A. E., & Steger, R. (1991). Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. *Coral Reefs*, *9*(4), 183–192. https://doi.org/10.1007/BF00290420

Donovan, M. K., Adam, T. C., Shantz, A. A., Speare, K. E., Munsterman, K. S., Rice, M. M., Schmitt, R. J., Holbrook, S. J., & Burkepile, D. E. (2020). Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *Proceedings of the National Academy of Science of the United States of America*, *117*, 5351–5357. https://doi.org/10.1073/pnas.1915395117

Doropoulos, C., Roff, G., Zupan, M., Nestor, V., Isechall, A. L., & Mumby, P. J. (2014). Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. *Coral Reefs*, *33*, 613–623. https://doi.org/10.1007/s00338-014-1149-y

Dudgeon, S. R., Aronson, R. B., Bruno, J. F., & Precht, W. F. (2010). Phase shifts and stable states on coral reefs. *Marine Ecology Progress Series*, *413*, 201–216. https://doi.org/10.3354/meps08751

Duursma, R. (2017). bootpredictlme4 GitHub repository. https://github.com/remkoduursma

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in coral reefs to provide ecosystem services. *OneEarth*, *4*, 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016

Edmunds, P. J., Doo, S. S., & Carpenter, R. C. (2020). Year-long effects of pCO_2 on the community structure of a tropical forereef assembled in outdoor flumes. *ICES Journal of Marine Science*, *77*, 1055–1065. https://doi.org/10.1093/icesjms/fsaa015

Fong, C. R., Gaynus, C. J., & Carpenter, R. C. (2020). Complex interactions among stressors evolve over time to drive shifts from short turfs to macroalgae on tropical reefs. *Ecosphere*, *11*(5), e03130. https://doi.org/10.1002/ecs2.3130

Ford, A. K., Van Hoytema, N., Moore, B. R., Pandihau, L., Wild, C., & Ferse, S. C. A. (2017). High sedimentary oxygen consumption indicates that sewage input from small islands drives benthic community shifts on overfished reefs. *Environmental Conservation*, *44*(4), 405–411. https://doi.org/10.1017/S0376892917000054

Fox, H. E., Harris, J. L., Darling, E. S., Ahmadia, G. N., Estradivari, & Razak, T. B. (2019). Rebuilding coral reefs: Success (and failure) of 16 years after low-cost, low-tech restoration. *Restoration Ecology*, *27*(4), 862–869. https://doi.org/10.1111/rec.12935

Fox, H. E., Mous, P. J., Pet, J. S., Muljadi, A. H., & Caldwell, R. L. (2005). Experimental assessment of coral reef rehabilitation following blast fishing. *Conservation Biology*, *19*(1), 98–107. https://doi.org/10.1111/j.1523-1739.2005.00261.x

Fox, H. E., Pet, J. S., Dahuri, R., & Caldwell, R. L. (2003). Recovery in rubble fields: Long-term impacts of blast fishing. *Marine Pollution Bulletin*, *46*, 1024–1031. https://doi.org/10.1016/S0025-326X(03)00246-7

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

González-Barrios, F. J., Cabral-Tena, R. A., & Alvarez-Filip, L. (2021). Recovery disparity between coral cover and the physical functionality of reefs with impaired coral assemblages. *Global Change Biology*, *27*(3), 640–651. https://doi.org/10.1111/gcb.15431

González-Rivero, M., Ferrari, R., Schönberg, C. H. L., & Mumby, P. J. (2012). Impacts of macroalgal competition and parrotfish predation on the growth of a common bioeroding sponge. *Marine Ecology Progress Series*, *444*, 133–142. https://doi.org/10.3354/meps09424

Guzman, C., Atrigenio, M., Shinzato, C., Aliño, P., & Conaco, C. (2019). Warm seawater temperature promotes substrate colonization by the blue coral, *Heliopora coerulea*. *PeerJ*, *7*, e7785. https://doi.org/10.7717/peerj.7785

Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y. W., Maughan, H., Pantos, O., Roach, T. N. F., Sanchez, S. E., Silveira, C. B., Sandin, S., Smith, J. E., & Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*, *1*(6), 16042. https://doi.org/10.1038/nmicrobiol.2016.42

Harii, S., Hongo, C., Ishihara, M., Ide, Y., & Kayanne, H. (2014). Impacts of multiple disturbances on coral communities at Ishigaki island, Okinawa, Japan, during a 15 year survey. *Marine Ecology Progress Series*, *509*, 171–180. https://doi.org/10.3354/meps10890

Hatcher, B. G. (1984). A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. *Coral Reefs*, *3*(4), 199–204. https://doi.org/10.1007/BF00288255

Hempson, T. N., Graham, N. A. J., MacNeil, M. A., Bodin, N., & Wilson, S. K. (2018). Regime shifts shorten food chains for mesopredators with potential sublethal effects. *Functional Ecology*, *32*(3), 820–830. https://doi.org/10.1111/1365-2435.13012

Hoey, A. S., & Bellwood, D. R. (2011). Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? *Ecology Letters*, *14*(3), 267–273. https://doi.org/10.1111/j.1461-0248.2010.01581.x

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, *265*(5178), 1547–1551. https://doi.org/10.1126/science.265.5178.1547

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*(7656), 82–90. https://doi.org/10.1038/nature22901

Hughes, T. P., Graham, N. A. J., Jackson, J. B. C., Mumby, P. J., & Steneck, R. S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*, *25*, 633–642. https://doi.org/10.1016/j.tree.2010.07.011

Hughes, T. P., Linares, C., Dakos, V., van de Leemput, I. A., & van Nes, E. H. (2013). Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology & Evolution*, *28*(3), 149–155. https://doi.org/10.1016/j.tree.2012.08.022

Hughes, T. P., Reed, D. C., & Boyle, M.-J. (1987). Herbivory on coral reefs: Community structure following mass mortalities of sea urchins.

Journal of Experimental Marine Biology and Ecology, *113*(1), 39–59. https://doi.org/10.1016/0022-0981(87)90081-5

Idjadi, J. A., Haring, R. N., & Precht, W. F. (2010). Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs. *Marine Ecology Progress Series*, *403*, 91–100. https://doi.org/10.3354/meps08463

Inoue, S., Kayanne, H., Yamamoto, S., & Kurihara, H. (2013). Spatial community shift from hard to soft corals in acidified water. *Nature Climate Change*, *3*(7), 683–687. https://doi.org/10.1038/nclimate1855

IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. E. S. Brondizio, J. Settele, S. Díaz, & H. T. Ngo (Eds.). IPBES Secretariat.

Johns, K. A., Emslie, M. A., Hoey, A. S., Osborne, K., Jonker, M. J., & Cheal, A. J. (2018). Macroalgal feedbacks and substrate properties maintain a coral regime shift. *Ecosphere*, *9*, e02349. https://doi.org/10.1002/ecs2.2349

Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., & Wilmshurst, J. M. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science*, *356*(6335), 270–275. https://doi.org/10.1126/science.aam9317

Knowlton, N. (2004). Multiple "stable" states in and the conservation of marine ecosystems. *Progress in Oceanography*, *60*, 387–396. https://doi.org/10.1016/j.pocean.2004.02.011

Kornder, N. A., Cappelletto, J., Mueller, B., Zalm, M. J. L., Martinez, S. J., Vermeij, M. J. A., Huisman, J., & de Goeij, J. M. (2021). Implications of 2D versus 3D surveys to measure the abundance and composition of benthic coral reef communities. *Coral Reefs*, *40*, 1137–1153. https://doi.org/10.1007/s00338-021-02118-6

Kuempel, C. D., & Altieri, A. H. (2017). The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Scientific Reports*, *7*, 39670. https://doi.org/10.1038/srep39670

Kuffner, I. B., & Paul, V. J. (2004). Effects of the benthic cyanobacterium *Lyngbya majuscula* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs*, *23*, 455–458. https://doi.org/10.1007/s00338-004-0416-8

Kulbicki, M., Parravicini, V., Bellwood, D. R., Arias-Gonzalez, E., Chabanet, P., Floeter, S. R., Friedlander, A., McPherson, J., Myers, R. E., Vigliola, L., & Mouillot, D. (2013). Global biogeographic of coral reef fishes: A hierarchical quantitative delineation of regions. *PLoS One*, *8*(12), e81847. https://doi.org/10.1371/journal.pone.0081847

Lamb, J. B., Willis, B. L., Fiorenza, E. A., Couch, C. S., Howard, R., Rader, D. N., True, J. D., Kelly, L. A., Ahmad, A., Jompa, J., & Harvell, C. D. (2018). Plastic waste associated with disease on coral reefs. *Science*, *359*, 460–462. https://doi.org/10.1126/science.aar3320

Lange, I. D., & Perry, C. T. (2020). A quick, easy and non-invasive method to quantify coral growth rates using photogrammetry and 3D model comparisons. *Methods in Ecology and Evolution*, *11*, 714–726. https://doi.org/10.1111/2041-210X.13388

Lesser, M. P., & Slattery, M. (2020). Will coral reef sponges be winners in the Anthropocene? *Global Change Biology*, *26*(6), 3202–3211. https://doi.org/10.1111/gcb.15039

Lin, Y. V., & Denis, V. (2019). Acknowledging differences: Number, characteristics, and distribution of marine benthic communities along Taiwan coast. *Ecosphere*, *10*(7), e02803. https://doi.org/10.1002/ecs2.2803

Loh, T.-L., McMurray, S. E., Henkel, T. P., Vicente, J., & Pawlik, J. R. (2015). Indirect effects of overfishing on Caribbean reefs: Sponges overgrow reef-building corals. *PeerJ*, *3*, e901. https://doi.org/10.7717/peerj.901

Loh, T.-L., & Pawlik, J. R. (2009). Bitten down to size: Fish predation determines growth form of the Caribbean coral reef sponge *Mycale laevis*. *Journal of Experimental Marine Biology and Ecology*, *374*, 45–50. https://doi.org/10.1016/j.jembe.2009.04.007

Madin, E. M. P., Darling, E. S., & Hardt, M. J. (2019). Emerging technologies and coral reef conservation: Opportunities, challenges, and moving forward. *Frontiers in Marine Science*, *6*, 727. https://doi.org/10.3389/fmars.2019.00727

Magel, J. M., Burns, J. H., Gates, R. D., & Baum, J. K. (2019). Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. *Scintific Reports*, *9*, 2512. https://doi.org/10.1038/s41598-018-37713-1

Maida, M., Sammarco, P. W., & Coll, J. C. (1995). Effects of soft corals on scleractinian coral recruitment. I: Directional allelopathy and inhibition of settlement. *Marine Ecology Progress Series*, *121*, 191–202. https://doi.org/10.3354/meps121191

Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M. G., Field, C. B., & Knowlton, N. (2020). Climate change and ecosystems: Threats, opportunities and solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190104. https://doi.org/10.1098/rstb.2019.0104

Maynard, J., van Hooidonk, R., Eakin, C. M., Puotinen, M., Garren, M., Williams, G., Heron, S. F., Lamb, J., Weil, E., Willis, B., & Harvell, C. D. (2015). Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. *Nature Climate Change*, *5*, 688–694. https://doi.org/10.1038/nclimate2625

McClanahan, T. R., Atewerberhan, M., Darling, E. S., Graham, N. A. J., & Muthiga, N. A. (2014). Biogeography and change among regional coral communities accross the Western Indian Ocean. *PLoS One*, *9*, e93385. https://doi.org/10.1371/journal.pone.0093385

McClanahan, T. R., Muthiga, N. A., & Coleman, R. A. (2011). Testing for top-down control: Can post-disturbance fisheries closures reverse algal dominance? *Aquatic Conservation*, *21*, 658–675. https://doi.org/10.1002/aqc.1225

McManus, J. W., Meñez, L. A. B., Kesner-Reyes, K. N., Vergara, S. G., & Ablan, M. C. (2000). Coral reef fishing and coral-algal phase shifts: Implications for global reef status. *ICES Journal of Marine Science*, *57*(3), 572–578. https://doi.org/10.1006/jmsc.2000.0720

McWilliam, M., Hoogenboom, M. O., Baird, A. H., Kuo, C.-Y., Madin, J. S., & Hughes, T. P. (2018). Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 3084–3089. https://doi.org/10.1073/pnas.1716643115

Mcwilliam, M., Pratchett, M. S., Hoogenboom, M. O., & Hughes, T. P. (2020). Deficits in functional trait diversity following recovery on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20192628. https://doi.org/10.1098/rspb.2019.2628

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *The BMJ*, *339*, b2535. https://doi.org/10.1136/bmj.b2535

Mumby, P. J., Steneck, R. S., Adjeroud, M., & Arnold, S. N. (2016). High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. *Oikos*, *125*, 644–655. https://doi.org/10.1111/oik.02673

Mumby, P. J., Steneck, R. S., & Hastings, A. (2013). Evidence for and against the existence of alternate attractors on coral reefs. *Oikos*, *122*(4), 481–491. https://doi.org/10.1111/j.1600-0706.2012.00262.x

Murfitt, S. L., Allan, B. M., Bellgrove, A., Rattray, A., Young, M. A., & Ierodiaconou, D. (2017). Applications of unmanned aerial vehicles in intertidal reef monitoring. *Scientific Reports*, *7*, 10259. https://doi.org/10.1038/s41598-017-10818-9

Neumann, M., Mues, V., Moreno, A., Hasenauer, H., & Seidl, R. (2017). Climate variability drives recent tree mortality in Europe. *Global Change Biology*, *23*(11), 4788–4797. https://doi.org/10.1111/gcb.13724

Newman, S. P., Meesters, E. H., Dryden, C. S., Williams, S. M., Sanchez, C., Mumby, P. J., & Polunin, N. V. C. (2015). Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology*, *84*, 1678–1689. https://doi.org/10.1111/1365-2656.12429

Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: Beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series*, *376*, 295–306. https://doi.org/10.3354/meps07815

Nugues, M. M., Smith, G. W., van Hooidonk, R. J., Seabra, M. I., & Bak, R. P. M. (2004). Algal contact as a trigger for coral disease. *Ecology Letters*, *7*, 919–923. https://doi.org/10.1111/j.1461-0248.2004.00651.x

Obura, D. O., Aeby, G., Amornthammarong, N., Appeltans, W., Bax, N., Bishop, J., Brainard, R. E., Chan, S., Fletcher, P., Gordon, T. A. C., Gramer, L., Gudka, M., Halas, J., Hendee, J., Hodgson, G., Huang, D., Jankulak, M., Jones, A., Kimura, T., … Wongbusarakum, S. (2019). Coral reef monitoring, reef assessment technologies, and ecosystem-based management. *Frontiers in Marine Science*, *6*, 580. https://doi.org/10.3389/fmars.2019.00580

Obura, D., Gudka, M., Rabi, F. A., Gian, S. B., Bijoux, J., Freed, S., Maharavo, J., Mwaura, J., Porter, S. N., Sola, E., Wickel, J., Yahya, S. A., & Ahamada, S. (2017). Coral reef status report for the Western Indian Ocean. Global Coral Reef Monitoring Network (GCRMN)/International Coral Reef Initiative (ICRI), pp. 144.

Olinger, L. K., Chaves-Fonnegra, A., Enochs, I. C., & Brandt, M. E. (2021). Three competitors in three dimensions: Photogrammetry reveals rapid overgrowth of coral during multispecies competition with sponges and algae. *Marine Ecology Progress Series*, *657*, 109–121. https://doi.org/10.3354/meps13579

Pearman, J. K., Leray, M., Villalobos, R., Machida, J., Berumen, M. L., Knowlton, N., & Carvalho, S. (2018). Cross-shelf investigation of coral reef cryptic benthic organisms reveals diversity patterns of the hidden majority. *Scientific Reports*, *8*, 8090. https://doi.org/10.1038/s41598-018-26332-5)

Pisapia, C., Hochberg, E. J., & Carpenter, R. (2019). Multi-decadal change in reef-scale production and calcification associated with recent disturbances on a Lizard Island reef flat. *Frontiers in Marine Science*, *6*(575). https://doi.org/10.3389/fmars.2019.00575

Plass-Johnson, J. G., Taylor, M. H., Husain, A. A. A., Teichberg, M. C., & Ferse, S. C. A. (2016). Non-random variability in functional composition of coral reef fish communities along an environmental gradient. *PLoS One*, *11*(4), e0154014. https://doi.org/10.1371/journal.pone.0154014

Porter, S. N., Branch, G. M., & Sink, K. J. (2013). Biogeographic patterns on shallow subtidal reefs in the Western Indian Ocean. *Marine Biology*, *160*, 1271–1283. https://doi.org/10.1007/s00227-013-2179-7

Pulsford, S. A., Lindenmayer, D. B., & Driscoll, D. A. (2016). A succession of theories: Purging redundancy from disturbance theory. *Biological Reviews*, *91*(1), 148–167. https://doi.org/10.1111/brv.12163

Ransome, E., Geller, J. B., Timmers, M., Leray, M., Mahardini, A., Sembiring, A., Collins, A. G., & Meyer, C. P. (2017). The importance of standardization for biodiversity comparisons: A case study using autonomous reef monitoring structures (ARMS) and metabarcoding to measure cryptic diversity on Mo'orea coral reefs, French Polynesia. *PLoS One*, *12*(4), e0175066. https://doi.org/10.1371/journal.pone.0175066

Rasher, D. B., & Hay, M. E. (2010). Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 9683–9688. https://doi.org/10.1073/pnas.0912095107

Rasher, D. B., Stout, E. P., Engel, S., Kubanek, J., & Hay, M. E. (2011). Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences USA*, *108*(43), 17726–17731. https://doi.org/10.1073/pnas.1108628108

Reichert, J., Tirpitz, V., Anand, R., Bach, K., Knopp, J., Schubert, P., Wilke, T., & Ziegler, M. (2021). Interactive effects of microplastic pollution and heat stress on reef-building corals. *Environmental Pollution*, *290*, 118010. https://doi.org/10.1016/j.envpol.2021.118010

Reverter, M., Jackson, M., Rohde, S., Moeller, M., Bara, R., Lasut, M. T., Reinach, M. S., & Schupp, P. J. (2021). High taxonomic resolution surveys and functional diversity analysis reveal multiple benthic regimes in North Sulawesi (Indonesia). *Scientific Reports*, *11*, 16554. https://doi.org/10.1038/s41598-021-95905-8

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., Eurich, J. G., & Hoey, A. S. (2018). Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology*, *24*(7), 3117–3129. https://doi.org/10.1111/gcb.14119

Richter, C., Wunsch, M., Rasheed, M., Kötter, I., & Badran, M. I. (2001). Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature*, *413*(6857), 726–730. https://doi.org/10.1038/35099547

Roach, T. N. F., Little, M., Arts, M. G. I., Huckeba, J., Haas, A. F., George, E. E., Quinn, R. A., Cobián-Güemes, A. G., Naliboff, D. S., Silveira, C. B., Vermeij, M. J. A., Kelly, L. W., Dorrestein, P. C., & Rohwer, F. (2020). A multiomic analysis of in situ coral–turf algal interactions. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(24), 13588–13595. https://doi.org/10.1073/pnas.1915455117

Robinson, J. P. W., Wilson, S. K., Robinson, J., Gerry, C., Lucas, J., Assan, C., Govinden, R., Jennings, S., & Graham, N. A. J. (2019). Productive instability of coral reef fisheries after climate-driven regime shifts. *Nature Ecology and Evolution*, *3*(2), 183–190. https://doi.org/10.1038/s41559-018-0715-z

Roe, D. (2019). Biodiversity loss more than an environmental emergency. *Lancet Planetary Health*, *3*(7), e287–e289. https://doi.org/10.1016/S2542-5196(19)30113-5

Roff, G., Doropoulos, C., Zupan, M., Rogers, A., Steneck, R. S., Golbuu, Y., & Mumby, P. J. (2015). Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia*, *178*(4), 1193–1203. https://doi.org/10.1007/s00442-015-3282-x

Roff, G., & Mumby, P. J. (2012). Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution*, *27*(7), 404–413. https://doi.org/10.1016/j.tree.2012.04.007

Rossi, P., Castagnetti, C., Capra, A., Brooks, A. J., & Mancini, F. (2020). Detecting change in coral reef 3D structure using underwater photogrammetry: critical issues and performance metrics. *Applied Geomatis*, *12*(Suppl. 1), S3–S17. https://doi.org/10.1007/s12518-019-00263-w

Rossi, P., Ponti, M., Righi, S., Castagnetti, C., Simonini, R., Mancini, F. Agrafiotis, P., Bassani, L., Bruno, F., Cerrano, C., Cignoni, P., Corsini, M., Drap, P., Dubbini, M., Garrabou, J., Gori, A., Gracias, N., Ledoux, J.-B., Linares, C., … Capra, A. (2021). Needs and gaps in optical underwater technologies and methods for the investigation of marine animal forest 3D-tructural complexity. *Frontiers in Marine Science*, *8*(171). https://doi.org/10.3389/fmars.2021.591292

Sawall, Y., Jompa, J., Litaay, M., Maddusila, A., & Richter, C. (2013). Coral recruitment and potential recovery of eutrophised and blast fishing impacted reefs in Spearmonde Archipelago, Indonesia. *Marine Pollution Bulletin*, *74*, 374–382. https://doi.org/10.1016/j.marpolbul.2013.06.022

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution*, *18*(12), 648–656. https://doi.org/10.1016/j.tree.2003.09.002

Schleyer, M. H., & Porter, S. N. (2018). Chapter one – Drivers of soft coral and stony coral community distribution on the high-latitude coral reefs of South Africa. In C. Sheppard (Ed.), *Advances in marine biology* (Vol. *80*, pp 1–55). Academic Press.

Schmitt, R. J., Holbrook, S. J., Davis, S. L., Brooks, A. J., & Adam, T. C. (2019). Experimental support for alternative attractors on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(10), 4372–4381. https://doi.org/10.1073/pnas.1812412116

Schoepf, V., Stat, M., Falter, J. L., & McCulloch, M. T. (2015). Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. *Scientific Reports*, *5*, 17639. https://doi.org/10.1038/srep17639

Schröder, A., Persson, L., & De Roos, A. M. (2005). Direct experimental evidence for alternative stable states: A review. *Oikos*, *110*(1), 3–19. https://doi.org/10.1111/j.0030-1299.2005.13962.x

Smith, J. E., Hunter, C. L., & Smith, C. M. (2010). The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia*, *163*, 497–507. https://doi.org/10.1007/s00442-009-1546-z

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A. L., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, *757*, 573–583. https://doi.org/10.1641/B570707

Stocks, G., Seales, L., Paniagua, F., Maehr, E., & Bruna, E. M. (2008). The geographical and institutional distribution of ecological research in the tropics. *Biotropica*, *40*(4), 397–404. https://doi.org/10.1111/j.1744-7429.2007.00393.x

Tebbett, S. B., Streit, R. P., & Bellwood, D. R. (2019). Expansion of a colonial ascidian following consecutive mass coral bleaching at Lizard Island, Australia. *Marine Environmental Research*, *144*, 125–129. https://doi.org/10.1016/j.marenvres.2019.01.007

Thinesh, T., Meenatchi, R., Jose, P. A., Kiran, G. S., & Selvin, J. (2019). Differential bleaching and recovery pattern of southeast Indian coral reef to 2016 global mass bleaching event: Ocurrence of stress-tolerant symbiont *Durusdinium* (Clade D) in corals in Palk Bay. *Marine Pollution Bulletin*, *145*, 287–294. https://doi.org/10.1016/j.marpolbul.2019.05.033

Tkachenko, K. S., Wu, B.-J., Fang, L.-S., & Fang, T.-Y. (2017). Dynamics of a coral reef community after mass mortality of branching *Acropora* corals and an outbreak of anemones. *Marine Biology*, *151*, 185–194. https://doi.org/10.1007/s00227-006-0467-1

Toth, L. T., Stathakopoulos, A., Kuffner, I. B., Ruzicka, R. R., Colella, M. A., & Shinn, E. A. (2019). The unprecedented loss of Florida's reef-building corals and the emergence of a novel coral-reef assemblage. *Ecology*, *100*(9), e02781. https://doi.org/10.1002/ecy.2781

Tribble, G. W., Sansone, F. J., Li, H.-Y., Smith, S. V., & Buddemeier, R. W. (1988). Material fluxes from a reef framework. In J. H. Choat (Ed.), *Proceedings of the 6th International Coral Reef Symposium* (pp. 577–582).

Van de Leemput, I. A., Hughes, T. P., van Nes, E. H., & Scheffer, M. (2016). Multiple feedbacks and the prevalence of alternate states on coral reefs. *Coral Reefs*, *35*, 857–865. https://doi.org/10.1007/s00338-016-1439-7

Vicente, J., Webb, M. K., Paulay, G., Rakchai, W., Timmers, M. A., Jury, C. P., Bahr, K., & Toonen, R. J. (2021). Unveiling hidden sponge biodiversity within the Hawaiian reef cryptofauna. *Coral Reefs*. https://doi.org/10.1007/s00338-021-02109-7

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Webster, F. J., Babcock, R. C., Van Keulen, M., & Loneragan, N. R. (2015). Macroalgae inhibits larval settlement and increases recruit mortality at Ningaloo Reef, Western Australia. *PLoS One*, *10*, e0124162. https://doi.org/10.1371/journal.pone.0124162

Wee, H. B., Reimer, J. D., Safuan, M., Saidin, J., Tan, C. H., & Bachok, Z. (2017). Zoantharian abundance in coral reef benthic communities at Terengganu Islands, Malaysia. *Regional Studies in Marine Science*, *12*, 58–63. https://doi.org/10.1016/j.rsma.2017.02.005

Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santana-Garcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., … Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. https://doi.org/10.1126/science.aad8745

Williams, G. J., & Graham, N. A. J. (2019). Rethinking coral reef functional futures. *Functional Ecology*, *33*(6), 942–947. https://doi.org/10.1111/1365-2435.13374

Williams, G. J., Graham, N. A. J., Jouffray, J.-B., Norström, A. V., Nyström, M., Gove, J. M., Heenan, A., & Wedding, L. M. (2019). Coral reef ecology in the Anthropocene. *Functional Ecology*, *33*(6), 1014–1022. https://doi.org/10.1111/1365-2435.13290

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

Work, T. M., Aeby, G. S., & Maragos, J. E. (2008). Phase shift from a coral to a corallimorph-dominated reef associated with a shipwreck on Palmyra atoll. *PLoS One*, *3*(8), e2989. https://doi.org/10.1371/journal.pone.0002989

Wunsch, M., Al-Moghrabi, S. M., & Kötter, I. (2000). Communities of coral reef cavities in Jordan, Gulf of Aqaba (Red Sea). *Proceedings of the 9th International Coral Reef Symposium*, *9*, 23–27.

Yu, W., Wang, W., Yu, K., Wang, Y., Huang, X., Huang, R., Liao, Z., Xu, S., & Chen, X. (2019). Rapid decline of a relatively high latitude coral assemblage at Weizhou Island, northern South China Sea. *Biodiversity Conservation*, *28*, 3925–3949. https://doi.org/10.1007/s10531-019-01858-w

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How to cite this article: Reverter, M., Helber, S. B., Rohde, S., de Goeij, J. M., & Schupp, P. J. (2022). Coral reef benthic community changes in the Anthropocene: Biogeographic heterogeneity, overlooked configurations, and methodology. *Global Change Biology*, 28, 1956–1971. https://doi.org/10.1111/gcb.16034