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Corals at the edge of environmental limits: A new conceptual framework to re-define marginal and extreme coral communities

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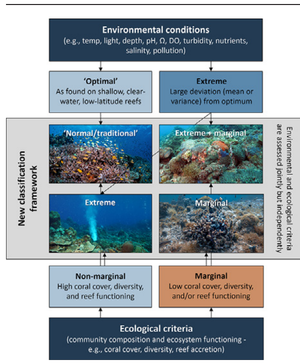
HIGHLIGHTS

- Extreme reefs are characterised by large deviations from optimal abiotic conditions.
- Marginal reefs have altered coral cover, community composition and ecosystem functioning.
- Extreme reefs can be adaptive refugia and natural laboratories for future ocean conditions.
- Marginal and extreme reefs differ in their conservation needs and priorities.
- Both are underrepresented in global conservation initiatives and need our attention.

GRAPHICAL ABSTRACT



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ABSTRACT

The worldwide decline of coral reefs has renewed interest in coral communities at the edge of environmental limits because they have the potential to serve as resilience hotspots and climate change refugia, and can provide insights into how coral reefs might function in future ocean conditions. These coral communities are often referred to as marginal or extreme but few definitions exist and usage of these terms has therefore been inconsistent. This creates significant challenges for categorising these often poorly studied communities and synthesising data across locations. Furthermore, this impedes our understanding of how coral communities can persist at the edge of their environmental limits and the lessons they provide for future coral reef survival. Here, we propose that marginal and extreme coral communities are related but distinct and provide a novel conceptual framework to redefine them. Specifically, we define coral reef extremeness solely based on environmental conditions (i.e., large deviations from optimal conditions in

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terms of mean and/or variance) and marginality solely based on ecological criteria (i.e., altered community composition and/or ecosystem functioning). This joint but independent assessment of environmental and ecological criteria is critical to avoid common pitfalls where coral communities existing outside the presumed optimal conditions for coral reef development are automatically considered inferior to coral reefs in more traditional settings. We further evaluate the differential potential of marginal and extreme coral communities to serve as natural laboratories, resilience hotspots and climate change refugia, and discuss strategies for their conservation and management as well as priorities for future research. Our new classification framework provides an important tool to improve our understanding of how corals can persist at the edge of their environmental limits and how we can leverage this knowledge to optimise strategies for coral reef conservation, restoration and management in a rapidly changing ocean.

Contents

1. Introduction

Most organisms have discrete tolerance limits to abiotic factors such as temperature, light, pH, and oxygen concentrations. The substantial heterogeneity in abiotic conditions across land- and seascapes often creates specialised populations of organisms living in conditions at the edge of their environmental tolerance limits (Hardie and Hutchings, 2010; Sexton et al., 2009). These extreme and/or marginal populations are of interest to researchers as they hold clues to physiological tolerance limits and environmental drivers of organismal abundance, species distributions, and evolutionary processes (Bridle and Vines, 2007; Brown et al., 1995). In an era of rapid climate change, populations of organisms at the edge of their environmental limits can be particularly useful in understanding how populations in more favourable habitats may respond to future climate scenarios (Kolzenburg, 2022), as conditions in some of these marginal or extreme environments match those expected under climate change.

Coral reefs are biodiversity hotspots of high socio-economic importance because they provide ecosystem services such as fisheries, tourism and coastal protection to millions of people worldwide (Fezzi et al., 2023; Fisher et al., 2015; Spalding et al., 2017). Yet, they are also one of the most threatened ecosystems under rapid climate change (e.g., Souter et al., 2021) because their primary ecosystem engineers - scleractinians corals - are highly sensitive to multiple climate change stressors. Ocean warming and marine heatwaves lead to mass bleaching events that result in coral mortality on regional to global scales (Hughes et al., 2019, 2018), while ocean acidification – a global decline in seawater pH – often decreases corals' ability to calcify and build reefs (Cornwall et al., 2021; Kornder et al., 2018). In addition, the loss of dissolved oxygen from ocean surface waters (ocean deoxygenation) and extreme low oxygen events (hypoxia) are increasingly recognized as a threat to tropical coral reefs (Altieri et al., 2017; Hughes et al., 2020). These global-scale climate change stressors further compound the multitude of stressors that directly threaten coral reefs on a local scale, including - but not limited to - invasive species, overfishing, coastal development, and associated declines in water quality (Harborne et al., 2017; Nalley et al., 2023, 2021). However, it is important to note that not all taxa present on coral reefs, or involved in the bioconstruction of the reef framework, are equally sensitive to these stressors, which has led to so-called phase shifts and dominance by non-coral taxa such as algae, sponges, soft corals or zoanthids (Bell et al., 2021; Dudgeon et al., 2010).

Despite the high ecological and socio-economic importance of coral reefs, they are in serious decline worldwide, with latest estimates indicating ~50 % loss of coral cover over the past 40 years (e.g., Tebbett et al., 2023). The global decline of coral reefs has renewed interest in environments where scleractinian corals persist at the edge of environmental limits to coral reef development (Burt et al., 2020; Camp et al., 2018a; Kleypas et al., 1999). In this review, we refer to them as "coral communities" instead of "coral reefs" because they encompass both accreting and non-accreting coral assemblages and may occur in biogenic (e.g., true coral reefs, coralline algal reefs, rhodolith beds) as well as non-biogenic reef environments (e.g., rocky reefs, sandstone reefs). We use this term in a broad sense where "coral community" is understood to include all taxa supported in these ecosystems. Importantly, these ecosystems may not necessarily be dominated by corals (e.g., corals growing on sponge reefs or in mangrove systems, Fig. S1f) and non-coral taxa such as coralline algae may be the main reef builders (Cornwall et al., 2023). We nevertheless refer to these ecosystems as coral communities due to our focus on scleractinian corals in this review.

The renewed interest in marginal and extreme coral communities is due to their potential to serve as (1) natural laboratories or "analogues" for future ocean conditions (Camp et al., 2019; Maggioni et al., 2021), (2) resilience hotspots that may harbor naturally stress-resistant coral species and/or communities (Palumbi et al., 2014; Riegl et al., 2012), and (3) refugia from climate change stressors (Kapsenberg and Cyronak, 2019; Kavousi and Keppel, 2017; Mies et al., 2020). The concepts of resistance and resilience are therefore key for understanding marginal and extreme coral communities, with resilience being the capacity of a system to resist and recover from a disturbance (Baumann et al., 2021; Holling, 1973). For example, thermally variable and extreme coral habitats, such as back-reef pools and intertidal habitats, have been shown to enhance heat tolerance of resident coral populations (Barshis et al., 2013; Safaie et al., 2018; Schoepf et al., 2020), while corals growing in the vicinity of CO_2 seeps can have traits that imply resistance to predicted future acidification levels (Agostini et al., 2021; Comeau et al., 2022; Wall et al., 2016). Examples for the refuge potential of marginal and extreme coral communities include turbid reefs which can act as potential short-term refugia from climate change because turbid waters mitigate coral bleaching during thermal stress events (Banha et al., 2020; Browne et al., 2019; Morgan et al., 2017; Sully and van Woesik, 2020). Marginal and extreme coral communities may also facilitate connectivity and gene flow across the seascape, with important implications for conservation and management (e.g., Studivan and Voss, 2018). Thus, while they are often less diverse and aesthetically less pleasing than clear-water coral reefs, they could play an important role in future coral persistence and have high research and conservation value. As coral ecosystems shift in species composition and structure, it is essential to understand future ecosystem functions (as defined by Brandl et al., 2019) and services in order to best manage and conserve these ecosystems and the services that they provide (Graham et al., 2014; Wilkinson, 2008).

Coral communities persisting at the edge of environmental limits have been referred to in the literature using a range of terms. Two of the most commonly used terms are "marginal" and "extreme" reefs, but the terms "variable" or "peripheral" reefs are also used (Camp et al., 2018a; Kleypas et al., 1999; Perry and Larcombe, 2003; Pratchett et al., 2013). However, while attempts have been made to offer definitions (Guinotte et al., 2003; Kleypas et al., 1999; Perry and Larcombe, 2003), this has proven difficult for several reasons (see section 2). Historically, the term marginal has been used for many decades in the context of coral reefs. In the early 1920s, Davis (1923) published a paper on the "marginal belts of the coral seas" which he defined as "having a probable width of about 5° between latitudes 25° and 30° north and south of the equator in the central and western parts of the Pacific Ocean". Some early research also used the term "marginal zone" to refer to the reef crest (Dryden, 1944; Hoffmeister, 1950). However, to the best of our knowledge, formal definitions of marginal reefs only followed in the late 1990s and early 2000s (see section 2).

In contrast to marginal reefs, the term "extreme reefs" has become popular mostly in recent years (Camp et al., 2018a; Rosser and Veron, 2011; Smith et al., 2017). However, it should be noted that several coral habitats have long been recognized to represent "extreme environments", including reef flat habitats (Coles et al., 1976; Glynn, 1968), the Persian/Arabian Gulf (e.g., Downing, 1985) and deep sea habitats (e.g., Raghukumar, 2017). The term extreme reefs is now increasingly used in the literature for shallow reef environments (see Burt et al., 2020; Camp et al., 2018a for maps of their distribution), with two special issues in scientific journals and two review articles dedicated to them in the last 5 years (Burt et al., 2020; Camp et al., 2018a). However, in contrast to marginal reefs, the term extreme reef has never been defined to our knowledge, particularly regarding any implied differences to marginal reefs. As a result, usage of the terms marginal and extreme has been inconsistent in the coral reef literature, with reviews on either type of reefs taking a very broad and inclusive approach (Camp et al., 2018a; Perry and Larcombe, 2003). For example, many reef systems mentioned in the first review on "natural extreme reef environments" (Camp et al., 2018a) have traditionally been included in previous definitions of marginal reefs (Guinotte et al., 2003; Kleypas et al., 1999; Perry and Larcombe, 2003), such as high-latitude reefs or turbid reefs. Similarly, another review has used the combined term "extreme and marginal reefs" (Burt et al., 2020), implying that these are similar yet somehow different reef types. The lack of clear definitions and inconsistent usage of these terms creates significant challenges for better understanding ecological dynamics and future trajectories of coral communities at the edge of their environmental limits. The goal of this review is therefore to revisit existing concepts of coral reef marginality and extremeness, and to provide a new conceptual framework that characterizes and classifies these important ecosystems in more detail and with greater consistency. This conceptual framework provides a new tool to improve our understanding of how corals can persist in a rapidly changing ocean and how we can leverage this knowledge to optimise strategies for coral reef conservation, restoration, and management.

2. Challenges in defining coral communities at the edge of environmental limits

Although formal definitions have been provided for marginal reefs, there is a lack of consensus regarding what marginality is (Guinotte et al., 2003; Kleypas et al., 1999; Perry and Larcombe, 2003). This has led to a range of criteria being used to define marginality (Table 1), including two definitions that focus exclusively on environmental conditions (Kleypas et al., 1999; Perry and Larcombe, 2003) and three definitions that focus more on ecological or community characteristics, either on their own or in combination with environmental criteria (Guinotte et al., 2003). Interestingly, one of these three definitions uses the term extreme, highlighting the challenges in defining coral communities at the edge of environmental limits.

One key challenge of defining marginal and extreme coral communities is that most definitions are subjective and implicitly require a reference point that compares marginal/extreme reefs to reefs in more traditional settings, hereafter referred to as 'normal' reefs (i.e., reefs in shallow, clear-water, tropical settings – see Fig. 1a). For example, Kleypas et al. (1999) defined marginal reefs as those "beyond 'normal' environmental limits of reef distribution". Yet, defining "normal environmental limits" or

Table 1
Existing definitions of "marginal" reefs. These definitions can be broadly separated into three groups: (1) definitions that only use environmental criteria, (2) definitions that only use ecological criteria, and (3) definitions that combine environmental and ecological criteria.

Reference	Definition
(1) Definitions using environmental criteria only	
Kleypas et al., 1999	Marginal reefs "exist near or beyond 'normal' environmental limits of reef distribution" or are defined "by their proximity to the minima or maxima of each variable".
Perry and Larcombe, 2003	"The term 'marginal' is used in a broad sense, to describe settings where coral communities or framework reefs occur either close to well-understood (or strongly perceived) environmental thresholds for coral survival (sensu Kleypas et al., 1999) or in areas characterised by 'suboptimal' or fluctuating environmental conditions."
(2) Definitions using ecological criteria only	
Guinotte et al., 2003 [a]	"Marginality may be defined in terms of organism and community condition (cover, composition, diversity, health) or metabolism."
(3) Definitions using both environmental and ecological criteria	
Guinotte et al., 2003 [b]	"Marginality may be defined in a purely statistical sense, identifying the subset of reef communities or conditions that are near the extreme of a particular suite of environmental variables or community conditions."
Guinotte et al., 2003 [c]	"Marginality may be defined on the basis of proximity to an environmental condition known or reasonably assumed, based on physiological or biogeographic evidence, to place an absolute limit on the occurrence of reef communities or key classes of reef organisms."

"well understood (or perceived) environmental thresholds" (Perry and Larcombe, 2003) is challenging due to a lack of high-quality data for many reef sites necessary to define environmental thresholds (see next paragraph). Although 'normal' reefs could refer to high diversity, high coral cover reefs typically found in shallow, clear, low-latitude settings, such a concept would be misleading for several reasons. For one, it is important to note that biodiversity encompasses not only taxonomic diversity but also phylogenetic and functional diversity (Le Bagousse-Pinguet et al., 2019). Second, high coral species richness may be a result of geographical proximity to centres of biodiversity, such as the Coral Triangle, as much as benign environmental conditions. In addition, reefs with high coral species richness and cover also exist in settings traditionally considered "sub-optimal", such as turbid, high-latitude or macrotidal environments (Fig. S1) (Browne et al., 2010; Richards et al., 2015; Sommer et al., 2014). Further, 'normal' reference reefs are also changing in composition and function as result of climate change impacts and local stressors, and hence these reference points may no longer represent what was once considered to be a pristine ecosystem. More broadly, current perceptions of what constitutes a healthy 'normal' coral reef are likely to be different from those of the 20th century due to the shifting baseline syndrome (but see Eddy et al., 2018; Knowlton and Jackson, 2008), which further complicates comparisons, and thus defining and identifying marginal and extreme coral communities.

A second related challenge of defining coral communities at the edge of their environmental limits is the lack of high-resolution environmental data for many, if not most, sites at relevant spatial and temporal scales (e.g., Camp et al., 2018a). Typically, only temperature is routinely measured locally because these measurements are easy and relatively inexpensive. In contrast, other environmental parameters (e.g., pH, aragonite/calcite saturation state, light, oxygen, turbidity, nutrients) that may be equally relevant as ecological drivers are often not assessed locally, likely due to a lack of low-cost, quality sensors that can be deployed for long time periods. Thus, adequate spatio-temporal resolution to assess the full extent of marginality or extremeness over daily/tidal/weekly/seasonal time scales is often missing. In addition, many of these coral communities are remote and often occur in environments that are highly variable over a range of spatio-temporal scales or otherwise logistically difficult to work in.

Third, limited interest in marginal and extreme coral communities (until recently) has resulted in the lack of historical baseline ecological data, and many sites are only now being discovered or measured. The term degraded, which is often applied to marginal coral communities, suggests that there has been a decline in reef health and function over time, but without appropriate baseline data, these assumptions may be incorrect. For example, some inshore turbid reefs of the Great Barrier Reef characterised by comparatively low coral species richness and cover have been considered degraded, yet palaeoecological studies have shown that they initiated and accreted in naturally turbid water conditions, and likely represent different and not degraded reef types (Perry et al., 2009). More coral community data, as well as high-resolution, long-term, multi-parameter abiotic datasets are therefore needed to improve our understanding of the environmental drivers of ecosystem structure and functioning in marginal and extreme coral communities and how they change over time.

The lack of a consensus on how to define marginal coral communities, combined with the lack of any definition for extreme communities, has resulted in inconsistent usage of these terms in the literature. This highlights that they likely mean different things to different people, and, as an increasing number of scientists are now studying these coral communities, it is necessary to (re-)define coral reef "marginality" and "extremeness". In this review, we provide a new conceptual framework that will allow for more detailed and consistent characterization and categorisation of these coral communities and specifically address the following five questions:

1. Are marginal and extreme reefs distinct types of coral communities existing at the edge of environmental limits?
2. Which criteria can be used to distinguish marginal and extreme coral communities?
3. Do marginal and extreme coral communities differ in their potential to serve as (i) natural "analogues" for future ocean conditions, (ii) resilience hotspots, and (iii) refugia? And do all sites in each category have the same potential, or is this site-specific?
4. What are the conservation and management priorities for marginal and extreme coral communities?
5. What are the priorities for future research to improve our understanding of marginal and extreme coral communities?

3. Are marginal and extreme reefs distinct types of coral communities existing at the edge of environmental limits?

Dictionary definitions of the terms marginal and extreme are generally different (Table 2), supporting the view that marginal and extreme coral communities should indeed represent distinct types of coral communities that exist at the edge of environmental limits. Definitions of marginal can be broadly grouped into two types, the first relating to extent, significance, and stature, and the second relating to spatial or geographical aspects. Specifically, marginal characterizes something that is "insignificant, minor or small" or "of little or less importance" as well as "relating to, or situated at, a margin or border" (Table 2). In contrast, extreme is defined as something that is "very large in amount or degree", "exceeding the ordinary, usual or expected" and "situated at the farthest possible point from a center" (Table 2). However, some overlap in meaning exists such as "situated at a margin or border" (marginal, Merriam Webster Dictionary) and "at the furthest point, especially from the center" (extreme, Cambridge Dictionary).

When examining existing definitions of marginal reefs (Table 1), it becomes clear that those focusing on environmental criteria (Guinotte et al., 2003; Kleypas et al., 1999; Perry and Larcombe, 2003) are generally more closely aligned with the meaning of extreme compared to marginal. Guinotte et al. (2003) even defined marginality as "reef communities or conditions that are near the *extreme* of a particular suite of environmental variables or community conditions" (emphasis added, definition [b]). In contrast, definitions that mostly rely on ecological criteria (e.g., Guinotte et al., 2003, definition [a]) appear more aligned with the meaning of marginal because community composition and ecosystem functioning of coral communities at the edge of environmental limits are often more "limited in extent, significance, or stature" (Merriam-Webster Dictionary, Table 2) compared to 'normal' reefs. We therefore argue that a new classification framework is required that re-defines extreme and marginal coral communities in a way that is more consistent with the defined meaning of these terms. We propose a new framework where (1) environmental criteria are

Table 2
Dictionary definitions of the terms "marginal" and "extreme". Only relevant definitions are listed for Merriam-Webster and Collins Dictionaries.

Dictionary	Marginal	Extreme
Cambridge	• very small in amount or effect • of little or less importance	• very large in amount or degree • very severe or bad • at the furthest point, especially from the centre
Merriam-Webster	• limited in extent, significance, or stature • not of central importance • of, relating to, or situated at a margin or border	• existing in a very high degree • going to great or exaggerated lengths • exceeding the ordinary, usual, or expected • situated at the farthest possible point from a center
Collins	• insignificant, minor, small • not considered central or important • of, in, on, or constituting a margin • close to a limit, especially a lower limit	• being of a high or of the highest degree or intensity • exceeding what is usual or reasonable; immoderate • very strict, rigid, or severe; or drastic • (prenominal) farthest or outermost in direction

assessed independently from ecological criteria, and (2) the term extreme is only applied to environmental conditions whereas marginal is only used for ecological criteria (Fig. 1, Table 3). In the following section, we discuss in more detail how the new classification framework can be used to differentiate marginal vs extreme coral communities using both environmental and ecological criteria.

4. Which criteria can be used to distinguish marginal and extreme coral communities?

4.1. Environmental criteria

4.1.1. Environmental extremeness

Key environmental parameters that influence the health of scleractinian corals and their ability to build reefs include, but are not limited to, temperature, light, pH, dissolved oxygen, salinity and water quality (e.g., nutrients, pollutants). Marginal and extreme coral communities are often characterised by “unfavourable” environmental conditions that deviate from what is traditionally considered optimal for the development of reefs built by scleractinian corals. While most people consider the warm, sunlit and nutrient-poor waters of shallow tropical reefs optimal, defining environmental limits for the development of reefs built by these corals – and thus, what constitutes extreme environmental conditions from a scleractinian coral point of view - remains challenging. Kleypas et al. (1999) identified five major physico-chemical factors as first-order determinants of global coral reef development and provided the following quantitative thresholds: weekly temperatures of 18–31.5 °C, salinities of 30–40 PSU, nutrient levels of <2 μmol L^{-1} nitrate and <0.4 μmol L^{-1} phosphate, light penetrating into depths >15 m, and an aragonite saturation state >3.5. Environments exceeding these values were considered “marginal” (sensu environmental marginality, Table 3). However, while this global-scale analysis represented a major step forward, resolution was limited to the spatial scale of one degree and the temporal scale of one month. Remote sensing products have become higher resolution since 1999 (moving from 1° x 1° resolution to 5 km × 5 km or even 350 m × 350 m resolution), but are still limited in their uses in nearshore areas, enclosed bays (with more land area in a single pixel than ocean), and across spatial scales <350 m. Additionally, the parameters available to monitor remotely do not fully encapsulate the parameters necessary for a holistic understanding of the complex dynamics of a coral ecosystem. Furthermore, renewed interest in coral communities at the edge of environmental limits and advances in logger technology have revealed the highly dynamic conditions that these communities are exposed to (e.g., Maggioni et al., 2021), yet limited data collected on multiple abiotic parameters at high frequency currently prevents a comprehensive analysis of the degree of extremeness encountered across these coral environments (Camp et al., 2018a; Zweifler et al., 2021). Therefore, until such data become more widely available, qualitative definitions of environmental extremeness must suffice.

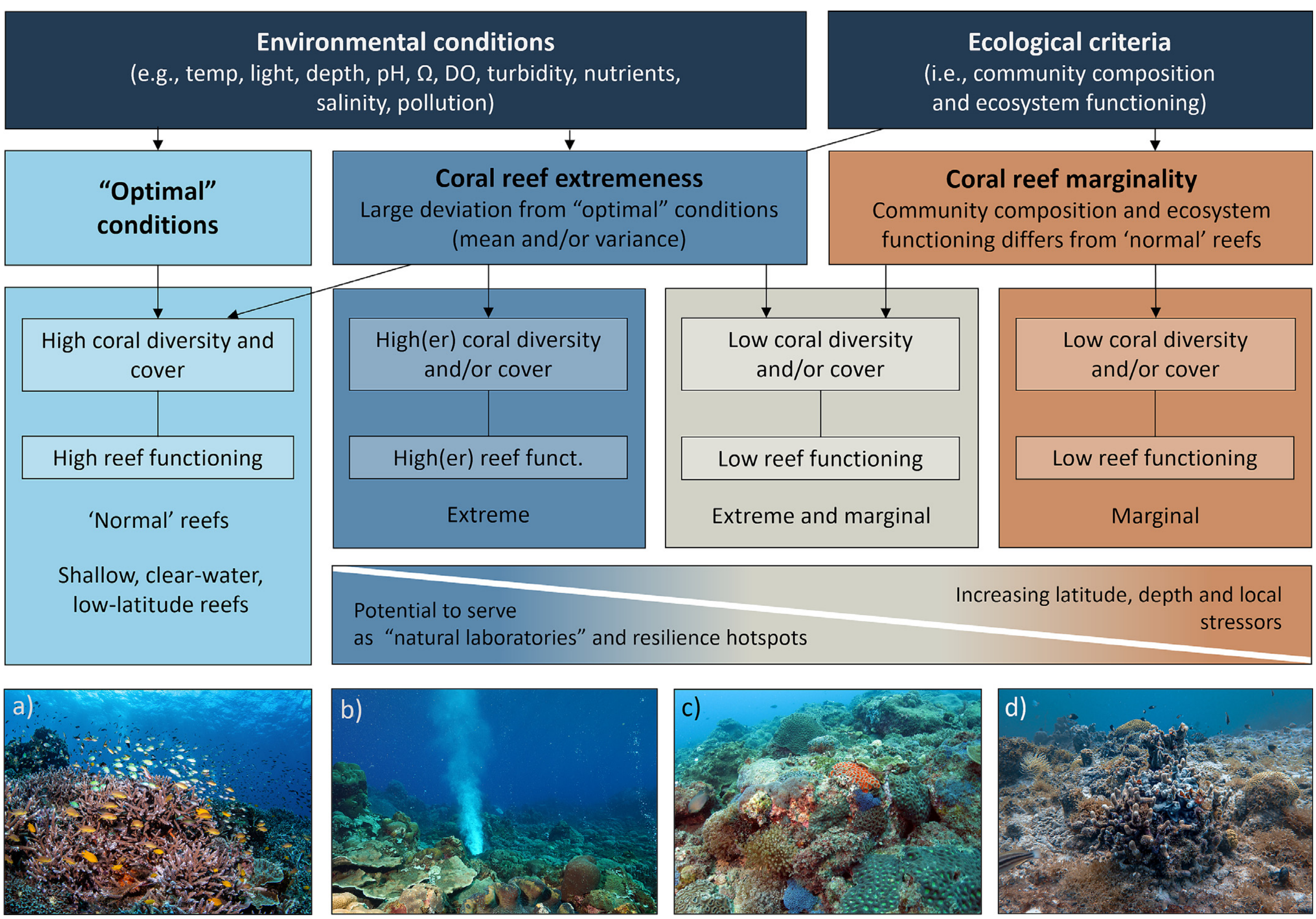

Fig. 1. A new classification framework to differentiate extreme versus marginal coral communities using environmental and ecological criteria. They are contrasted with ‘normal’ coral reefs that exist under optimal environmental conditions. Photos show illustrative examples of each type: (a) ‘normal’ coral reef in Indonesia (Credit: Brook Peterson | Ocean Image Bank), (b) extreme coral community near a CO_2 vent in Papua New Guinea (Credit: T. Shlesinger), (c) extreme and marginal high-latitude coral community at the Sunshine coast, Australia (Credit: B. Sommer), (d) marginal coral community surrounded by rubble and macroalgae, Curaçao, southern Caribbean (Credit: Lars ter Horst). For more examples, see Fig. S1. Note that extreme coral communities tend to have higher coral cover, diversity and reef functioning than marginal coral communities but these metrics may not be as high as on ‘normal’ reefs.

Table 3
Overview of existing versus new concepts of coral reef "marginality". Existing concepts (left column) can be broadly separated into three groups: (1) spatial/geographical marginality, (2) environmental marginality, and (3) ecological marginality. The right column relates these three existing concepts to the new conceptual framework presented in this review which defines coral reef extremeness solely based on environmental conditions and coral reef marginality solely based on ecological criteria.

Existing concepts of coral reef marginality	New framework (this review)
(1) Spatial/geographical marginality	
• defines marginality based on occurrence at high latitude (independent of environmental or ecological criteria)	• use of this concept is ***discouraged*** due to potential for confusion with other concepts of coral reef marginality
• key reference: Davis, 1923	
• consistent with the dictionary meaning of the term "marginal"	
(2) Environmental marginality	
• defines marginality based on presence of unfavourable or extreme abiotic conditions	• the new framework proposes to refer to this concept of marginality as ***coral reef extremeness***
• key references: Kleypas et al., 1999; Perry and Larcombe, 2003; Guinotte et al., 2003	
• more consistent with the dictionary meaning of the term "extreme"	
(3) Ecological marginality	
• defines marginality based on altered organism, community or ecosystem condition compared to reefs in shallow, clear-water, tropical settings	• the new framework proposes to refer to this concept as ***coral reef marginality***
• key reference: Guinotte et al., 2003	• structural marginality refers to aspects of ecosystem structure (e.g., coral cover, diversity, community composition)
• more consistent with the dictionary meaning of the term "marginal"	• functional marginality refers to aspects of ecosystem functioning (e.g., metabolism, reef growth)

Here, we define extreme environmental conditions as those that represent large deviations from "optimal" environmental conditions such as those outlined in Kleypas et al. (1999), both in terms of mean and/or variance (Fig. 1). This definition is closely aligned with existing definitions of coral reef marginality that relied on environmental criteria (Table 1) (Guinotte et al., 2003; Kleypas et al., 1999; Perry and Larcombe, 2003) and focuses on the general environmental conditions present at a location, thus excluding stochastic extreme events such as cyclones or marine heatwaves. Assessment of whether a given coral community is exposed to extreme environmental conditions therefore necessarily remains somewhat subjective at present. However, as more data become available, future global analyses should focus on defining quantitative thresholds at the reef scale, both for mean and variance. For the latter, this could include metrics such as a certain standard deviation from the mean or coefficient of variation (e.g., Camp et al., 2019), daily or seasonal range (e.g., Safaie et al., 2018), or skewness and kurtosis (Ateweberhan and McClanahan, 2010; Zinke et al., 2018). For example, some of the most extreme daily ranges have been reported for macrotidal reef flats and tide pools (up to 11 °C, 1.4 pH units and 440 μM dissolved oxygen) (Cornwall et al., 2018; Gruber et al., 2017; Schoepf et al., 2020; Smit and Glassom, 2017), while coefficients of variation were typically an order of magnitude higher (>0.01–0.02) for these three parameters in mangrove lagoons compared to nearby reference reefs (Camp et al., 2019). Due to the lack of quantitative thresholds at present, we strongly encourage scientists to state explicitly why they consider environmental conditions to be extreme at a given location and to make their data publicly available for future re-use. Furthermore, in the following we discuss aspects that should be considered when determining whether a coral community should be classified as extreme.

Environmental extremeness can occur over a range of both temporal and spatial scales. On a temporal scale, many coral communities at the edge of environmental limits exist in a range of settings where environmental parameters vary over diel, tidal, seasonal, episodical, lunar or other temporal scales. In these environments, extreme conditions are only reached for certain periods of time (i.e., large deviations from optimal conditions in terms of variance) which is contrasted by coral communities that are characterised by chronic or permanent extreme conditions (i.e., a shift in mean conditions). How these parameters vary over time as well as the extent of their variance has important implications for biological processes and can impose severe restrictions on coral (reef) health and functioning. On a diel/tidal scale, communities with highly fluctuating extreme conditions include, for example, macrotidal reefs in NW Australia (Fig. S1b) (Cornwall et al., 2018; Schoepf et al., 2015) or corals growing in mangrove-dominated environments (Fig. S1f) (e.g., Camp et al., 2019; Stewart et al., 2022) and semi-enclosed bays (Fig. S1c) (Camp et al., 2017; Golbuu et al., 2016; Maggioni et al., 2021). In contrast, the Persian-Arabian Gulf is characterised by the most extreme seasonal variability (e.g., Riegl and Purkis, 2012). Examples for coral communities exposed to chronically extreme conditions include corals growing in the vicinity of CO_2 vents (Fig. 1b) (Comeau et al., 2022; Fabricius et al., 2011; Pichler et al., 2019), turbid reefs in the Southwestern Atlantic (Santana et al., 2023; Teixeira et al., 2021) and on the inshore Great Barrier Reef (Browne et al., 2013a; Morgan et al., 2016), and eutrophied and/or polluted urban reefs (Browne et al., 2015; Guzman et al., 2020; Pizarro et al., 2017). While all these examples feature extreme environmental conditions, it is important to note that some – but not all - of them also have significantly altered organism and community condition compared to 'normal' reefs (see below), and should then be classified as extreme *and* marginal (Table S1).

Environmental extremeness also varies substantially over a range of spatial scales, including at the regional scale (e.g., latitude) and at the local scale with changes in depth, currents and microclimate or due to anthropogenic influences (e.g., eutrophication, sedimentation, pollution). Mesophotic coral communities, in particular, represent some of the most extreme coral habitats. Hermatypic corals (sensu Schuhmacher and Zibrowius, 1985) can occur over large depth ranges (e.g., Lesser et al., 2010), extending coral reef development into greater depths (30–150 m) in many locations despite limiting light levels, altered light spectra and low pH and aragonite saturation state (Lesser et al., 2018). These extreme conditions at greater depths typically result in reduced coral cover, species richness and altered reef functioning compared to 'normal' reefs (Kahng et al. 2010; Lesser et al., 2018) but not always (Hoeksema et al., 2017; Pyle et al., 2016). Similar to deep or mesophotic coral communities, high-latitude reefs and coral communities are among those most commonly and most consistently referred to as marginal reefs (e.g., Celliers and Schleyer, 2002; Perry and Larcombe, 2003; Soares et al., 2020). However, they illustrate the existing confusion about terms such as marginal, extreme and peripheral – as well as the controversy surrounding marginal reefs being considered degraded or the "poor cousins" of 'normal' reefs (Perry and Larcombe, 2003) – like no other type of marginal/extreme coral community, and are therefore discussed in more detail in the next section.

4.1.2. Case study: high-latitude coral communities

Several different concepts of coral reef 'marginality' appear to have been applied routinely to high-latitude reefs, including geographical, ecological and environmental 'marginality' (Table 3). This has led to significant confusion as to what 'marginality' is as these concepts have routinely been used interchangeably. The three most common concepts are discussed below.

The first concept of coral reef marginality uses latitude as a simple, general criterion to classify high-latitude coral communities as marginal, independent of environmental or ecological criteria. We refer to this concept as "geographical marginality". The concept goes back to at least the 1920s, when Davis' (1923) defined the "marginal belts of the coral seas" as "having a probable width of about 5° between latitudes 25° and 30° north and south of the equator". Given that one meaning of the term marginal is "of, relating to, or situated at a margin or border" (Merriam-Webster Dictionary, Table 2) and that high-latitude coral communities are located at or near the poleward range limits of most tropical reef organisms, this concept is indeed consistent with dictionary definitions of marginal and one of the few objective criteria currently in use. Nevertheless, we argue that this concept is problematic because it has too often been confused - and used interchangeably - with the concept of "ecological marginality" (see next).

Ecological marginality is related to the different community composition and ecosystem functioning that characterizes many high-latitude coral communities compared to 'normal' reefs (Fig. 1c). Many – though certainly not all – high-latitude coral communities have reduced coral cover, species richness or reef growth (Harriott et al., 1995; Macintyre, 2003; Veron, 1992) and are ecologically distinct from 'normal reefs' as they are shaped by trait-mediated environmental filtering processes that reduce the available regional species pool to taxa that are able to persist in high-latitude conditions based on their shared and evolutionary histories (Sommer et al., 2017, 2014). This has shaped the misperception that they are generally "degraded" or the "poor cousins" of 'normal' reefs (Perry and Larcombe, 2003). Although this perception is aligned with one meaning of the term marginal, namely being "limited in extent, significance, or stature" (Merriam-Webster Dictionary, Table 2), it becomes problematic when applied interchangeably with the concept of geographical marginality because this results in any high-latitude coral community being labelled as marginal, independent of whether ecological criteria have been assessed and found to be different from 'normal' reefs.

The third concept of coral reef marginality focuses on the fact that many definitions of marginal reefs are based on the existence of extreme environmental conditions (Kleypas et al., 1999; Perry and Larcombe, 2003; see Table 1). This concept could be referred to as "environmental marginality" but dictionary definitions of the terms marginal and extreme (Table 2) suggest that the meaning of extreme is better aligned with the existence of extreme environmental conditions, i.e., those that strongly differ from those perceived to be 'normal' or 'optimal' for coral reef development (Kleypas et al., 1999). Furthermore, this concept is problematic because many – but not all – high-latitude coral communities occur in locations with extreme environmental conditions (Johannes et al., 1983; Schleyer et al., 2018; Yamano et al., 2001), thus it is not helpful when attempting to distinguish between marginal and extreme coral communities. For example, the Houtman Abrolhos Islands off the coast of Western Australia (28–29°S) have highly diverse coral communities dominated by *Acropora* spp. (37 genera) but coexist with fleshy macroalgae, including kelp, more commonly found in cooler waters (minimum average monthly temperature is ~20 °C) (Johannes et al., 1983).

Due to the complexities outlined above, we recommend to classify high-latitude coral communities according to our new classification framework where they should be considered (1) extreme if extreme environmental conditions exist (see previous section), (2) marginal if ecological criteria indeed indicate that community composition and ecosystem functioning are substantially different from 'normal' reefs (see next section), or (3) extreme *and* marginal if both criteria are met.

4.2. Ecological criteria (community composition and ecosystem functioning)

Our new classification framework proposes to use ecological criteria only to determine whether a coral community should be referred to as marginal or not (Fig. 1). Coral communities that occur close to environmental thresholds for coral survival are often (though not always) characterised by low coral cover, reduced species richness and altered ecosystem functioning compared to 'normal' reefs with more favourable conditions (Guinotte et al., 2003; Perry and Larcombe, 2003; Soares et al., 2020). We therefore define coral reef marginality as coral communities with a community composition and/or ecosystem functioning that differs substantially from those on reefs with optimal conditions (Fig. 1). Although this may refer to any reef taxa, emphasis is typically placed on scleractinian corals due to their dual role as reef builders and ecosystem engineers. Our definition agrees with the dictionary meaning of marginal as being "limited in extent, significance, or stature" (Merriam-Webster Dictionary, Table 2).

We further distinguish between two aspects of ecological marginality: structural and functional marginality (Table 3). Ecosystem structure refers to attributes that can be evaluated with point-in-time measurements such as abiotic criteria and community composition (e.g., nutrient concentrations or biological diversity), whereas ecosystem functioning refers to key biophysical processes that are measured repeatedly, thus capturing the dynamic processes taking place in an ecosystem over time (e.g., calcium carbonate production, nutrient cycling or productivity) (Brandl et al., 2019; Palmer and Febria, 2012). Although the term "function" has many meanings in coral reef ecology (Bellwood et al., 2019), Brandl et al. (2019) recently identified eight complementary core processes that define ecosystem functioning on coral reefs: calcium carbonate production and bioerosion, primary production and herbivory, secondary production and predation, and nutrient uptake and release. Importantly, ecosystem structure and functioning are often intrinsically linked. For example, a live coral cover threshold of ~10 % has been identified as critical to maintaining net reef growth on Caribbean reefs (Perry et al., 2013). Similarly, nutrient pollution enhances productivity and framework dissolution in algae- but not in coral-dominated reef communities (Roth et al., 2021).

4.2.1. Structural coral reef marginality

Many coral communities at the edge of environmental limits have coral cover, species richness and/or community composition (e.g., Macintyre, 2003; Moses et al., 2003; Yates et al., 2014) that differ substantially from 'normal' coral reefs, which can be due to evolutionary and biogeographic processes as well as more extreme environmental conditions. Since these parameters are related to ecosystem structure (e.g., Palmer and Febria, 2012), we refer to this type of coral reef marginality as structural ecological marginality (Table 3). This is further in agreement with one of the definitions of marginality provided by Guinotte et al. (2003), although they did not explicitly state that these parameters are "reduced" or "altered" (definition [a], Table 1). As for the environmental criteria discussed above, quantitative thresholds do not currently exist to objectively define what constitutes "substantially reduced or altered" coral cover, species richness and community composition. Such metrics could, for example, focus on species composition, species richness, diversity indices (e.g., Shannon's H index) or species evenness. As what is considered low or high diversity depends on the regional biogeographic context (e.g., Great Barrier Reef, Caribbean), we recommend that these metrics (e.g., local diversity) are assessed against the available regional species pool (i.e., gamma diversity), such as species composition of high-latitude eastern Australian reefs as subsets of the Great Barrier Reef species pool (Sommer et al., 2017).

Type sites for marginal systems with low coral cover and/or species richness include, for example, the turbid bays of Cape Verde where a total of 5 coral species occur and *Siderastrea radians* forms unusual, large pavements (Moses et al., 2003). Similarly, mangrove habitats in the U.S. Virgin Islands and on the Great Barrier Reef feature diverse coral communities (33–34 species) (Camp et al., 2019; Yates et al., 2014) but have <5 % coral cover that is highly patchy (Camp et al., 2019). Some high-latitude coral communities are also "classic" marginal communities with low coral cover and/or species richness (Booth and Sear, 2018; Macintyre, 2003; Veron, 1992) where non-acroporids such as merulinids or *Turbinaria* become dominant (Ross et al., 2018; Yamano et al., 2001). Importantly, the altered ecosystem structure at many of these marginal sites is often due to the presence of extreme environmental conditions, thus many sites are examples for coral communities that are both marginal and extreme (Table S1).

It is further important to note here that many coral communities exist under extreme environmental conditions but nevertheless have high coral cover and species richness. For example, intertidal reefs in the Kimberley region in NW Australia host 225 species from 60 genera despite a tidal range of up to 12 m and highly dynamic environmental conditions (Richards et al., 2015). Similarly, ~100 coral species were observed near CO_2 seep sites in Papua New Guinea, which co-exist with dominant massive *Porites* (Comeau et al., 2022), while the semi-enclosed, low-pH bays at the Rock Islands, Palau, have 23–63 % coral cover and 12 genera/transect (Barkley et al., 2015; Shamberger et al., 2013). These communities should be classified as extreme but not marginal in our new classification framework (Fig. 1, Table S1), highlighting the importance of assessing environmental and ecological criteria independently.

4.2.2. Functional coral reef marginality

As a consequence of suboptimal environmental conditions, coral communities persisting at the edge of environmental limits may not only have reduced or altered ecosystem structure (e.g., low coral cover and/or species richness) but also altered or reduced ecosystem functioning (Perry et al., 2013; Riegl, 2001; Roth et al., 2021). We propose that these communities should generally be classified as marginal coral communities and refer to this type of coral reef marginality as functional ecological marginality (Table 3). Reef accretion, in particular, has traditionally played a key role in assessing coral reef marginality because it is tightly linked to two of eight core processes that underlie coral reef functioning – calcium carbonate production and bioerosion (Brandl et al., 2019). In addition, positive net vertical accretion is closely linked to many ecosystem services that coral reefs provide, including habitat structure provision and coastline protection from storms and erosion (e.g., Beck et al., 2018). It should be noted, however, that calcium carbonate production can also stem from non-coral taxa such as calcareous algae and bryozoans (Cornwall et al., 2023), while habitat structure may be provided by sponges, for example. Furthermore, non-framework reefs or non-accreting coral communities, especially at high latitude, have often been considered "classic" marginal systems (e.g., Macintyre, 2003). Nevertheless, beyond positive net reef vertical accretion, quantitative thresholds do not currently exist for any of the other core processes that underlie coral reef functioning (Brandl et al., 2019) because many aspects of reef functioning remain heavily understudied, particularly in extreme and marginal coral communities. This should therefore be a priority for future research (Table 4).

Type sites for functionally marginal coral communities include, for example, many non-accreting high-latitude coral communities (Booth and Sear, 2018; Macintyre, 2003; Veron, 1992) where framework building potential can be impaired despite often high coral species richness and cover due to frequent disturbances (Riegl, 2003, 2001). Reduced ecosystem functioning can also be the consequence of severe reductions in coral cover caused by repeated disturbances or long-term degradation as observed in the Caribbean where 37 % of surveyed reefs were found to be non-accreting or net-erosional (Morris et al., 2022; Perry et al., 2013). Many coral communities in the Caribbean are therefore examples for marginal communities that have altered community composition and ecosystem functioning in the absence of extreme environmental conditions and should therefore be classified as marginal but not extreme (Fig. 1d). Conversely, reef-building potential can be maintained under extreme environmental conditions. For example, high reef accretion rates occur on inshore reefs of the Great Barrier Reef despite high turbidity (Browne et al., 2013b), and active (though very low) net calcium carbonate production has been documented in Singapore despite the highly urbanized setting (Browne et al., 2015; Januchowski-Hartley et al., 2020) or on the very high latitude reefs at Iki Island, Japan (34°N) (Yamano et al., 2001).

Table 4
Priorities for future research on coral communities at the edge of environmental limits. The priorities listed here are intended to complement the list of research priorities provided in Camp et al. (2018a).

Research priorities
• Studies that collect both environmental data and ecological data in tandem at a high enough resolution to be meaningful for understanding the system at large
• Assessing historical trajectories of marginal and extreme coral communities, for example by integrating paleo-proxy studies assessment of coral community structure over time, while also encouraging contemporary baseline studies to facilitate future assessment of historical trajectories
• Research into the aspects of variability that drive coral stress responses (e.g., frequency, amplitude, duration, rate of change)
• Focus on a wider range of coral species beyond commonly studied genera such as *Acropora* or *Porites*
• Studying interactions between key community members, such as coral, crustose coralline algae and other macroalgae, and how these relationships change with changing abiotic conditions, thus moving away from single organism studies to community level analyses and ecosystem level outcomes
• The role of non-coral taxa in shaping ecological dynamics and future trajectories, especially in subtropical ecosystems, where tropicalisation and altered species interactions are already transforming ecosystems (e.g., Vergés et al., 2019)
• Determining multiple aspects of reef functioning in marginal and extreme coral communities
• Experimental tests to determine whether organisms from marginal or extreme systems have elevated resistance to sustained (chronic) future climate change stressors, ideally using at least two future emissions scenarios as organisms might be resistant to mild but not severe levels of these stressors
• Understanding the time scales and molecular mechanisms required to achieve enhanced resistance and survival in the long-term, as well as how long favourable traits are maintained in novel environments
• Research into how biological responses differ across life stages

4.2.3. Case study: "degraded" coral communities

The term "degraded" has commonly been applied to marginal coral communities with altered ecological criteria but – similar to the term marginal itself – is actually poorly defined. In fact, the term degraded implies that a decline in reef health and function has occurred over time yet this assumption can be incorrect (e.g., Perry et al., 2009), particularly in the absence of ecological baseline data. In our new classification framework, we argue that both the ecological status of a degraded community and its cause need to be assessed in order to determine whether it should be classified as extreme, marginal or both. We therefore propose that the term degraded should only be used when ecological baseline data exist to confirm a decline in reef health and function over time. Importantly, this needs to occur in the context of environmental history or the historical trajectory of the community because prior to the degradation, they may have been 'normal' reefs, extreme or "naturally" marginal communities. For example, Florida's subtropical reefs were already referred to as marginal (e.g., Glynn, 1973) prior to their extensive degradation since the late 1970s and 1980s which resulted in unprecedented loss of coral cover and reef functioning (Morris et al., 2022; Toth et al., 2019). Similarly, lagoonal reefs in Bahía Almirante and the Bocas del Toro archipelago on the Caribbean coast of Panama were always considered extreme but relatively healthy coral communities due to high live coral cover and species richness but have become increasingly marginal and degraded due to increasing sediment and nutrient loads and hypoxia events (Altieri et al., 2017; Aronson et al., 2014; Guzmán, 2003).

If the cause of the degradation is due to extreme environmental conditions, such as eutrophication or other forms of pollution, and the coral community has suffered a loss of species richness, cover or ecosystem functioning, it should be classified as both extreme and marginal (Fig. 1). However, if the altered ecological criteria are due to factors that are unrelated to general environmental extremeness, such as overfishing, cyclones or coral disease outbreaks, then the community should be classified as marginal but not extreme. We further argue that it is important to consider whether the degradation is likely reversible or permanent, and propose that the term degraded should only be applied to coral communities where this has been shown to be a chronic and likely irreversible state. In particular, we caution against using the term degraded where stochastic extreme events such as marine heatwaves or cyclones have led to coral mass mortality and thus temporary 'marginality' or degradation but recovery is ongoing or still possible, especially for 'normal' reefs. We therefore recommend that use of the term degraded should be carefully considered in light of environmental and ecological baseline data, historical trajectories of decline, and future recovery potential.

5. How to use the new classification framework

Given the large diversity and inherent complexity of coral communities persisting at the edge of environmental limits, assessing their extremeness or marginality will require careful consideration of the criteria listed above. Since quantitative thresholds do not exist for most criteria, what is considered "large" deviations from optimal environmental conditions or "low" coral cover and reef functioning is somewhat subjective. It is therefore critical that the terms marginal and extreme are not used without explicitly stating how such a conclusion has been reached. To aid this process, we have developed a checklist that users can follow to guide and document their assessment, and applied it to a diverse range of coral communities persisting at the edge of environmental limits to illustrate how this new framework facilitates the assessment of coral reef marginality or extremeness (Table S1).

1. Both environmental and ecological criteria need to be assessed to make a sound judgment of whether a coral community should be classified as marginal, extreme, or both. Importantly, independent but joint assessment of these criteria will prevent the common assumption that all coral communities at the edge of environmental limits are the "poor cousins" of 'normal' reefs (Perry and Larcombe, 2003).
2. Regarding environmental extremeness, a coral community would be classified as extreme if at least one parameter is considered to represent a large deviation from optimal environmental conditions (either in terms of mean or variance).
3. Regarding ecological marginality, a coral community would be classified as marginal if at least two of the following parameters are considered substantially different from 'normal' reefs: coral cover, community composition, species richness or ecosystem functioning. We suggest that at least two parameters need to be substantially different to fulfill this criterion because this could otherwise lead to 'normal', functioning reefs inadvertently being classified as marginal. For example, some coral reefs e.g. in the Seychelles have mono-specific fields of *Acropora* (Gardner et al., 2019) but are nevertheless 'normal', functioning reefs.
4. Coral communities that are considered extreme with respect to environmental conditions and marginal with respect to their ecological condition would be classified as systems that are both extreme and marginal, with clear documentation regarding which criteria were considered marginal and extreme.
5. If known, the environmental history or historical trajectory of a coral community should be considered and discussed, particularly in the context of local anthropogenic stressors and a presumed decline in reef functioning and health.

Although our new framework represents a major step forward, it comes with certain caveats. One important limitation is the lack of quantitative thresholds for most criteria. We therefore caution that it is currently not possible to provide a single, universal definition for coral reef extremeness and marginality – as has also been the case for previous definitions of marginal reefs (e.g., Guinotte et al., 2003) or the term "super-corals" (Camp et al., 2018b). Nevertheless, we consider it critical to alert the community to the fact that these terms have been used inconsistently in the literature and have distinct meanings, and argue that the conceptual framework provided here is a significant step forward in highlighting the environmental and ecological parameters needed to contextualise marginality and extremeness, which has important implications for guiding future research and managing and conserving these systems. Once more high-resolution data for a wide range of parameters and locations become available, it should be a priority to provide more quantitative metrics to define coral reef marginality and extremeness.

We further note that each type of marginal or extreme coral community (e.g., turbid reefs or high-latitude reefs) comprises many different, individual locations that may differ strongly in terms of environmental or ecological parameters. As a consequence, different locations might fall into different categories (i.e., extreme or marginal or both). For example, both Singapore's inshore reefs and several inshore reef sites on the Great Barrier Reef are labelled as turbid reefs (Browne et al., 2015, 2013b; Morgan et al., 2016). Yet, based on our new conceptual framework, here we re-define (most) of Singapore's reefs as extreme *and* marginal due to both chronic environmental conditions influenced by land reclamation and reduced coral cover and reef function (Januchowski-Hartley et al., 2020). In contrast, Great Barrier Reef sites such as Paluma Shoals, which experience extreme fluctuations in turbidity due to wind-driven resuspension, have both high coral cover and species richness, and, therefore, would be considered to be an extreme but not marginal reef. It is also critical to recognise that all researchers are inherently biased by the specific conditions present at their respective study sites and need to be cautious when extrapolating from one location to another, even if both locations represent the same type of marginal or extreme coral communities (e.g., turbid reefs).

In addition, it is important to realise that significant complexity and heterogeneity can exist even within individual locations for several reasons. First, extreme environments are never equally extreme to all resident taxa and species. For example, in Curaçao, broadcast spawning corals species showed much greater difference in population structure and density between environmentally extreme inland bays and more typical, clear-water reefs compared to brooding species, indicating that inland bays are much more extreme to broadcast spawners than brooders (Vermeij et al., 2007). Second, some locations will be extreme or marginal with regards to only one environmental or ecological parameter, respectively, whereas others will be marginal or extreme with regards to multiple parameters, thus representing varying degrees of extremeness or marginality.

Third, naturally the robustness of assessments to determine marginality or extremeness will depend on how many environmental parameters or ecological criteria will be measured at high enough spatio-temporal resolution. For example, when abiotic parameters are measured only via spot measurements restricted to certain times of the day, tidal cycle or season, true extremeness will likely be underestimated. Similarly, ecosystems are always in flux due to recurrent biological and physical disturbances, thus ecological criteria will vary naturally over time and should ideally be assessed over longer temporal scales (e.g., Hughes and Connell, 1999). We therefore need to acknowledge that (some) communities may be more (or less) marginal or extreme than we think given that it is impossible to measure all environmental and ecological parameters at high enough spatio-temporal resolution. This further highlights the need to explicitly state which parameters are being referred to when categorising a system as marginal or extreme. Finally, we need to recognise that in the future, more coral communities will become (even more) marginal or extreme due to intensifying global and local stressors, which in turn will also affect the more benign reference reefs that are so often taken as the "norm" for coral growth and reef development (Dixon et al., 2022; Guinotte et al., 2003).

6. Do marginal and extreme coral communities differ in their potential to serve as natural "analogues" for future ocean conditions, resilience hotspots and refugia?

Based on the criteria discussed above, we propose that marginal and extreme coral communities do not generally have the same potential to serve as natural "analogues" for future ocean conditions, resilience hotspots and refugia. Importantly, we also caution that while some generalisations can be made for certain types of marginal or extreme coral communities, this potential will likely depend strongly on the specific environmental conditions and ecological criteria at a given location.

"Natural analogues" for future ocean conditions are coral reef environments where resident organisms already experience conditions predicted to occur under future climate scenarios (i.e., high temperatures, low pH and low dissolved oxygen). However, most, if not all such environments are imperfect analogues for future ocean conditions due to the fluctuating rather than chronic nature of the climate change stressor/s or the presence of co-occurring stressors (e.g., Pichler et al., 2019; Maggioni et al., 2021). We therefore argue against the use of this term and instead propose that these are unique natural laboratories that provide the opportunity to investigate how corals and other reef-associated organisms can gain tolerance to suboptimal environmental conditions in situ and over ecologically realistic time scales (Burt et al., 2020; Camp et al., 2018a).

Extreme coral communities have significant potential to serve as natural laboratories for future ocean conditions if at least one of the three climate change stressors (i.e., warming, acidification and deoxygenation/hypoxia) reaches levels predicted to occur under future climate scenarios. Due to the large diversity of extreme coral communities, they include sites where only one climate change stressor is present (e.g., high temperatures in tide pools or back-reef areas, low pH near CO_2 vents) (Fabricius et al., 2011; Palumbi et al., 2014; Schoepf et al., 2015), as well as multi-stressor sites that simulate two or all three co-occurring climate change stressors (e.g., mangrove habitats and semi-enclosed lagoons) (Camp et al., 2019; Golbuu et al., 2016; Maggioni et al., 2021). The extent of stress exposure may also vary, with some sites exposed to future stress levels only temporarily due to strong diel or tidal variability (e.g., tide pools or coral communities with neighbouring seagrass fields), while others are characterised by chronic stress levels (e.g., the Persian/Arabian Gulf where the world's warmest reefs occur, or coral communities near CO_2 vents). Sites with either fluctuating or chronic stress levels can serve as valuable natural laboratories but those with chronic temperature, pH or dissolved oxygen levels simulate future ocean conditions more closely than those with fluctuating levels. Finally, many sites representing natural laboratories occur in remote locations often far from human impacts (e.g., back-reef pools in American Samoa, Fig. S1a), whereas others are characterised by co-occurring local stressors that can have either natural (e.g., the Bouraké lagoon in New Caledonia, Fig. S1c) or anthropogenic causes or both (e.g., inland bays in Curaçao) (Debrot et al., 1998; Maggioni et al., 2021). While the absence of local stressors facilitates interpretation of the main drivers of coral responses to future ocean conditions, increasing human impacts on coral reefs worldwide highlight the need to investigate more locations where future climate change and local stressors interact. We therefore strongly encourage researchers to quantify co-occurring stressors and to state the limitations of each site in representing future ocean conditions to ensure appropriate interpretation of the results.

Resilience hotspots or so-called "adaptive refugia" are areas where environmental conditions enhance a species' adaptive capacity to one or several stressors, including climate change stressors (Kapsenberg and Cyronak, 2019). It is important to note that adaptive refugia differ fundamentally from other types of refugia, such as "spatial refugia" where a species' biogeographic range experiences less intense stress exposure relative to sister populations (Kapsenberg and Cyronak, 2019). Since extreme coral communities, as well as those that are both extreme and marginal, are characterised by the presence of non-optimal, stressful environmental conditions, only these coral communities have the potential to serve as resilience hotspots. However, we caution that this potential may be limited to near-future climate conditions (i.e., the next few decades) because their adaptive capacity may become increasingly overwhelmed as climate change stressors are superimposed on already extreme environmental conditions. There is evidence that this may already be occurring now as several thermally variable reef environments have suffered extensive bleaching despite hosting more heat-resistant coral populations (Brown et al., 2022; Klepac and Barshis, 2020; Le Nohaïc et al., 2017). Intensifying climate change therefore increases the risk that lethal thresholds will be exceeded in locations where current extremeness is already close to lethal limits, i.e., 'what does not kill you, makes you stronger – until it kills you'.

Spatial refugia are defined as "habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions" (Keppel and Wardell-Johnson, 2012). They can serve as a "slow lane" for biodiversity because they can protect native species and ecosystems from the negative effects of climate change, at least in the short term (Morelli et al., 2020). Some refugia have the ability to provide long-term (over several generations) mitigation of environmental changes that make surrounding areas unsuitable and are therefore distinct from so-called *refuges* that only provide "short-term spatial and/or temporal shelter from environmental stressors or advantages in biotic interactions" (Kavousi and Keppel, 2017). The capacity of refugia to effectively shield corals and reef-associated organisms depends on many factors, but long-term buffering and protection from multiple climate change stressors is essential for effective coral reef refugia (Dixon et al., 2022; Kavousi and Keppel, 2017).

Given the rapid pace of climate change and accelerating decline of coral reefs worldwide, we argue that only very few effective coral reef refugia exist that fulfill the criteria listed above. This also applies to many extreme/marginal coral communities that have been proposed as spatial refugia in the past because most have inherent characteristics that limit their suitability (Glynn, 1996; Riegl and Piller, 2003; Soares, 2020). For example, it has been suggested that high-latitude coral communities may act as refugia from rising ocean temperatures but bleaching events documented at various high-latitude reefs (e.g., Celliers and Schleyer, 2002; Dalton et al., 2020; Kim et al., 2019) and lower light levels and aragonite saturation states (Beger et al., 2014; Muir et al., 2015) likely limit their potential to serve as refugia. Furthermore, reef growth in high-latitude settings can rapidly turn on or off due to high sensitivity to climate and oceanographic changes (Lybolt et al., 2011; Pereira-Filho et al., 2021). Notably, species migrations and associated changes in species interactions (e.g., herbivory, competition) are already reorganising subtropical and temperate ecosystems globally, a phenomenon called tropicalisation (Vergés et al., 2014). Tropicalisation trajectories vary among regions and taxa and often have unexpected consequences (e.g., overgrazing of kelp beds by range expanding herbivores and competitive release of corals; Ling et al., 2018). For instance, in Japan, some subtropical rocky reefs previously dominated by cold-water kelp are now occupied by corals (Kumagai et al., 2018; Vergés et al., 2014), while subtropical coral assemblages in eastern Australia have remained stable over a twenty-year period (Mizerek et al., 2021) despite considerable warming and concomitant loss of kelp and tropicalisation of fish assemblages (Vergés et al., 2016) similar to patterns observed in Japan. These examples highlight that the refuge capacity of high-latitude reefs for corals is difficult to predict (Beger et al., 2014). Similarly, coral communities that experience favourable conditions due to upwelling, internal wave cooling or neighbouring seagrass/macroalgal communities should rather be characterised as refugees (sensu Kavousi and Keppel, 2017) because shelter from environmental stressors is temporary or associated with other stressors, such as high nutrients and/or low pH (Kapsenberg and Cyronak, 2019; Manzello et al., 2008; Wall et al., 2015). However, some extreme and/or marginal coral communities may indeed represent effective spatial refugia, such as nearshore turbid reefs where turbid waters mitigate heat-stress induced bleaching (Banha et al., 2020; Browne et al., 2019; Morgan et al., 2017; Sully and van Woesik, 2020). However, they may not fulfill all criteria proposed by Kavousi and Keppel (2017) for climate change refugia as they likely do not, for example, protect against other climate stressors such as ocean acidification. In addition, given the proximity of some of these sites to human populations, it is uncertain whether their potential as refugia can be sustained in the coming decades.

We therefore conclude that both marginal and extreme coral communities can play an important role in facilitating the persistence of future coral reefs, with extreme coral communities having the greatest potential to serve as adaptive refugia and natural laboratories for future ocean conditions, while some extreme and/or marginal coral communities may represent spatial refugia or refuges. However, more research is needed to understand the trade-offs and costs of survival in marginal and extreme coral communities (Camp et al., 2018a).

7. What are the conservation and management priorities for marginal and extreme reefs?

In addition to their research and intrinsic ecological values, many coral communities at the edge of their environmental limits also have high conservation value, for example, because of their potential to serve as natural laboratories, resilience hotspots and climate change refugia (see above) (Camp, 2022; Camp et al., 2018a). However, extreme and marginal coral communities nevertheless seem to be underrepresented in existing global conservation initiatives. For example, the 50 Reefs Initiative, which used Modern Portfolio Theory to identify reef areas with the highest chance of surviving projected climate change (Beyer et al., 2018), includes only one area that represents extreme and/or marginal coral communities: the Abrolhos Archipelago, Brazil, which is characterised by high sedimentation, turbidity and nutrient levels (Leão et al., 2003; Mies et al., 2020; Santana et al., 2023). The large diversity and heterogeneity of extreme and marginal coral communities makes it difficult to recommend conservation and management actions that are universally applicable across locations. Nevertheless, a thorough examination of reef settings and ecological state (marginal/non-marginal) can be used to inform management strategies. In general, we propose that marginal and/or extreme coral communities have different conservation and management needs and priorities.

Extreme coral communities tend to have particularly high conservation value for two reasons. First, persistence in extreme environmental conditions makes them ideal natural laboratories to investigate responses to future ocean conditions as well as resilience hotspots where naturally stress-resistant coral communities can occur. Identifying areas in which populations, species and functional groups are known to be resistant or sensitive to environmental disturbance is critical for designing adaptive marine protected networks (Bates et al., 2019; Webster et al., 2017). Stress-resistant coral populations possess traits favourable for survival and persistence under future ocean conditions (Burt et al., 2020; Camp et al., 2018a) and can thus provide opportunities for genetic rescue to coral populations maladapted to various climate change stressors (e.g., Bay et al., 2017; Matz et al., 2018). They are also important for pro-active management approaches, including reef restoration and assisted evolution (Camp, 2022; van Oppen et al., 2017, 2015). Second, extreme coral communities tend to have high ecosystem health and functioning, which is generally thought to enhance overall resilience. Although empirical evidence for this theory is not as strong as expected (Bates et al., 2019; Baumann et al., 2021), the high research and conservation value of extreme coral communities makes them prime candidates for the "protect" and "recover" management strategies outlined in Darling et al.'s (2019) framework for effective coral reef management in the Anthropocene. However, it is important to note that these strategies may lead to the so-called protection paradox (sensu Bates et al., 2019) where protected areas can, in fact, have lower resilience to disturbance events such as mass bleaching due to a higher abundance of heat-sensitive species that were only able to persist in these areas.

In contrast, we propose that marginal coral communities, where corals often are not the dominant taxa, tend to differ in their conservation values and needs. For example, many marginal coral communities are characterised by few stress-resistant coral species, high levels of endemism, small population sizes, geographic isolation and low functional redundancy, making them vulnerable to both local and global stressors (Soares, 2020). On Australia's high-latitude reefs for example, endemic coral species (e.g., *Pocillopora aliciae*), subtropical specialists and species close to their northern distributional limits (e.g., *Coscinaraea marshae*) have been more vulnerable to bleaching than those that are normally among the first to bleach in the tropics (e.g., *Acropora* spp.) (Cant et al., 2021; Kim et al., 2019; Thomson et al., 2011). These features might limit the overall resilience of marginal coral communities and increase the risk of long-term, irreversible degradation from multiple stressors, although some high-latitude reefs have been remarkably stable over the last two decades despite being warming hotspots (Mizerek et al., 2021).

This raises the question whether limited resources should be prioritised for often costly active management interventions such as habitat restoration, whose likelihood of success might be limited in these already marginal settings (see Fig. 3 in Beger et al., 2014). For example, calcification rates of coral reef calcifiers, as well as reef accretion, may be constrained in these settings, making restoration particularly challenging. Beger et al. (2014) therefore recommended the establishment of no-take reserves to reduce local impacts, foster resilience and anticipate climate change impacts such as species migrations on high-latitude reefs. Conversely, for degraded reefs, the "transform" management strategy, which recommends transforming existing management, or ultimately assisting societies to transform away from reef-dependent livelihoods (Darling et al., 2019), may be most appropriate. Importantly, we certainly do not advocate "giving up" on marginal coral communities. For example, if they provide important ecosystem services to local communities (e.g., food, shoreline protection) or if the cause for decline can be eliminated relatively easily, these locations should be prioritised under the "recover" strategy which recommends mitigating local stressors and investing in coral reef rehabilitation and restoration (Darling et al., 2019). In addition, some marginal coral communities may play an important role as refuges in adaptive marine park networks, for example cooler upwelling or turbid areas, from which impacted areas may be replenished through time (Bates et al., 2019). Furthermore, the protection paradox implies that many marginal coral communities may have higher resilience than extreme or 'normal' reefs as they are often already dominated by weedy or stress-resistant coral species (Bates et al., 2019).

Another important consideration is that marginal coral communities tend to differ in community composition (i.e., structural ecological marginality) and support high diversity and abundance of other taxa (e.g., macroalgae, soft corals, ascidians and other non-coral invertebrates) that perform important functions in these marginal systems. These distinct ecological characteristics give them high conservation value (Sommer, 2022) and need to be considered when designing conservation and management strategies for marginal coral communities. For example, high-latitude reefs often host unusual species combinations, such as tropical corals and temperate macroalgae (e.g., *Ecklonia radiata*, kelp) co-occurring at their pole- and equatorward range limits, respectively (Fig. S1d). These habitat forming species support high diversity of associated taxa (e.g., fishes, mobile invertebrates) and are differentially affected by warming, which causes complex and hard to predict impacts for the wider ecosystem (Beger et al., 2014; Vergés et al., 2019; Wernberg et al., 2016). Notably, species range shifts and associated changes in species interactions are creating novel ecosystem configurations that pose major challenges to traditional conservation approaches, which typically focus on maintaining local biodiversity patterns. Vergés et al. (2019) therefore recommend to also consider new strategies that might alleviate predicted structural or functional changes, such as the establishment of fisheries that target range-expanding species, and assisted migration and evolution strategies to facilitate large habitat formers like corals or kelp seaweeds.

These examples highlight some of the complexities involved in conserving and managing the diverse array of extreme and/or marginal coral communities. We therefore recommend that any management strategy should be developed jointly with local stakeholders and integrate traditional and Indigenous knowledge along with Western science (Ogar et al., 2020). Furthermore, as it is increasingly unrealistic that coral reefs can return to historical pristine conditions, conservation and management efforts need to be directed more appropriately towards achievable goals (Graham et al., 2014) and be accompanied by rapid reductions in greenhouse gas emissions to safeguard coral reef futures (IPCC, 2019).

8. What are the priorities for future research to improve our understanding of marginal and extreme coral communities?

As coral communities persisting at the edge of environmental limits have only recently attracted more scientific attention and continue to be understudied, the priorities for future research outlined by Camp et al. (2018a) remain valid despite significant progress being made in the field. For example, recent work has revealed the range of abiotic conditions that characterise such coral communities (e.g., Maggioni et al., 2021) or the traits and fitness trade-offs associated with surviving under sub-optimal conditions (e.g., Camp et al., 2019; Sommer et al., 2021). Research priorities outlined by Camp et al. (2018a) included, for example, improved reporting of both mean and variance as well as measurement time frames for environmental parameters, research into the fitness trade-offs underlying survival under sub-optimal conditions, and improving our understanding of how multiple stressors interact over a range of temporal scales. However, to enable more quantitative definitions of marginal and extreme coral communities, one research priority stands out as particularly important: the collection of longer-term, high-resolution abiotic and ecological baseline data sets that include multiple parameters across different temporal and spatial scales. This will be critical to enable the identification of quantitative thresholds to better define what constitutes extremeness and marginality, such as "extreme" variance, "low" coral cover or "reduced" reef functioning. Nevertheless, we have identified here several additional priorities for future research (Table 4) that complement the list already provided in Camp et al. (2018a) and need to be addressed to advance our understanding of how coral communities can persist at the edge of their environmental limits.

9. Conclusion

Here, we have shown that marginal and extreme coral communities are distinct communities with high but different research and conservation values and developed a novel, simple framework that allows for better classification of these important but understudied coral communities. Our new conceptual framework provides a list of criteria and a checklist that can be used to characterise and re-define marginal and extreme coral communities in a way that is more consistent with the defined meaning of these terms. Furthermore, independent but joint assessment of environmental and ecological criteria makes it straightforward to define coral reef extremeness based on environmental conditions and marginality based on community composition and ecosystem functioning (Fig. 1). This new approach will not only discourage the common notion of all marginal reefs being “poor cousins” but also agrees with Perry and Larcombe's (2003) view that marginal and extreme coral communities should be considered “alternative states of development rather than disturbed or restricted versions of the coral reefs that develop in the low-latitude, warm, clear-water settings” - i.e., they represent coral communities in their own right that should not be directly compared to ‘normal’ reefs. We acknowledge that this framework may not fit perfectly for all coral communities at the edge of environmental limits due to their remarkable diversity. We therefore encourage researchers to consider this framework and use it to explain their reasoning behind calling a specific site ‘marginal’ or ‘extreme’ in order to help build consensus thinking on these definitions across the field. Finally, we call on all researchers working on marginal and extreme coral communities to adopt a data-driven approach to site classification and collect, publish, and archive site-specific abiotic and biotic data for use by others to facilitate future comparisons and synthesis across locations.

CRediT authorship contribution statement

Verena Schoepf: Conceptualization, Methodology, Investigation, Visualization, Writing – original draft. **Justin H. Baumann:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Daniel J. Barshis:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Nicola K. Browne:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Emma F. Camp:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Steeve Comeau:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Christopher E. Cornwall:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Héctor M. Guzmán:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Bernhard Riegl:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Riccardo Rodolfo-Metalpa:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Brigitte Sommer:** Conceptualization, Methodology, Investigation, Writing – review & editing.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary Information

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