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Shifting paradigms in restoration of the world's coral reefs

Running head: Shifting paradigms in coral reef restoration

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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) are 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 in order to enhance climate resilience of coral reefs.

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 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 over-harvesting, 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 like corals, may cause a reduced calcification rate (Andersson & Gledhill, 2003) 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 1981/82, 1997/98, 2001/02, 2005/06, 2010 and 2014/16. 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 coral reefs will face temperature extremes annually from between the mid-2050s and the mid-2070s (van Hooidonk *et al.*, 2013, 2016), and possibly even from as early as the mid-2030s (The Conversation, 2016b). Given recovery of coral cover from severe coral mortality to the pre-disturbance 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 2014-16 (Eakin *et al.*, 2016; Normile, 2016) indicates 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 and 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) pre-conditioning or epigenetic programming, i.e., 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 elevated temperature and $p\mathrm{CO}_2$ 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)), ability of species to cross-fertilise 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 favourable 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 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, over-harvesting, 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 (see below) 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 world-wide (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, or massive), 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 like the Eastern Tropical Pacific and Hawaii versus 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, i.e., 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 to 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, i.e., 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 lead 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; Csaszar *et al.*, 2009; Voolstra *et al.*, 2009; DeSalvo *et al.*, 2010; 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, $p\mathrm{CO}_2$ 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 $p\mathrm{CO}_2$ 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 pre-conditioning of the coral *Porites porites* with elevated $p\mathrm{CO}_2$ resulted in slower rates of calcification and feeding when they were subsequently submitted to experimental heat stress (Towle *et al.*, 2016). Further, while colonies of *Acropora aspera* enhanced their thermal bleaching tolerance following pre-conditioning with heat, this was not the case for *A. millepora* (Middlebrook *et al.*, 2008). Photosymbionts inhabiting *A. millepora* colonies that were pre-conditioned by warming had improved their ability to dispose of excess light energy as heat compared to those in non-conditioned 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 $p\mathrm{CO}_2$, but the relative frequency and importance of this transgenerational plasticity is 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, 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, i.e., 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: 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 behaviour of a recipient organism) that induce attachment and metamorphosis in coral larvae (Negri *et al.*, 2003; Webster *et al.*, 2004; Tebben *et al.*, 2011; Tebben *et al.*, 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 additional 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 overgrowth by filamentous algae by coating settlement surfaces with non-toxic 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 inter-crossing, 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 inter-crossing has 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 non-model 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 as well as socio-economic 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 to 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 in order 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, the assisted evolution tools have neither 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 is 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 cryo-preservation (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.

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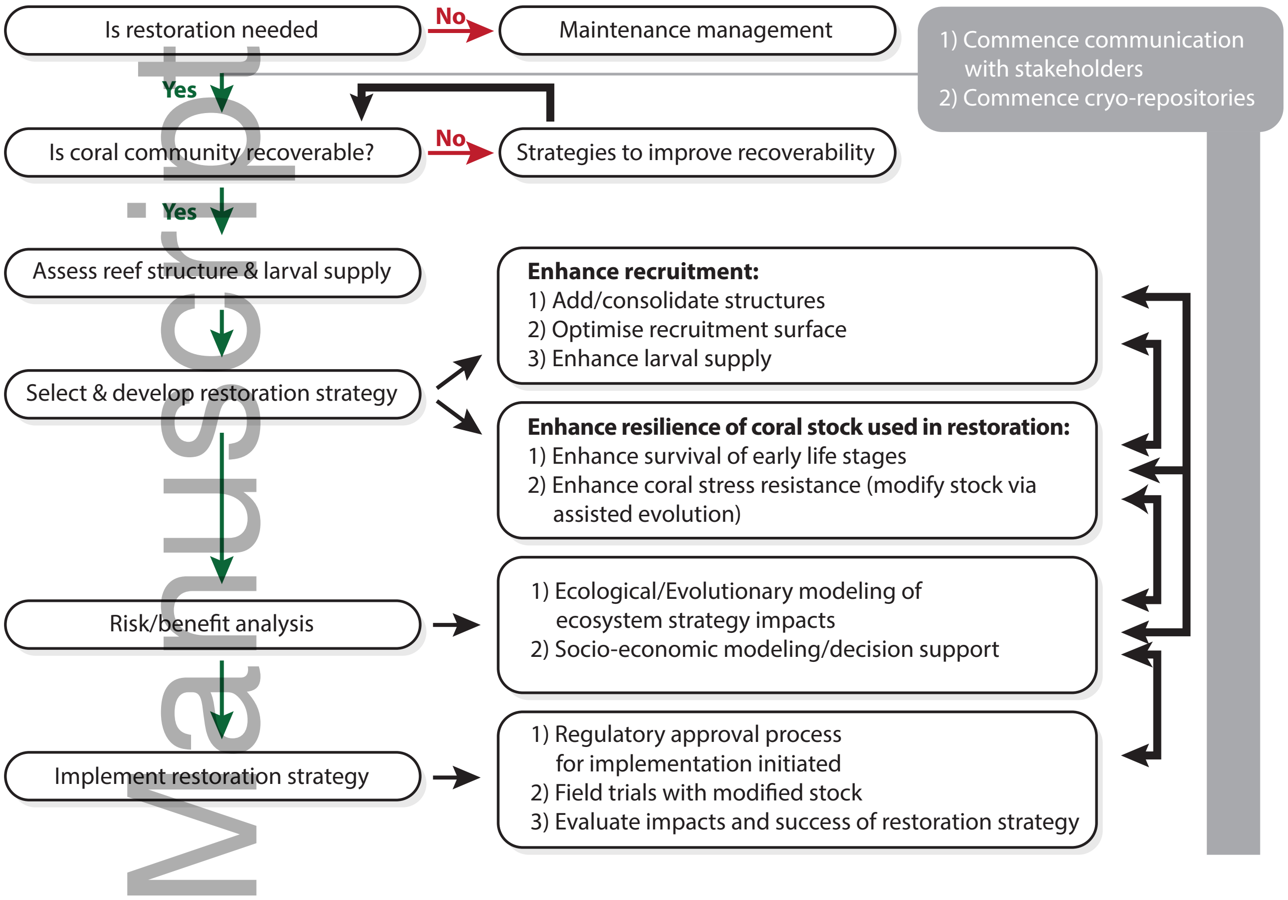
Figure 1: Intraspecific variation in bleaching tolerance in sympatry. Two adjacent *Orbicella faveolata* colonies in the upper Florida Keys showing different bleaching responses to thermal stress in September 2015. Photocredit: NOAA-Southeast Fisheries Science Center.

Figure 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, etc.). 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 cryo-repositories are ongoing throughout the process.


Is restoration needed
No
Maintenance management
1) Commence communication with stakeholders
2) Commence cryo-repositories
Yes
Is coral community recoverable?
No
Strategies to improve recoverability
Yes
Assess reef structure & larval supply
Enhance recruitment:
1) Add/consolidate structures
2) Optimise recruitment surface
3) Enhance larval supply
Select & develop restoration strategy
Enhance resilience of coral stock used in restoration:
1) Enhance survival of early life stages
2) Enhance coral stress resistance (modify stock via assisted evolution)
Risk/benefit analysis
1) Ecological/Evolutionary modeling of ecosystem strategy impacts
2) Socio-economic modeling/decision support
Implement restoration strategy
1) Regulatory approval process for implementation initiated
2) Field trials with modified stock
3) Evaluate impacts and success of restoration strategy