Life on the edge: Hawaiian model for coral evolution

Debashish Bhattacharya *,1, Timothy G. Stephens,1 Amanda I. Tinoco,2 Robert H. Richmond,3 Phillip A. Cleves2
1Department of Biochemistry and Microbiology, Rutgers University, New Brunswick, New Jersey
2Department of Embryology, Carnegie Institution for Science, Baltimore, Maryland
3Kewalo Marine Laboratory, University of Hawaii at Manoa, Honolulu, Hawaii

Abstract
Degradation and loss of coral reefs due to climate change and other anthropogenic stressors has fueled genomics, proteomics, and genetics research to investigate coral stress response pathways and to identify resilient species, genotypes, and populations to restore these biodiverse ecosystems. Much of the research and conservation effort has understandably focused on the most taxonomically rich regions, such as the Great Barrier Reef in Australia and the Coral Triangle in the western Pacific. These ecosystems are analogous to tropical rainforests that also house enormous biodiversity and complex biotic interactions among different trophic levels. An alternative model ecosystem for studying coral reef biology is the relatively species poor but abundant coral reefs in the Hawaiian Archipelago that exist at the northern edge of the Indo-Pacific coral distribution. The Hawaiian Islands are the world’s most isolated archipelago, geographically isolated from other Pacific reef systems. This region houses about 80 species of scleractinian corals in three dominant genera (Porites, Montipora, and Pocillopora). Here we briefly review knowledge about the Hawaiian coral fauna with a focus on our model species, the rice coral Montipora capitata. We suggest that this simpler, relatively isolated reef system provides an ideal platform for advancing coral biology and conservation using multi-omics and genetic tools.

The earliest stony corals (Scleractinia) were not reef builders, but rather, small, solitary polyps that were azooxanthellate (Veron 1995; Campoy et al. 2020; Gault et al. 2021). By virtue of the algal endosymbiosis and subsequent metabolic integration of the holobiont members (i.e., cnidarian host, Symbiodiniaceae algal symbionts, prokaryote microbiome, endolithic algae, viruses; Knowlton and Rohwer 2003; Bosch and McFall-Ngai 2011), coral reefs cover 255,000 km² of the planet’s surface (Spalding and Grenfell 1997) and house ca. 25% of marine biodiversity (Reaka-Kudla 1997; Knowlton et al. 2010). As with all sessile marine organisms, corals have evolved specialized reproductive strategies and mechanisms to cope with stress over the course of their long lifespans that can extend to centuries (Strathmann 1990; Kaplan 2009). These adaptations have allowed corals to flourish since their radiation in the Devonian, 324–447 Ma that was concomitant with establishment of photosymbiosis (McFadden et al. 2021, but see also Lajeunesse et al. 2018 for a discussion of the timing of diversification of Symbiodiniaceae), surviving mass extinction events and multiple biotic crises (Bhattacharya et al. 2016). Coral ecosystems are threatened by anthropogenic climate change that results in repeated episodes of damaging thermal stress, reduced ambient pH, and other environmental perturbations (Kleypas et al. 2021; Sutherland et al. 2021). These stresses can result in dysbiosis and the subsequent loss of the algal endosymbionts that provide substantial nutrition to the host coral. The whitening of coral colonies, known as “bleaching” (due to the loss of color in corals conferred by algal pigments), may lead to sublethal stress, outright coral mortality, and widespread reef degradation (Muscatine and Porter 1977; National Academies of Sciences, Engineering, and Medicine 2019). Therefore, a major focus of coral research is the response of the coral holobiont to climate change-associated stressors, in particular increased sea surface temperature and ocean acidification (Hoegh-Guldberg et al. 2007). An obstacle to these efforts is the lack of fundamental knowledge about the processes that govern the biology and stress responses of the coral holobiont. Increasing amounts of genomic and other omics resources are being generated for corals (Barshis et al. 2013; National Academies of Sciences, Engineering, and Medicine 2019; Tishlhammer et al. 2020, 2021), but these studies often target distantly related species. Given that coral holobiont interactions will reflect local conditions (Murphy *Correspondence: dbhattac@rutgers.edu

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et al. 2019), both biotic (e.g., microbiome, disease, presence/absence of other reef dwellers such as fish and algae) and abiotic (e.g., thermal stress [annual temperature minima and maxima], light levels, and water flow), a major focus of coral research is developing local model systems that are amenable to manipulation and interpretation. We suggest that the Hawaiian Archipelago offers an ideal (of many potential) testbeds for developing knowledge about corals using a variety of tools, with a focus here on multi-omics and genetic methods. The Hawaiian Archipelago (Fig. 1a) is at the northern limit of coral distribution in the Indo-Pacific and is therefore relatively “simple” in terms of species numbers. Compared to other hotspots such as the Coral Triangle where more than 600 species exist (Veron et al. 2009), Hawaiian reefs are dominated by three genera (Porites, Montipora, and Pocillopora; Fig. 1b) that comprise < 80 species in total.

Despite this paucity of biodiversity, the Hawaiian Islands may represent a hotspot for the rapid evolution and adaptation of species that can provide novel insights into functional diversification, unavailable in ubiquitously distributed coral species (Olson 2004). Due to its isolated position in subtropical regions of the Indo-Pacific (Simon 1987; Veron 1995), the waters off Hawai‘i house many endemic coral species (Hughes et al. 2002). The resulting low gene flow and genetic drift can result in genome growth due to repeat, transposon, and gene family expansion, as recently postulated for Montipora capitata (Shumaker et al. 2019). The existing data are consistent with work done on Drosophila subobscura that has shown high frequencies of the bilbo and gypsy transposable elements (TEs) due to recent bottlenecks (García Guerrero et al. 2008). The fossil record provides evidence for genetic bottlenecks associated with Hawaiian corals that is explained by repeated invasions by marine species that have become extinct and been replaced by others (Kay and Palumbi 1987). Although corals can be transported long distances either as larvae or via rafting, existing data suggest that these modes of dispersal have not broadly impacted Hawaiian coral genetic diversity (Jokiel 1987). The subtropical countercurrent is the most likely delivery system for the coral reef biota from the Indo-West Pacific (Grigg 1981; Fletcher et al. 2008). The North Hawaiian Ridge Current and the Hawai‘i Lee Current are the major surface currents that move in a northwesterly direction around the Archipelago and mediate local particle dispersal (Wren et al. 2016). Conditions prior to and during “El Nino” events can also affect current patterns and connectivity among Pacific coral populations (Richmond 1990).

Beyond coral species, the marine habitat of the Hawaiian Archipelago displays some of the highest levels of endemism worldwide, including mesophotic coral ecosystems, with 100% of fish species from deep coral reefs in the northwestern islands reported to be endemic (Kosaki et al. 2017). Endemic seaweeds (e.g., species of Ulva and Umbraulva) and sponges, of which many of the latter remain to be characterized, have also been identified in this region (Spalding et al. 2019). The terrestrial flora and fauna in the Archipelago are well-studied and given the massive radiation of taxa such as Hawaiian honeycreepers, spiders, and the “silversword alliance,” a broader and more sustained evolutionary response to isolation has occurred on land (Simon 1987; Olson 2004; Patton et al. 2021).

Given these data, it is of interest to ask if a putative “Hawai‘i effect” (colloquial term) due to geographic isolation of Hawaiian coral species has, for example, resulted in genome growth due to population bottlenecks and genetic drift, and genetic innovations related to local adaptation. Because well-characterized adaptive radiations have occurred among terrestrial fauna in Hawai‘i, similar genomic and species radiations may be occurring in corals, but perhaps in a less obvious manner in terms of morphology, consistent with recent discoveries of cryptic species across reef-building corals (Fuller et al. 2020;
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Burgess et al. 2021; Rose et al. 2021). It should be noted that work in the Coral Triangle shows that this region has relatively low coral endemicity. Rather, its high coral diversity is explained by range expansion of species that have evolved elsewhere (Huang et al. 2017). Therefore, the Hawaiian endemics, as storehouses of genetic diversity, may play an important role in coral range expansion to other sites and are therefore worthy of protection, even though the region has lower overall species diversity. A key driver of genetic diversity among Hawaiian corals may be the volcanic hotspot that has created these islands (Wilson 1963), forging constantly changing habitats. The Hawaiian chain ranges in age from 0.4 million years (Ma) for the Big Island of Hawai‘i to 3.7 Ma for O‘ahu to 5.1 million years for Kaua‘i (Clague and Dalrymple 1987) (Fig. 1a). Recurrent dispersal and extinction events recorded in the fossil history of Hawaiian marine fauna (Jokiel 1987; Kay and Palumbi 1987; Spalding et al. 2019) provide an ideal testbed to ask questions about how isolation and disturbance breed innovation. It is, for example, possible that the closely related morphotypes observed in extant Montipora (e.g., Fig. 1c) and in Porites species, and other coral taxa in Hawai‘i (Baums et al. 2012; Concepcion et al. 2014) would potentially be the “seed” for future endemics in isolated environments that did not face repeated gain and loss of habitat as is the case for the Hawaiian island chain. Existing knowledge therefore suggests that omics and genetic analysis of Hawaiian corals could provide valuable insights into the impact of recent origin and isolation on genome structure and content in long-lived sessile species. In this way, the Hawaiian Islands may represent the coral analog of the “warm little pond” of fundamental innovations (i.e., origin of complex molecules) described by C.R. Darwin in an 1871 letter to J.D Hooker (Letter no. 7471, Darwin Correspondence Project 1871).

We of course note that Hawai‘i is one of many model reef systems that is available for addressing questions regarding coral biology and evolution, using different species as targets for investigation. For example, isolated reefs are also present in the Chagos Archipelago, Kiribati, and the Bahamas (among others), that could be used to study the influence of geographic isolation on genome evolution. Interestingly, these reefs have also been impacted by warming oceans, even though they may be far from human populations (Bruno and Valdivia 2016). With regard to reverse genetic manipulations, several tractable coral models already exist, in addition to M. capitata, that can be used to test hypotheses about gene function in different species with different life histories (e.g., vertical or horizontal transmission of photosymbionts). For example, Cleves and colleagues used the CRISPR/Cas9 genome editing tool to make mutations in target genes in the ecologically important reef-building corals, Acropora millepora (Cleves et al. 2018). They then used these new genetic tools to demonstrate that heat shock transcription factor 1 (HSF1) was required for coral tolerance to heat stress (Cleves et al. 2020a,b). These results position CRISPR/Cas9 as a powerful tool to disrupt specific genes in a variety of broadcast spawning corals to characterize their involvement in regulating heat and bleaching tolerance and other traits of interest. By comparing discoveries using several genetically tractable model corals, both endemic and cosmopolitan, we can increase the likelihood of identifying the conserved molecular underpinnings of ecologically important traits that can be generalized across the diversity of reef-building coral species.

Coral evolution under climate change

Hawaiian coral reefs are largely fully functioning and vibrant ecosystems, although many disturbed sites such Hono-lulu Harbor exist (with a unique “Harbor Porites”; Brown et al. 2020), and provide ideal models for uncovering site-specific adaptations (e.g., Tisthammer and Richmond 2018). Geographic isolation of Hawaiian coral species provides the opportunity to track genome evolution in natural populations experiencing different selective pressures. To reach these goals, it is important to begin sampling extant coral populations thoroughly to generate their baseline genetic architecture. These data can be used to identify genetic sweeps due to ongoing environmental pressures such as climate change and other anthropogenic stressors. For example, population genomic analysis of Acropora tenuis in the Great Barrier Reef revealed signatures of natural selection in the animal genome with regard to genes involved in osmotic regulation, skeletal development, and the algal symbiosis, likely driven by post-glacial climate change (Cooke et al. 2020). In contrast, the genomes of corals in the world’s warmest reefs in the Persian/Arabian Gulf show evidence of selective sweeps that impact genes potentially involved in thermal adaptation (Smith et al. 2022). The restricted gene flow of corals within the Hawaiian Islands should allow us to identify and track genetic selection in these natural populations. In addition, the Hawaiian Islands have both highly disturbed and pristine reefs that are close in proximity and create potential hybridization zones for admixture between populations which can be used to identify adaptive alleles (Tisthammer et al. 2020, 2021). For example, there may be populations with differential bleaching histories that have zones of admixture based on unique geography (Fig. 2). These hybridization zones would generate natural crosses between bleaching affected and bleaching naïve populations. Multi-omics scans and corresponding phenotyping within these zones and the non-admixed populations would allow mapping of host genetic loci, symbiont strains, and other factors controlling selected traits in corals (Fig. 2). Finally, with the successful application of reverse genetic technologies to Hawaiian corals (Cleves et al. 2018, 2020a,b), these hypotheses about local adaptation can be validated and further studied to understand how stress tolerance evolves at the molecular level.

In addition to observing how evolution “plays out” in natural populations by screening corals from these populations for
variability with respect to resilience or susceptibility to stress, there is an opportunity to identify highly resilient individuals (genotypes) or populations that may be useful for studying the molecular basis of evolved stress tolerance and for conservation efforts. This approach has already proven successful in identifying resilient coral in other reefs (Brown et al. 2020; Cunning et al. 2021). However, the isolated, simpler nature of the Hawaiian Islands system should enable relatively tractable approaches to determine how stress tolerant individuals are distributed and maintained across the Archipelago. This information will provide a valuable model for understanding how adaptation can arise and spread in a sessile coral population, thereby providing insights into the evolutionary capacity of other coral reef ecosystems.

**M. capitata as a model species**

Although the diversity of species on Hawaiian reefs is relatively low, there is still great value in developing a single coral model system for both laboratory and field studies. Of the different Hawaiian coral species, the hermaphroditic, broadcast spawning rice coral, *M. capitata*, has emerged as a highly promising model for studying coral genomics, genetics, evolution, and disease (Cleves et al. 2020a, b; Van Etten et al. 2020; Brown et al. 2021). This conclusion is based on several key traits that, in combination, support the importance of this coral model:

1. *M. capitata* is widely distributed in both shallow and deep waters off the Hawaiian Islands (e.g., Fig. 3a; https://www.pacioos.hawaii.edu/projects/coral/) and is a dominant reef builder in the region.

2. *Montipora* species are widely distributed across the Indian and Pacific Oceans making *M. capitata* an important model, not just for the Hawaiian Islands, but also for the Great Barrier Reef and the Coral Triangle.

3. Use of neutral genetic markers initially suggested overall, low population diversity (Franklin et al. 2013; Concepcion et al. 2014). However, more recent genome wide studies (Helmkampf et al. 2019; Caruso et al. 2021; Stephens et al. 2021) demonstrate that *M. capitata* in Hawai‘i is an outbreeding species with high standing genetic variation: that is, heterozygosity rate of ca. 1.3% (Helmkampf et al. 2019). The latter data make *M. capitata* an ideal model for uncovering the genetic basis of local adaptation, under the same paradigm that model system researchers employ to create in-bred lines to study these processes.

4. Existing data (Frazier et al. 2017; Helmkampf et al. 2018; Shumaker et al. 2019; Williams et al. 2021a) show *M. capitata* to be robust to short-term thermal stress with the ability to sustain itself during periods of bleaching, most likely through heterotrophic feeding (Grottoli

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**Fig. 2.** Schematic model illustrating how analysis of two partially overlapping *Montipora capitata* populations that inhabit divergent environments can be used to uncover alleles associated with local adaptation. This approach can be applied to any coral species in Hawai‘i or elsewhere.

**Fig. 3.** Analysis of *Montipora capitata* at HIMB. (a) Scaled percent cover of *M. capitata* in Kāne‘ohe Bay, O‘ahu, showing the location of HIMB. Image adapted from the Pacific Islands ocean observing system (https://www.pacioos.hawaii.edu/projects/coral/) (Franklin et al. 2013). (b) Injection of Cas9 protein and guide RNA into one-cell stage embryos of *M. capitata* to facilitate gene knockdown. Note the algal symbions (brown dots) already present in the embryos. Image created by P. A. Cleves.
et al. 2006). This species also has a perforate skeleton to sequester algal symbionts in more protected tissues, that allow quick recovery from bleaching events. However, a recent study using analysis of compound-specific isotopes found that *M. capitata* lacks trophic plasticity when compared to *Pocillopora meandrina* (Wall et al. 2021). This trait, and its manifestation in different *M. capitata* populations, offers the opportunity to study coral biology in both non-bleached and bleached colonies of this species and to follow colonies through single or multiple bleaching-to-recovery cycles.

5. Mass spawning, whereby sperm and egg bundles are released, generally occurs three times a year during the New Moon in June, July, and August in Kāneʻohe Bay, Oʻahu, although the timing and extent of gamete release can vary widely in different years (Padilla-Gamiño and Gates 2012). Regular spawning events make *M. capitata* amenable to microinjection to deliver reverse genetic regents (including CRISPR/Cas9) in which controlled crosses can be used to study the phenotype resulting from gene knockdowns in newly settled recruits (Cleves et al. 2018, 2020a,b). Microinjection of 1-cell zygotes in *M. capitata* has been tested (by P.A.C.) and shown to function well in this species (Fig. 3b);

6. In *M. capitata*, algal symbionts are transmitted vertically via the egg (Fig. 3b; Padilla-Gamiño et al. 2012), allowing study of the relationship between gene function and symbiont biology and retention during early development.

7. A chromosomal level assembly was recently generated for *M. capitata* using the Dovetail Omni-C library prep and scaffolding with HiRise that identified (as previously predicted in other *Montipora* species; Kenyon 1997) 14 putative chromosomes in this species with a genome of size ca. 650 Mbp (D.B., Hollie M. Putnam, T.G.S., unpubl.).

8. *Montipora* species have great diversity in their algal symbiont communities (*Cladocopium* and *Durusdinium* species) that provides the opportunity to study how different host-symbiont genotype combinations (e.g., via shuffling; Quigley et al. 2019) respond to changing environmental conditions.

9. And finally, *Montipora* populations and species in Hawai‘i show significant phenotypic plasticity, and evidence exists of genetic differentiation among the branching, plating (Fig. 1c), and different color ecotypes of *M. capitata* (Cunha et al. 2019). This trait may allow the investigation, using omics and CRISPR/Cas9 approaches, of the genetic basis of specific types of phenotypic plasticity that occur in *M. capitata* and other Hawaiian coral species.

There are already extensive transcriptomic and metabolomic analyses that have been done with Hawaiian *M. capitata* that provide a strong molecular foundation for interpreting the population genetic studies. These studies have begun to unravel the stress response pathways in this species and to identify markers of coral health. Heat-responsive gene networks (Fig. 4a) contain conserved genes (e.g., Tob/BTG, transcription coactivator YAP1 and HSF1) and a variety of “dark” (also known as orphan [ORFan]) genes (Tautz and Domazet-Lošo 2011; Cleves et al. 2020a,b) of unknown function at hub and peripheral positions (Shumaker et al. 2019; Yoshioka et al. 2022). A recent project completed by our group at the Hawai‘i Institute of Marine Biology (HIMB) in O‘ahu placed *M. capitata* under a 2.7°C temperature increase over a 5-week period (T1–T5). Untargeted hydrophilic interaction liquid chromatography (HILIC)–mass spectrometry (LC–MS) analysis of the holobiont revealed hundreds of interesting features from the coral samples (300 known, ~2100 unknown). The machine learning technique, PLS-DA, demonstrated that the metabolic profiles differed greatly between ambient temperature exposed and heat-stressed corals (Williams et al. 2021b). We identified several known compounds from well-characterized biosynthetic pathways from *M. capitata* that may be involved in the heat-stress phenotype such as methionine and methionine sulfoxide, which were both upregulated in response to heat stress. Novel metabolomic features that may diagnose thermal stress prior to visible bleaching were also found. Foremost of these were several dipeptides that showed a time-dependent increase under high-temperature (Fig. 4b).

Ongoing work aims to develop field-deployable tools for assessing coral health, based on markers identified from metabolomic, gene expression, and protein accumulation data and machine learning approaches. These tools will enable large scale non-invasive monitoring programs that can be used to make informed decisions about coral reef conservation and restoration. For example, the Bhattacharya lab and collaborators have adapted inexpensive Urinalysis reagent test strips (Accutest URS-14100), used for human health monitoring, to analyze metabolite extracts from ambient and heat-stressed corals (unpubl. data). They have also developed smartphone apps for field analysis of coral test strip results (*TestStripDX*; https://github.com/dbsymbiosis/TestStripDX) and assessment of colony color scores (*CoralDX*; https://github.com/dbsymbiosis/CoralDX). The latter is a minimally invasive and widely used method to approximate the extent of coral bleaching (i.e., loss of algal symbionts) that normally required a significant amount of manual image processing but can be greatly simplified and automated using machine learning (Siebeck et al. 2006; Williams et al. 2021b). The Bhattacharya lab and collaborators are also actively exploring the use of nanowell impedance sensors, which are antibody-functionalized wells with nanoelectrodes for measuring changes in impedance due to protein binding. This approach allows quantification of thermal stress related protein accumulation, identified from *M. capitata* proteomic data as being significantly up (e.g., isocitrate dehydrogenase [NADP], mitochondrial) or down (e.g., growth factor receptor bound protein [GRB]10) regulated, in field-collected samples (unpubl.)
data). These tools hold the promise of making assessment of coral health less expensive, larger scale, and more accessible to affected communities. The latter is particularly important for developing countries which may have limited access to the advanced and expensive techniques often deployed in modern coral conservation, and who stand to be disproportionately affected by climate change driven shifts in reef ecosystems.

Beyond these studies, a wide range of research has been done on Hawaiian *M. capitata*, particularly in the well-characterized Kāne‘ohe Bay system. Recent work includes demonstrating the minimal contribution of heterotrophy to holobiont amino acid composition (Wall et al. 2021), defining the negative impacts of thermal stress on reproductive plasticity (e.g., sperm motility) (Henley et al. 2021), identifying the persistent metabolomic signatures of bleaching history in *M. capitata* colonies (Roach et al. 2021), and characterizing the impacts of near-shore stressors such as suspended sediment concentrations and lowered salinity on *M. capitata* fertilization success and larval settlement (Lager et al. 2020). This species has also been a model for identifying novel metabolites of biological significance such as the montiporic acids (MAs) that were initially identified in eggs of Australian *M. digitata*. These compounds exhibit antimicrobial activity and cytotoxicity against leukemia cells (Fusetani et al. 1996) and reduce photosynthetic capacity in coral algal symbionts (Hagedorn et al. 2015). Recently, MAs were found to be abundant in ambient temperature and heat-stressed lab cultures of *M. capitata* colonies.

**Fig. 4.** Omics analysis of *Montipora capitata*. (a) Subnetwork of a group of significantly upregulated transcription factors in response to thermal stress. The yellow nodes indicate dark genes of unknown function (i.e., identified using BLASTP against the nr database; E-value $\leq 10^{-5}$ cutoff) with only hits to cnidarians. (b) Annotated thermal stress network of metabolite cooccurrence in *M. capitata* after 2 weeks of thermal stress (for details, see Williams et al. 2021b). The highly accumulating dipeptides are shown as triangles (under both positive and negative ionization modes) and other metabolites are shown as circles with annotations, when available. Metabolite intensity and the direction of correlation are shown in the legend.
M. capitata, as well as being present in field samples (Williams et al. 2021b). These corals were studied during the June spawning period, thereby likely explaining MA richness (i.e., the metabolite was packaged into eggs) in the animal tissues. This brief accounting of past work on M. capitata in Kāneʻohe Bay and elsewhere in Hawai‘i demonstrates that future multi-omics and genetics research with this species can draw upon a rich source of existing knowledge to guide data interpretation and reach conclusions about the basis of holobiont resilience. A final research area of high interest involves a close relative of M. capitata in the South Pacific that has spread rapidly in Ulithi Atoll (Federated States of Micronesia), acting as an opportunistic species in disturbed areas (Crane et al. 2017). Therefore, this species has some interesting ecological traits at sites beyond Hawai‘i that are worthy of study using omics methods.

Future prospects

Several hypotheses can be posited about Hawaiian corals that merit exploration using M. capitata and other species. First, we expect that morphological and genotypic variation may be unlinked in some cases and will need to be investigated. Therefore, a detailed accounting of standing genetic variation and its relationship to different morphotypes and reef locations will be highly beneficial. The relationship between morphotype and phylogenetic position among Montipora species has been studied in the past using microsatellites, genetic markers, and RADseq (Cunha et al. 2019).

In the future, this type of research should be transitioned to low coverage genome resequencing and/or RNA-seq data drawn from different sites in the Hawaiian Archipelago. The recent chromosome-level assembly of M. capitata (such data are needed from other species) is ideal for this purpose. The existing framework of Hawaiian coral species population structure needs to be augmented with multi-omics and genetic analyses to understand how genomes in an isolated island chain have evolved under different selective regimes found in pristine vs. highly disturbed habitats such as Honolulu Harbor and Pearl Harbor (Brown et al. 2020). Fundamental questions about how genomes are shaped by population biogeography, local adaptation, and ecological parameters will be addressed by such studies. The identification of hybrid zones with divergent populations will allow us to identify adaptive alleles. We anticipate that gene family expansion and contraction, repeat growth and shrinkage, and ploidy changes (e.g., Flot et al. 2008; Baums et al. 2009) will likely play central roles in the evolution of Hawaiian corals species, as well as varying reproductive strategies to deal with divergent environmental and biotic constraints. All these ideas and observations make the Hawaiian Islands an ideal testbed for advancing coral and marine science in general.

Data availability statement

No new data were generated for this study. Existing data for the Montipora capitata genome is available under BioProject PRJNA509219 and the assembly is at http://cyanophora.rutgers.edu/montipora/.

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Conflict of interest

None declared.