Chapter 1

Introduction to the book *Coral reef conservation and restoration in the omics age*

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Coral reefs not only support a vast amount of marine biodiversity (Fisher et al. 2015), but provide critical goods and services to humankind, such as coastal protection, commercial fisheries, and pharmaceuticals, and have important recreational and cultural value (Moberg and Folke 1999). The need to protect and restore coral reefs has, however, never been more urgent than today. A suite of human activities with local and global scale consequences for the environment have contributed to the decline of coral reefs. These include coastal development and related terrestrial run-off and sewage outflow causing habitat destruction, nutrification, sedimentation and pollution; overharvesting of commercially valuable species; the introduction of foreign species; and the excessive emission of carbon dioxide and other greenhouse gasses causing ocean acidification and warming (Jackson et al. 2001; Pandolfi et al. 2003; Hughes et al. 2007; De'ath et al. 2012). Of these anthropogenic disturbances, the rise of sea surface temperatures (IPCC 2021) is currently the biggest threat to the persistence of coral reefs because it is a global threat that causes an increase in the frequency, intensity and duration of summer heatwaves (Oliver et al. 2019). The critical symbiosis between corals and their microbial photosymbionts (Symbiodiniaceae) often breaks down during these periods of unusually high temperature, causing a paling of the coral tissues due to a loss of the Symbiodiniaceae (called coral bleaching) (Hoegh-Guldberg 1999). Corals rely on their symbiosis with Symbiodiniaceae as the symbionts provide corals with most of their energy (Muscatine and Porter 1977; Yellowlees et al. 2008; Kopp et al. 2013), and they often die if the symbiosis cannot re-establish. The Symbiodiniaceae also accelerate calcification rates and thus the formation of the coral skeleton (Pearse and Muscatine 1971; Barnes and Chalker 1990) which functions as the reef's real estate providing a home to at least a third of all marine multicellular eukaryotes (Fisher et al. 2015).

Widespread coral bleaching events that affect the majority of corals present on reefs as well as many reefs within a region are called mass bleaching events. The first global mass coral bleaching event in 1997-1998 resulted in a loss of ~8% of the world's coral. Recovery to pre-1998 levels ensued in the following decade, but subsequent mass bleaching events and other disturbances between 2009 and 2018 reduced global coral cover by ~14% (Souter et al. 2021). Larger declines in regional coral cover are often seen immediately following mass bleaching events. For example, on the Great Barrier Reef, about half of the coral cover was lost due to the back-to-back mass bleaching events of 2016 and 2017. Climate models predict further warming will occur and even if we can keep warming at 1.5°C above pre-industrial temperatures, up to 90% of the world's coral reefs could be lost (van Hooidonk et al. 2016; Bindoff et al. 2019).

In addition to increasing the frequency and magnitude of coral bleaching events, climate change related temperature anomalies are believed to drive increases in coral disease incidence (Bruno et al. 2007; Ruiz-Moreno et al. 2012; Randall and van Woesik 2015; Howells et al. 2020). Coral disease outbreaks have also been associated with overfishing (Raymundo et al. 2009) and poor water quality (Haapkylä et al. 2011; Pollock et al. 2014; Lamb et al. 2018). Considerable losses of coral cover worldwide have been attributed to coral disease, particularly in the Caribbean (Ruiz-Moreno et al. 2012).

The United Nations have declared the period 2021-2030 the Decade on Ecosystem Restoration (https://www.iucn.org/theme/nature-based-solutions/initiatives/decade-ecosystem-restoration).

Restoration is defined as “any intentional activity that initiates or accelerates the recovery of an ecosystem from a degraded state” (IPBES 2018). Sadly, the decay of coral reefs has progressed to a state where conservation, “the study of the loss of Earth’s biological diversity and the ways this loss can be prevented” (https://www.britannica.com), may no longer be sufficient to preserve biodiversity and ecosystem functions and services, and restoration efforts need to be considered (Bay et al. 2019; National Academies of Sciences and Medicine 2019; Hein et al. 2021; Knowlton et al. 2021).

Coral reef conservation and restoration consist of actions that are proactive (i.e., aimed at protecting and enabling recovery) or reactive (aimed at repairing ecosystem function and assisting recovery of a degraded reef system) (Hein et al. 2021). The former include actions such as climate change mitigation, reef shading and cooling, the establishment of marine protected areas, and water quality management, whereas the latter are comprised of interventions like coral gardening, larval enhancement, assisted evolution, biobanking, algal removal and substrate manipulation. The development of novel ecosystem conservation and restoration tools relies on scientific research across disciplines, such as social science, mechanical engineering, geo-engineering, bio-engineering, ecology, reproductive biology, microbiology, genetics and omics research (i.e., genomics, epigenomics, transcriptomics, proteomics, metabolomics). While a large amount of genetics and omics research relevant to coral reef conservation and restoration has been conducted and is ongoing, uptake of omics research data into conservation and restoration planning has been limited. This book focuses on reef-building corals and their associated microalgal and bacterial symbionts, because corals are foundation and keystone taxa of coral reefs. It highlights the value of omics data in many aspects of coral reef conservation and restoration and has packaged information that tends to be scattered in the scientific literature. The book is aimed at researchers, students, and reef managers with an interest in the field.

Chapters 2 to 5 focus on genetic variation encoded in the genome of the coral host animal. In Chapter 2, Riginos and Beger review spatial genetic and genomic approaches to assess coral connectivity and adaptive potential. They describe how genetic connectivity and adaptative genetic variation can be measured, what the challenges in measuring these parameters are, and how this information can be incorporated in spatial planning and coral reef management. An important conclusion is that the design of networks that support evolutionary resilience and especially evolutionary rescue can help corals cope with the contemporary climate crisis. High levels of genetic diversity reflect a high adaptive potential; maintaining or restoring genetic diversity in coral populations is therefore an important component of conservation and restoration. In Chapter 3, Baums et al. discuss how genetic diversity can be measured and maximised in coral reef restoration initiatives. The authors caution that selection for enhanced tolerance to one stressor, such as elevated temperature, may jeopardise tolerance to other stressors and can result in the loss of genetic diversity. Further, captive rearing itself (without selection for certain traits) can inflict genetic bottlenecks and cause genetic erosion. The various aquaculture steps that may contribute to uneven genet contribution to batch cultures, from gamete spawning to larval settlement and the outplanting phase, are evaluated. Baums et al. stress that the maintenance of genetic diversity must not be overlooked in restoration programs and provide guidelines for the development of genetic management plans. Howells and co-authors (Chapter 4) delve deeper into the topic of adaptive genetic variation that exists in the coral host genome and genomic loci that underpin thermal tolerance, how it arises, and how it can be detected and monitored by phenotypic and genomic methods. The authors provide evidence for the existence of coral adaptation to the local thermal environment and the heritability of heat tolerance traits. Further, they urge that knowledge on adaptive genetic variation be used to (1) prioritise reefs for protection, (2) select coral brood stock for reef restoration, (3) predict coral responses to climate change, and (4) assess the risks and benefits of genetic interventions. The chapter ends by stressing the need for translation of complex genomic, environmental and modeling data into formats that allow uptake by reef managers and other stakeholders. In Chapter 5, Drury et al.

explore intraspecific selective breeding, the reproductive crossing of specific individuals to produce offspring that have improved desired trait values, to enhance coral climate resilience. All coral selective breeding studies to date are restricted to a single generation of breeding. Based on four case studies, the authors show that the average survivorship of selected coral offspring (F1 resulting from crosses of tolerant corals) is higher compared with that of the unselected control offspring (F1 offspring of most sensitive corals). Coral phenotypes, their genotypes or information on their local environment can be used to choose parental brood stock, and in some instances the microalgal symbiont community composition can also be a trait relevant for parental brood selection. Drury and co-authors provide a step-by-step selective breeding workflow and discuss the risk and limitations of and future directions for selective breeding of corals.

The contribution of omics approaches to understanding the roles of coral-associated microbes and the value of microbes for coral reef conservation and restoration are addressed in chapters 6 to 8. In Chapter 6, Shah et al. review genomic features of the Symbiodiniaceae, how genome sequence data can provide insight into their evolutionary diversification and how they can guide efforts aimed at the bioengineering of more resilient coral reefs. The authors stress the enormous genomic diversity and divergence among Symbiodiniaceae taxa revealed by genome sequence analyses and highlight the need for additional data to fully understand coral-Symbiodiniaceae interactions in the context of coral resilience. Maher and co-authors review the literature on the diversity, composition and function of coral-associated bacteria in Chapter 7. These authors discuss possible bacterial pathogens and parasites known from corals, the way in which antimicrobials produced by some bacteria shape bacterial communities and how bacteria contribute to the expansion of the metabolic capabilities of the coral holobiont. The chapter summarises published works on coral-associated bacterial community variability and dynamics in response to environmental stress, and synthesises how bacterial communities may contribute to coral holobiont resilience. Certain changes in the bacterial communities may be used as early warning systems of coral stress and have value in reef health monitoring, and microbiome manipulation may accelerate host acclimatisation or adaptation. Van Oppen and Nitschke review how coral microbiome manipulation may enhance coral thermal bleaching resilience in Chapter 8, with a focus on Symbiodiniaceae and bacteria. The authors summarise current knowledge on the mechanisms responsible for thermal bleaching, describe the importance of omics approaches in microbiome engineering efforts, highlight key knowledge gaps, and provide direction to the field based on the premise that these interventions need to be self-sustaining to make them financially viable. Encouragingly, experimental evolution of Symbiodiniaceae has resulted in strains able to enhance thermal bleaching tolerance of corals following their introduction into corals. For the development of bacterial probiotics, they recommend to first identify culturable bacteria that are stably associated with their coral host, located within the coral tissue and ideally maternally transmitted. Experimental evolution can subsequently be used to enhance trait values if required.

Chapters 9 to 12 address how omics approaches other than genomics have been applied to corals and discuss their current and anticipated future value for coral reef conservation and restoration. In chapter 9, Aranda leads us through the state-of-play of coral acclimatisation (i.e., acquired tolerance) to environmental stress and its underlying epigenetic mechanisms. The chapter includes a brief history of the young field of epigenetics, the molecular mechanisms underpinning epigenetic changes as well as those behind epigenetic transcriptional memory and finishes by proposing a model for epigenetic memory and acquired tolerance in corals. Aranda concludes that there is some evidence for environmental memory induced by previous stress events that makes corals more tolerant to future events, and that in some instances this may be passed on to the next generation. However, there is a general lack of long-term monitoring of individual corals, and evidence of an adaptive value of epigenetic marks is often not provided. In Chapter 10, Kenkel and Wright synthesise existing transcriptomics studies on corals, ways by which gene expression can be measured for individual coral holobiont members and for the holobiont as a whole, and what the applications of transcriptomics are for coral reef conservation and restoration. The authors conclude that one of the most promising applications is the development of targeted biomarkers, both diagnostic and predictive. Further, in addition to providing data on patterns of gene expression, RNAseq data can be used to estimate genetic variation and divergence in holobiont members and this has been successfully used to reveal cryptic species. Finally, partnerships between researchers and practitioners are highlighted as key to accelerate the integration of transcriptomics into conservation and restoration policy and practice. Chapter 11 (by Cleves) addresses how reverse genetics in corals can inform conservation efforts. The genetic basis of coral heat tolerance remains poorly understood because the function of gene candidates cannot be tested without reverse genetic tools. The chapter reviews recent advances in reverse genetics in cnidarians other than corals, the state-of-play of genetic tools for corals and provides a roadmap for tool development in corals. Cleves contends that reverse genetics will help unveil the genes and main cellular mechanisms underpinning bleaching and may be used to enhance coral thermal tolerance via knock-ins of certain alleles allowing testing of trade-offs against enhanced thermal tolerance. However, the author warns against rushing to release transgenic corals into the wild. In Chapter 12, Lawson and co-authors discuss omics approaches that examine the metabolites representing the end- (or by-/waste-) products of cellular processes, as well as the elemental building blocks for all metabolites. These approaches help decipher the functional roles of corals within coral reef ecosystems. Available methods and progress in the field are reviewed for elementomics, classical metabolomics, lipodomics and volatilomics. The authors propose these methods can be used in conservation and restoration initiatives for identifying thermally resistant coral colonies, as early warning biomarkers and for reef health monitoring, and for guiding genetic engineering efforts aimed at enhancing tolerance. The chapter ends by providing a roadmap for prioritising research and development of the metabolomics disciplines reviewed.

Chapter 13 (Richards *et al.*) addresses the emerging field of biodiversity monitoring via environmental DNA (eDNA) analysis, explains what eDNA is, the methods and workflow used, and reviews its applications relevant to coral reefs. The authors discuss the spatial and temporal scales over which eDNA in various reef habitats can be assessed and what the strengths and limitations of the eDNA approach are. The chapter ends with a view to the future of eDNA and eRNA and concludes that eDNA has an important role in biodiversity research which, coupled with appropriate communication of the extent of coral reef biodiversity loss, critically contributes to achieving action on climate change. Bouwmeester and colleagues discuss current advances in coral cryopreservation in Chapter 14. The primary aim of freezing coral alive is to preserve extant genetic diversity for future reef restoration, with the facilitation of scientific coral research being a secondary aim. The authors present the rationale for and challenges of the methods used to cryopreserve coral sperm, larvae, algal symbionts, and coral fragments. Coral eggs have not yet been successfully cryopreserved. Population genetic and genomic approaches will inform the number of genets that need to be preserved to represent the genetic diversity that exists within a population or species. The authors stress that as reefs are disappearing rapidly, it is critical for cryobiologists to collaborate with engineers to address issues of scalability and develop user-friendly, cost-effective and field-ready methods. Further, engagement with other stakeholders of coral reefs is vital. The book ends with a brief synthesis of chapters 2-14 (Chapter 15).

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