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Perspective

Enhancing coral bleaching predictive tools through integrating sensitivity to heat exposure

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ABSTRACT

Predicting coral bleaching events has been key to reef conservation management efforts. Current satellite-based bleaching prediction tools offer effective regional-scale alerts of bleaching risk, but lack reliability at the reef-scale. Bleaching models focus on predicted heat exposure during summer, omitting critical factors that influence heat stress responses and the subsequent coral reef community bleaching severity. The IPCC framework however assesses the susceptibility of a system to be harmed by climate change based on exposure, sensitivity, and adaptive capacity. In this perspective, we propose integrating the IPCC vulnerability framework to develop a holistic coral bleaching prediction model that accounts for reef-scale exposure to heat stress, species-specific sensitivity, and adaptive capacity. We specifically recommend: 1) incorporating historical temperature metrics to account for acclimatisation responses, 2) including community composition metrics to better reflect variations in sensitivity at the reef scale, and 3) addressing environmental conditions to identify potential refugia and refine predictions. We discuss these factors and the feasibility to inform metrics for use in prediction tools. Historical temperature is identified as a primary target, with community composition and environmental drivers recommended for further exploration as data availability improves. Future assessments of these **sensitivity metrics** should be integrated into an **experimental framework** to further refine and improve prediction tools. This perspective underscores the urgency of refining coral bleaching prediction models and directly supports reef conservation efforts in the face of climate change.

1. Introduction

Coral reefs are among the world's most biodiverse and ecologically important ecosystems, yet they are increasingly vulnerable to climate and other anthropogenic threats. They provide habitat to over 25 % of all marine life (El-Naggar, 2020) – some as critical nurseries and breeding grounds for keystone and charismatic species (Moberg and Folke, 1999). In addition to their inherent natural value, reefs support the lives and livelihoods of around one billion people in coastal communities by providing food and jobs (Costanza et al., 2014), whilst dispersing wave energy to mitigate storm effects, therein protecting coastlines from erosion (Sheppard et al., 2005). Increasing anthropogenic impacts threaten the health and future survival of coral reef ecosystems and, therefore, the goods and services they provide (Hughes et al., 2017a). Heat stress induced by climate change poses the greatest threat, leading to more frequent and severe coral bleaching events globally (Mydlarz et al., 2010; Meissner et al., 2012).

Mass coral bleaching was first reported in the Pacific and Indian Oceans in 1982 and 1983, with moderate bleaching also reported in the southern Caribbean (Parmesan et al., 2022; Coffroth et al., 1990). The first documented global bleaching event (defined as significant impacts in all three tropical ocean basins) occurred in 1998 (Wilkinson, 1998)

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and was associated with strong El Niño conditions (Oliver et al., 2009). The second documented global-scale bleaching event was recorded in 2010 during a comparatively weaker El Niño (Oliver et al., 2009; Tun et al., 2010). A third global bleaching event occurred from 2014 to 2017, affecting over 70 % of the world's coral reefs (Eakin et al., 2019; Hughes et al., 2017b) and coincided with (then) record-breaking sea-surface temperature (SST) in reef locations across the globe over a prolonged period, resulting in high coral mortality (Eakin et al., 2019). A fourth global mass bleaching event has recently been declared, underscoring the persistent threat to reefs worldwide (Oceanic and Administration, 2024; Hoegh-Guldberg et al., 2023).

The Great Barrier Reef (GBR), the world's largest coral reef ecosystem, is an iconic example of the accelerating impacts of global change. Overall the reef has experienced bleaching events in 1998, 2002, 2006, 2016, 2017, 2020, 2022, and now currently unfolding again in 2024 (Fig. 1) (Thiault et al., 2021). At the time of writing, analysis of the 2024 bleaching events is underway, with early estimates demonstrating 2024 is likely the most severe and extensive event on record for the ecosystem (Authority, 2024). Despite extensive research, effectively managing coral bleaching remains a significant challenge. Crucial to effective management and conservation of coral reefs through the coral reef crisis is effective, real-time, accurate and responsive bleaching predictions and alerts specific to management needs (Ainsworth et al., 2021).

Coral bleaching prediction tools include satellite-based current assessments (nowcasts) and model-based seasonal outlooks (forecasts) (Liu et al., 2008; Maynard et al., 2009). Nowcasts assess current conditions based on real-time satellite SST data to inform stakeholders of the existing threat and guide reactive conservation responses; e.g., impact surveys, where reef closures to recreational activities may limit reef damage and promote recovery (Liu et al., 2018; Strong et al., 2006; Vila et al., 2022). Forecasts predict future conditions using seasonal climate models and provide reef managers with additional lead-time to plan proactive responses (Liu et al., 2008). They could also guide monitoring responses and research efforts to target reefs at risk of bleaching, which in turn increases knowledge of the causes and consequences of the event(s). Although useful, there are still challenges in accurately predicting mass coral bleaching months in advance.

Currently satellite-based coral bleaching predictions singularly focus on heat exposure through the measure of ocean surface temperatures converted to heat stress metrics (Liu et al., 2017; Garde et al., 2013). Accumulated heat stress (combination of duration and intensity) is the primary driving factor for mass coral bleaching events and subsequent heat-induced mortality. There are also other factors that have been associated with the severity of coral bleaching responses across the scales of coral colony, species, and community. Current bleaching thresholds and bleaching risk tools were built in the 90s with pre-disturbance reefs and their diverse composition in mind (Liu et al., 2014). As we see increased disturbance events, coral communities worldwide are bleaching more regularly. Incorporating satellite temperature-based measures that are reflective of multiple biophysical and historical drivers of coral sensitivity and adaptive capacity (which have so far been neglected in prediction tools) has the potential to improve bleaching predictions and allow for reef-specific bleaching warnings to be communicated in real-time, globally. As ecosystems are being continuously restructured, bleaching thresholds that have been tested and reviewed also require further evaluation to ensure their relevance in light of ongoing environmental changes (McClanahan et al., 2019; McClanahan and Azali, 2021). In this perspective, we explore how the IPCC vulnerability framework can be applied to coral bleaching prediction models, providing a mechanism to incorporate factors that influence both exposure and sensitivity (Birkmann et al., 2012). This framework has been applied to coral reefs in the context of social science (van Hooidonk et al., 2020) or hazard risk assessment (Kim et al., 2023), but its **application in the ecological context of coral bleaching** represents a novel approach that goes beyond existing prediction tools focused solely on heat exposure.

The IPCC vulnerability framework (Birkmann et al., 2012) is composed of three factors that interact to determine the vulnerability of an ecosystem to climate change:

- **Exposure (E)** – the direct stress upon an ecosystem;
- **Sensitivity (S)** – the pre-disposition of a given ecosystem to be impacted by or susceptible to stress; and
- **Adaptive capacity (AC)** – the ability of surviving individuals within the ecosystem to moderate potential/future impacts (resilience), to take advantage of opportunities and/or to cope with consequences (adaptive capacity).

This sensitivity and prediction framework can be applied to satellite predictions of coral bleaching at the scale of coral reef ecosystems (Fig. 2).

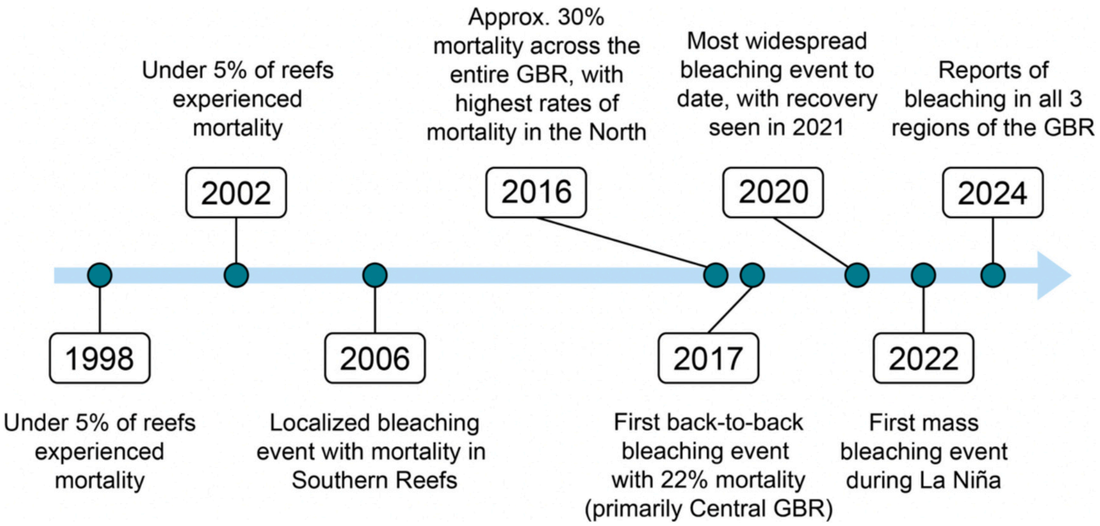

Fig. 1. Coral bleaching history on the Great Barrier Reef from 1998 to 2024 (Credit: Dr. Emma Rehn). All years were documented mass coral bleaching events on the GBR, aside from 2006, which was a localised inshore event in the southern sector.

1.1. Exposure

Current satellite products provide the exposure component of the vulnerability framework metrics by describing heat stress accumulation (Liu et al., 2017; Maynard et al., 2008). The strong link between coral bleaching and heat stress exposure has provided the foundation for the development and use of satellite SST-based prediction tools, which are now recognised as a core component of coral bleaching monitoring and are widely used to inform and focus conservation management activities (Maynard et al., 2009; Brown, 1997; Hoegh-Guldberg, 1999).

NOAA's Coral Reef Watch (CRW) program monitors accumulated heat stress on reefs worldwide, with reference to locally-specific climatological baselines to underpin nowcasting (Supp. 1). The widely used Degree Heating Week (DHW) metric is derived from the maximum of the monthly-mean climatologies (MMM), in which SST values at least 1 °C above the MMM in the prior 12-weeks are accumulated at a resolution of 5 by 5 km (Liu et al., 2003). DHW of 2–3 °C-weeks has been linked to the possibility of mild coral bleaching; 4–6 °C-weeks with probable coral bleaching; and > 8 °C-weeks increased likelihood of severe coral bleaching and coral mortality (Hughes et al., 2017b; Liu et al., 2003; Liu et al., n.d.; Hughes et al., 2018). The heritage version of the DHW product was generated biweekly at a resolution of 50 km, reasserting to need to test current thresholds and tools to leverage the available data at higher spatial and temporal resolutions effectively. ReefTemp Next Generation (RTNG, Supp. 1) is a regional product suite specifically generated for the GBR and forms a part of the Great Barrier Reef Marine Park Authority's (GBRMPA) strategic bleaching response framework (Garde et al., 2013; Maynard et al., 2008). The RTNG product differs from NOAA's CRW DHW metric primarily in its use of **monthly climatological baselines** (December to March) rather than a single maximum monthly mean climatology (MMM) baseline. Additionally, RTNG has a **higher spatial resolution** (0.02°, ~2 km) compared to the 0.05° (~5 km) resolution of CRW. These differences allow RTNG to provide **region-specific, high-resolution heat stress data** that complements the global-scale NOAA product, to inform bleaching risk and response planning for GBR conservation managers and reef scientists (Maynard et al., 2009; Garde et al., 2013). This would be adapted considering both satellite measurable and non-satellite measurable factors.

While DHW has been widely adopted as a key metric for predicting coral bleaching, there is ongoing debate in the literature regarding its effectiveness and whether it requires modification (McClanahan and Azali, 2021; DeCarlo, 2020). Some studies suggest that the relationship between DHW and coral bleaching may not be linear, with empirical data revealing weak or hump-shaped correlations between DHW and coral mortality (McClanahan and Azali, 2021). The use of the MMM + 1 °C threshold, in particular, has been challenged for not consistently predicting bleaching, with research indicating that more regionally specific or multi-dimensional models—incorporating factors such as peak temperatures, cold temperature durations, and temperature variability—could improve predictive power (McClanahan et al., 2019; DeCarlo, 2020; Donner, 2011). Additionally, as coral communities acclimatise and adapt to changing SST conditions, the predictive accuracy of the current DHW metric may diminish (McClanahan, 2017). **However, this debate is not the primary focus of this perspective. Instead, we aim to explore other critical factors missing from current prediction models, particularly those related to coral community sensitivity and adaptive capacity.**

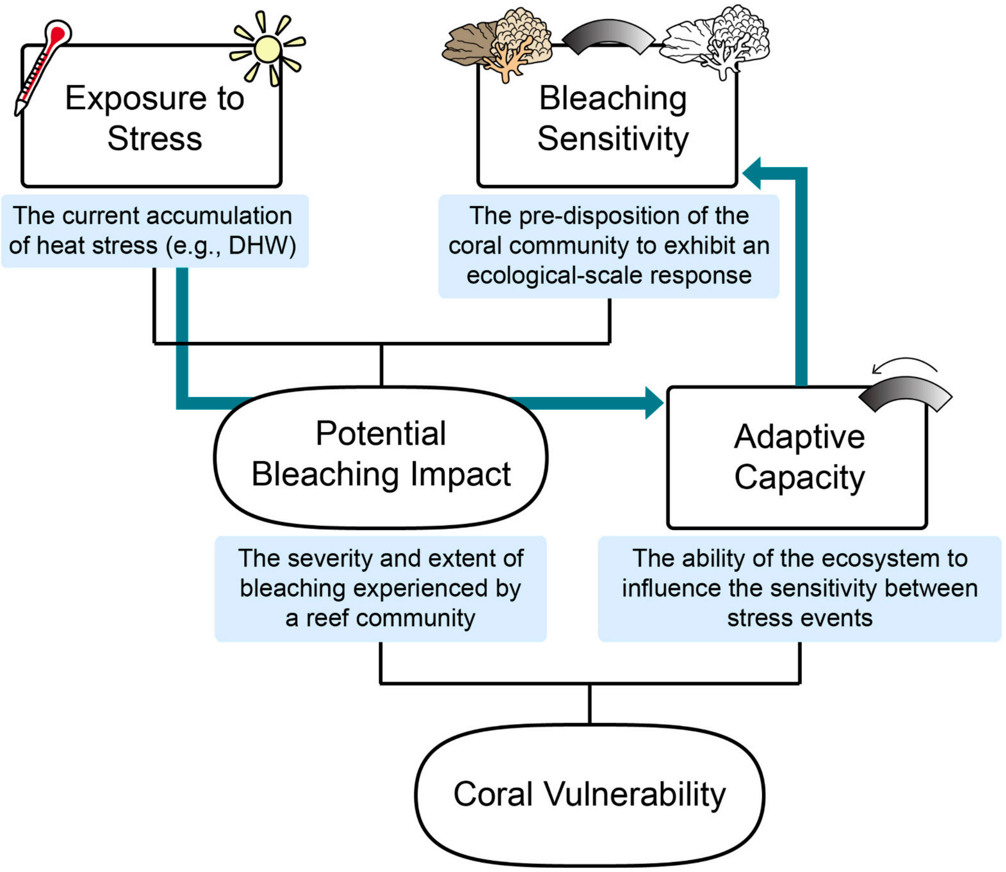

Fig. 2. The IPCC vulnerability framework applied to corals, showing exposure to stress, bleaching sensitivity, and adaptive capacity as vulnerability components. Arrows indicate relationship pathways – exposure can trigger adaptive capacity to influence sensitivity (Credit: Dr. Emma Rehn).

Sensitivity at a coral reef community level (aligning with a satellite pixel scale) relates to the prevalence of bleaching response within the coral community at a reef scale. Colony-scale sensitivity to a stress exposure can vary between individuals and species: it is the combined response across a community that gives the aggregated, ecological-scale sensitivity (influencing the occurrence and severity of bleaching on a reef). Thermal sensitivity at this scale can be influenced by the community composition of corals, the local temperature range (both daily and seasonally), and the occurrence of historical stress exposure (beyond both upper and lower limits) (Middlebrook et al., 2008; Heron et al., 2016a; Heron et al., 2016b). In this perspective, the integration of sensitivity into prediction models is presented and recommendations for implementation discussed.

1.2. Adaptive capacity

The adaptive capacity of a reef community is revealed by changes to the sensitivity between stress events (Birkmann et al., 2012). As for sensitivity, the capacity of individual colonies to adapt can be variable (and taxon-dependent) and it is the aggregation of these to the community-scale that can be related to satellite monitoring.

Inherent within the complexity of advancing coral bleaching predictions is the range of scales over which information related to the key aspects of the IPPC framework – exposure, sensitivity, and adaptive capacity - is available. The resolution of satellite SST monitoring tools is at a scale of multiple kilometres (ca. 1–20 km) (Merchant et al., 2019), whereas physiological responses occur within individual coral colonies. Evaluating acclimatisation of colonies is limited by the broader scale of satellite data. Coral bleaching events are observed, and their impacts managed, at a community-to-reef scale. Bridging between these scales to create holistic bleaching predictions requires aggregating the breadth of scientific and conservation information now available from the smallest to broader scales (Liu et al., 2017; Garde et al., 2013). Similarly, understanding of community to colony-level responses needs to be carefully considered in how it can best inform potential improvements to broad-scale satellite predictions.

2. Exploring coral bleaching from the perspective of the IPCC framework

Coral bleaching is a generalised stress response of the coral animal, resulting in the breakdown of an otherwise productive symbiosis, through the significant loss of endosymbiotic dinoflagellates and/or the associated pigments within the coral tissue, causing coral colonies to pale or whiten in colour (Brown, 1997). Coral bleaching is observed as approximately 50 % or more loss in symbiont density (Franklin et al., 2006; Brown et al., 1995)) and while predominantly occurring on shallow reefs, studies have also reported bleaching within the mesophotic zone to depths of 90 m (Diaz et al., 2023). Environmental triggers of coral bleaching include extreme high and low temperature (Brown, 1997; Glynn, 1996; Warner et al., 1999; Lesser and Farrell, 2004; Paz-García et al., 2012; Hoegh-Guldberg et al., 2005), coupling of anomalous temperature and solar radiation (Baird et al., 2018), low salinity (Downs et al., 2009; Berkelmans and Oliver, 1999; Dias et al., 2019; Chavanich et al., 2009; Gegner et al., 2017; Ochsenkühn et al., 2017), low pH (Anthony et al., 2008), microbial infection (Rosenberg, 2004; Rosenberg and Ben-Haim, 2002), pollution (Cunning and Baker, 2013; Meehan and Ostrander, 1997), and phosphate (Morris et al., 2019; Rosset et al., 2017; Wiedenmann et al., 2013), essential metals (Ferrier-Pagès et al., 2018), or oxygen starvation (Coles and Brown, 2003; Altieri et al., 2017; Alderdice et al., 2022; Johnson et al., 2021). However, elevated summertime temperatures, when coupled with elevated solar irradiance during clear-calm days, is the primary driver of mass bleaching events associated with anomalous SST conditions (Brown, 1997; Glynn, 1996).

2.1. Exposure

While heat is the primary stressor causing widespread mass coral bleaching (Glynn, 1996; Baird et al., 2018; Jones et al., 1998; Downs et al., 2013), thermal variability across reef areas during temperature anomalies can be used to calculate how heat stress exposure is avoided (noting the assumption that a typically cooler reef area remains cooler than other areas during periods of extreme temperature). Bleaching also inherently involves light (Baird et al., 2018; Rosic et al., 2020; Kuanui et al., 2020)), with increasing light the thermal threshold for bleaching is reduced (Iglesias-Prieto and Trench, 1994). A satellite-based predictive product that combines SST and irradiance, being developed by CRW, demonstrated that incorporating short-term photo-acclimation increased the accuracy of bleaching predictions on the GBR (Skirving et al., 2018). While this tool is not currently operational (regionally or globally), it does illustrate that there are other satellite-measurable factors that can contribute to the exposure term.

2.2. Sensitivity

The current use of locally-specific temperature thresholds for bleaching predictions from satellite tools exemplifies the upscaling of colony-level responses to the scale of satellite-derived data pixels (Liu et al., 2017; Garde et al., 2013). There is the potential for short-term (acclimatisation) responses to therefore also inform the interpretation of satellite-derived heat exposures. For example, ecological memory, defined as the potential for an ecosystem's history to influence future ecological response (Johnstone et al., 2016; Peterson, 2002; Ogle et al., 2015) may play a role on coral reefs, where prior thermal stress events may alter future responses (Hughes et al., 2019; Stuart-Smith et al., 2018). Importantly, the community-scale concept of ecological memory is underpinned by aggregated colony-scale changes, which could include surviving colony acclimatisation to heat stress transferring to the broader scale (Hughes et al., 2019), as well as mortality transforming species composition (Stuart-Smith et al., 2018).

Community-scale sensitivity has been exhibited in differential responses to heat exposure and been linked to acclimatisation. For instance, during the 1998 global mass bleaching event, significant bleaching was recorded on Singaporean reefs (particularly for branching corals), whilst no bleaching was recorded on reefs in Sumatra, Indonesia, or Tioman Island, Malaysia (Guest et al., 2012). During the subsequent global mass bleaching event in 2010, reefs that had experienced high levels of bleaching showed relative resilience to the next heat stress exposure, with a higher prevalence of bleaching observed in massive corals over branching. The previously unaffected regions that had not experienced heat stress in 1998, like Sumatra, experienced high levels of bleaching (Guest et al., 2012). On the Great Barrier Reef, regions exposed to high heat stress in 2016 appeared to exhibit ecological memory, resulting in reduced bleaching and mortality during the 2017 mass bleaching event (Hughes et al., 2019). Past bleaching exposure is hypothesised to have reduced bleaching sensitivity by either community-scale acclimatisation or changed community composition (Lachs et al., 2023).

High-mortality heat stress events have altered community composition and diversity decline on reefs of the GBR (Hughes et al., 2017b). Fast-growing genera (e.g., *Acropora*) recolonize first after disturbance, quickly dominating the reef community and decreasing reef resilience (Kubicek et al., 2012; Birkeland, 1997). Where heat stress is less severe, bleaching occurs selectively among species, whereas higher levels of heat stress affect taxa broadly (Hughes et al., 2017b; Watt-Pringle et al., 2022). This is particularly important as observed bleaching severity can change across a heat stress severity gradient depending on the indicator species chosen. Long-term monitoring in Wakatobi, Indonesia revealed that percentage cover prior to and immediately after a bleaching event had an effect on species' recovery success potentially due to the Allee effect, which inhibits reproduction and recolonisation of species present at low population densities (Watt-Pringle et al., 2022). Evidence relating to adaptive responses to heat stress in host, symbiont, and bacterial mutualists may also provide an insight into how well coral communities can adapt in the future with repeated exposure to heat stress. While little is known about the capacity for transgenerational inheritance, some evidence supporting the passing down of epigenetic changes to provide transgenerational plasticity exists, but further studies are required (Torda et al., 2017; Putnam et al., 2020; Quigley et al., 2019). These are important aspects to consider as community-level sensitivity to bleaching will depend on dynamic shifts in community composition that occur.

Coral bleaching sensitivity is more complex to parameterize than exposure and requires a detailed understanding of the underlying connections with past disturbance, including causes for spatial variation in bleaching responses. Different historical disturbances across reefs produce variable community composition and sensitivities to bleaching

Table 1
Sub-pixel factors of bleaching sensitivity.

	Sensitivity factor	Description	Refs
Physical factors	Sub-pixel temperature variation	Variation is affected by flow, turbidity, depth, wave exposure, shading, and reef zones.	Ainsworth et al. (Ainsworth et al., 2021)
	Flow	High flow provides partial refugia to corals through increasing mixing by tides and currents that slow the warming rate. This will affect corals differently based on their size and morphology, changing the surface area to which the coral is exposed to the water column.	Page et al. (Page et al., 2021), Jimenez et al. (Jimenez et al., 2011)
	Turbidity	Turbidity reduces bleaching impact through limiting benthic irradiance and enhancing heterotrophy.	Guest et al. (Guest et al., 2016)
	Depth	The importance of depth is illustrated by shallow reefs typically being the first to bleach (Kenkel and Matz, 2016). With increasing depth, coral exposure to sunlight decreases, but the coral response can be complex. There are examples of shallow corals that have adapted to high light and temperature variability during low tide, suggesting enhanced tolerance due to the high stress environment (Meissner et al., 2012; Pineda et al., 2013). In contrast, some corals experience mortality following repeated subaerial exposure during low tides.	Cosbie et al. (Crosbie et al., 2019), Muir et al. (Muir et al., 1864)
	Pollution	Pollution, including nutrient runoff (Donovan et al., 2020), sedimentation (Wear and Thurber, 2015), and chemical contaminants (Brown, 2000), can exacerbate coral bleaching by increasing stress on coral communities. It may reduce water quality or cause eutrophication, making them more susceptible to heat stress or disease (Wear and Thurber, 2015).	Donovan et al. (Donovan et al., 2020), Wear & Thurber (Wear and Thurber, 2015), Brown (Brown, 2000)
Colony characteristics	Size	Size changes the surface area exposed to the physical factors of bleaching. The effect of size on bleaching susceptibility is debated and differs across taxa and bleaching severity experienced.	Ortiz et al. (Ortiz, 2009), Shenkar et al. (Shenkar et al., 2005), Burn et al. (Burn et al., 2023), Brandt (Brandt, 2009)
	Morphology	Coral genera exhibiting fast-growing life histories (e.g., branching and tabular corals) are generally considered more susceptible to bleaching than mound corals with stress-tolerant life histories. Fast-growing corals (e.g., species in Acroporidae and Pocilloporidae) are thought to allocate energy to growth rather than stress tolerance, whereas massive and sub-massive coral species (e.g., species in Poritidae and Merulinidae, previously Faviidae) allocate energy into (mechanical or heat) stress-tolerant structures and therefore less to growth. However, these ideas concerning bleaching susceptibility across different taxa have been challenged by observations and analysis of coral morphotypes that have exhibited unusual responses to heat stress.	Hughes et al. (Hughes et al., 2017b), Hughes et al. (Hughes et al., 2019), Darling et al. (Darling et al., 2013), Pratchett et al. (Pratchett et al., 2013)
	Taxon susceptibility	There exists high variability in bleaching susceptibility within and between species, genera, and families of corals. Inconsistencies in bleaching susceptibility were found among growth forms in a review of 95 studies published from 1982 to 2011.	McCowen et al. (McCowan et al., 2012)
	Symbiont population and coral-associated microbial communities	Symbiont shuffling can alter bleaching sensitivity depending on heat tolerance of symbionts, while coral-associated microbial communities also play a significant role by modulating coral health and thermal tolerance through their influence on nutrient cycling, and pathogen resistance.	Cunning et al. (Cunning et al., 1809), Silverstein et al. (Silverstein et al., 2017), Mouchka et al. (Mouchka et al., 2010), Bourne et al. (Bourne et al., 2008), Lesser et al. (Lesser et al., 2007), Ritchie et al. (Ritchie and Smith, 2004)
Community characteristics	Community composition	The aggregated sensitivity of the community will reflect the different sensitivities of the community's taxa and therefore will change depending on the community composition. Community composition may change due to mortality – as susceptible species die off, the community shifts, often favouring more resilient species. Mortality will therefore play a role in shaping community composition and the overall sensitivity of the community (as illustrated in Fig. 3b and c).	Hughes et al. (Hughes et al., 2019)
	Geomorphology and location	Different reef regions have been found to have variable aggregated sensitivity, with variation in bleaching occurrence across inshore and offshore reefs, as well as in different parts of the reef (slope, lagoon, flats) with different geomorphology	Berkelmans et al. (Berkelmans et al., 2004), Liang et al. (Liang et al., 2021), Semprucci et al. (Semprucci et al., 2018)

(Hughes et al., 2019; Pratchett et al., 2020), which leads to community-scale changes in bleaching sensitivity. An ideal bleaching prediction model which accounts for sensitivity would incorporate complex coral community factors and real-time data regarding taxa and morphotype responses. However, achieving this globally as events emerge through an ecosystem is challenging, requiring local interpretation of satellite products and the responses occurring on reefs. To achieve incorporating sensitivity, we propose including satellite-measurable historical temperature (i.e., thermal variance and recent heat stress exposure) as well as non-satellite-measurable factors (see below, in Section 3.1). Community shifts that occur due to repeated disturbance events could potentially also be accounted for with historical temperature.

2.3. *Adaptive capacity*

Understanding the extent of adaptive capacity at either colony or community scale prior to an exposure event may not be feasible, given the multiple potential factors involved (e.g., colony-scale: symbiont reshuffling (Quigley et al., 2019; Cunning et al., 1809; Silverstein et al., 2017), bacterial community shifts (Bourne et al., 2008; Ziegler et al., 2017), thermal acclimatisation (Coles and Brown, 2003; Hoadley et al., 2016; Ateweberhan et al., 2013; Brown and Cossins, 2011), genetic adaptation (Coles and Brown, 2003; Kenkel and Matz, 2016); community-scale: coral composition (Hughes et al., 2017b; Hughes et al., 2018; Watt-Pringle et al., 2022)). As noted, the ecological memory of the 2016 GBR heat stress was observed during the 2017 GBR heat stress event, reflecting the capacity for reefs to change their sensitivity. Ainsworth et al. (Ainsworth et al., 2016) focused on within-summer SST trajectories and prior heat exposure (priming) of GBR corals and the effects on bleaching and mortality. A ‘protective’ trajectory, in which SST rose slightly above then returned below the local MMM before warming above the local bleaching threshold (MMM + 1 °C), resulted in lower cell mortality than trajectories without the initial mild warming. Taken together, evidence suggests that changes in sensitivity occur during a bleaching event, influencing the capacity of reefs to acclimatise, and may underpin adaptation. Because of this strong link with sensitivity, we focus on sensitivity factors to incorporate the adaptive capacity as well.

3. Bleaching sensitivity factors to consider for coral bleaching prediction tools

3.1. *Satellite-measurable SST bleaching factors*

3.1.1. *Thermal variance*

Although the importance of historical temperature in defining long-term average thresholds for summertime heat exposure is highlighted within existing satellite monitoring products, temperature and stress variability and trends are not, but have potential to influence broad-scale bleaching sensitivity. Reefs in areas of higher diurnal temperature variability have a lower bleaching response than those with lower daily temperature ranges (Pineda et al., 2013). Similar reduced sensitivity to heat exposure has been observed for reef regions with high within-summer temperature variability (McClanahan and Maina, 2003; Oliver and Palumbi, 2011). Intra-annual temperature variability has also been linked with reef-scale patterns of bleaching response, where areas with greater annual temperature range experience less bleaching than those with smaller annual range (Safaie et al., 2018). The ENSO cycle is also an important consideration due to the variability in SST and heat stress patterns it causes (Williams et al., 2010; Thompson and Van Woesik, 2009). It is therefore important to consider temperature variability and stress over various time scales and how these measurable temperature features of reefs can be accounted for in predictions.

3.1.2. *Recent heat stress exposure*

Recent heat stress (within the past year to several years) can also reduce reef-scale sensitivity to bleaching either through enhanced tolerance of surviving corals or the mortality of susceptible corals among a community (Hughes et al., 2019; Thompson and Van Woesik, 2009). Existing satellite-based SST products offer insights on long- and short-term historical temperature, spanning from weeks to decades. These data can provide metrics of historical temperature variability (annually and seasonally), past heat stress events (over the span of multiple years), pre-conditioning prior to summer (within the year), and the development trajectory of heat stress, each of which could influence the sensitivity of corals to heat stress exposure. The potential importance of historical temperature on bleaching susceptibility during hot summers has been indicated by bleaching simulations. Logan et al. (Logan et al., 2014) simulated potential bleaching considering two adaptive responses: directional genetic selection (a long-term change to sensitivity), through a decadally-increasing bleaching threshold in response to projected warming; and symbiont shuffling (a short-term response), through temporary increases in the bleaching threshold following bleaching stress. Incorporating both adaptive responses showed that future predictions of coral mortality were lower than in a scenario with neither, with up to 14 % of reef pixels studied avoiding high-frequency bleaching by 2100. When compared with past bleaching events, the ‘no adaptive response’ simulation hindcast much higher bleaching and mortality rates (overprediction) than had been observed, consistent with the proposition that some adaptive response may have already occurred (Logan et al., 2014).

Whilst the effect of summertime heat stress is increasingly understood, attention to temperature exposure prior to the onset of summer is also needed. With climate change projected to affect winter SST and variability, it is vital to consider the effects of cold and warm winters on the bleaching sensitivity the following summer. Little is known about the effects of a warm winter, whether increasing community-level sensitivity to bleaching or, on the contrary, pre-conditioning for thermal tolerance. Winter-time effects on observed coral disease outbreaks within the GBR (Heron et al., 2010) suggest that effects on bleaching sensitivity are plausible. Similarly, the effect of cold stress on bleaching sensitivity remains poorly understood. Coral bleaching has been observed at a community scale during unusually cold events (Hoegh-Guldberg et al., 2005; Hoegh-Guldberg and Fine, 2004; Lirman et al., 2011). Notably, the reporting of one of these events (Lirman et al., 2011) observed that the typically most-heat tolerant taxa were the most impacted by cold stress. Potential colony-level physiological responses to cold stress have been posited as similar to those from heat stress (Saxby et al., 2003), which suggests that they could also translate to observed responses at the community level. Decreased lipid content, as observed following anomalously cold exposure of corals in the Mexican Pacific, could affect the capacity for corals to resist subsequent heat stress (Rodríguez-Troncoso et al., 2010; Bellworthy and Fine, 2021). These studies suggest a potential role of cold historical temperature in influencing bleaching sensitivity. Furthermore, it is then also logical to consider the potential influence of springtime temperature conditions in modifying bleaching sensitivity (e.g., through pre-conditioning coral reefs prior to a subsequent heat stress event).

3.2. *Non-satellite measurable SST bleaching factors*

We acknowledge the extensive body of literature surrounding coral bleaching sensitivity and the myriad factors that can influence community-level responses to bleaching – many of which are not measurable or inferred by satellite temperature measures. Sub-pixel spatial patterns in temperature, as well as small-scale gradients in other physical parameters can affect heat exposure and bleaching sensitivity (Table 1). Similarly, characteristics of individual colonies can influence differential responses, which can aggregate to affect the community-level response (Table 1). However, **in this perspective, we focus on identifying aspects of coral bleaching sensitivity that can be translated into practical metrics for coral bleaching prediction**

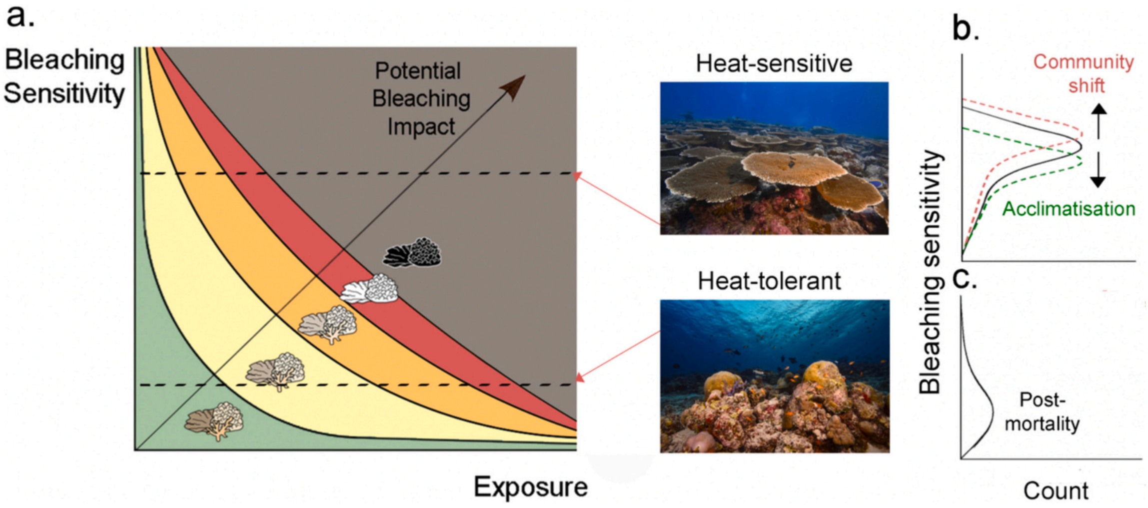

Fig. 3. a) Potential bleaching impact as a function of exposure and sensitivity. Contours represent the impact (green: low likelihood of bleaching impact, red: high impacts from bleaching, grey: coral mortality). b) Potential changes in population distribution of a theoretical reef community impacted by repeated disturbance events. The black population curve represents a diverse community before disturbance events. c) Example community structure of a reef post-disturbance with little to no recovery. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tools. s. Factors such as community composition and biophysical interactions (e.g., high flow leading to locally-reduced temperature; wave exposure affecting morphology types found in different reef zones – and therefore community composition) are difficult to quantify directly, but their role in shaping community sensitivity remains critical. It is therefore important to evaluate the complexities of these factors before considering their implementation into predictive models.

4. Key recommendations for improving bleaching predictions based on the vulnerability framework

Despite demonstrated variable sensitivity from both field and experimental studies, current prediction tools have yet to include these crucial discoveries. Looking towards the IPCC vulnerability framework, the magnitude of bleaching impact on a reef community is a direct function of exposure and sensitivity, which in turn determines the overall vulnerability of a reef system (Fig. 3). We propose three achievable areas of consideration for improvement in predictions which can be supported by satellite-derived data:

Image 1. Variable bleaching responses of coral species during the 2017 coral bleaching event on the Great Barrier Reef at moderate levels of heat stress (image credit: N. Cantin / AIMS).

1) historical temperature,
2) community composition, and
3) environmental conditions.

Incorporating metrics of historical temperature dynamics, or historical temperature, can introduce variability in community-scale sensitivity and vulnerability for prediction models. Altered sensitivity, whether reduced by acclimatisation/adaptation to past temperature conditions or increased by pre-summer stress can be incorporated through satellite-measurable SST-based metrics of historical temperature. As has been demonstrated by Logan et al. (Logan et al., 2014), bleaching and mortality models that overpredicted coral mortality benefitted from the inclusion of acclimatisation and adaptive responses, but determining how predictive models would benefit from this inclusion should be a priority. Various coral bleaching prediction models have overpredicted or underpredicted heat stress (likely due to different reasons) and could potentially benefit from the addition of a sensitivity metric (Liu et al., 2018; Spillman and Smith, 2021; Spillman et al., 2013). Testing the accuracy of different models under different climatic scenarios is therefore crucial to identify where sensitivity metrics are needed. Understanding the nuances of historical temperature requires assessing both long-term trends and short-term fluctuations that could alter coral community sensitivity to bleaching. Drawn from data compatible with that used in current prediction models (i.e., Coral Reef Watch), long-term historical temperature products are available for reefs worldwide (Heron et al., 2016b) that complement short-term factors from profiles of recent stress exposure to describe sensitivity. For instance, exploring variations in temperature trajectories leading up to summer, rates of temperature increase, bouts of cold or heat stress occurring prior to summer, recovery times, or the historical annual temperature range can reveal critical insights into differences in coral community bleaching response. Moreover, it is essential to consider factors beyond just the summer months, that may hint at community-scale ecological memory (reducing sensitivity) or recent stress (increasing sensitivity). Translating these factors into SST-based metrics could then help include variation in bleaching sensitivity and vulnerability driven by differences in historical temperature.

Different reef communities exhibit different levels of bleaching sensitivity, which change with repeated exposure to stress (Fig. 3). This can be demonstrated by a reef that is dominated by fast-growing and heat-sensitive taxa, in contrast to a less diverse reef that may have not recovered sensitive taxa post-disturbance. The latter would have low

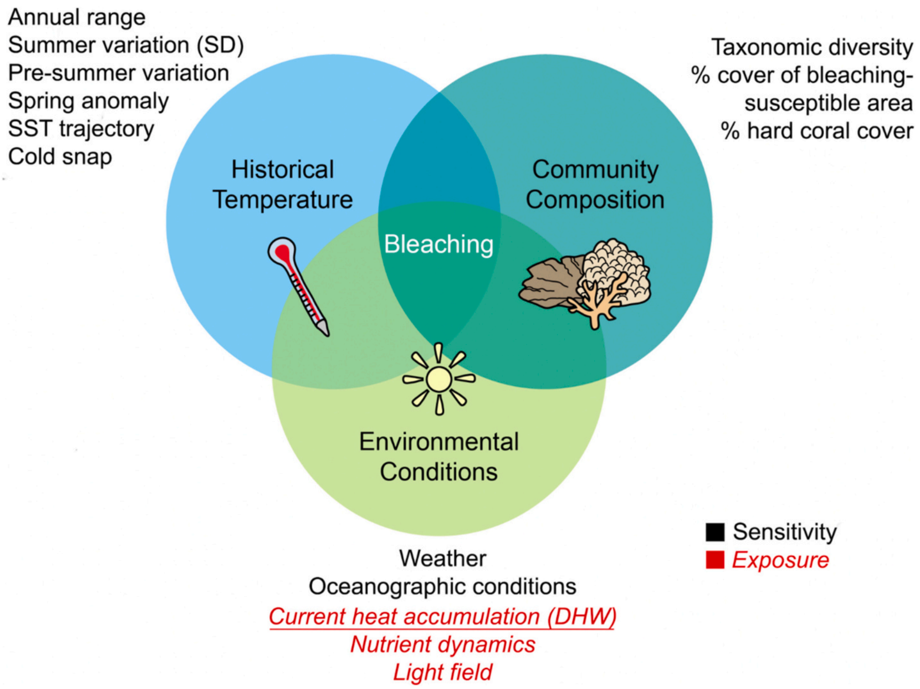

Fig. 4. Factors that could improve coral bleaching prediction. Metrics are proposed for historical temperature, community composition, and environmental conditions. Bleaching impact will depend on a combination of these factors. Current heat accumulation (DHW) is underlined as it already forms the basis of current coral bleaching prediction models. Oceanographic conditions include flow, turbidity, depth, water quality/pollution. (Credit: Dr. Emma Rehn).

coral cover that is dominated by more heat-tolerant taxa. For a given exposure, the more-sensitive reef experiences higher impacts than the tolerant reef (and will be positioned at different positions on the sensitivity axis of Fig. 3a). Although this dynamic between sensitivity and exposure may apply to all morphotypes in a community, it does not imply that the bleaching impact to individual morphotypes is equal (Image 1). Following a disturbance event, a population could shift towards fast-growing, but more heat-sensitive coral species, a likely shift that occurs on recovering reefs that have experienced some coral mortality (as reflected by the red population curve in Fig. 3b). Following recovery, this community would have a lower overall sensitivity (as reflected by the green population curve in Fig. 3b). If heat stress is sufficient to result in the mortality of sensitive taxa, the reef composition could transition to a less-diverse and lower-coral cover community. The population would shift to heat-tolerant taxa, which are more likely to survive, as seen in Fig. 3c. Although this community would have reduced sensitivity, the overall resilience of the community could be negatively impacted (Alvarez-Filip et al., 2013; Kubicek et al., 2019), due to lower coral diversity and coral cover (as seen in Fig. 3b and c, where coral cover, the area under the curve, is lower in c than in b). Furthermore, recovery would likely see a predominance of the fastest-growing, heat-sensitive species, leading to a shift in the distribution to higher sensitivity and vulnerability (red dashed line, Fig. 3b). These examples of the dynamics of heat stress events, community composition, coral cover, and bleaching susceptibility indicate that there may be value in incorporating community composition metrics into prediction models.

In contrast to historical SST information, community composition (Fig. 4) data are not currently consistently available for global coral reefs. Where available, information concerning the current state and the temporal variation of such factors can be used to interpret heat stress predictions, and such opportunities could be tested and developed regionally. For example, on the GBR permanent long-term ecological monitoring and bleaching survey data exist on wide spatial scales (Mellin et al., 2020)). Potential also exists in incorporating community composition through remote sensing, with methods in this field being continuously tested and fine-tuned for greater accuracy (Mumby et al., 2004; Roelfsema and Phinn, 2010).

Other environmental factors have the potential to synergistically increase coral bleaching impacts, influencing bleaching sensitivity, whilst increasing exposure to different types of stress. Oceanic conditions such as depth, flow, and geomorphology have the potential to influence the vulnerability of a reef. For this, bathymetric gradients for the GBR have been derived from high-resolution (30 m) data (Beaman, 2018), which could provide descriptive information on the distribution of corals and their proximity to deeper and cooler water. The Allen Coral Atlas can also provide information on habitat type and geomorphology (Atlas, 2020). This could account for refuge areas where reefs may not feel the impacts of high heat stress. Other factors that can provide synergistic effects include ocean acidification, pollution, disease, overfishing, and sedimentation (Anthony et al., 2008; Ateweberhan et al., 2013; Bozec and Mumby, 2015), but the direct relationships between these variables are quite uncertain, so quantifying these synergies is imperative if future nowcasting and forecasting systems are to incorporate such effects.

Hastily incorporating too many variables does risk overcomplicating prediction models. To avoid this, we suggest that considering historical temperature serves as an ideal primary target to improve due to the global availability of SST data. Aside from data availability, the practicality of deriving historical temperature metrics from the same satellite-derived dataset as current heat exposure metrics aids in the ease of modelling historical temperature into current prediction tools. With previous simulations having shown overpredictions of coral bleaching

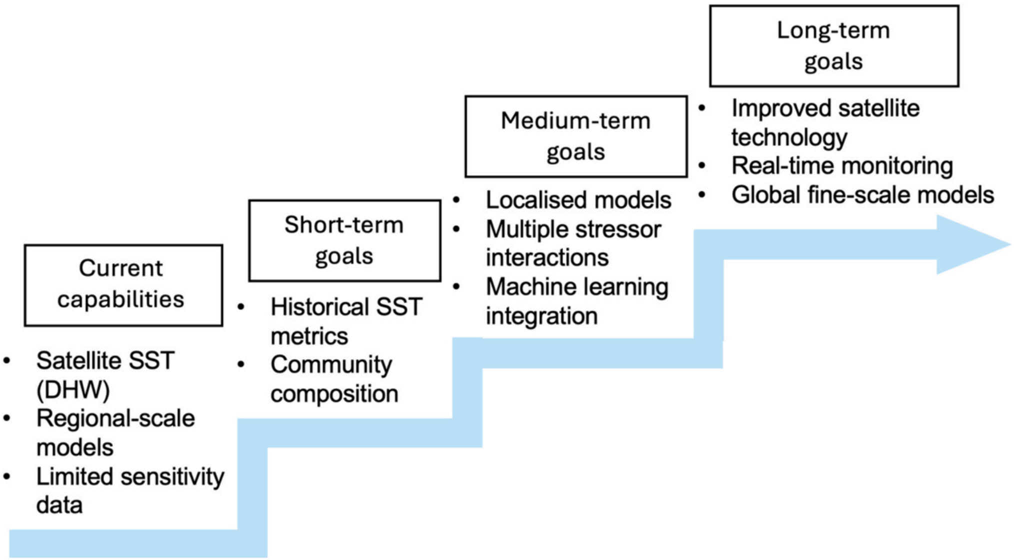

Fig. 5. Roadmap illustrating potential improvements to coral bleaching prediction tools from current capabilities to future innovations. The roadmap outlines immediate recommendations (short-term), emerging capabilities (medium-term), and long-term visionary goals to enhance the accuracy and reliability of prediction models.

(Liu et al., 2018; Logan et al., 2014), the biological significance of including historical temperature is also highlighted and needs to be further tested. After this, incorporating a community composition metric, in regions where sufficient data are available from a suitable monitoring program, is a sensible priority, as this can provide sensitivity information at the sub-pixel scale. After considering historical temperature and community composition, we recommend the development of localised prediction models that account for regionally important oceanographic processes. Additionally, as our understanding of synergies between stressors such as heat, pollution, and nutrient dynamics becomes better quantified, these interactions should be incorporated into prediction models. Addressing these synergies will help to capture the complex, non-linear responses of coral reefs to multiple co-occurring stressors, enhancing the predictive power and ecological relevance of future models. Emerging technologies, such as machine learning, offer powerful tools for integrating these multidimensional datasets and enhancing model performance. Machine learning approaches could uncover complex, nonlinear relationships among stressors that may be missed by traditional methods.

Looking outside of improvements to modelling bleaching parameters, there also exists space for improvements in satellite SST prediction. All current coral bleaching forecasts are affected by difficulties in forecasting SST; any unreliability in forecast SST propagates to heat stress products. Looking towards the long-term future, we envision significant advancements in satellite technology and the development of global fine-scale prediction models. Improvements in satellite SST forecasting, including enhanced cloud masking, aerosol impact assessment, and diurnal variability estimation, will be essential for reducing uncertainties in SST predictions (O'Carroll et al., 2019). For bleaching forecasts, the accuracy in assessing anomalously high SST is the main concern, given that differences of $+1$ °C can distinguish between a heat stress event and a period of no bleaching (Goreau and Hayes, 2005). Beyond current capabilities, future satellite systems could provide higher-resolution spatial and temporal data on both SST and additional environmental variables, enabling truly global prediction models (Fig. 5).

5. Conclusion

Improving the accuracy of coral bleaching prediction tools can be achieved through incorporating metrics that describe bleaching exposure and community-level sensitivity. Our primary recommendation centres on harnessing community-level acclimatisation recorded through historical temperature—both long-term trends and recent effects. Leveraging existing datasets, where available, can preliminarily identify which metrics best inform sensitivity. As the complex interactions affecting coral bleaching susceptibility are better understood, and more available, testing community composition is recommended, followed by additional environmental and biological factors. Future assessment of sensitivity metrics can then be included in an experimental framework to inform development of prediction tools.

Improving coral bleaching prediction tools offers a multitude of advantages by informing stakeholders regarding climate threats to coral reefs. By achieving reliable long-term future bleaching projections, advocacy for coral reef conservation can have an even stronger backing by science. Increasing certainty of bleaching predictions will achieve more appropriate and immediate action to underpin evidence-based policy. The ongoing restructuring of coral reef communities due to frequent disturbance events necessitates updates to our prediction tools. Built before such events became commonplace, these tools must now reflect the dynamic changes in sensitivity occurring across reefs globally. With these escalating impacts of climate change in mind, the imperative to refine coral bleaching prediction models is urgent for the conservation of coral reef communities worldwide.

CRediT authorship contribution statement

Valerie J. Cornet: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Neal E. Cantin:** Writing – review & editing, Supervision, Conceptualization. **Karen E. Joyce:** Writing – review & editing, Supervision, Conceptualization. **William Leggat:** Writing – review & editing. **Tracy D. Ainsworth:** Writing – review & editing. **Scott F. Heron:** Writing – review & editing, Supervision, Conceptualization.

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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Data availability

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

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