



The ReFuGe 2020 Consortium—using “omics” approaches to explore the adaptability and resilience of coral holobionts to environmental change

ReFuGe 2020 Consortium[†]

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Human-induced environmental changes have been linked directly with loss of biodiversity. Coral reefs, which have been severely impacted by anthropogenic activities over the last few decades, exemplify this global problem and provide an opportunity to develop research addressing key knowledge gaps through “omics”-based approaches. While many stressors, e.g., global warming, ocean acidification, overfishing, and coastal development have been identified, there is an urgent need to understand how corals function at a basic level in order to conceive strategies for mitigating future reef loss. In this regard, availability of fully sequenced genomes has been immensely valuable in providing answers to questions of organismal biology. Given that corals are metaorganisms comprised of the coral animal host, its intracellular photosynthetic algae, and associated microbiota (i.e., bacteria, archaea, fungi, viruses), these efforts must focus on entire coral holobionts. The Reef Future Genomics 2020 (ReFuGe 2020) Consortium has formed to sequence hologenomes of 10 coral species representing different physiological or functional groups to provide foundation data for coral reef adaptation research that is freely available to the research community.

Keywords: coral reef ecosystem, global environmental change, adaptation, resilience, Great Barrier Reef, Red Sea, holobiont, metaorganism

Overview

Scleractinian or stony corals are a foundation species of reef ecosystems, as their carbonate skeletons provide the structural habitat complexity necessary to maintain millions of vertebrate and invertebrate marine organisms (Reaka-Kudla, 1997). Over 500 million people and billion-dollar industries, including fisheries and tourism, depend on healthy reef ecosystems (Cesar, 2002). Increases in atmospheric CO₂ concentrations place reef-building corals at risk due to potential rises in water temperatures and ocean acidity. While research focusing on adaptability and response of corals to “future ocean” conditions is steadily increasing (Kleypas et al., 2006; Hoegh-Guldberg et al., 2007a; Császár et al., 2010; Hofmann et al., 2010; Iguchi et al., 2011; Voolstra et al., 2011; Sawall et al., 2015), these studies typically focus on ecosystem scale consequences of environmental change or study the effect on distinct coral compartments.

Relatively few studies target the entire coral holobiont (i.e., the coral metaorganism consisting of the coral animal host, its intracellular algae, and other microbiota) as the functional unit, potentially missing important interactions among members of the holobiont association that contribute to stress tolerance. However, a growing number of studies are now

emphasizing the validity of the metaorganism concept (McFall-Ngai et al., 2013), with functional studies elucidating these fundamental interactions also in aquatic and marine organisms (Bolnick et al., 2014; Franchini et al., 2014; McFall-Ngai, 2014). These studies commonly focus on bacterial-host interactions and demonstrate how bacteria fundamentally alter host organism development, ecology, and evolution (Bosch and McFall-Ngai, 2011). An exception is the study of coral-algal symbioses. *Symbiodinium* sp., the photosynthetic algal symbiont of reef-building corals was formally described in 1962 (Freudenthal, 1962), and the partnership between the coral animal host and its algal symbiont has long been recognized to provide the foundation of coral reef ecosystems. Whereas the algal symbionts provide energy to their hosts in the form of photosynthates, the coral animal provides a sheltered, light-rich environment and inorganic nutrients (Muscatine and Cernichiar, 1969; Falkowski et al., 1984). Currently, there is an urgent requirement for understanding coral resilience and their capacity to adapt in a holobiont framework to provide threshold values for coral reef stewardship (*sensu* Steffen et al., 2015). The long history of research detailing the intricacies of the coral-algal symbiosis and more recent studies on bacterial interactions can now provide the building blocks to understand coral metaorganism function using the new suite of genomic-based approaches.

Although we focus here primarily on coral species from Australia's Great Barrier Reef, our considerations are likely to apply to all coral reefs. We use the term “resilience” in reference to the capacity of an ecosystem or organism to absorb and recover from a perturbation (e.g., toxic agricultural runoffs or temperature spikes) and “adaptability” in reference to the capacity for a lineage or species to adjust to (rapidly) changing circumstances (e.g., a higher average ambient temperature), including potential changes to the composition of the ecosystem. In this context, resilience and adaptation can result in the ecosystem maintaining critical functions and services.

Rather than defining a set of “critical” species to investigate, we define a set of signature genera that represent different physiological or functional coral groups that together form the core of the ecosystem. We acknowledge that coral reefs are highly complex systems in which mechanisms of resilience may not be obvious (e.g., Bellwood et al., 2006), but we also believe that modern genomic approaches may provide equally important insight to the ability of corals to respond to climate change (e.g., Shinzato et al., 2011). We provide an overview of how contemporary genomic tools can be used to provide information pertinent to better understanding how corals function at a basic level, which we expect to be helpful in informing management and conservation of coral reefs. Specifically, we highlight how such tools can be used to explore genetic diversity within and among these species, the genetic basis of relevant traits and their patterns of inheritance, and the dynamic changes that occur during acclimation and adaptation.

This article is structured into four parts: (1) strategic considerations of the composition of complex ecosystems and selection of core functional coral groups; (2) insights from pioneering studies on adaptation in *Drosophila*, stickleback fish

and other species groups that might inform similar research on corals; (3) description of coral ecosystems and the threats arising from environmental change; and (4) a case study on genomic approaches to understand adaptability of corals.

Strategic Considerations and Approach

Environmental change may intensify selective pressures acting on organisms. Although our overall concern is the resilience of a given ecosystem as a whole, it is more practical to consider the responses of individual component species, especially those that play key roles in the ecosystem. Understanding which species can or cannot cope will provide a baseline (i.e., which species might be expected to persist) and constrain models of ecosystem function that depend on the sum of individual responses and the synergies among them. “Foundation species”, those that provide habitat for others and simultaneously facilitate higher diversity, are increasingly recognized as significant factors at the ecosystem level (Bruno et al., 2003). The heritable effects of genes in these foundation species extend to higher levels, contributing to ecosystem phenotypes that other species may rely on (Whitham et al., 2006). In the example at hand, the coral is a metaorganism consisting of the coral animal, photosynthetic dinoflagellate symbionts, and species-specific assemblages of microorganisms, collectively referred to as the coral holobiont (Rohwer et al., 2002). Population and quantitative genetic analyses of the coral holobiont allow us to elucidate heritable components of ecosystem phenotypes and provide an evolutionary framework in which to understand the effect of climate change on organisms that in turn affect ecosystem processes. In this regard, it is important to incorporate knowledge about metaorganism function from ecological and evolutionary studies, since an important aspect of coral resilience might lie in understanding how the coral-algae-microbe symbioses co-evolved and how this in turn connects genomes and phenotypes (Bosch and McFall-Ngai, 2011). In other words, an increased understanding of the evolutionary forces that shape metaorganisms and their hologenomes will help to assist and mitigate detrimental effects of environmental change on corals and their reef ecosystems, and support efforts of building coral resilience through assisted evolution (van Oppen et al., 2015).

The primary question is how to identify the species that are likely to be most informative for assessing resilience and adaptability of the ecosystem in question, and thus should be prioritized for study. We posit that there exist certain core coral genera that reflect distinct physiological groups, which should become the initial focus, but will be expanded as the ability to gather data advances. Given the above, the criteria for selection should be (i) genera or species that occur (or have very close relatives) in equivalent ecosystems around the world, and are thus generally typical and representative of that type of ecosystem; and (ii) among these, species that are amenable to experimental assessment and manipulation in enclosed environments (i.e., aquaria). Given the ongoing advance of sequencing technology, selecting species with relatively small genomes (for efficiency of assembly and analysis) is not a primary criterion, but might be considered downstream in the selection

process. Compromises will have to be made, and known and unknown blind spots accepted, if we are to make a start and not be inhibited by the scope of the problem and our current ignorance.

For the experimental component, we propose a three-pronged approach: (i) identification of genomic, epigenomic, and transcriptomic variation across natural clines of the environmental factor of interest; (ii) experimental assessment of the ability of variants from each end of the clines to withstand a controlled progression to the other extreme and determine how time-sensitive and reversible this response may be; and (iii) genome-scale sequencing to examine the genomic, epigenomic, and transcriptomic changes that may have occurred as part of an adaptive response and how they correspond to the variation that is observed naturally. In making these suggestions, we note the enormous recent increase in DNA-sequencing capacity, and the corresponding reduction in cost, that make large-scale surveys increasingly feasible. We suggest that any strategy must be tractable, yet scalable to benefit from ever-improving sequencing technologies. Further, although there are many sequencing projects underway, the concerted work of a group of researchers will facilitate coordination, and thus helps to streamline and channel sequencing efforts. For instance, the Global Invertebrate Genomics Alliance (GIGA) was formed to coordinate current efforts generating and analyzing invertebrate non-arthropod genomic data (GIGA Community of Scientists, 2014). This becomes especially important in conducting downstream comparative analyses and providing a data infrastructure that allows easy access and retrieval of genomic baseline data.

The Genetics of Adaptation: Insights from the Fruit Fly *Drosophila* and Other Model Systems

Studies on various other species groups including the fruit fly *Drosophila*, the rockcress *Arabidopsis*, stickleback fish *Gasterosteus*, and other model organisms have been particularly informative in understanding the heritability of different traits and the response of different species to environmental change and selection at the genetic and genomic levels. The *Drosophila* work was initiated in *D. melanogaster* and has focused on environmental gradients, particularly latitudinal climatic gradients (see Schmidt et al., 2005; Hoffmann and Weeks, 2007). Genetic analyses along gradients have been used to identify genes and genetic polymorphisms that appear involved in evolutionary adaptation to different climates (e.g., Schmidt et al., 2005; Paaby et al., 2010; Telonis-Scott et al., 2011). Some of these polymorphisms are shifting in response to recent climate change (Umina et al., 2005). Regions of the genome that have diverged between the ends of climatic gradients have been identified (González et al., 2010; Fabian et al., 2012), and transcriptomes from gradient ends have also been compared (Chen et al., 2012). Environmental gradients have been used to link adaptation to genetic polymorphisms in many other species; notable examples include polymorphisms affecting salinity in *Gasterosteus* (Barrett et al., 2008) or flowering time in *Arabidopsis* (Caicedo et al., 2004).

Although great progress has been made in understanding the genetic basis of adaptive variation in *Drosophila* and other organisms, it remains difficult to make direct connections between genetic polymorphisms and traits associated with climate adaptation (Chung et al., 2014). The effects of candidate genetic polymorphisms identified from different types of experiments and/or clinal analysis need to be tested on randomized genetic backgrounds to assess their impact on traits that vary along gradients (Lee et al., 2011). This is facilitated by tools available in model organisms, including *D. melanogaster*, which allow the expression of specific genes to be modified, and effects of polymorphisms to be assessed in controlled backgrounds. A combination of approaches has allowed the adaptive significance of particular genetic changes to be identified: for instance, expression of the *ebony* gene affects body pigmentation (Pool and Aquadro, 2007; Telonis-Scott et al., 2011), which in turn may influence fitness under different climatic conditions (Parkash et al., 2008) and shows clinal patterns (Telonis-Scott et al., 2011); a set of polymorphisms in the regulatory region influences expression of this gene (Takahashi and Takano-Shimizu, 2011).

The genus *Drosophila* itself and related genera contain an enormous range of species adapted to different climatic regions. It is now possible to map traits that influence climate adaptation onto *Drosophila* phylogeny to develop a detailed understanding of limits to climate adaptation, controlling for environmental effects by rearing the species in a common environment (Strachan et al., 2011; Kellermann et al., 2012). Clear links have been established between traits and species distributions including resistance to desiccation, cold, and heat. There is strong phylogenetic signature in these traits, and clades can be identified that seem to lack evolutionary potential because all the related species show a similar stress response (e.g., desiccation resistance in *D. birchii* and other species from wet tropical environments (Hoffmann et al., 2003; Kellermann et al., 2009). To understand why trait evolution might be limited within particular species and clades, candidate genes and genetic processes are being mapped onto phylogenies (Reis et al., 2011). Within *Drosophila* phylogenies, evolutionary responses to environmental factors appear related to gene duplication and gene loss within particular gene families (Zhong et al., 2013). *De-novo* evolution of genes seems to be a rich source for adaptive evolution in *Drosophila* lineages (Chen et al., 2010). While immediate responses to selection under climate change may depend on standing genetic variation, genomic changes might nevertheless contribute to adaptive changes across a few decades (Izutsu et al., 2012). Genetic adaptation will also depend on other factors like patterns of gene flow that can be maladaptive and limit local adaptation (Magiafoglou and Hoffmann, 2003) and/or maternal effects that can result in the transmission of stress resistance from mothers to offspring (Jenkins and Hoffmann, 1994).

Coral Reefs and Environmental Change

Phylogenetic constraints outlined in species of *Drosophila* are likely to occur in many other species groups, particularly for upper thermal limits (Araújo et al., 2013). This is of particular significance as most corals live close to their thermal

tolerance limits, and hence may be severely affected by global warming and increasing sea surface temperatures (SST). To better understand the consequences of environmental change for coral reefs, a closer look at the ecology of coral organisms is needed.

Over the past century, coral reefs have been in global decline—more than 50% of extant reefs are severely degraded and most of the remainder are under serious threat (Hoegh-Guldberg, 1999). The causes of reef loss are varied and complex, but a major current concern is that global changes in climate may drive increasingly more frequent and widespread coral bleaching events and thus exacerbate reef loss (Hoegh-Guldberg, 1999). Reefs flourished in pre-industrial times, when the pH of the ocean was around 8.1, but the advent of the industrial period has led to increasing atmospheric CO₂, and the oceans have become both warmer and more acidic. Average SSTs in the tropical oceans have increased by around 0.6°C over the past century, and much greater changes are forecast to occur in the twenty-first century if present rates of emission continue (Bindoff et al., 2007). Mass coral bleaching events, resulting in widespread mortality, are a consequence of thermal anomalies that are likely to increase in frequency and extent as a function of higher ocean temperatures (Hughes et al., 2003). This effect may be compounded by the decreases in pH that occur as atmospheric CO₂ equilibrates with seawater, as calcification becomes increasingly more energetically costly under more acidic conditions (Anthony et al., 2008).

Although corals may be able to adapt to a changing world, the main concern is that they may be unable to do so rapidly enough to keep pace with current rates of change, which are orders of magnitude more rapid than occurred during ice age transitions (Hoegh-Guldberg et al., 2007b). Corals have relatively long generation times (10–100 years), and thus evolve on far longer timescales than, for example, fruit flies. Factors that can potentially mitigate the slow evolutionary rate include high levels of genetic diversity and the large effective population sizes in at least some species. Moreover, the coral holobiont as a metaorganism may evolve much more rapidly than can the coral animal because the symbiotic dinoflagellates and microorganisms associated with corals are themselves highly variable and have short generation times, provided that there is enough flexibility in these associations. Of note, the contribution of phenotypic plasticity in corals, i.e., the development of different phenotypes from a single genotype depending on the environment, might be an important contributor to the response to environmental change, and hence, coral resilience (Todd, 2008). While light and water movement are recognized important variables in determining coral shape and form, it was recently shown that seawater acidification can also cause a shift in coral skeleton morphology, in concert with and probably to evade the consequences of a decrease in coral calcification rates (Tambutté et al., 2015). As such, plastic responses in corals (including all holobiont compartments) might in themselves be adaptive and improve fitness, i.e., growth, reproduction, or survival (Gotthard and Nylin, 1995). Availability of large-scale gene expression data will make it possible to study plasticity from a molecular perspective, e.g., determining how many and which

genes vary in expression between different phenotypes of a plastic trait, thereby helping to uncover the cellular mechanism(s) involved (Aubin-Horth and Renn, 2009).

Genetic diversity within a location may also provide scope for selection for change in local thermal tolerance. For instance, recent work on *Acropora hyacinthus* has shown that within a single site, local acclimatization and adaptation contribute equally to thermal tolerance (Palumbi et al., 2014). Importantly, this was reflected in patterns of gene expression, providing a direction for further studies. However, our understanding of genetic diversity within coral populations is generally at an early stage, leaving a large series of unanswered questions including (i) which species will be most sensitive to the predicted change in sea surface temperature and ocean acidity; (ii) where resistant genotypes might be found for potential use in captive breeding, translocation, or assisted migration programs, and for DNA banks; (iii) what is the natural level of gene flow among populations within a reef system, e.g., along the Great Barrier Reef; (iv) the expected rate of adaptive response, if any, in different species; and (v) how differences in the microbial communities associated with a coral affect its capacity for phenotypic response, and how heritable that might be. We can begin to address these questions within an initial set of signature genera as further outlined below.

Case Study: Genomic Approaches to Assess Adaptability of Corals to Climate Change

Building on insights into the genomic bases of adaptation in model organisms including *Drosophila*, genome science has the potential to rapidly advance our understanding of the adaptive capacity of reef-building corals (Stapley et al., 2010; Shinzato et al., 2011). While we acknowledge the inherent differences between fruit flies and corals, development and testing of hypotheses in model organisms can act as a springboard to inform coral biology (Baumgarten et al., 2015). Given the urgency of the problem and decreasing costs of sequencing technologies, the authors of this paper have formed the Reef Future Genomics 2020 Consortium (ReFuGe 2020), within which our “Sea-quence” project has identified a framework of molecular datasets that we anticipate will provide novel insights into the adaptive landscape of reef-building corals, their dinoflagellate symbionts, and the associated microbial communities (<http://refuge2020.com/>).

For the Sea-quence project, we have initially selected 10 species of tropical corals from a diverse set of genera for deep genomic and transcriptomic sequencing of all coral holobiont compartments, i.e., *de-novo* genome and transcriptome sequencing of the coral host, associated *Symbiodinium* types, and microbial (including viral) metagenomes and metatranscriptomes for each selected coral species. We included corals that are broadly distributed across environmental gradients, physiologically diverse, and easily identified in the field. While it is impossible to cover the full diversity of the order Scleractinia, we selected species within genera that represent different physiological groups, e.g., thermally

TABLE 1 | Selection of 10 initial coral species and organismal attributes targeted for hologenome sequencing in the ReFuGe 2020 Consortium.

Morphological group	Coral species	Coral temperature tolerance	Coral growth rate [#]	Symbiont transmission mode [*]	Symbiont diversity
Massive corals	<i>Porites lutea</i>	High	Slow	Vertical	C types
	<i>Goniastrea aspera</i>	High	Slow	Vertical/Horizontal ^a	C, D types
Branching corals	<i>Stylophora pistillata</i> **	Low	Slow	Vertical	A, C types
	<i>Acropora millepora</i> **	Low	Fast	Horizontal	C, D types
	<i>Porites cylindrica</i>	High	Intermediate	Vertical	C types
Tabular corals	<i>Acropora hyacinthus</i>	Low	Fast	Horizontal	C, D types
Foliaceous corals	<i>Montipora aequiturbiculata</i>	Low ^b	Intermediate	Vertical	C, D types
Encrusting corals	<i>Montipora spumosa</i>	Unknown	Intermediate	Vertical	N/A
Solitary corals	<i>Fungia fungites</i>	Moderate ^c	Slow	Assumed vertical	C, D types
Non-symbiotic corals	<i>Madrepora oculata</i>	Low ^d /High ^e	Slow	N/A	N/A

Species selection will be expanded in the course of the work of the Consortium (<http://refuge2020.com/>).

^{*}Symbiont transmission data based on Baird et al. (2009).

[#]Growth rate based on slow <15 mm/year, intermediate 15–30 mm/year, fast >30 mm/year.

^{**}De-novo sequencing complete (Miller/Ball/Foret and Voolstra/Aranda labs).

^aAccording to Sakai (1997).

^bAccording to Marshall and Baird (2000).

^cAccording to Hoeksema (1991).

^dAccording to Naumann et al. (2014).

^eAccording to Roder et al. (2013).

susceptible as well as tolerant genera (e.g., *Porites* and *Acropora*) (Marshall and Baird, 2000). We also considered the mode of reproduction, extent of existing resources and datasets, ease of collection and cultivation, and diversity and transmission mode of the symbiont. The 10 species are broadly distributed across the Indo-Pacific and occupy a wide range of thermal environments, making it likely that the results will be broadly applicable (Table 1). We anticipate the initial species selection will be expanded in the course of the work of the ReFuGe 2020 Consortium. A current overview is available on the ReFuGe 2020 webpage (<http://refuge2020.com/our-research/research-progress>). At the time of writing of this manuscript, genomic DNA from several coral holobionts has been sequenced (data are accessible at <https://ccgapps.com.au/bpa-metadata/gbr/>).

Availability of *de-novo* reference genome sequences of 10 coral genomes and associated microorganisms will be instrumental in providing answers to basic and specific questions of coral biology. For instance, the provision of annotated holobiont gene sets will allow the elucidation of the metabolic, immunological, and physiological capacities encoded in coral metaorganisms as well as the determination of a core set of orthologous genes that allows deciphering the mechanistic underpinnings of coral biology. The availability of reference genomic resources is invaluable for informing downstream experimental approaches, such as transcriptional, protein, and epigenetic profiling. As described above for *Drosophila*, we aim to explore genomic, epigenomic, and transcriptomic variation along latitudinal gradients to uncover acclimation and adaptation potential of selected genera. For instance, along the 1000-km north-south gradient of the Great Barrier Reef water temperatures differ by about 2°C. Along this transect, experiments have revealed that corals from the southern Great Barrier Reef are much more susceptible to thermal stress than are those from the northern region (Ulstrup et al., 2006; Cooper et al., 2011).

Complementing such data with analyses of selected target or similar species from “extreme” environments (“extreme phenotype sequencing”), e.g., the Red Sea (Arif et al., 2014; Sawall et al., 2014) or Arabian Gulf (Hume et al., 2013, 2015), provides the opportunity to determine how standing genetic variation, phenotypic plasticity, population size, and genomic architecture translate into adaptability of coral organisms and resilience of reef ecosystems. In combination with manipulative experiments, genetic variability can potentially be partitioned into that relating to tolerance to water temperature vs. the many other environmental factors that co-vary with it. Understanding which elements are associated with “climate change tolerant” coral species will present opportunities for management strategies aiming to preserve the resilience of coral reef regions. Generation of holobiont genome reference data is not an end (Richards, 2015), but rather the foundational necessity for research targeting resilience and adaptability of coral holobionts. As such, it substantiates, rather than replaces, other efforts of coral reef research.

Conclusions

Here we have outlined a genomics framework focusing on signature coral genera for which hologenomes will be generated to better understand resilience and adaptability of coral holobionts and by extension reef ecosystems. Under the “Sea-quence” project the ReFuGe 2020 Consortium generates and analyzes a set of genomic reference data to interrogate the adaptive potential of different functional groups. Our approach leverages the enormous scope and capacity of sequencing technology to query genetic diversity and to profile real-time genomic responses to environmental stress. On this road we have adopted lessons from adaptation research in *Drosophila* and other species. Our approach is an important first step to generate

foundation data for coral reef adaptation research, freely available to the research community, to make better predictions about

which species may be expected to persist, under what conditions, and why.

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