INVITED REVIEW

Shifting paradigms in restoration of the world's coral reefs

MADELEINE J. H. VAN OPPEN[1,2] (iD), RUTH D. GATES[3], LINDA L. BLACKALL[2], NEAL CANTIN[1], LEELA J. CHAKRAVARTI[1,4,5], WING Y. CHAN[1,2], CRAIG CORMICK[6], ANGELA CREAN[7], KATARINA DAMJANOVIC[1,2], HANNAH EPSTEIN[1,4,5,8], PETER L. HARRISON[9], THOMAS A. JONES[10], MARGARET MILLER[11], RACHEL J. PEARS[12], LESA M. PEPLOW[1], DAVID A. RAFTOS[13], BRITTA SCHAFFELKE[1], KRISTEN STEWART[14], GERGELY TORDA[1,8], DAVID WACHENFELD[12], ANDREW R. WEEKS[2] and HOLLIE M. PUTNAM[3,*]

[1]Australian Institute of Marine Science, PMB No. 3, Townsville MC, QLD 4810, Australia, [2]School of BioSciences, University of Melbourne, Parkville, VIC 3010, Australia, [3]Hawaii Institute of Marine Biology, Kaneohe, HI 96744, USA, [4]AIMS@JCU, James Cook University, Townsville, QLD 4811, Australia, [5]College of Marine and Environmental Sciences, James Cook University, Townsville, QLD 4811, Australia, [6]ThinkOutsideThe, 12 Giffen Close, Holt, ACT 2615, Australia, [7]School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia, [8]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia, [9]Marine Ecology Research Centre, School of Environment, Science and Engineering, Southern Cross University, Lismore, NSW, Australia, [10]USDA-Agricultural Research Service, Forage and Range Research Laboratory, Logan, UT 84322-6300, USA, [11]National Oceanic and Atmospheric Administration-National Marine Fisheries Service, Miami, FL, USA, [12]Great Barrier Reef Marine Park Authority, PO Box 1379, Townsville, QLD 4810, Australia, [13]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia, [14]SUNY College of Environmental Science and Forestry, Syracuse, NY 13210-2788, USA

Abstract

Many ecosystems around the world are rapidly deteriorating due to both local and global pressures, and perhaps none so precipitously as coral reefs. Management of coral reefs through maintenance (e.g., marine-protected areas, catchment management to improve water quality), restoration, as well as global and national governmental agreements to reduce greenhouse gas emissions (e.g., the 2015 Paris Agreement) is critical for the persistence of coral reefs. Despite these initiatives, the health and abundance of corals reefs are rapidly declining and other solutions will soon be required. We have recently discussed options for using assisted evolution (i.e., selective breeding, assisted gene flow, conditioning or epigenetic programming, and the manipulation of the coral microbiome) as a means to enhance environmental stress tolerance of corals and the success of coral reef restoration efforts. The 2014–2016 global coral bleaching event has sharpened the focus on such interventionist approaches. We highlight the necessity for consideration of alternative (e.g., hybrid) ecosystem states, discuss traits of resilient corals and coral reef ecosystems, and propose a decision tree for incorporating assisted evolution into restoration initiatives to enhance climate resilience of coral reefs.

Keywords: assisted evolution, climate change, coral reefs, global warming, hybrid ecosystems, rehabilitation, restoration, scleractinia

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Introduction

Human activities that began with the industrial revolution in the late 18th century have driven an incredibly rapid increase in greenhouse gas concentrations in the

*Present address: Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

Correspondence: Madeleine J. H. van Oppen, tel. +61 3 83448286, fax +61 383447909, e-mail: madeleine.van@unimelb.edu.au

Earth's atmosphere. As a result, air and ocean temperatures have risen and continue to rise at a pace not experienced by life on Earth for at least 50 and possibly even hundreds of millions of years (Hönisch *et al.*, 2012; Wright & Schaller, 2013; Zeebe *et al.*, 2014). These global environmental changes, as well as the often more localized direct human impacts such as overharvesting, destructive fishing, anchor damage, ship groundings, and pollution, have precipitated broad ecological declines, shifts, and extinctions across a variety of

ecosystems (Parmesan, 2006), including coral reefs (Pandolfi *et al.*, 2003).

Higher-than-usual seawater temperatures can break down the obligate association between the reef-building coral animal and its dinoflagellate endosymbionts (*Symbiodinium* spp.), causing coral bleaching and often extensive mortality (Hoegh-Guldberg, 1999). Ocean acidification (OA) is a consequence of atmospheric carbon dioxide entering the water column, resulting in an increase in hydrogen ion concentration that shifts the seawater carbonate chemistry, resulting in a lower pH. OA increases the energetic demands for calcifying organisms such as corals, may cause a reduced calcification rate (Andersson & Gledhill, 2013), and may exacerbate the negative impact of elevated temperature by reducing the corals' bleaching tolerance limits (Anthony *et al.*, 2008). A number of severe bleaching events have assaulted coral reefs around the world over the past 35 years, including in 1981/1982, 1997/1998, 2001/2002, 2005/2006, 2010, and 2014/2016. The most recent events have seen extreme bleaching with 75% of the corals bleached in some locations in Hawaii (Minton *et al.*, 2015) and 93% of surveyed reefs on the Great Barrier Reef (GBR) exhibiting some level of bleaching with >50% coral mortality observed at many locations in the northern GBR (Great Barrier Reef Marine Park Authority, 2016; The Conversation, 2016a). Climate models predict that most of the world's coral reefs will face temperature extremes annually before the end of this century (Van Hooidonk *et al.*, 2013, 2016), with some experiencing such conditions from as early as the mid-2030s (The Conversation, 2016b). Given recovery of coral cover from severe coral mortality to the predisturbance state takes multiple decades (Connell *et al.*, 1997; Coles & Brown, 2007; Emslie *et al.*, 2008; Done *et al.*, 2010; Jackson *et al.*, 2014), climate projections portray a grim future for coral reefs. Thus, in addition to global efforts to reduce greenhouse gases, a toolbox of options is urgently needed for coral reef rehabilitation, repair, and restoration activities.

A glimmer of hope comes from the observations of an increase in bleaching tolerance at a small number of Indo-Pacific reefs following successive bleaching events (Maynard *et al.*, 2008; Berkelmans, 2009; Guest *et al.*, 2012; Penin *et al.*, 2013), indicating that adaptation or acclimatization to extreme temperature anomalies can occur naturally under certain circumstances. Conversely, the loss of >40% of the world's coral reefs over the past four decades (Burke *et al.*, 2011) and the extensive coral mortality experienced during the recent global bleaching event of 2014–2016 (Eakin *et al.*, 2016; Normile, 2016) indicate that the rate of temperature increase is outpacing the natural rate of evolution of thermal tolerance in corals, threatening coral reef

ecosystem persistence into the future. Edwards & Gomez (2007) concluded that *'there is little that managers can do in the face of the large-scale "natural" drivers of degradation such as climate change related mass bleaching, storms, tsunamis, and disease outbreaks'*. We have recently argued that this message may be overly pessimistic in relation to large-scale drivers such as ocean warming and that the climate resilience of corals may be augmented through assisted evolution (van Oppen *et al.*, 2015). Such innovative management methods represent a major change to our thinking about and approach to coral reef restoration (i.e., a shifting paradigm) and would increase the probability of survival of corals used for restoring degraded reefs as well as enhance the resilience of remaining natural coral populations. The present opinion paper addresses a number of issues relevant in this context: It (1) discusses the need for consideration of alternative ecosystems that maintain varying levels of functionality (i.e., diversity, goods, and services) where a return to the historical ecosystem state is no longer feasible, (2) characterizes the ecosystem attributes and coral traits that are most critical for climate resilience, (3) discusses the challenges of interventions focused on enhanced climate resilience (assisted evolution), and (4) proposes a decision framework for the incorporation of assisted evolution into coral restoration practice. We provide criteria to guide coral reef managers in decision making for implementation of coral stock obtained *via* assisted evolution, with the goal of promoting more climate resilient reef ecosystems.

Assisted evolution and related terms

Assisted evolution is the acceleration of natural evolutionary processes to enhance certain traits (Jones & Monaco, 2009; van Oppen *et al.*, 2015). These processes include genetic adaptation, transgenerational changes through epigenetic mechanisms, and modifications in the community composition of microbes associated with the target organism. For reef-building corals, we are currently evaluating whether environmental stress tolerance can be increased using the following assisted evolution approaches: (1) preconditioning or epigenetic programming, that is, the exposure of adult coral colonies to environmental stress with the aim to induce heritable, increased stress tolerance and fitness in their offspring, (2) manipulation of the community composition of microbial organisms associated with the coral holobiont (the microbiome); corals associate with a wide range of microbial organisms, including *Symbiodinium*, prokaryotes, fungi, and viruses, (3) laboratory evolution of cultured *Symbiodinium* under the elevated temperature and pCO_2 selection followed by

inoculation of coral hosts with the evolved algal cultures, and (4) selective breeding of the coral host. The latter is guided by relative bleaching tolerance in sympatry (Fig. 1) or allopatry (e.g., along the latitudinal gradient on the GBR (van Oppen *et al.*, 2014; Dixon *et al.*, 2015)), the ability of species to cross-fertilize, and genetic markers of relative stress tolerance (Jin *et al.*, 2016). While assisted evolution is a holistic term that incorporates genetic, epigenetic, and microbiome evolutionary changes, there are other terms used in the literature that focus specifically on genetic changes to increase the fitness of populations:

Genetic rescue (*sensu* restoration; Tallmon *et al.*, 2004; Hedrick, 2005) is the improvement in reproductive fitness and increase in genetic diversity through outcrossing of a population previously suffering low genetic diversity and inbreeding depression. Genetic rescue is applicable to small threatened populations and has been used successfully in conservation efforts to recover populations of species such as the Florida panther (Johnson *et al.*, 2010), the mountain pygmy possum (Weeks *et al.*, 2015), the greater prairie chicken (Bateson *et al.*, 2014), an adder (Madsen *et al.*, 1999), and the Mexican wolf (Fredrickson *et al.*, 2007).

Assisted gene flow (Aitken & Whitlock, 2013) is the managed movement of individuals with favorable traits (alleles/genotypes) into populations (unidirectional) to reduce local maladaptation to climate or other environmental change (either current or future change). Assisted gene flow can be used in the context of small and declining populations (Aitken & Whitlock, 2013) or keystone, foundation, and resource production species that have large population sizes (Broadhurst *et al.*, 2008; Aitken & Whitlock, 2013). Corals, as an example of a foundation species, have been proposed previously

Fig. 1 Intraspecific variation in bleaching tolerance in sympatry. Two adjacent *Orbicella faveolata* colonies in the upper Florida Keys showing different bleaching responses to thermal stress in September 2015. Photocredit: NOAA-Southeast Fisheries Science Center.

as candidates for assisted gene flow (Hoegh-Guldberg *et al.*, 2008; Riegl *et al.*, 2011) to counter the effects of climate change. While assisted gene flow has been proposed as a key conservation action to combat climate change and other threatening processes, relatively few examples of assisted gene flow are available in the literature.

Evolutionary rescue refers to adaptation at a rate that results in survival of a population that is threatened with extinction (and characterized by a negative growth rate) by environmental change (Orr & Unckless, 2014). Small populations are less likely than large populations to experience evolutionary rescue because they are more likely to lack genetic variation necessary for adaptation and therefore at a higher risk of extirpation before rescue. Evidence for evolutionary rescue mostly comes from empirical experiments with microbes (Gonzalez & Bell, 2013). At a time of rapid environmental change, it is difficult to predict species and populations that will survive through evolutionary rescue (Aitken & Whitlock, 2013).

Other terms are also used in the literature in the context of biodiversity conservation (e.g., gene pool mixing, genetic adaptation, targeted gene flow, assisted migration), but are essentially similar to one of the above.

Restoring coral reef ecosystems

Ecological restoration is 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed' (SER, 2004), where the restored community needs to be self-sustainable (SER, 2004; Edwards & Gomez, 2007). Traditionally, the focus of most restoration initiatives has been to return to a pre-disturbance state (Perring *et al.*, 2015), but when ecosystems have changed beyond their long-term 'natural' variability it may not be practical or possible to restore them to their historical conditions. Unfortunately, this limitation is increasingly becoming the norm in terrestrial and marine ecosystems alike, including coral reefs. Climate change, poor water quality, coastal developments, destructive fishing, overharvesting, and invasive species are among the many perturbations that in combination have altered the structure and species composition of coral reef ecosystems. Therefore, the broader and more flexible concept of 'intervention ecology' (Hobbs *et al.*, 2011), proposed originally for terrestrial systems, may be an appropriate consideration for coral reefs. Intervention ecology focuses on managing for future change but uses history to guide (1) the retention of historical states where possible, or (2) the development of new systems that meet desired ecosystem attributes and maintain the goods and services provided by

the historical system (Jackson & Hobbs, 2009; Hobbs *et al.*, 2011; Higgs *et al.*, 2014).

Historical (pristine) coral reefs are generally characterized by high coral cover and recruitment rates, high fish biomass, and high algal grazing rates, resulting in extensive three-dimensionality and biodiversity (Graham *et al.*, 2013). A reduction in coral cover, fish biomass, biodiversity, and structural relief has occurred on many contemporary reef systems as a result of a number of anthropogenic disturbances (Pandolfi *et al.*, 2003). Such reefs may still be dominated by coral, but coral species composition may have changed, or they may have reached an alternative state dominated by other organisms, and it is unlikely a return to the historical state is possible (Graham *et al.*, 2013). If the historical ecosystem state is no longer attainable through natural recovery processes or through human intervention, either 'hybrid' (those retaining some original characteristics as well as novel elements) or 'novel' (those that differ in composition and/or function from present and past systems) ecosystems are two possible alternative restoration objectives that have been considered in terrestrial restoration initiatives (Hobbs *et al.*, 2009). Novel coral reef ecosystems, composed almost entirely of species that were not formerly native to the geographic location or that might exhibit different functional properties, or both (Hobbs *et al.*, 2009), are unlikely to be considered in coral reef restoration initiatives in the near future, but we propose that the hybrid system concept receives further attention. The challenge, however, is to define the desired attributes of hybrid ecosystems (i.e., the restoration goals) and the interventions required for establishing and maintaining alternative ecosystem states (i.e., hybrid ecosystems), as restoration goals are context dependent and will differ between locales. Defining these is critical for developing the actions required for restoration, and for identifying the coral traits that should be targeted and improved using assisted evolution methods.

Coral reefs are integral to coastal and economic stability and valued in the billions of dollars annually (Costanza *et al.*, 1997, 2014; Bishop *et al.*, 2012; Stoeckl *et al.*, 2014). Therefore, primary considerations for restoration include the attributes: coral cover, biodiversity, self-sustainability, functional diversity and redundancy, structural complexity (Kuffner & Toth, 2016), and, chiefly, resilience (i.e., the magnitude of the perturbation that can be buffered by an ecosystem prior to changes in ecosystem structure (Holling & Gunderson, 2001). Live coral cover is an important reef ecosystem attribute and one of the most widely used metrics of coral reef performance worldwide (Gardner *et al.*, 2003; De'ath *et al.*, 2009; Edmunds *et al.*, 2014). For example, scleractinian (stony) coral cover is the primary explanatory variable of fish abundance at Lizard Island (GBR), in comparison with other attributes such as specific coral morphology cover (i.e., branching, corymbose, ormassive), benthic habitat diversity and complexity, and species richness (Komyakova *et al.*, 2013). This suggests a critical need to maintain both coral cover and diversity at a locally informed threshold in the hybrid ecosystem state; coral reef structure and function can be strongly location specific (e.g., low diversity functional reefs such as the Eastern Tropical Pacific and Hawaii vs. diverse reefs such as in the central Indo-Pacific). For Caribbean reefs, it has been suggested that ~10% live coral cover is critical for maintaining positive calcium carbonate production rates and thus reef growth (Perry *et al.*, 2013).

Self-sustainability at a locally defined amount of mean coral cover and diversity that is able to support a locally defined amount of diversity of other reef organisms (i.e., a benefit to the natural organisms that comprise the ecosystem) is another desired attribute. Further, the system should have the capacity to adapt to future environmental perturbations. The broad strategy of maximizing genetic and epigenetic variation upon which selection can act in stochastic environments should be used as part of the management portfolio. We recognize that not all perturbations are predictable, but for the primary elements of concern at the global scale such as increased water temperature and ocean acidification, actions can be taken for enhancing adaptation and acclimatization to such stressors (Dixon *et al.*, 2015; Putnam *et al.*, 2016), while considering potential ecological trade-offs as a consequence of the enhanced traits. For instance, thermal tolerance acquired by hosting clade D *Symbiodinium* is associated with slower growth (Little *et al.*, 2004), as well as lower lipid storage, and smaller egg sizes during reproduction in the coral, *Acropora millepora* (Jones & Berkelmans, 2011).

Further, it is well established that coral reefs are major biodiversity 'hotspots' (Roberts *et al.*, 2006) and that sustaining biodiversity provides ecosystem function as well as goods and services (Mace *et al.*, 2012). Functional redundancy, that is, different species with similar roles in communities that can be substituted with little impact on ecosystem processes and function, will enhance or protect ecosystem performance under environmental perturbation (Nystrom, 2006). For example, functional redundancy resulted in a regime shift from an algal- to coral-dominated state, not due to the presence of large herbivores typical of reefs (parrotfish and surgeon fish) as expected, but to the functional redundancy of a batfish (*Platax pinnatus*) in a primary herbivore role (Bellwood *et al.*, 2006). It is therefore recommended to ensure functional redundancy remains.

Critical coral traits for climate resilience: targets for assisted evolution

Ocean warming and acidification are the main stressors related to increasing greenhouse gas concentrations in the atmosphere that threaten scleractinian corals, the system engineers of coral reefs. Related to climate warming are a number of additional perturbations that impact negatively on reef-building corals, that is, more extreme wet seasons causing seawater salinity to drop and influxes of pollutants and nutrients to rise, an increase in disease incidence (Maynard et al., 2015), and an increased frequency and intensity of storms and cyclones. Therefore, the critical climate resilience traits of corals include tolerance to warmer and acidified waters, disease resistance, tolerance to fluctuations in salinity and exposure to nutrients, herbicides and other pollutants, and higher skeletal densities to better withstand storms and cyclones and to maintain the ability to provide coastal protection. To obtain corals with these traits, some approaches can be guided by coral phenotypes, but other methods require knowledge of the cellular processes and genetic architecture underpinning these desired traits. Considerable progress has been made in dissecting organismal responses to environmental stress (Kültz, 2003, 2005), including corals (Kenkel et al., 2014), and we discuss how this knowledge can inform assisted evolution approaches to enhance coral stress tolerance.

Certain facets of the cellular stress response are not stressor specific (Gasch et al., 2000; Kültz, 2005; Anderson et al., 2015). Instead, a diverse array of stressors leads to an increase of toxic chemicals in the cell (particularly reactive oxygen species [ROS]) that cause damage to macromolecules (e.g., membrane lipids, DNA, and proteins). The universal 'minimal cellular stress response' has evolved to recruit the same set of cellular functions irrespective of the stressor. This includes cell cycle control, protein chaperoning and repair, DNA and chromatin stabilization and repair, removal of damaged proteins, and certain aspects of metabolism (Kültz, 2003). Further, while there are many taxon-specific stress response genes, many of the genes and proteins involved in the minimal cellular stress response are conserved across all kingdoms of life (Kültz, 2003). Targeting genes that underpin the minimal cellular stress response (for instance, through marker-assisted selective breeding (Lande & Thompson, 1990)) thus provides an opportunity to develop coral stock with enhanced tolerance to a number of stressors simultaneously. In support of this notion, a recent study showed that the same quantitative trait loci (QTLs) for antioxidant capacity in corals are informative for relative tolerance to temperature anomalies and poor water quality

(Jin et al., 2016). In another example, conspecific corals from a warm backreef location had higher levels of ubiquitin-conjugated protein than those from a cooler forereef location, which were maintained after transplantation to the cooler site (Barshis et al., 2010). Ubiquitination is a process by which proteins are tagged for degradation and the cell rids itself of damaged proteins, and is an element of the minimal cellular stress response. Further, many coral and Symbiodinium gene expression studies have demonstrated that genes known to form part of the minimal cellular stress response (Kültz, 2003, 2005) are regulated in response to heat (Desalvo et al., 2008, 2010; Csaszar et al., 2009; Voolstra et al., 2009; Kenkel et al., 2011; Meyer et al., 2011; Barshis et al., 2013; Polato et al., 2013; Levin et al., 2016), pollutants (Morgan et al., 2005), UV radiation, and salinity (Edge et al., 2005). Innate immune response genes have also been found to be regulated in corals exposed to environmental stress (Barshis et al., 2013; Pinzón et al., 2015). This is unsurprising given high levels of ROS are known to trigger the coral host innate immune response (Weis, 2008). Other calcifying marine invertebrates, such as oysters, show regulation of the same sets of genes involved in innate immunity and the minimal cellular stress response when exposed to elevated temperature, pCO_2, or infected with a pathogen (Anderson et al., 2015). The increased climate resilience in the Sydney oyster, as a by-product of selective breeding for pathogen resistance (Parker et al., 2011; Thompson et al., 2015), confirms that selection on components of the minimal cellular stress response may have positive effects on tolerance to a number of different stressors. Such cross-tolerance has also been documented for other organisms including crop plants (Perez & Brown, 2014).

The existence of a universal, minimal cellular stress response further indicates that enhanced resistance of corals to stressors such as temperature and pCO_2 may be accomplished by exposure to another (and perhaps single) stressor that is easy to simulate in the laboratory, such as high light intensity, and perhaps can even be applied at small scales in the field. Higher levels of natural solar radiation experienced by one side (the west side) of hemispherical colonies of the coral, Goniastrea aspera (proposed reclassification: Coelastrea aspera; Huang et al., 2014), subsequently conferred increased thermal bleaching tolerance to the west sides compared to their east sides (Brown et al., 2002; Brown & Dunne, 2008). These results support the presence of (minimal) stress responses in corals that are not specific to a particular stressor and justify further research to explore the efficacy of conditioning with only one stressor to attempt the augmentation of general stress tolerance in corals. However, this field of research is still in its

infancy, with some studies showing contrasting effects. For instance, laboratory preconditioning of the coral *Porites porites* with elevated pCO$_2$ resulted in slower rates of calcification and feeding when they were subsequently subjected to experimental heat stress (Towle *et al.*, 2016). Further, while colonies of *Acropora aspera* enhanced their thermal bleaching tolerance following preconditioning with heat, this was not the case for *A. millepora* (Middlebrook *et al.*, 2008). Photosymbionts inhabiting *A. millepora* colonies that were preconditioned by warming had improved their ability to dispose of excess light energy as heat compared to those in nonconditioned colonies, but were no more tolerant to subsequent bleaching (Middlebrook *et al.*, 2012). Positive transgenerational acclimatization and parental effects have been documented in the coral *Pocillopora damicornis* following preconditioning of parents to high temperature and pCO$_2$, but the relative frequency and importance of this transgenerational plasticity are even less well understood (Putnam & Gates, 2015).

Integration of assisted evolution into coral reef restoration: a decision tree

van Oppen *et al.* (2015) previously proposed four approaches to develop coral stock with enhanced environmental stress resistance, and research is underway to assess the value of each of these in different environmental settings. It is important that assisted evolution becomes embedded within coral reef restoration initiatives, because the worldwide extensive loss of coral cover suggests natural rates of evolution of stress tolerance are too slow to maintain functional coral reef ecosystems into a future characterized by rapid climate change. As with any restoration initiative, assisted evolution approaches need to be guided by historical information, contribute to the restoration of ecological structure and function, and developed stock needs to have the ability to adapt further to contemporary selection pressures (i.e., sufficient levels of genetic diversity need to be maintained). This means that coral stock enhanced for climate resilience needs to be developed for a number of coral species representing different functional groups, including the rapidly growing branching corals, as well as species with massive and encrusting morphologies. We suggest a process that considers the lowest levels of intervention first and progressing to more aggressive intervention only when necessary (Edwards & Clark, 1999; Jones, 2003; Edwards & Gomez, 2007; Hobbs *et al.*, 2014). The process is iterative and forms part of an adaptive management framework, the outcomes of which feed back into the process with the aim of improved reef status.

One of the initial considerations of this approach is to determine whether restoration is required (Fig. 2). Restoration may be desired under a number of scenarios, including when coral cover is approaching or has declined below a certain threshold, or when coral functional, species, or genetic diversity has declined significantly. If restoration is desired, an assessment of recoverability is necessary, as a reef may not be currently recoverable when for example it is chronically polluted, it has no or few herbivores, and it has high numbers of predators such as crown-of-thorns starfish (COTS) or is exposed to a high disturbance frequency. In those instances, strategies to enhance recoverability would be the primary intervention effort, such as catchment management, the establishment of marine-protected areas and/or no-take zones, macroalgal removal, and active COTS control (Anthony, 2016).

If a reef is deemed in need of restoration and is also recoverable, the next step is to explore the key missing links in the recovery chain, that is, are the physical structures of the reef and microbial biofilms suitable for larval recruitment (suitability) and is larval supply sufficient (connectivity/supply). If a sufficiently large number of larvae reach the reef, but recruitment is poor, options to enhance recruitment include the following: removal of fine sediments or deployment of artificial reef settlement structures, the optimization of the three-dimensionality of recruitment surfaces, and the coating of recruitment surfaces with biota and semiochemicals (i.e., chemical signals from one organism that modify the behavior of a recipient organism) that induce attachment and metamorphosis in coral larvae (Negri *et al.*, 2003; Webster *et al.*, 2004; Tebben *et al.*, 2011, 2015). If the reef substratum is healthy and suitable for larval recruitment but few larvae reach the reef, the number of larvae reaching the reef substratum can be actively increased by collecting coral spawning slicks, rearing the embryos to mature larvae in *in situ* floating nurseries, and pumping mature larvae onto the substratum (Heyward *et al.*, 2002; Edwards *et al.*, 2015). Alternatively, larvae can be reared *ex situ* and subsequently released onto the reef (Guest *et al.*, 2014; Chamberland *et al.*, 2015), or gravid colonies can be transplanted prior to the reproductive season (Horoszowski-Fridman *et al.*, 2011). A combination of adding physical structures, optimization of the recruitment surfaces, and enhancement of larval supply may also be considered.

A key issue in coral reef restoration is the resilience of the coral stock used for restoration. Early coral life stages generally have very high levels of mortality during their first year of life (Wilson & Harrison, 2005; Edwards & Gomez, 2007; Guest *et al.*, 2014). Survival of early recruits may be increased through minimizing
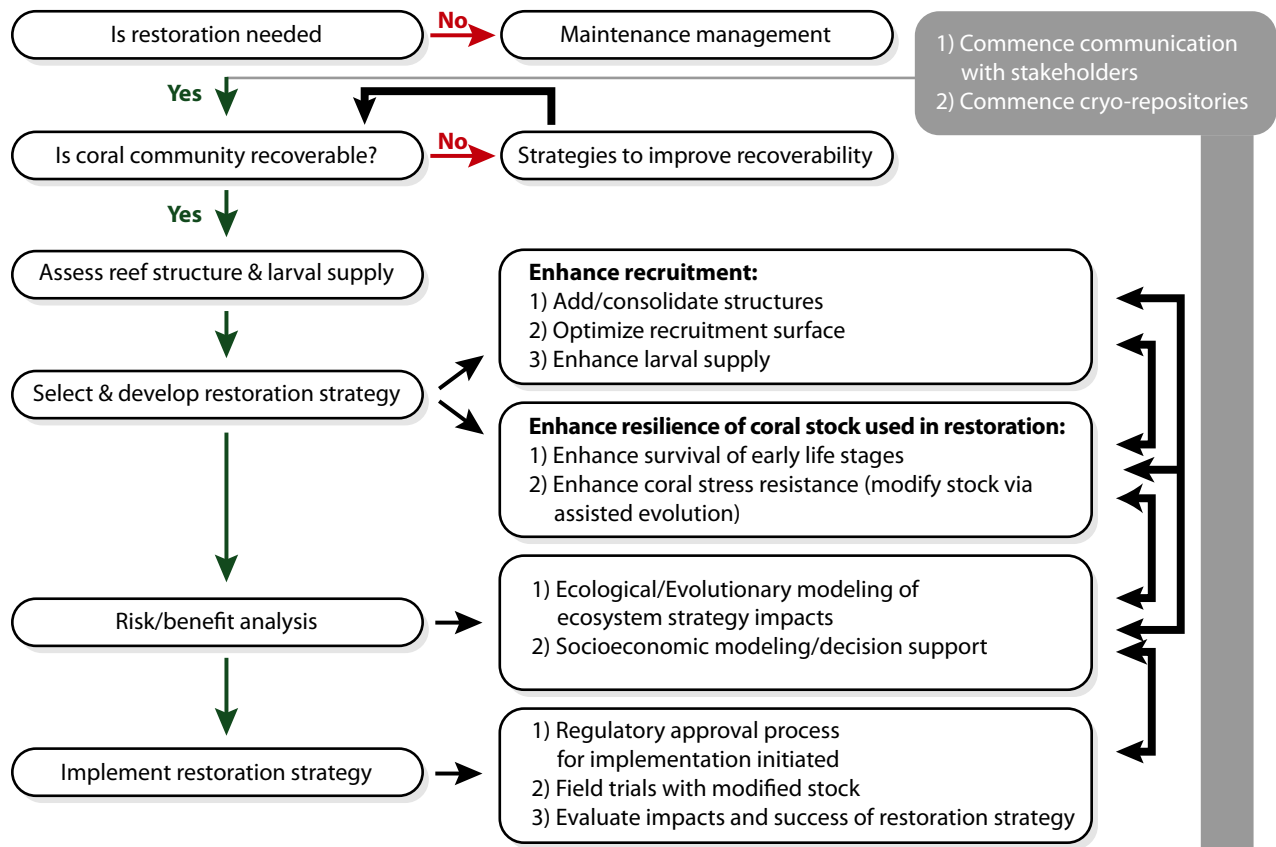
Fig. 2 Proposed decision tree for coral reef restoration including assisted evolution. The various steps in the tree are explained in the section *Integration of assisted evolution into coral reef restoration: a decision tree* in the text. The selection of the restoration strategy depends on the causes underlying the lack of recovery as well as the restoration targets (e.g., historical or hybrid ecosystem, percent coral cover, coral diversity). The process is iterative and forms part of an adaptive management framework, the outcomes of which feed back into the process with the aim of improved reef status. Communication strategies and cryorepositories are ongoing throughout the process.

overgrowth by filamentous algae by coating settlement surfaces with nontoxic antifoulants (Tebben *et al.*, 2014), an approach that has not yet seen any large-scale testing, or through the use of a protected nursery grow-out stage to allow the recruits to increase in size before deployment onto the reef. Most coral reef restoration initiatives have used coral fragments obtained by breaking adult coral colonies into smaller pieces, and in some cases, fragments are subsequently attached to a line or hard substrate and grown out in an *in situ* floating nursery before being explanted into the reef environment (Rinkevich, 2014). This approach overcomes the high mortality associated with small recruit size but has a number of disadvantages, including the generally low genotypic diversity in the restoration stock obtained in this way and the possible negative impact it has on the reef, as healthy corals are sacrificed to produce the fragments.

The enhancement of coral resilience to environmental stress through assisted evolution is aiming at increasing survival of coral stock used for restoration (van Oppen *et al.*, 2015). Within two of the proposed assisted evolution approaches for corals (modification of microbial community composition and selective breeding), the level of intervention can be scaled based on the genetic correspondence of the enhanced material to the native stock. Our guidelines follow those of rangeland restoration practitioners (Jones, 2003), who recommend that in the development of more resilient stock, the most 'local' options must always be considered before any non-native ones. There is extensive evidence for local adaptation in corals (Berkelmans & van Oppen, 2006; Dixon *et al.*, 2015). Correspondingly, the different options for sourcing stress-resistant microbes (e.g., algal endosymbionts, prokaryotes, fungi) to inoculate corals are colonies growing on the same reef, a more distant reef in the same region, or from a completely different part of the world (Riegl *et al.*, 2011). For selective breeding, intraspecific hybridization can be conducted using colonies from distinct habitats on the same reef (e.g., slope

and flat), colonies from nearby reefs, or colonies from more distant reefs. Alternatively, colonies belonging to different species can be crossed to create interspecific hybrids (Willis *et al.*, 1997). It should be noted that even if a genetically more distant breeding stock is initially used to develop the desired stock, backcrossing to the native population for multiple generations may increase the proportion of native genetic material. Subsequent intercrossing, in combination with selection for the desired trait at each generation, may result in increased fitness. Resistance to fungal blight disease has been introduced into the American chestnut in this manner. The American chestnut once dominated North America, but was decimated following the introduction of a fungus over a century ago that causes chestnut blight. Initially, the American chestnut was hybridized with the Chinese chestnut (which has blight resistance encoded by a number of genes that are absent in the American chestnut), generating an F1 generation (50% American chestnut). Three backcross generations to the American chestnut followed by two generations of intercrossing have resulted in a BC_3F_3 generation (94% American chestnut), but with enhanced disease resistance compared to the original American chestnut (Clark *et al.*, 2016).

In an alternate approach to develop blight-resistant American chestnut trees, an oxalate oxidase gene from wheat was inserted into the American chestnut genome through genetic transformation; the transgenic trees show enhanced pathogen resistance (Zhang *et al.*, 2013; Newhouse *et al.*, 2014) because the enzyme product directly neutralizes the main weapon of the fungus, oxalate. While genetic engineering techniques can be challenging, especially in nonmodel organisms, and also tend to receive considerable public resistance, such approaches may produce desirable results faster and at a lower cost compared to selective breeding (Dominguez *et al.*, 2015; Bolukbasi *et al.*, 2016). However, a detailed understanding of the disease etiology and the cellular pathways underlying environmental stress responses is required to direct such biotechnological approaches. In this context, the development of QTLs for environmental stress tolerance in corals (Jin *et al.*, 2016), and the growing body of knowledge on the interactions between coral host and *Symbiodinium* symbionts (Barott *et al.*, 2015; Parkinson *et al.*, 2015), the host and symbiont genes regulated in response to stress (Barshis *et al.*, 2013; Levin *et al.*, 2016) or under selection from environmental variables such as temperature (Lundgren *et al.*, 2013; Bay & Palumbi, 2014), are important developments.

All of the interventions listed above must be guided by agreed-upon restoration goals and be subjected to rigorous risk/benefit analyses that incorporate both ecological/evolutionary impacts on coral reef ecosystems and socioeconomic aspects such as the cost and public acceptance of the intervention. These analyses will assist in the development of a regulatory framework to decide whether an intervention should/can be implemented and when. The first steps to implementing restoration of a reef using modified stock would be controlled laboratory trials, followed by small-scale field trials, for example, on isolated reefs that do not provide surrounding reefs with dispersing coral larvae. Hence, knowledge of reef connectivity and gene flow is a critical component of the risk/benefit analyses.

A hypothetical example of how to use the proposed decision tree (Fig. 2): the 2016 bleaching event on the GBR

In early 2016, the GBR experienced the most severe coral bleaching event on record. More than 50% of coral was lost from many reefs in the northern third of the GBR as a consequence, with little to no bleaching-related mortality observed in the central and southern sectors of the GBR (Great Barrier Reef Marine Park Authority, 2016; The Conversation 2016a). This contrasts with the patterns of other severe mass bleaching events on the GBR where the greatest impacts were recorded in the central and southern GBR (Berkelmans *et al.*, 2004).

'Is restoration needed?' is the first point in the suggested decision tree (Fig. 2). There are many questions about the prospect for the far northern GBR to recover naturally. Will the remaining corals be able to produce sufficient larvae that can recruit onto the denuded areas? Will coral larvae from the Torres Strait and Papua New Guinea to the north, from the Coral Sea to the east, from more southern GBR reefs, or from deeper waters be dispersed and recruit to the northern GBR and help restore coral cover and diversity? Has there been a shift in coral community composition, with some of the more bleaching-sensitive taxa being specifically decimated? The answers to these questions are mostly unknown and are being assessed with ongoing surveys following the bleaching event. If coral cover shows few or no signs of recovery over the next several years, active restoration efforts may be desired.

'Is the coral community recoverable?' is the next question in the decision tree. Given there is no substantial coastal development north of Cooktown and water quality is good, the answer to this question will likely be 'yes'. This will also depend on the progression of a COTS outbreak which is currently taking place on the GBR.

'Are reef structure and larval supply adequate for new recruitment?' Surveys are required to examine

whether reefs have accumulated a large amount of rubble and/or sediment, which would reduce successful larval settlement and juvenile survival. While unsuitable reef structures are more likely to be an issue in the case of disturbances such as ship groundings or cyclones rather than bleaching, reefs that are denuded of coral may erode and lose their three-dimensional structure. If the reef structure is appropriate, the question is whether larval supply is sufficient for natural recovery to occur. This can be assessed based on the numbers of new recruits observed on the northern reefs over the next few years. Population genetic/genomic studies in the northern GBR and surrounding regions provide insight into patterns of coral dispersal. *Acropora* coral populations in the northern GBR have been shown to be largely open with high levels of gene flow, suggesting that natural larval supply from within the northern GBR can be high (van Oppen *et al.*, 2011; Lukoschek *et al.*, 2016), but dispersal in brooding corals is likely to be more restricted and connectivity patterns are more complex (Torda *et al.*, 2013; Warner *et al.*, 2015). Connectivity with the Torres Strait, Papua New Guinea, or the Coral Sea is not well understood and should be examined further. Biophysical models (Luick *et al.*, 2007; Hock *et al.*, 2014; Thomas *et al.*, 2014) are not well developed for corals in the northern GBR and surrounding regions; hence, this is another area of research requiring more attention.

The next step in the decision tree is to 'select and develop restoration strategy'. The preferred strategy will depend on in-field observations. If recruit survivorship is low, but further temperature anomalies or other significant disturbances have been absent, the bleaching event and coral loss may have disturbed the natural microbial biofilms lining the reef substratum, affecting juvenile coral fitness traits, such as growth rate and competitive ability. Little is known about the composition of a healthy microbial biofilm and whether or how it can be modified or restored. It is feasible that a dipstick-type biosensor for rapid, simple, and inexpensive microbiome DNA testing could be developed in the next 5–10 years, provided this research is appropriately resourced. If the bleaching event has caused an imbalance between coral and algal cover, then competition for space with benthic algae may have become so intense that coral recruit survival becomes too low to restore coral cover. The use of larvae settled *ex situ* onto settlement substrata that contain antifouling coating (Tebben *et al.*, 2014), followed by deployment onto the disturbed reefs, may be considered. *Ex situ* settlement of larvae allows for the simultaneous use of coral stock enhanced for thermal tolerance to prepare the reef for recurring temperature extremes.

Another approach under this hypothetical example is to take a proactive stance and increase stress resistance in corals along the length of the GBR in response to the recent extensive coral mortality in the northern GBR. Such an early intervention approach would require the implementation of assisted evolution methods and the deployment of stock with enhanced environmental stress tolerance onto healthy reefs with the aim to increase resilience. At present, neither the assisted evolution tools have been sufficiently developed nor their risks and benefits assessed to permit taking this step. We encourage investment in this research area so that assisted evolution and the use of coral stock enhanced for environmental stress tolerance can be realistically evaluated for coral reef restoration initiatives as necessity dictates in the near future.

Conclusions

We are entering an era of innovative coral reef restoration in the next 5–10 years, which may include the use of (semio)chemicals, optimized biofilms, and modified coral stock. We acknowledge that assisted evolution approaches in corals are in the proof-of-concept stage, and the scaling up of current experiments both spatially and across taxa and functional groups is eventually required for these to be implemented in coral reef restoration efforts. Advancement of methods for the large-scale rearing and deployment of coral stock manipulated for enhanced stress resistance are therefore urgently required. A pressing need also exists to preserve a representative portion of the extant genetic diversity by establishing coral and *Symbiodinium* genomic repositories using cryopreservation (Hagedorn *et al.*, 2012), analogous to seed banks established for plants (Westengen *et al.*, 2013; Haidet & Olwell, 2015). Finally, an active dialogue between scientists, coral reef managers, policy makers, politicians, and the general public needs to occur at all steps in the decision tree. In this way, we will ensure stakeholder involvement in setting directions and priorities for the research and development aspects of reef restoration, as well as practical uptake of strategies and optimal restoration practice in the future.

Acknowledgements

References

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 367.

Anderson K, Taylor DA, Thompson EL, Melwani AR, Nair SV, Raftos DA (2015) Meta-analysis of studies using suppression subtractive hybridization and microarrays to investigate the effects of environmental stress on gene transcription in oysters. *PLoS ONE*, **10**, e0118839. doi:10.1371/journal.pone.0118839.

Andersson AJ, Gledhill D (2013) Ocean acidification and coral reefs: effects on breakdown, dissolution, and net ecosystem calcification. *Annual Review of Marine Science*, **5**, 321–348.

Anthony KR (2016) Coral reefs under climate change and ocean acidification: challenges and opportunities for management and policy. *Annual Review of Environment and Resources*, **41**, 59–81.

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17442–17446.

Barott KL, Venn AA, Perez SO, Tambutté S, Tresguerres M (2015) Coral host cells acidify symbiotic algal microenvironment to promote photosynthesis. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 607–612.

Barshis DJ, Stillman JH, Gates RD, Toonen RJ, Smith LW, Birkeland C (2010) Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? *Molecular Ecology*, **19**, 1705–1720.

Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral resilience to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 1387–1392.

Bateson ZW, Dunn PO, Hull SD, Henschen AE, Johnson JA, Whittingham LA (2014) Genetic restoration of a threatened population of greater prairie-chickens. *Biological Conservation*, **174**, 12–19.

Bay RA, Palumbi SR (2014) Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology*, **24**, 2952–2956.

Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping functional group drives coral-reef recovery. *Current Biology*, **16**, 2434–2439.

Berkelmans R (2009) Bleaching and mortality thresholds: how much is too much? In: *Coral Bleaching: Patterns, Processes, Causes and Consequences* (eds van Oppen MJH, Lough JM), pp. 103–119. Springer-Verlag, Berlin, Heidelberg.

Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London – Series B: Biological Sciences*, **273**, 2305–2312.

Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs*, **23**, 74–83.

Bishop RC, Chapman DJ, Kanninen BJ, Krosnick JA, Leeworthy B, Meade NF (2012) Total economic value for protecting and restoring Hawaiian coral reef ecosystems: Final Report. NOAA Office of National Marine Sanctuaries, Office of Response and Restoration, and Coral Reef Conservation Program, Silver Spring, MD. NOAA Technical Memorandum CRCP 16, 406 pp.

Bolukbasi MF, Gupta A, Wolfe SA (2016) Creating and evaluating accurate CRISPR-Cas9 scalpels for genomic surgery. *Nature Methods*, **13**, 41–50.

Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, Mcdonald M, Vesk PA, Yates C (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications*, **1**, 587–597.

Brown BE, Dunne RP (2008) Solar radiation modulates bleaching and damage protection in a shallow water coral. *Marine Ecology Progress Series*, **362**, 99–107.

Brown B, Dunne R, Goodson M, Douglas A (2002) Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs*, **21**, 119–126.

Burke L, Reytar K, Spalding M, Perry A (2011) *Reefs at risk revisited*, ISBN 978-1-56973-762-0.

Chamberland VF, Vermeij MJ, Brittsan M *et al.* (2015) Restoration of critically endangered elkhorn coral (*Acropora palmata*) populations using larvae reared from wild-caught gametes. *Global Ecology and Conservation*, **4**, 526–537.

Clark SL, Schlarbaum SE, Saxton AM, Hebard FV (2016) Establishment of American chestnuts (*Castanea dentata*) bred for blight (*Cryphonectria parasitica*) resistance: influence of breeding and nursery grading. *New Forests*, **47**, 243–270.

Coles S, Brown E (2007) Twenty-five years of change in coral coverage on a hurricane impacted reef in Hawai'i: the importance of recruitment. *Coral Reefs*, **26**, 705–717.

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs*, **67**, 461–488.

Costanza R, D'arge R, De Groot R *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–260.

Costanza R, De Groot R, Sutton P *et al.* (2014) Changes in the global value of ecosystem services. *Global Environmental Change*, **26**, 152–158.

Csaszar NBM, Seneca FO, van Oppen MJH (2009) Variation in antioxidant gene expression in the scleractinian coral Acropora millepora under laboratory thermal stress. *Marine Ecology-Progress Series*, **392**, 93–102.

De'ath G, Lough JM, Fabricius KE (2009) Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–119.

Desalvo MK, Rvoolstra C, Sunagawa S *et al.* (2008) Differential gene expression during thermal stress and bleaching in the Caribbean coral *Montastraea faveolata*. *Molecular Ecology*, **17**, 3952–3971.

Desalvo MK, Sunagawa S, Voolstra CR, Medina M (2010) Transcriptomic responses to heat stress and bleaching in the elkhorn coral *Acropora palmata*. *Marine Ecology Progress Series*, **402**, 97–113.

Dixon GB, Davies SW, Aglyamova GA, Meyer E, Bay LK, Matz MV (2015) Genomic determinants of coral heat tolerance across latitudes. *Science*, **348**, 1460–1462.

Dominguez AA, Lim WA, Qi LS (2015) Beyond editing: repurposing CRISPR-Cas9 for precision genome regulation and interrogation. *Nature Reviews Molecular Cell Biology*, **17**, 5–15.

Done T, Devantier L, Turak E, Fisk D, Wakeford M, Van Woesik R (2010) Coral growth on three reefs: development of recovery benchmarks using a space for time approach. *Coral Reefs*, **29**, 815–833.

Eakin C, Liu G, Gomez A *et al.* (2016) Global coral bleaching 2014–2017: status and an appeal for observations. *Reef Encounter*, **31**, 20–26.

Edge SE, Morgan MB, Gleason DF, Snell TW (2005) Development of a coral cDNA array to examine gene expression profiles in *Montastraea faveolata* exposed to environmental stress. *Marine Pollution Bulletin*, **51**, 507–523.

Edmunds PJ, Adjeroud M, Baskett ML *et al.* (2014) Persistence and change in community composition of reef corals through present, past, and future climates. *PLoS ONE*, **9**, e107525.

Edwards AJ, Clark S (1999) Coral transplantation: a useful management tool or misguided meddling? *Marine Pollution Bulletin*, **37**, 474–487.

Edwards AJ, Gomez ED (2007) *Reef Restoration Concepts and Guidelines: Making Sensible Management Choices in the Face of Uncertainty. Capacity Building for Management Programme/Coral Reef Targeted Research*. The Coral Reef Targeted Research & Capacity Building for Management Program, St Lucia, Australia.

Edwards AJ, Guest JR, Heyward AJ, Villanueva RD, Baria MV, Bollozos IS, Golbuu Y (2015) Direct seeding of mass-cultured coral larvae is not an effective option for reef rehabilitation. *Marine Ecology Progress Series*, **525**, 105–116.

Emslie M, Cheal A, Sweatman H, Delean J (2008) Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series*, **371**, 177–190.

Fredrickson RJ, Siminski P, Woolf M, Hedrick PW (2007) Genetic rescue and inbreeding depression in Mexican wolves. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 2365–2371.

Gardner TA, Cote IM, Gill JA, Gant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.

Gasch AP, Spellman PT, Kao CM *et al.* (2000) Genomic expression programs in the response of yeast cells to environmental changes. *Molecular Biology of the Cell*, **11**, 4241–4257.

Gonzalez A, Bell G (2013) Evolutionary rescue and adaptation to abrupt environmental change depends upon the history of stress. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **368**, 20120079.

Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norstrom AV, Nystrom M (2013) Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, **11**, 541–548.

Great Barrier Reef Marine Park Authority (2016) *Interim Report: 2016 Coral Bleaching Event on the Great Barrier Reef*. GBRMPA, Townsville.

Guest JR, Baird AH, Maynard JA *et al.* (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE*, **7**, e33353.

Guest JR, Baria MV, Gomez ED, Heyward AJ, Edwards AJ (2014) Closing the circle: is it feasible to rehabilitate reefs with sexually propagated corals? *Coral Reefs*, **33**, 45–55.

Hagedorn M, Carter V, Martorana K *et al.* (2012) Preserving and using germplasm and dissociated embryonic cells for conserving Caribbean and Pacific coral. *PLoS ONE*, **7**, e33354.

Haidet M, Olwell P (2015) Seeds of success: a national seed banking program working to achieve long-term conservation goals. *Natural Areas Journal*, **35**, 165–173.

Hedrick P (2005) Genetic restoration': a more comprehensive perspective than 'genetic rescue. *Trends in Ecology & Evolution*, **20**, 109.

Heyward A, Smith LD, Rees M, Field SN (2002) Enhancement of coral recruitment by *in situ* mass culture of coral larvae. *Marine Ecology Progress Series*, **230**, 113–118.

Higgs E, Falk DA, Guerrini A *et al.* (2014) The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment*, **12**, 499–506.

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24**, 599–605.

Hobbs RJ, Hallett LM, Ehrlich PR, Mooney HA (2011) Intervention ecology: applying ecological science in the twenty-first century. *BioScience*, **61**, 442–450.

Hobbs RJ, Higgs E, Hall CM *et al.* (2014) Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment*, **12**, 557–564.

Hock K, Wolff NH, Condie SA, Anthony K, Mumby PJ (2014) Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *Journal of Applied Ecology*, **51**, 1188–1196.

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.

Hoegh-Guldberg O, Hughes L, Mcintyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345–346.

Holling CS, Gunderson LH (2001) Resilience and adaptive cycles. In: *Panarchy: Understanding Transformations in Human and Natural Systems* (eds Gunderson LH, Holling CS), pp. 25–62. Island Press, Washington, DC.

Hönisch B, Ridgwell A, Schmidt DN *et al.* (2012) The geological record of ocean acidification. *Science*, **335**, 1058–1063.

Horoszowski-Fridman YB, Izhaki I, Rinkevich B (2011) Engineering of coral reef larval supply through transplantation of nursery-farmed gravid colonies. *Journal of Experimental Marine Biology and Ecology*, **399**, 162–166.

Huang D, Benzoni F, Fukami H, Knowlton N, Smith ND, Budd AF (2014) Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*, **171**, 277–355.

Jackson ST, Hobbs RJ (2009) Ecological restoration in the light of ecological history. *Science*, **325**, 567.

Jackson J, Donovan M, Cramer K, Lam V (2014) Status and trends of Caribbean coral reefs: 1970–2012, Global Coral Reef Monitoring Network. 304 p.

Jin YK, Lundgren P, Lutz A *et al.* (2016) Genetic markers for antioxidant capacity in a reef-building coral. *Science Advances*, **2**, e1500842.

Johnson WE, Onorato DP, Roelke ME *et al.* (2010) Genetic restoration of the Florida panther. *Science*, **329**, 1641–1645.

Jones TA (2003) The restoration gene pool concept: Beyond the native versus non-native debate. *Restoration Ecology*, **11**, 281–290.

Jones AM, Berkelmans R (2011) Tradeoffs to thermal acclimation: energetics and reproduction of a reef coral with heat tolerant *Symbiodinium* type-D. *Journal of Marine Biology*, **2011**. doi:10.1155/2011/185890.

Jones TA, Monaco TA (2009) A role for assisted evolution in designing native plant materials for domesticated landscapes. *Frontiers in Ecology and the Environment*, **7**, 541–547.

Kenkel CD, Aglyamova G, Alamaru A *et al.* (2011) Development of gene expression markers of acute heat-light stress in reef-building corals of the genus *Porites*. *PLoS ONE*, **6**, e26914.

Kenkel C, Sheridan C, Leal MC *et al.* (2014) Diagnostic gene expression biomarkers of coral thermal stress. *Molecular Ecology Resources*, **14**, 667–678.

Komyakova V, Munday PL, Jones GP (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, **8**, 1–12.

Kuffner IB, Toth LT (2016) A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conservation Biology*, **30**, 706–715.

Kültz D (2003) Evolution of the cellular stress proteome: from monophyletic origin to ubiquitous function. *Journal of Experimental Biology*, **206**, 3119–3124.

Kültz D (2005) Molecular and evolutionary basis of the cellular stress response. *Annual Reviews in Physiology*, **67**, 225–257.

Lande R, Thompson R (1990) Efficiency of marker-assisted selection in the improvement of quantitative traits. *Genetics*, **124**, 743–756.

Levin RA, Beltran VH, Hill R, Kjelleberg S, Mcdougald D, Steinberg PD, van Oppen MJH (2016) Sex, scavengers, and chaperones: transcriptome secrets of divergent *Symbiodinium* thermal tolerances. *Molecular Biology & Evolution*, **33**, 2201–2215. doi:10.1093/molbev/msw119.

Little AF, van Oppen MJH, Willis BL (2004) Flexibility in algal endosymbioses shapes growth in reef corals. *Science*, **304**, 1492–1494.

Luick JL, Mason L, Hardy T, Furnas MJ (2007) Circulation in the Great Barrier Reef Lagoon using numerical tracers and in situ data. *Continental Shelf Research*, **27**, 757–778.

Lukoschek V, Riginos C, van Oppen MJH (2016) Congruent patterns of connectivity can inform management for broadcast spawning corals on the Great Barrier Reef. *Molecular Ecology*, **25**, 3065–3080.

Lundgren P, Vera JC, Peplow L, Manel S, van Oppen MJH (2013) Genotype-environment correlations in corals from the Great Barrier Reef. *BMC Genetics*, **14**, 9.

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology and Evolution*, **27**, 19–25.

Madsen T, Shine R, Olsson M, Wittzell H (1999) Conservation biology: restoration of an inbred adder population. *Nature*, **402**, 34–35.

Maynard JA, Anthony KRN, Marshall PA, Masiri I (2008) Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology*, **155**, 173–182.

Maynard J, Van Hooidonk R, Eakin CM *et al.* (2015) Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. *Nature Climate Change*, **5**, 688–694.

Meyer E, Aglyamova G, Matz M (2011) Profiling gene expression responses of coral larvae (Acropora millepora) to elevated temperature and settlement inducers using a novel RNA-Seq procedure. *Molecular Ecology*, **20**, 3599–3616.

Middlebrook R, Hoegh-Guldberg O, Leggat W (2008) The effect of thermal history on the susceptibility of reef-building corals to thermal stress. *Journal of Experimental Biology*, **211**, 1050–1056.

Middlebrook R, Anthony KRN, Hoegh-Guldberg O, Dove S (2012) Thermal priming affects symbiont photosynthesis but does not alter bleaching susceptibility in *Acropora millepora*. *Journal of Experimental Marine Biology and Ecology*, **432**, 64–72.

Minton D, Amimoto R, Friedlander A, Stamoulis K, Conklin E (2015) Baseline Biological Surveys of 'A'alapapa Reef, O'ahu, Hawai'i 2014 -2015. In: *TNC Technical Report prepared for the Lanikai Beach and Park Foundation*. 58 pp.

Morgan MB, Edge SE, Snell TW (2005) Profiling differential gene expression of corals along a transect of waters adjacent to the Bermuda municipal dump. *Marine Pollution Bulletin*, **51**, 524–533.

Negri AP, Webster NS, Hill RT, Heyward AJ (2003) Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. *Marine Ecology Progress Series*, **223**, 121–131.

Newhouse AE, Polin-Mcguigan LD, Baier KA *et al.* (2014) Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. *Plant Science*, **228**, 88–97.

Normile D (2016) El Niño's warmth devastating reefs worldwide. *Science*, **352**, 15–16.

Nystrom M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio*, **35**, 30–35.

van Oppen MJH, Peplow LM, Kininmonth S, Berkelmans R (2011) Historical and contemporary factors shape the population genetic structure of the broadcast spawning coral, *Acropora millepora*, on the Great Barrier Reef. *Molecular Ecology*, **20**, 4899–4914.

van Oppen MJH, Puill-Stephan E, Lundgren P, De'ath G, Bay LK (2014) First generation fitness consequences of interpopulational hybridisation in a Great Barrier Reef coral and its implications for assisted migration management. *Coral Reefs*, **33**, 607–611.

van Oppen MJH, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 2307–2313.

Orr HA, Unckless RL (2014) The population genetics of evolutionary rescue. *PLoS Genetics*, **10**, e1004551.

Pandolfi JM, Bradbury RH, Sala E *et al.* (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science*, **301**, 955–958.

Parker L, Ross PM, O'Connor WA (2011) Populations of the Sydney rock oyster, *Saccostrea glomerata*, vary in response to ocean acidification. *Marine Biology*, **158**, 689–697.

Parkinson JE, Banaszak AT, Altman NS, Lajeunesse TC, Baums IB (2015) Intraspecific diversity among partners drives functional variation in coral symbioses. *Scientific Reports*, **5**. doi:10.1038/srep15667.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Penin L, Vidal-Dupiol J, Adjeroud M (2013) Response of coral assemblages to thermal stress: are bleaching intensity and spatial patterns consistent between events? *Environmental Monitoring and Assessment*, **185**, 5031–5042.

Perez IB, Brown PJ (2014) The role of ROS signaling in cross-tolerance: from model to crop. *Frontiers in Plant Science*, **5**, 754.

Perring MP, Standish RJ, Price JN *et al.* (2015) Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere*, **6**, 1–25.

Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature Communications*, **4**, 1402.

Pinzón JH, Kamel B, Burge CA, Harvell CD, Medina M, Weil E, Mydlarz LD (2015) Whole transcriptome analysis reveals changes in expression of immune-related genes during and after bleaching in a reef-building coral. *Royal Society Open Science*, **2**, 140214.

Polato NR, Altman NS, Baums IB (2013) Variation in the transcriptional response of threatened coral larvae to elevated temperatures. *Molecular Ecology*, **22**, 1366–1382.

Putnam HM, Gates RD (2015) Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. *The Journal of Experimental Biology*, **218**, 2365–2372.

Putnam HM, Davidson J, Gates RD (2016) Ocean acidification influences DNA methylation and phenotypic plasticity in environmentally susceptible corals. *Integrative and Comparative Biology*, **56**, E177.

Riegl BM, Purkis SJ, Al-Cibahy AS, Abdel-Moati MA, Hoegh-Guldberg O (2011) Present limits to heat-adaptability in corals and population-level responses to climate extremes. *PLoS ONE*, **6**, e24802.

Rinkevich B (2014) Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? *Current Opinion in Environmental Sustainability*, **7**, 28–36.

Roberts CM, Mittermeier CG, Schueler FW (2006) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **1280**, 1280–1284.

SER (2004) The SER Primer on Ecological Restoration. Version 2. Society for Ecological Restoration Science and Policy Working Group. Available at: http://www.ser.org,

Stoeckl N, Farr M, Larson S, Adams VM, Kubiszewski I, Esparon M, Costanza R (2014) A new approach to the problem of overlapping values: a case study in Australia's Great Barrier Reef. *Ecosystem Services*, **10**, 61–78.

Tallmon DA, Luikart G, Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution*, **19**, 489–496.

Tebben J, Tapiolas DM, Motti CA *et al.* (2011) Induction of larval metamorphosis of the coral *Acropora millepora* by tetrabromopyrrole isolated from a *Pseudoalteromonas* bacterium. *PLoS ONE*, **6**, e19082.

Tebben J, Guest JR, Sin TM, Steinberg PD, Harder T (2014) Corals like it waxed: paraffin-based antifouling technology enhances coral spat survival. *PLoS ONE*, **9**, e87545.

Tebben J, Motti C, Siboni N *et al.* (2015) Chemical mediation of coral larval settlement by crustose coralline algae. *Scientific Reports*, **5**. doi:10.1038/srep10803.

The Conversation (2016a) How much coral has died in the Great Barrier Reef's worst bleaching event? Available at: http://theconversation.com/how-much-coral-has-died-in-the-great-barrier-reefs-worst-bleaching-event-69494 (accessed 29 November 2016).

The Conversation (2016b) Great Barrier Reef bleaching would be almost impossible without climate change. Available at: http://theconversation.com/great-barrier-reef-bleaching-would-be-almost-impossible-without-climate-change-58408 (accessed 29 April 2016).

Thomas CJ, Lambrechts J, Wolanski E, Traag VA, Blondel VD, Deleersnijder E, Hanert E (2014) Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef. *Ecological Modelling*, **272**, 160–174.

Thompson EL, O'Connor W, Parker L, Ross P, Raftos DA (2015) Differential proteomic responses of selectively bred and wild-type Sydney rock oyster populations exposed to elevated CO_2. *Molecular Ecology*, **24**, 1248–1262.

Torda G, Lundgren P, Willis B, van Oppen MJH (2013) Revisiting the connectivity puzzle of the common coral Pocillopora damicornis. *Molecular Ecology*, **22**, 5805–5820.

Towle EK, Baker AC, Langdon C (2016) Preconditioning to high CO_2 exacerbates the response of the Caribbean branching coral *Porites porites* to high temperature stress. *Marine Ecology Progress Series*, **546**, 75–84.

Van Hooidonk R, Maynard JA, Planes S (2013) Temporary refugia for coral reefs in a warming world. *Nature Climate Change*, **3**, 508–511.

Van Hooidonk R, Maynard J, Tamelander J *et al.* (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports*, **6**. doi: 10.1038/srep39666.

Voolstra CR, Schnetzer J, Peshkin L, Randall CJ, Szmant AM, Medina M (2009) Effects of temperature on gene expression in embryos of the coral *Montastraea faveolata*. *BMC Genomics*, **10**, 1.

Warner PA, van Oppen MJ, Willis BL (2015) Unexpected cryptic species diversity in the widespread coral Seriatopora hystrix masks spatial-genetic patterns of connectivity. *Molecular Ecology*, **24**, 2993–3008.

Webster NS, Smith L, Heyward A, Watts J, Webb R, Blackall LL, Negri AP (2004) Metamorphosis of a scleractinian coral in response to microbial biofilms. *Applied and Environmental Microbiology*, **70**, 1213–1221.

Weeks AR, Moro D, Thavornkanlapachai R, Taylor HR, White NE, Weiser EL, Heinze D (2015) *Conserving and Enhancing Genetic Diversity in Translocation Programs. Advances in Reintroduction Biology of Australian and New Zealand Fauna.* CSIRO Publishing, Melbourne, 127–140.

Weis VM (2008) Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. *Journal of Experimental Biology*, **211**, 3059–3066.

Westengen OT, Jeppson S, Guarino L (2013) Global ex-situ crop diversity conservation and the Svalbard Global Seed Vault: assessing the current status. *PLoS ONE*, **8**, e64146.

Willis BL, Babcock RC, Harrison PL, Wallace CC (1997) Experimental hybridisation and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs*, **16**(Suppl.), 553–565.

Wilson J, Harrison P (2005) Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. *Coral Reefs*, **24**, 418–421.

Wright JD, Schaller MF (2013) Evidence for a rapid release of carbon at the Paleocene-Eocene thermal maximum. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 15908–15913.

Zeebe RE, Dickens GR, Ridgwell A, Sluijs A, Thomas E (2014) Onset of carbon isotope excursion at the Paleocene-Eocene thermal maximum took millennia, not 13 years. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, E1062–E1063.

Zhang B, Oakes AD, Newhouse AE, Baier KM, Maynard CA, Powell WA (2013) A threshold level of oxalate oxidase transgene expression reduces *Cryphonectria parasitica*-induced necrosis in a transgenic American chestnut (*Castanea dentata*) leaf bioassay. *Transgenic Research*, **22**, 973–982.