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# Restore or Redefine: Future Trajectories for Restoration

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Global habitat deterioration of marine ecosystems has led to a need for active interventions to halt or reverse the loss of ecological function. Restoration has historically been a key tool to reverse habitat loss and restore functions, but the extent to which this will be sufficient under future climates is uncertain. Emerging genetic technologies now provide the ability for restoration to proactively match adaptability of target species to predicted future environmental conditions, which opens up the possibility of boosting resistance to future stress in degraded and threatened habitats. As such, the choice of whether to restore to historical baselines or anticipate the future remains a key decision that will influence restoration success in the face of environmental and climate change. Here, we present an overview of the different motives for restoration – to *recover* or *revive* lost or degraded habitats to extant or historical states, or to *reinforce* or *redefine* for future conditions. We focus on the genetic and adaptive choices that underpin each option and subsequent consequences for restoration success. These options span a range of possible trajectories, technological advances and societal acceptability, and represent a framework for progressing restoration of marine habitat forming species into the future.

**Keywords:** assisted adaptation, provenance, kelp, climate change, evolution, synthetic biology

## INTRODUCTION

Habitat deterioration and destruction threaten global ecological functions and result in significant loss of social and economic values (Hoffmann et al., 2010; Venter et al., 2016; Powers and Jetz, 2019). Recognizing this threat, the UN has declared 2021–2030 the “decade of restoration” (FAO, 2019) with the aim to restore 350 million hectares of degraded ecosystems, and massively scale up restoration efforts to promote resilience to climate and anthropogenic change and reverse biodiversity loss. In particular, there is an urgent need for marine restoration initiatives to combat and reverse existing habitat loss (e.g., Krumhansl et al., 2016; Filbee-Dexter and Wernberg, 2018),

and even pre-empt future habitat loss (Gattuso et al., 2015; Hughes et al., 2017). As such, both preventive (passive) and adaptive (active) restoration measures are globally supported as viable options under future climates (IPCC, 2019).

Successful, large scale restoration efforts will require robust, science-based practices that consider the fundamental question: “to what time point should we restore?” Historically, restoration has sought to replicate what was lost and to recover properties of populations or communities (species, structure, ecosystem services) to historic states that are putatively adapted to extant environmental conditions. However, ongoing habitat deterioration and climate change is outpacing the ability of many species to adapt, challenging the assumption that restoration to historic states will be sufficient to ensure persistence into the future (Hobbs et al., 2009; Van Oppen et al., 2015; Perring et al., 2015; Breed et al., 2018, 2019; Gurgel et al., 2020). Instead, improving or redesigning properties of lost habitats to withstand predicted future conditions may confer greater restoration success. Moreover, restoration could also include anticipatory actions (prior to loss) to proactively boost resilience and adaptive capacity of extant populations to predicted future conditions (assisted adaptation, Aitken and Whitlock, 2013; Van Oppen et al., 2017). Thus, the decision whether to restore to extant or historical baselines, versus some predicted but uncertain future state is likely to be central to restoration success into the future.

Given that habitat resilience (the capacity to resist or recover from perturbation) and adaptive capacity to cope with environmental change will be influenced by underlying genetic properties of populations (genetic diversity, composition of genes and alleles; Wernberg et al., 2018), determining provenance (the origin and diversity of donor individuals) and thus, choosing an historic versus unknown future genetic baseline is a key consideration in contemporary restoration science (Breed et al., 2018). Although genetic baselines are not static and change through time, here we define a genetic baseline as the level of the genetic diversity and structure chosen and initially replicated in a restoration program through provenance decisions. Current best practice recommends local provenance for restoration, that is, that donor adults or propagules are sourced within contemporary extant genetic boundaries to maintain locally adapted genotypes and avoid maladaptation and genetic pollution (e.g., SERA, 2017). Moreover, characterizing and replicating extant levels of genetic diversity and structure is recommended to ensure sufficient diversity for adaptation (Bischoff et al., 2010; Wood et al., in press). Unfortunately, restoration, particularly in marine systems, has historically been conducted in the absence of formal genetic assessments, which may contribute to poor outcomes to date (McKay et al., 2005; Mijangos et al., 2015; Crouzeilles et al., 2016). Although current restoration efforts are increasingly incorporating empirical assessments of genetic provenance into practice<sup>1</sup> (e.g., Evans et al., 2018; Wood et al., in press), the extent to which this will confer success under future scenarios of climate and anthropogenic stress remains a critical uncertainty (Weeks et al., 2011; Perring et al., 2015).

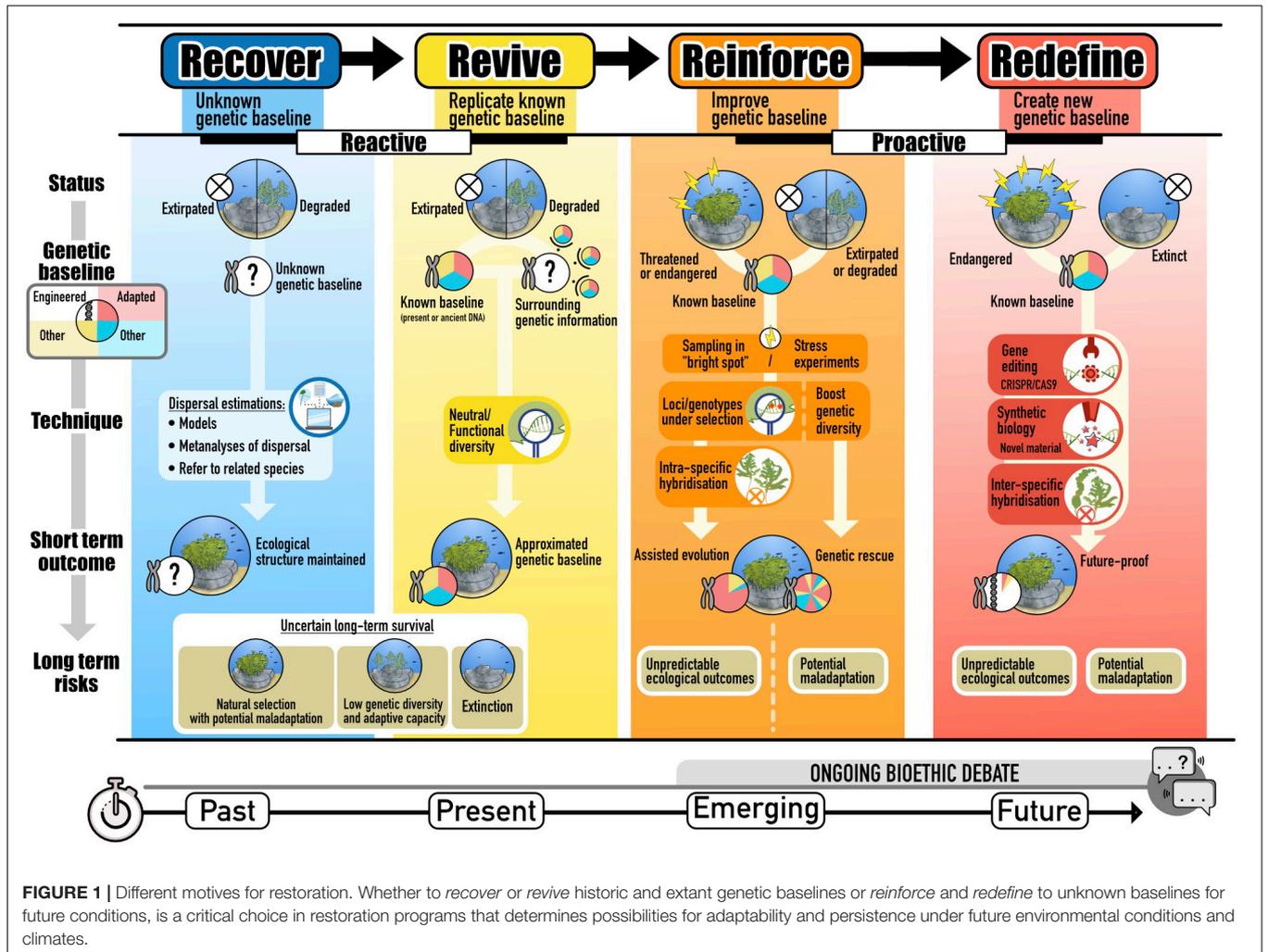
<sup>1</sup>www.operationcrayweed.org

Predicted increases in climate and anthropogenic stress have prompted calls for “future-proof” restoration practices that reinforce or even redesign historic and extant genetic baselines to confer increased resilience to future conditions and stressors in restored populations (Van Oppen et al., 2017; Breed et al., 2018, 2019; Ralls et al., 2018; Wood et al., 2019; Sgrò et al., 2011). Critically, both reinforcing and redefining existing genetic baselines can be applied similarly through traditional restoration programs after loss or degradation, or as a preventative measure prior to any impact occurring. Reinforcing genetic baselines could be achieved via increasing genetic diversity in restored populations to provide sufficient adaptive capacity to cope with future change. Another strategy involves matching predicted environmental and anthropogenic conditions to the ability of individuals and populations to adapt through addition of resilient genotypes identified through experimentation (Breed et al., 2019) or genome wide association studies (GWAS; Van Oppen et al., 2015; Rinkevich, 2019). Completely redefining genetic baselines and population resilience is now possible with emerging genetic technologies (Popkin, 2018). For example, synthetic biology and gene editing using tools such as CRISPR/CAS9 can be harnessed to create or spread novel or engineered beneficial genetic elements within restored or vulnerable populations (Coleman and Goold, 2019) and allow bespoke restoration or assisted adaptation programs to be designed for specific stressors of interest.

Here, we focus on kelp forests, critical marine habitats in decline, to present a framework to guide the design of restoration initiatives as a function of four possible motives: *Recover*, *Revive*, *Reinforce*, and *Redefine* (Figure 1). Importantly, this framework does not only apply to kelp forests but to restoration efforts more broadly. *Recover* and *revive* center on contemporary, reactive restoration practices that seek to return already degraded habitat to historic or extant baselines. In contrast, *reinforce* and *redefine* seek to proactively anticipate future conditions and boost resilience in lost, degraded or vulnerable habitats. This framework spans a range of possible trajectories, technological advances and societal acceptability and represents a platform for progressing marine restoration into the future. We discuss techniques for estimating appropriate genetic provenance in cases where prior genetic data is limited and pathways to develop preventative strategies that anticipate and boost resilience to future stress.

## KELP FORESTS – CRITICAL HABITATS IN DECLINE

Kelp forests are highly productive seascapes dominated by large brown seaweeds (Wernberg and Filbee-Dexter, 2019). They are particularly prominent in temperate to polar environments where they are the foundations for immense biodiversity and valuable ecological services such as important recreational and commercial fisheries (Wernberg et al., 2019b). The best available evidence suggests that 40–60% of the world’s kelp forests have been in decline over the past 50 years (Krumhansl et al., 2016; Wernberg et al., 2019b) as a consequence of a variety of direct



**FIGURE 1 |** Different motives for restoration. Whether to *recover* or *revive* historic and extant genetic baselines or *reinforce* and *redefine* to unknown baselines for future conditions, is a critical choice in restoration programs that determines possibilities for adaptability and persistence under future environmental conditions and climates.

and indirect stressors including warming, marine heatwaves, eutrophication and increasing herbivory from range-shifting warm-water herbivores (Vergés et al., 2014; Filbee-Dexter and Wernberg, 2018). For example, in Australia, kelp forests of laminarian kelp and fucoids (e.g., *Ecklonia radiata*, *Scyothalia dorycarpa*, *Phyllospora comosa*) are found throughout the Great Southern Reef along the southern coastline of the continent (Coleman and Wernberg, 2017; Wernberg et al., 2019a). In recent decades, almost every part of this unique large-scale ecosystem has experienced localized to regional decline and loss of kelp forests due to a range of processes including eutrophication, over grazing, warming, and marine heatwaves (Coleman et al., 2008; Connell et al., 2008; Ling et al., 2009; Vergés et al., 2016; Wernberg et al., 2016; Carnell and Keough, 2019). In almost all cases in Australia and globally, kelp loss has been persistent with no signs of natural recovery. Instead, kelp forests have been replaced by alternate habitats including turf algae (Filbee-Dexter and Wernberg, 2018) or urchin barrens (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015) which create strong reinforcing feedbacks that prevent natural recovery of kelp. This provides strong impetus and motivation to apply interventions

such as restoration, especially where the initial stressor no longer occurs (e.g., Coleman et al., 2008) or can be controlled (e.g., Sanderson et al., 2015; Layton et al., 2020).

The first published studies on kelp forest restoration stem from the 1960s–1970s in Japan and North America (Carlisle et al., 1964; North, 1976; Kuwahara et al., 2006). Although the number of kelp restoration attempts has increased exponentially since then, such efforts are generally of limited duration (<2 years), small in scale (<0.1 ha) and have had limited success (Eger et al., 2019). Moreover, these efforts have generally lacked empirical data of underlying patterns of genetic diversity and structure (particularly functional genetic diversity), and often have not considered demographic history and ecological processes influencing kelp populations, all of which may have contributed to poor restoration outcomes. There are however some notable ongoing projects that address some of these concerns. For example, the Wheeler North Reef in southern California has successfully established a giant kelp forest community at a large scale (70 hectares of artificial reef structure) to compensate for the loss of natural giant kelp forests due to impacts from a nuclear power station (Schroeter et al., 2018). The

343 Korean government has also developed a major marine seaweed  
 344 foresting program and has already restored over 3,000 hectares  
 345 of seaweed forests since 2009 (Lee, 2019). In Sydney, Australia,  
 346 a project is also ongoing that aims to re-establish lost forests  
 347 of *P. comosa* at the scale of the initial degradation –70 km  
 348 of metropolitan coastline<sup>2</sup> (Campbell et al., 2014; Wood et al.,  
 349 in press). The projects that have seen sustained success have  
 350 generally been well financed, have often been coordinated by  
 351 regulatory bodies, carried out over a sustained periods of time, or  
 352 harnessed the power of local community engagement to deliver  
 353 lasting results (Eger et al., 2019; DeAngelis et al., 2020; Layton  
 354 et al., 2020). While these projects are currently in the minority,  
 355 interest in kelp restoration is accelerating and we are at the  
 356 point where we can adequately learn from our past mistakes  
 357 and enhance restoration of our underwater forests (Eger et al.,  
 358 2019). Central to the success of these future efforts, however,  
 359 is determining which environmental conditions to restore to  
 360 and, therefore, whether to recover or revive genetic baselines,  
 361 or reinforce and redefine them. These issues are common not  
 362 only to kelp forests restoration but also to marine and terrestrial  
 363 restoration more broadly.

364

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## 366 **RECOVER – RESTORATION THAT** 367 **REPLICATES UNKNOWN GENETIC** 368 **BASELINES** 369

370 Marine restoration initiatives have historically operated in  
 371 the absence of empirical genetic data, instead focusing on  
 372 restoring community and habitat structure, functions and  
 373 biodiversity (e.g., Campbell et al., 2014; Marzinelli et al.,  
 374 2016; Verdura et al., 2018). This is partly a reflection of the  
 375 historically high costs, complexity and inaccessibility of genomic  
 376 techniques to assess baseline genetic diversity and structure using  
 377 high throughput methods. Nonetheless, restoration practices  
 378 have typically informally considered genetic baselines through  
 379 available scientific literature on related taxa, knowledge of direct  
 380 dispersal distances where measurable, incorporation of general  
 381 genetic principles into practice (e.g., mixing populations to avoid  
 382 inbreeding and ensure diversity) or through expert opinion.  
 383 For example, global meta-analyses for marine algae have shown  
 384 that scales of dispersal and population connectivity are generally  
 385 limited to ~50 km (Durrant et al., 2014), which can be used  
 386 as a general rule of thumb for provenance when empirical data  
 387 for the species of interest is lacking. Alternatively, estimates  
 388 of oceanographic dispersal distance relative to properties of  
 389 propagules (Gaylord et al., 2006) can sometimes be used to infer  
 390 appropriate provenance in the absence of data (e.g., Coleman  
 391 et al., 2011b; Coleman et al., 2013), with consideration of  
 392 potential barriers to dispersal or genetic breaks (e.g., Coleman  
 393 and Brawley, 2005; Coleman and Kelaher, 2009; Alberto et al.,  
 394 2010; Durrant et al., 2018).

395 The risk associated with restoring populations in the absence  
 396 of empirical genetic knowledge is that restored populations will  
 397 inadvertently lack diversity or appropriate adaptive capacity to

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 399 <sup>2</sup>[www.operationcrayweed.com](http://www.operationcrayweed.com)

cope with extant or future conditions (e.g., Williams, 2001), 400  
 which may be particularly pertinent for species that exhibit small 401  
 scale dispersal and are therefore susceptible to reduced gene flow, 402  
 increased inbreeding or asexual propagation (e.g., Guillemain 403  
 et al., 2008; Coleman et al., 2011a, 2019; Coleman and Wernberg, 404  
 2018; Miller et al., 2019). This risk is exacerbated given increasing 405  
 habitat fragmentation and deterioration often characterizes 406  
 the seascapes from which donor adults or propagules must 407  
 be sourced for restoration (Coleman and Kelaher, 2009). 408  
 Inadvertently sourcing donor plants from outside locally adapted 409  
 populations could cause maladaptation and decreased fitness 410  
 relative to appropriate provenance (Sexton et al., 2011), which 411  
 may contribute to the general lack of successes in marine 412  
 restoration to date (e.g., see Rinkevich, 2014 for a coral example). 413  
 Obtaining genetic baselines is, however, now within reach of most 414  
 restoration programs due to the increasing sophistication and 415  
 reduced cost of modern genetic techniques (e.g., sequencing) that 416  
 allow for assessments of population genetic structure without 417  
 lengthy development stages (Narum et al., 2013). We argue that 418  
 such assessments should now be planned and budgeted for prior 419  
 to implementation in future restoration initiatives by adapting 420  
 existing frameworks (e.g., Hoffmann et al., 2015). 421

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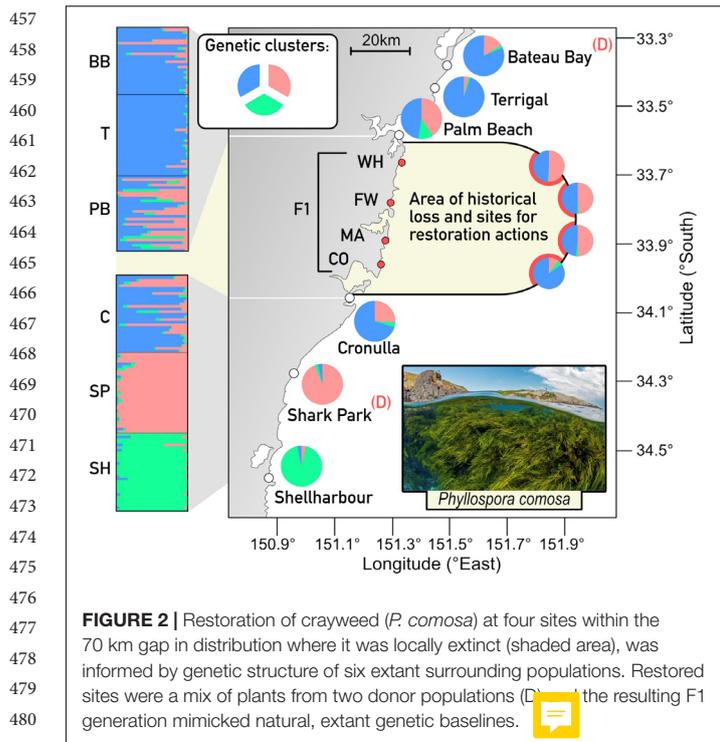
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## 424 **REVIVE – RESTORING EXTANT OR** 425 **HISTORIC GENETIC BASELINES** 426

427 Contemporary restoration programs should aim, at a minimum,  
 428 to replicate natural genetic baselines informed by empirical  
 429 genetic data. Given that “before” data collected prior to loss  
 430 rarely exist (Grant et al., 2017), population genetic diversity and  
 431 structure should be assessed within surrounding, putatively non-  
 432 impacted populations. This can then be replicated within restored  
 433 populations through careful selection of donor populations  
 434 and individuals (Figure 2). Such genetic assessments can now  
 435 be done with less cost and effort than previously with the  
 436 advent and accessibility of high throughput sequencing and  
 437 should be included as “best-practice” in restoration programs.  
 438 Moreover, modern genomic techniques (e.g., genotyping by  
 439 sequencing of single nucleotide polymorphisms; SNPs) allow  
 440 both neutral and functional or adaptive genetic diversity to be  
 441 characterized simultaneously, an advance that is set to improve  
 442 restoration outcomes through refined provenance decisions.  
 443 While there are no current examples of its use in the literature  
 444 in the context of restoration, genotyping by sequencing of tens  
 445 of thousands of SNP loci, along with reference genomes to  
 446 identify functions, is providing detailed extant baselines for key  
 447 foundation species of kelp (e.g., *E. radiata*), that will soon allow  
 448 replication (or bespoke manipulation, see section “Reinforce –  
 449 Improving Genetic Baselines for Future Conditions”) of neutral  
 450 and functional diversity and structure in restoration programs.

451 Restoration informed by underlying patterns of genomic  
 452 diversity and structure was recently implemented for one of the  
 453 largest kelp restoration programs globally, Operation Crayweed<sup>3</sup>  
 454 (Wood et al., in press). Prior to restoration, population genetic

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 456 <sup>3</sup>[www.operationcrayweed.org](http://www.operationcrayweed.org)



diversity and structure of the endemic crayweed (*P. comosa*) was characterized throughout its entire distribution and within 180 km either side of the intended restoration areas (Figure 2; Coleman et al., 2008; Coleman and Kelaher, 2009; Wood et al., in press). Natural level of genetic diversity and structure were mimicked in restoration programs by sourcing and mixing adult donor plants from two sites that represented the genetic clusters that occur within an 80 km radius of where *Phyllospora* was lost (Figure 2; Wood et al., in press). This avoided mixing distant genetic clusters that were not representative of the region and was also a practical distance to ensure donor plant survival during transplantation. The success of this approach was evidenced by rapid recruitment and an F1 generation that had near identical genetic properties to donor plants and sites (Figure 2; Wood et al., in press). This is among the most successful restoration programs globally and there are now self-sustaining crayweed populations with likely F3–4 generations in some restored sites.

To ensure empirical genetic data is utilized to facilitate informed provenance decisions, data on genetic diversity and structure and their links to environmental conditions should be made publicly available to stakeholders and non-experts including community groups and governments who often implement restoration programs. For example, the restore and renew website for terrestrial plants<sup>4</sup> (Rossetto et al., 2019) allows users to define a site to be restored, choose appropriate provenance within defined genetic populations and even provides provenance options to improve resilience (see “Revive – Restoring Extant or Historic Genetic Baselines”). No such platforms exist for marine systems but development of new

<sup>4</sup>restore-and-renew.org.au

marine restoration methods that will increase accessibility of marine restoration to diverse user groups and over large scales, will necessitate similar initiatives to ensure scientifically informed provenance decisions are made within the decade of restoration.

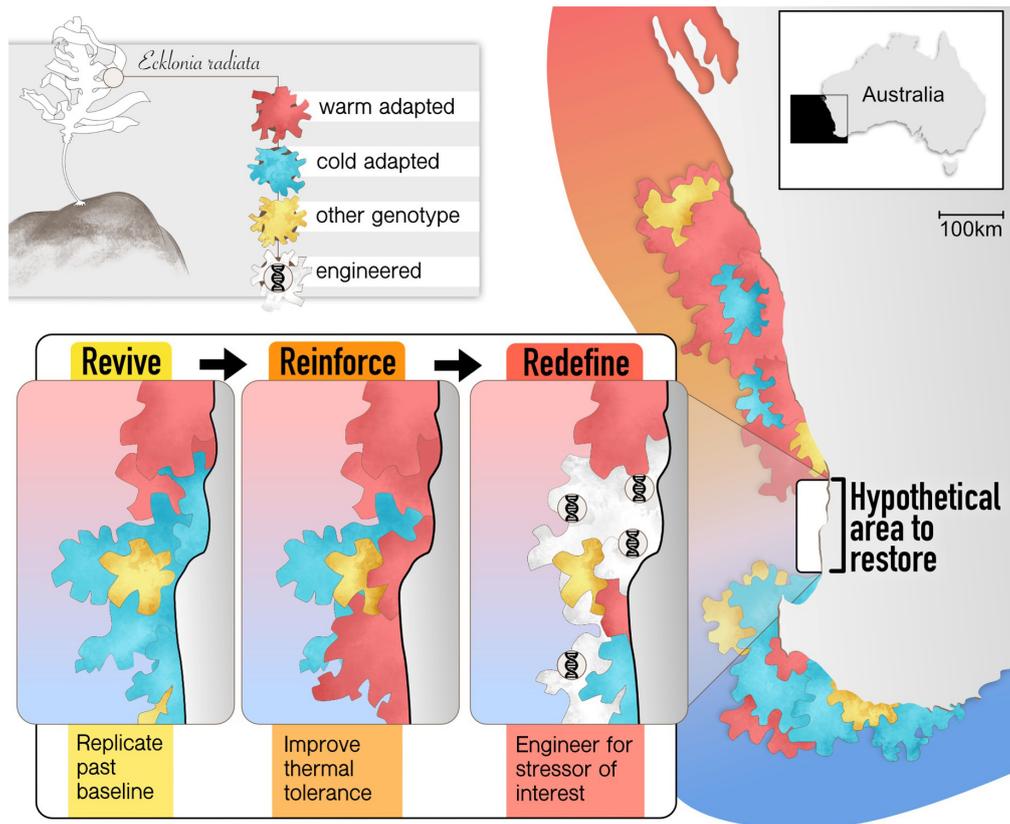
## DYNAMIC BASELINES – WHY WE SHOULD NOT REPLICATE WHAT WAS LOST

In rare cases baseline genetic data from lost or vulnerable populations are available and can theoretically be replicated. For example, rare “before” and “after” data has revealed massive change in baseline levels of genetic diversity and structure in three species of kelps that were impacted by a heatwave off Western Australia (Coleman et al., 2011b; Wernberg et al., 2018; Gurgel et al., 2020). Under a scenario of restoration that seeks to replicate what was lost, such “before” estimates can be used as a guide for provenance. This may be desirable where legislation dictates the necessity for a baseline (McAfee et al., 2019) or there are concerns surrounding genetic pollution (Potts et al., 2003). However, these studies have also revealed that genetic “baselines” are not static but are naturally dynamic properties of populations that can change rapidly (within a few months), due to redistribution of existing genetic variants through dispersal or selection (Torda et al., 2017; Gurgel et al., 2020).

This raises the important question of whether it is desirable to replicate exactly what was lost, or to embrace the dynamic nature of baselines and make informed decisions to reinforce or redefine them to an unknown future state (Figures 1, 3). Kelp loss and change in genetic baselines may naturally enhance resilience to future stress through selection. Thus, restoring kelp forests using past genetic baselines may, therefore, actually create populations that are more vulnerable to the events or stressors that caused loss in the first place providing a mechanistic basis and impetus for reinforcing as a restoration goal. Predicting future genetic response can be enhanced by the incorporation of neutral and functional genetic variation into species distribution models under projected future environmental scenarios (Bay et al., 2017; Razgour et al., 2019). Given naturally shifting baselines and environmental changes that are increasingly overwhelming the intrinsic capacity of organisms to adapt and survive in parts of their range (Deutsch et al., 2015; Segan et al., 2016) it is imperative to explore the potential to enhance or reinforce the resilience of ecosystems through restoration (Hobbs et al., 2017) as well as proactively reinforce resilience in habitats that will be threatened under future scenarios of change.

## REINFORCE – IMPROVING GENETIC BASELINES FOR FUTURE CONDITIONS

Often termed “assisted adaptation” or “assisted evolution,” the idea of reinforcing genetic baselines is to introduce diversity or genotypes that will enhance resilience to future stressors in restored or threatened populations. While there are scientific and ethical challenges to adoption of such approaches



**FIGURE 3 |** Potential scenarios for kelp restoration for a hypothetical area to be restored off Western Australia. Frequencies of putative warm (red) and cool (blue) adapted genotypes have been identified along a gradient of ocean temperature (shaded background) which could be utilized to revive or reinforce kelp forests against future thermal stress. Kelps with engineered genetic elements could be used to redefine the genetic baseline.

(Coleman and Goold, 2019; Filbee-Dexter and Smajdor, 2019), the continued anthropogenic alteration of habitats and emergence of novel ecosystems place such interventions firmly at the forefront of restoration science.

The terms assisted adaptation or evolution capture numerous approaches for manipulating natural genetic properties of populations in order to increase their ability to adapt to changing environmental conditions. Such measures include moving resilient individuals to vulnerable populations to increase their capacity to resist or recover from disturbances (known as assisted gene flow or assisted migration; Figure 3). This could be achieved through targeted sourcing of donor plants using laboratory selection experiments or through identification of natural selection in the field (Zhang et al., 2011; Robinson et al., 2013; Gurgel et al., 2020). Another proposed strategy is “genetic rescue” whereby genetic diversity is enhanced in populations that have limited adaptive capacity, rather than entirely new genotypes introduced. Opting for boosting genetic diversity also reduces risks of negative fitness trade-offs by increasing the overall range of responses to various environmental conditions without aiming at improving one specific function. This approach has enhanced seagrass restoration success with greater productivity and biodiversity in experimental plots with

increased genetic diversity (Reynolds et al., 2012). Similarly, higher genetic diversity in kelp forests may also confer greater resilience to climate stressors (Wernberg et al., 2018). Finally, resilience may be increased by utilizing intra-specific hybrid vigor or heterosis whereby crossing individuals from different populations (often not connected by contemporary gene flow) increases fitness relative to pure breeds (e.g., Sexton et al., 2011), although this idea may be underpinned by mechanisms including increase in genetic diversity *per se*, addition of more resilient genes or epigenetic responses (Fujimoto et al., 2018).

Given the controversial nature of restoration strategies that seek to reinforce or improve extant genetic baselines, prioritization and careful selection of candidate species or sites is vital, as is experimentation to provide proof of concept that such strategies will work under a range of current and potential future stressors. It may be most appropriate to consider assisted adaptation in areas where species are already threatened or endangered, where projections of loss are severe or where impacts of loss will have widespread economic and ecological effects (e.g., foundation species; Baums, 2008; Aitken and Whitlock, 2013). Australian kelps meet all these criteria because a lack of poleward landmasses and warm currents along both coastlines

685 create a unique scenario whereby species are locked into an  
 686 ever narrowing thermal niche (Coleman et al., 2011b, 2017;  
 687 Martínez et al., 2018). Projections for Australian kelps under  
 688 climate change scenarios reveal an average loss of 78% of current  
 689 distributions under the immediate RCP 6.0 scenario (Martínez  
 690 et al., 2018), which may present logical targets for assisted  
 691 adaptation and improving extant genetic baselines. This could  
 692 be done through genomic identification of heritable loci under  
 693 selection for certain stressors combined with manipulative stress  
 694 experiments using multiple stressors that test the resilience of  
 695 genotypes possessing such loci and assess potential trade-offs.  
 696 Genotypes that perform well can then be cultured for enhanced  
 697 seeding into restored populations (Figure 2; Weeks et al.,  
 698 2011; Webster et al., 2017; Fredriksen et al., 2020). Given that  
 699 such approaches, however, could lead to detrimental trade-offs  
 700 (maladaptation) and decreased resilience to non-target stressors  
 701 (Hereford, 2009; Anderson et al., 2014), a portfolio approach  
 702 whereby assisted adaptation is paired with other approaches  
 703 including enhancing diversity or connectivity, protecting a wide  
 704 range of seascapes and minimizing stressors (Webster et al., 2017)  
 705 may provide more security in uncertain futures.

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## 708 **REDEFINE – CREATE A NOVEL GENETIC** 709 **STATE**

710

711 Scientific advances are providing never-before imagined  
 712 solutions to emerging environmental problems, with synthetic  
 713 biology and CRISPR/CAS9 gene editing tools among the fastest  
 714 developing and transformative scientific fields (Lin and Qin,  
 715 2014; Wang et al., 2016; Piaggio et al., 2017). These technologies  
 716 involve the creation of novel and engineered genetic variation  
 717 that could be utilized in a restoration context to redefine extant  
 718 genetic baselines and future resilience of species and populations  
 719 to change (Figure 3; Coleman and Goold, 2019). The potential  
 720 application of such technologies is vast, at times controversial,  
 721 and technological advances have outpaced social, ethical and  
 722 practical considerations. Here, we discuss some of the potential  
 723 applications of synthetic biology and gene editing in restoration.  
 724 Rather than advocate or oppose their use, we identify where and  
 725 when they may play a role in restoration science. Regardless of  
 726 whether these techniques will ever be socially acceptable or even  
 727 necessary, this is a discussion that must be had early on.

728 Synthetic biology, or the engineered creation of novel genetic  
 729 variation, is a fast developing and transformative scientific  
 730 field. It can involve both genetic and metabolic engineering to  
 731 create new functions in living cells or the creation of entirely  
 732 new cells with synthetic components. Synthetic biology has  
 733 been enabled through the decreasing costs of sequencing and  
 734 synthesis of DNA, availability of extensive databases including  
 735 information on sequences and functions, and the standardization  
 736 of parts (genetic elements, proteins, organisms) which allows  
 737 for increasing predictability in biological organisms, facilitating  
 738 their use in a more designed approach as biological devices  
 739 (Canton et al., 2008). Synthetic biology has also been enabled by  
 740 development of the CRISPR/Cas9 genome editing tool (Pretorius,  
 741 2017) that cleaves viral double stranded DNA and allows for

742 very precisely targeted changes to be made in a genome,  
 743 as long as an organism is genetically tractable (Doudna and  
 744 Charpentier, 2014). Examples of the use of CRISPR/Cas9 range  
 745 from introducing a point mutation in a species genome to  
 746 affect the quantity of metabolites (Shih et al., 2016), engineering  
 747 speciation through designer karyotypes (Luo et al., 2018), or  
 748 creating sequence specific anti-microbials through microbiome  
 749 engineering (Bikard et al., 2014).

750 In conjunction with the availability of vast metagenomic  
 751 data, it should be possible for scientists to map the genetic  
 752 characteristics of resilient species or entire populations that  
 753 are thriving despite stress, through natural and manipulative  
 754 experiments. Resilient genetic elements could then help guide  
 755 synthetic biology/genome engineering design principles. For  
 756 example, traits from populations of marine organisms which  
 757 have adapted to adverse conditions (e.g., polluted areas or  
 758 warm range edges) could be introduced into related species or  
 759 impacted populations to improve resilience to those stressors.  
 760 The nature of these genetic elements could range from  
 761 advantageous single nucleotide polymorphisms (SNPs; Doudna  
 762 and Charpentier, 2014), to different genetic alleles/genes or  
 763 even foreign/synthesized DNA (Williams et al., 2017), to larger  
 764 duplications, inversions or deletions of entire chromosome arms  
 765 (Luo et al., 2018). Synthetic biology could even be applied to  
 766 restore extinct species. Such approaches are being considered in  
 767 terrestrial contexts, with various groups attempting to resurrect  
 768 extinct species (known as “de-extinction”), such as the great  
 769 auk and the woolly mammoth (Corlett, 2017). Indeed, by  
 770 extensive and rigorous bio-banking it may be possible, in the  
 771 long term, to attempt to partially recreate extinct species and  
 772 biomes using synthetic biology and store adaptive potential  
 773 (Hodgins and Moore, 2016). Thus, to enable future restoration,  
 774 bio-banking and *ex situ* conservation approaches should be  
 775 promptly considered to allow the possibility for habitat recreation  
 776 into the future.

777 Another technique that constitutes redefining extant  
 778 genetic baselines is assisted evolution through inter-specific  
 779 hybridization or heterosis. This utilizes the phenomenon of  
 780 hybrid vigor, whereby species F1 hybrids display greater fitness  
 781 than pure breeds and is an emerging idea that has been suggested  
 782 as a tool to enhance survival and persistence of foundation  
 783 species under future climates (Rinkevich, 2014; Van Oppen  
 784 et al., 2015; Wood et al., 2019). In an assisted evolution context,  
 785 inter-specific hybridization would be facilitated where it would  
 786 otherwise not occur spatially, temporally (e.g., reproductive  
 787 isolation) or within evolutionary time frames that would match  
 788 the rapid pace of climate change. For example, hybrids of both  
 789 kelp and coral have been shown to have greater thermal tolerance  
 790 (Chan et al., 2018; Martins et al., 2019) which could be utilized  
 791 in a restoration or assisted adaptation context that accepts  
 792 redefining genetic baselines by mixing species gene pools.

793 At present, redefining extant genetic baselines in natural  
 794 ecosystems is perhaps most palatable and ethically acceptable  
 795 in the extreme case of stopping species extinction. Given the  
 796 transformative nature and unpredictability of creating new  
 797 genetic states, we suggest a starting point may be to prioritize  
 798 species with little chance of persistence under future climate

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799 conditions. Again, Australian kelps provide the perfect example  
 800 of such a situation because rapid warming, a narrowing thermal  
 801 niche combined with high endemism (Phillips, 2001) create  
 802 conditions that will see many species extinct within the next  
 803 century (Martínez et al., 2018). For example, the endemic  
 804 furoid *P. comosa* (Coleman and Wernberg, 2017) is predicted  
 805 to be completely lost by 2100 under future scenarios of climate  
 806 change given extant temperature tolerances. Moreover, this  
 807 species possesses a shallow history with low genetic diversity and  
 808 structure (Coleman and Kelaher, 2009; Coleman et al., 2011a;  
 809 Durrant et al., 2015), likely limiting its possible responses to  
 810 change. Given that no other extant species seem to provide  
 811 the same functions as *P. comosa* (Marzinelli et al., 2014, 2016),  
 812 this warrants prompt discussion on the potential for genetic  
 813 engineering of novel elements to boost thermal resilience as well  
 814 as limit the effects of additional stressors (Coleman and Goold,  
 815 2019). Without such interventions, this key foundation species  
 816 may be lost forever.

817 Assisted adaption, gene editing and hybridization raise  
 818 complex ethical issues, which largely center on whether we should  
 819 be deliberately introducing new genetic entities into natural  
 820 ecosystems. From an ethical perspective, this shift in restoration  
 821 focus from “revive” to “redefine” is significant (Camacho,  
 822 2010). Redefining genetic baselines can create problematic value  
 823 judgments, such as prioritizing some species or properties  
 824 over others, effectively deciding the winners and losers of  
 825 the Anthropocene. These strategies to alter populations to  
 826 withstand future stress also transform our role from *guardians*  
 827 to *engineers* and *designers* of natural systems, which we do  
 828 not fully comprehend, and can move ecosystems toward states  
 829 that they have never been in before. As a result, we are  
 830 determining the value of species and ecosystems based on the  
 831 degree to which they match our current ideals of how things  
 832 should be – targeting a more intact, familiar ecosystem that  
 833 has been genetically manipulated to resist certain types of  
 834 environmental stress, instead of an unpredictable and unfamiliar  
 835 ecosystem that is transforming due to human activity. The  
 836 use of adaptive or assisted evolution is also complicit with a  
 837 worldview of environmental manipulation and commodification  
 838 of natural systems that could perpetuate the damaging habits  
 839 and dispositions which have caused the habitat loss in the first  
 840 place (Sandler, 2013). Even if not morally wrong itself, adapted  
 841 or assisted evolution may increase reliance on biotechnological  
 842 intervention or even be used to justify continuing harmful  
 843 practices in the future.

844 Conversely, inaction or passive decisions (i.e., not using all  
 845 available tools to potentially save a species or habitat from  
 846 disappearing) may also be unethical. If we have reason to  
 847 predict that not acting will cause more harm than acting, then  
 848 intervention seems to be the best course of action available. In  
 849 an ideal world, we would reduce emissions and mitigate human  
 850 impacts in time to remain in the “revive” space of conservation.  
 851 Yet, we are in a state of crisis that we know will severely impact  
 852 our environment and future generation (Gattuso et al., 2015). In  
 853 light of this pressing reality, it could be argued that we have a  
 854 moral responsibility to take risks we can reasonably predict will  
 855 help to repair human-caused damage – as long as we are not

reckless or negligent in doing so (Douglas, 2003). At a minimum, 856  
 we should seek to thoroughly understand the potential impact 857  
 of using all the tools available to us now, so that we will be 858  
 in a position to choose these options should some catastrophic 859  
 scenario arise in the future (e.g., “arm the future argument” 860  
 outlined by Gardiner, 2010). 861

At a more practical level, there are several first steps we 862  
 can take toward including ethical considerations in decisions 863  
 to use assisted evolution tools. First, we can ensure that a 864  
 minimum standard of risk assessment of potential impact on 865  
 the environment is conducted. This could include controlled 866  
 manipulative experiments on novel or engineered genotypes to 867  
 assess their performance and interactions in natural settings. 868  
 Second, that informed consent of stakeholders is obtained 869  
 and that no conflicts of interest exist in the relationships 870  
 between researchers/managers and local communities. Finally, 871  
 we can develop policy and guidelines for the use of these 872  
 tools in specific systems. Regardless, there is a pressing need 873  
 for prompt collaboration and dialogue among geneticists, 874  
 synthetic biologists, ecologists, and conservationists to identify 875  
 opportunities for use of these transformative technologies and 876  
 ensure that extant research directions are set on trajectories to 877  
 allow these currently disparate fields to converge toward practical 878  
 restoration solutions. While the application of such techniques 879  
 to natural settings is currently controversial (Filbee-Dexter and 880  
 Smajdor, 2019) they should remain at the forefront of discussions 881  
 to future-proof marine ecosystems and restoration practices 882  
 (Coleman and Goold, 2019). 883  
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## 886 RESTORE OR REDEFINE: A BROADLY 887 APPLICABLE FRAMEWORK 888

889 While we have focused here on kelp forests, the framework  
 890 presented is broadly applicable to any marine or terrestrial  
 891 restoration program. Indeed, it may even be more easily  
 892 applied and adopted for restoration of species that are  
 893 more genetically tractable than kelps. Genomic techniques  
 894 might be more rapidly developed in taxa for which DNA  
 895 extraction and subsequent sequencing techniques are more  
 896 easily applied. Further, genomic resources are more developed  
 897 for key model species such as corals, making progress  
 898 toward *revive* and *redefine* more tangible. Indeed, genetics  
 899 and provenance are emerging considerations in coral reef  
 900 restoration guidelines (Baums et al., 2019) and standard  
 901 practices that are easily accessible to managers and practitioners  
 902 (e.g., [www.reefresilience.org](http://www.reefresilience.org)). For such taxa, progress toward  
 903 empirically incorporating appropriate genetic baselines to  
 904 restoration programs should be more rapid. The goal to  
 905 redefine genetic baselines in restoration programs may also  
 906 be more tangible for taxa that have direct economic value  
 907 (e.g., harvested species), where breeding programs often involve  
 908 detailed genomic assessments linking performance and traits to  
 909 environmental conditions. Regardless, restoration of foundation  
 910 macrophytes (e.g., saltmarsh, seagrass, mangroves) and animals  
 911 (e.g., oyster beds, corals) that underpin vast biodiversity of  
 912 marine systems is gaining increasing traction, funding and

sophistication with great potential toward achieving the aims of the United Nations decade of restoration.

## CONCLUSION

Whether to recover and restore historic and extant genetic baselines, or reinforce and redefine them to some unknown future state, will fundamentally affect the resilience and adaptive capacity of restored populations (Hobbs et al., 2009; Van Oppen et al., 2015; Breed et al., 2018, 2019; Wood et al., 2019) but is largely untested for marine systems. Here, we discuss the application of both traditional and modern genomic tools for characterizing (e.g., genotyping by sequencing) and manipulating (CRISPR/Cas9) the genetic composition of lost or degraded marine habitats. The increasing accessibility of these genomic techniques means that future marine restoration efforts can, and should, proceed with the best available genetic data and technologies. At a minimum, baseline empirical genetic data should inform provenance decisions and, where acceptable, incorporate assisted adaptation strategies.

More broadly, it is clear that restoration in the traditional sense of returning a system to a past state, is unlikely to be sufficient or effective under future climates (Van Oppen et al., 2017). Instead, restoration should seek to reinforce and perhaps even redefine populations and species to withstand future environmental conditions and stressors. However, this raises profound and challenging management (to what baseline should we “restore?”), technical (how do we achieve that baseline in a practical sense?) and ethical (what right do we have to introduce novel genetic entities into the marine environment?) questions that will determine our ongoing relationship with nature. We argue for a worldwide move among marine managers and scientists toward prompt consideration of more interventionist

approaches. The failure to consider and prepare for such approaches, despite ethical debates, is also an ethical decision with potentially serious environmental consequences of inaction.

Marine restoration will benefit from learnings from the history of biomedical fields, where technological developments and associated benefits have often outstripped the social and ethical dialogue necessary for implementation. Prompt dialogue is thus required among scientists, policy makers and the broader community on setting restoration targets, including the increasing need to restore for future conditions and the implications of using novel or engineered genetic entities (Coleman and Goold, 2019). Scientific agendas should be set on trajectories to provide the underpinnings for such decisions. Only then can we ensure that our valuable marine habitats continue to deliver ecosystem goods and services in the face of increasing environmental change.

## AUTHOR CONTRIBUTIONS

MC conceived the idea and led the manuscript. All authors wrote sections and edited the manuscript. AM produced the figures.

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## REFERENCES

- Aitken, S. N., and Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annu. Rev. Ecol. Evol. Systemat.* 44, 367–388. doi: 10.1146/annurev-ecolsys-110512-135747
- Alberto, F., Raimondi, P. T., Reed, D. C., Coelho, N. C., Leblois, R., Whitmer, A., et al. (2010). Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. *Ecology* 91, 49–56. doi: 10.1890/09-050.1
- Anderson, J. T., Lee, C.-R., and Mitchell-Olds, T. (2014). Strong selection genome-wide enhances fitness trade-offs across environments and episodes of selection. *Evolution* 68, 16–31. doi: 10.1111/evo.12259
- Baums, I. B. (2008). A restoration genetics guide for coral reef conservation. *Mol. Ecol.* 17, 2796–2811. doi: 10.1111/j.1365-294x.2008.03787.x
- Baums, I. B., Baker, A. C., Davies, S. W., Grottoli, A. G., Kenkel, C. D., Kitchen, S. A., et al. (2019). Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecol. Appl.* 29, e01978.
- Bay, R. A., Rose, N., Barrett, R., Bernatchez, L., Ghalambor, C. K., Lasky, J. R., et al. (2017). Predicting responses to contemporary environmental change using evolutionary response architectures. *Am. Nat.* 189, 463–473. doi: 10.1086/691233
- Bikard, D., Euler, C. W., Jiang, W., Nussenzweig, P. M., Goldberg, G. W., Duportet, X., et al. (2014). Exploiting crisper-cas nucleases to produce sequence-specific antimicrobials. *Nat. Biotechnol.* 32, 1146–1150. doi: 10.1038/nbt.3043

- Bischoff, A., Steinger, T., and Müller-Schärer, H. (2010). The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. *Restor. Ecol.* 18, 338–348. doi: 10.1111/j.1526-100x.2008.00454.x
- Breed, M. F., Harrison, P. A., Bischoff, A., Durruty, P., Gellie, N. J. C., Gonzales, E. K., et al. (2018). Priority actions to improve provenance decision-making. *BioScience* 68, 510–516. doi: 10.1093/biosci/biy050
- Breed, M. F., Harrison, P. A., Blyth, C., Byrne, M., Gaget, V., Gellie, N. J. C., et al. (2019). The potential of genomics for restoring ecosystems and biodiversity. *Nat. Rev. Genet.* 20, 615–628. doi: 10.1038/s41576-019-0152-0
- Camacho, A. E. (2010). Assisted migration: redefining nature and natural resource law under climate change. *Yale J. Regul.* 27, 171.
- Campbell, A. H., Marzinelli, E. M., Verges, A., Coleman, M. A., and Steinberg, P. D. (2014). Towards restoration of missing underwater forests. *PLoS ONE* 9:e84106. doi: 10.1371/journal.pone.0084106
- Carlisle, J. G., Turner, C. H., and Ebert, E. E. (1964). *Artificial Habitat in the Marine Environment*. Sacramento, CA: Resources Agency of California.
- Carnell, P. E., and Keough, M. J. (2019). Reconstructing historical marine populations reveals major decline of a kelp forest ecosystem in Australia. *Estuar. Coasts* 42, 765–778. doi: 10.1007/s12237-019-00525-1
- Chan, W. Y., Peplow, L. M., Menéndez, P., Hoffmann, A. A., and Van Oppen, M. J. H. (2018). Interspecific hybridization may provide novel opportunities for coral reef restoration. *Front. Mar. Sci.* 5:160. doi: 10.3389/fmars.2018.00160
- Coleman, M. A., and Brawley, S. H. (2005). Spatial and temporal variability in dispersal and population genetic structure of a rockpool alga. *Mar. Ecol. Prog. Ser.* 300, 63–77. doi: 10.3354/meps300063

- 1027 Coleman, M. A., Cetina-Heredia, P., Roughan, M., Feng, M., Sebille, E., and  
1028 Kelaher, B. P. (2017). Anticipating changes to future connectivity within a  
1029 network of marine protected areas. *Global Change Biol.* 23, 3533–3542. doi:  
10.1111/gcb.13634
- 1030 Coleman, M. A., Chambers, J., Knott, N. A., Malcolm, H. A., Harasti, D., Jordan, A.,  
1031 et al. (2011a). Connectivity within and among a network of temperate marine  
1032 reserves. *PLoS ONE* 6:e20168. doi: 10.1371/journal.pone.0020168
- 1033 Coleman, M. A., Roughan, M., Macdonald, H. S., Connell, S. D., Gillanders, B. M.,  
1034 Kelaher, B. P., et al. (2011b). Variation in the strength of continental boundary  
1035 currents determines continent-wide connectivity in kelp. *J. Ecol.* 99, 1026–1032.  
doi: 10.1111/j.1365-2745.2011.01822.x
- 1036 Coleman, M. A., Clark, J. S., Doblin, M. A., Bishop, M. J., and Kelaher, B. P.  
1037 (2019). Genetic differentiation between estuarine and open coast ecotypes of  
1038 a dominant ecosystem engineer. *Mar. Freshw. Res.* 70, 977–985.
- 1039 Coleman, M. A., Feng, M., Roughan, M., Cetina-Heredia, P., and Connell, S. D.  
1040 (2013). Temperate shelf water dispersal by Australian boundary currents:  
1041 Implications for population connectivity. *Limnol. Oceanogr. Fluids Environ.* 3,  
295–309. doi: 10.1215/21573689-2409306
- 1042 Coleman, M. A., and Goold, H. (2019). Harnessing synthetic biology for kelp forest  
1043 conservation. *J. Phycol.* 55, 745–751. doi: 10.1111/jpy.12888
- 1044 Coleman, M. A., and Kelaher, B. P. (2009). Connectivity among fragmented  
1045 populations of a habitat-forming alga, *Phyllospora comosa* (Phaeophyceae,  
1046 Fucales) on an urbanised coast. *Mar. Ecol. Prog. Ser.* 381, 63–70. doi: 10.3354/  
meps07977
- 1047 Coleman, M. A., Kelaher, B. P., Steinberg, P. D., and Millar, A. J. K. (2008). Absence  
1048 of a large brown macroalga on urbanised rocky reefs around Sydney, Australia,  
1049 and evidence for historical decline. *J. Phycol.* 44, 897–901. doi: 10.1111/j.1529-  
8817.2008.00541.x
- 1050 Coleman, M. A., and Wernberg, T. (2017). Forgotten underwater forests: the  
1051 key role of fucoids on Australian temperate reefs. *Ecol. Evol.* 7, 8406–8418.  
doi: 10.1002/ece3.3279
- 1052 Coleman, M. A., and Wernberg, T. (2018). Genetic and morphological diversity in  
1053 sympatric kelps with contrasting reproductive strategies. *Aquat. Biol.* 27, 65–73.  
doi: 10.3354/ab00698
- 1054 Connell, S. D., Russell, B. D., Turner, D. J., Shepherd, S. A., Kildea, T., Miller, D.,  
1055 et al. (2008). Recovering a lost baseline: missing kelp forests from a metropolitan  
1056 coast. *Mar. Ecol. Prog. Ser.* 360, 63–72. doi: 10.3354/meps07526
- 1057 Corlett, R. T. (2017). A bigger toolbox: biotechnology in biodiversity conservation.  
1058 *Trends Biotechnol.* 35, 55–65. doi: 10.1016/j.tibtech.2016.06.009
- 1059 Crouzeilles, R., Curran, M., Ferreira, M. S., Lindenmayer, D. B., Grelle, C. E. V.,  
1060 and Rey Benayas, J. M. (2016). A global meta-analysis on the ecological drivers  
1061 of forest restoration success. *Nat. Commun.* 7:11666.
- 1062 DeAngelis, M. B., Sutton-Grier, E. A., Colden, A., Arkema, K. K., Baillie, J. C.,  
1063 Bennett, O. R., et al. (2020). Social factors key to landscape-scale coastal  
1064 restoration: lessons learned from three U.S. case studies. *Sustainability* 12:869.  
doi: 10.3390/su12030869
- 1065 Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H., and Huey, R. (2015). Climate change  
1066 tightens a metabolic constraint on marine habitats. *Science* 348, 1132–1135.  
doi: 10.1126/science.aaa1605
- 1067 Doudna, J. A., and Charpentier, E. (2014). The new frontier of genome engineering  
1068 with Crispr-Cas9. *Science* 346, 1258096. doi: 10.1126/science.1258096
- 1069 Douglas, H. (2003). The moral responsibilities of scientists. *Am. Philos. Quart.* 40,  
1070 59–68.
- 1071 Durrant, H. M. S., Barrett, N. S., Edgar, G. J., Coleman, M. A., and Burridge,  
1072 C. P. (2015). Shallow phylogeographic histories of key species in a biodiversity  
1073 hotspot. *Phycologia* 54, 556–565. doi: 10.2216/15-24.1
- 1074 Durrant, H. M. S., Barrett, N. S., Edgar, G. J., Coleman, M. A., and Burridge,  
1075 C. P. (2018). Seascape habitat patchiness and hydrodynamics explain genetic  
1076 structuring of kelp populations. *Mar. Ecol. Prog. Ser.* 587, 81–92. doi: 10.3354/  
meps12447
- 1077 Durrant, H. M. S., Burridge, C. P., Kelaher, B. P., Barrett, N. S., Edgar, G. J., and  
1078 Coleman, M. A. (2014). Implications of macroalgal isolation by distance for  
1079 networks of marine protected areas. *Conserv. Biol.* 28, 438–445. doi: 10.1111/  
cobi.12203
- 1080 Eger, A. M., Marzinelli, E., Steinberg, P. D., & Verges, A. (2019). “Worldwide  
1081 synthesis of kelp forest restoration,” eds O. S. F. Portal.
- 1082 Evans, S. M., Sinclair, E. A., Poore, A. G. B., Bain, K. F., and Vergés, A.  
1083 (2018). Assessing the effect of genetic diversity on the early establishment  
of the threatened seagrass *Posidonia australis* using a reciprocal-transplant  
experiment. *Restor. Ecol.* 26, 570–580. doi: 10.1111/rec.12595
- 1085 FAO (2019). *New Century Decade on Ecosystem Restoration Offers Unparalleled*  
1086 *Opportunity for Job Creation, Food Security and Addressing Climate Change.*  
Available at: <http://www.fao.org/news/story/en/item/1182090/icode/>.
- 1087 Filbee-Dexter, K., and Scheibling, R. E. (2014). Sea urchin barrens as alternative  
1088 stable states of collapsed kelp ecosystems. *Mar. Ecol. Prog. Ser.* 495, 1–25.  
doi: 10.3354/meps10573
- 1089 Filbee-Dexter, K., and Smajdor, A. (2019). Ethics of assisted evolution in marine  
1090 conservation. *Front. Mar. Sci.* 6:20. doi: 10.3389/fmars.2019.00020
- 1091 Filbee-Dexter, K., and Wernberg, T. (2018). Rise of turfs: a new battlefield for  
1092 globally declining kelp forests. *BioScience* 68, 64–76. doi: 10.1093/biosci/bix147
- 1093 Fredriksen, S., Filbee-Dexter, K., Norderhaug, K. M., Steen, H., Bodvin, T.,  
1094 Coleman, M. A., et al. (2020). Green gravel: a novel restoration tool to combat  
1095 kelp forest decline. *Sci. Rep.* 10:3983.
- 1096 Fujimoto, R., Uezono, K., Ishikura, S., Osabe, K., Peacock, W. J., and Dennis, E. S.  
1097 (2018). Recent research on the mechanism of heterosis is important for crop and  
1098 vegetable breeding systems. *Breed. Sci.* 68, 145–158. doi: 10.1270/jsbbs.17155
- 1099 Gardiner, S. (2010). “Is arming the future with geoengineering really the lesser evil?  
1100 Some doubts about the ethics of intentionally manipulating the climate system,”  
1101 in *Climate Ethics: Essential Readings*, eds S. Gardiner, S. Caney, D. Jamieson, and  
1102 H. Shue (Oxford: Oxford University Press), 30.
- 1103 Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W. W. L., Howes, E. L., Joos, F., et al.  
1104 (2015). Contrasting futures for ocean and society from different anthropogenic  
1105 Co2 emissions scenarios. *Science* 349:aac4722. doi: 10.1126/science.aac4722
- 1106 Gaylord, B., Reed, D. C., Raimondi, P. T., and Washburn, L. (2006). Macroalgal  
1107 spore dispersal in coastal environments: mechanistic insights revealed by theory  
1108 and experiment. *Ecol. Monogr.* 76, 481–502. doi: 10.1890/0012-9615(2006)  
076%5B0481:msdice%5D2.0.co;2
- 1109 Grant, P. R., Grant, B. R., Huey, R. B., Johnson, M. T. J., Knoll, A. H., and Schmitt,  
1110 J. (2017). Evolution caused by extreme events. *Philos. Trans. R. Soc. B-Biol. Sci.*  
372:20160146.
- 1111 Guillemin, M.-L., Faugeron, S., Destombe, C., Viard, F., Correa, J. A., and Valero,  
1112 M. (2018). Genetic variation in wild and cultivated populations of the haploid-  
1113 diploid red alga *Gracilaria chilensis*: how farming practices favor asexual  
1114 reproduction and heterozygosity. *Evolution* 62, 1500–1519. doi: 10.1111/j.1558-  
5646.2008.00373.x
- 1115 Gurgel, C. F. D., Camacho, O., Minne, A. J. P., Wernberg, T., and Coleman, M. A.  
1116 (2020). Marine heatwave drives cryptic loss of genetic diversity in underwater  
1117 forests. *Curr. Biol.* [Epub ahead of print].
- 1118 Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs.  
1119 *Am. Nat.* 173, 579–588. doi: 10.1086/597611
- 1120 Hobbs, R. J., Higgs, E., and Harris, J. A. (2009). Novel ecosystems: implications for  
1121 conservation and restoration. *Trends Ecol. Evol.* 24, 599–605. doi: 10.1016/j.tree.  
2009.05.012
- 1122 Hobbs, R. J., Higgs, E. S., and Hall, C. M. (2017). Expanding the portfolio:  
1123 conserving nature’s masterpieces in a changing world. *BioScience* 67, 568–575.  
doi: 10.1093/biosci/bix043
- 1124 Hodgins, K. A., and Moore, J. L. (2016). Adapting to a warming world: Ecological  
1125 restoration, climate change, and genomics. *Am. J. Bot.* 103, 590–592. doi: 10.  
3732/ajb.1600049
- 1126 Hoffmann, A., Griffin, P., Dillon, S., Catullo, R., Rane, R., Byrne, M., et al.  
1127 (2015). A framework for incorporating evolutionary genomics into biodiversity  
1128 conservation and management. *Clim. Change Responses* 2:1.
- 1129 Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart,  
1130 S. H. M., et al. (2010). The impact of conservation on the status of the world’s  
1131 vertebrates. *Science* 330:1503.
- 1132 Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S.,  
1133 Jackson, J. B. C., et al. (2017). Coral reefs in the Anthropocene. *Nature* 546,  
82–90.
- 1134 IPCC, (2019). *Summary for Policymakers. Ipcc Special Report on the Ocean and*  
*Cryosphere in a Changing Climate.* Geneva: IPCC.
- 1135 Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J.,  
1136 Cavanaugh, K. C., et al. (2016). Global patterns of kelp forest change over the  
1137 past half-century. *Proc. Natl. Acad. Sci. U.S.A.* 113, 13785–13790.
- 1138 Kuwahara, H., Watanuki, A., Aota, T., Ando, W., Kawai, T., Terawaki, T., et al.  
1139 (2006). Trends in literature on seaweed restoration techniques on barren  
1140 grounds in Japan. *J. Fish. Eng.* 43, 81–87.

- 1141 Layton, C., Coleman, M. A., Marzinelli, E. M., Steinberg, P. D., Swearer, S. E.,  
1142 Vergés, A., et al. (2020). Kelp forest restoration in Australia. *Front. Mar. Sci.*  
1143 7:74. doi: 10.3389/fmars.2020.00074
- 1144 Lee, S. G. (2019). "Marine stock enhancement, restocking, and sea ranching in  
1145 Korea," in *Wildlife Management – Failures, Successes and Prospects*, eds J. R.  
1146 Kideghesho, and A. A. Rija (London: IntechOpen).
- 1147 Lin, H., and Qin, S. (2014). Tipping points in seaweed genetic engineering: scaling  
1148 up opportunities in the next decade. *Mar. Drugs* 12, 3025–3045. doi: 10.3390/  
1149 md12053025
- 1150 Ling, S. D., Johnson, C. R., Frusher, S. D., and Ridgway, K. R. (2009). Overfishing  
1151 reduces resilience of kelp beds to climate-driven catastrophic phase shift.  
1152 *Proc. Natl. Acad. Sci. U.S.A.* 106, 22341–22345. doi: 10.1073/pnas.090752  
1153 9106
- 1154 Ling, S. D., Scheibling, R. E., Rassweiler, A., Johnson, C. R., Shears, N., Connell,  
1155 S. D., et al. (2015). Global regime shift dynamics of catastrophic sea urchin  
1156 overgrazing. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20130269. doi: 10.1098/rstb.  
1157 2013.0269
- 1158 Luo, J., Sun, X., Cormack, B. P., and Boeke, J. D. (2018). Karyotype engineering  
1159 by chromosome fusion leads to reproductive isolation in yeast. *Nature* 560,  
1160 392–396. doi: 10.1038/s41586-018-0374-x
- 1161 Martínez, B., Radford, B., Thomsen, M. S., Connell, S. D., Carreño, F., Bradshaw,  
1162 C. J. A., et al. (2018). Distribution models predict large contractions of  
1163 habitat-forming seaweeds in response to ocean warming. *Divers. Distribut.* 24,  
1164 1350–1366. doi: 10.1111/ddi.12767
- 1165 Martins, N., Pearson, G. A., Gouveia, L., Tavares, A. I., Serrão, E. A., and  
1166 Bartsch, I. (2019). Hybrid vigour for thermal tolerance in hybrids between the  
1167 allopatric kelps *Laminaria digitata* and *L. pallida* (Laminariales, Phaeophyceae)  
1168 with contrasting thermal affinities. *Eur. J. Phycol.* 54, 548–561. doi: 10.1080/  
1169 09670262.2019.1613571
- 1170 Marzinelli, E. M., Campbell, A. H., Verges, A., Coleman, M. A., Kelaher, B. P.,  
1171 and Steinberg, P. D. (2014). Restoring seaweeds: does the declining fucooid  
1172 *Phyllospora comosa* support different biodiversity than other habitats? *J. Appl.*  
1173 *Phycol.* 26, 1089–1096. doi: 10.1007/s10811-013-0158-5
- 1174 Marzinelli, E. M., Leong, M. R., Campbell, A. H., Steinberg, P. D., and Verges, A.  
1175 (2016). Does restoration of a habitat-forming seaweed restore associated faunal  
1176 diversity? *Restor. Ecol.* 24, 81–90. doi: 10.1111/rec.12292
- 1177 McAfee, D., Doubleday, Z. A., Geiger, N., and Connell, S. D. (2019). Everyone  
1178 loves a success story: optimism inspires conservation engagement. *BioScience*  
1179 69, 274–281. doi: 10.1093/biosci/biz019
- 1180 McKay, J. K., Christian, C. E., Harrison, S., and Rice, K. J. (2005). "How local  
1181 is local?"—A review of practical and conceptual issues in the genetics of  
1182 restoration. *Restor. Ecol.* 13, 432–440. doi: 10.1111/j.1526-100x.2005.00058.x
- 1183 Mijangos, J. L., Pacioni, C., Spencer, P. B. S., and Craig, M. D. (2015). Contribution  
1184 of genetics to ecological restoration. *Mol. Ecol.* 24, 22–37. doi: 10.1111/mec.  
1185 12995
- 1186 Miller, A., Coleman, M., Clark, J., Cook, R., Naga, Z., Doblin, M., et al. (2019). Local  
1187 thermal adaptation and limited gene flow constrain future climate responses of  
1188 a marine ecosystem engineer. *Evol. Appl.* 1–17.
- 1189 Narum, S. R., Buerkle, C. A., Davey, J. W., Miller, M. R., and Hohenlohe, P. A.  
1190 (2013). Genotyping-by-sequencing in ecological and conservation genomics.  
1191 *Mol. Ecol.* 22, 2841–2847. doi: 10.1111/mec.12350
- 1192 North, W. J. (1976). Aquacultural techniques for creating and restoring beds of  
1193 giant kelp, *Macrocystis* spp. *J. Fish. Res. Board Canada* 33, 1015–1023. doi:  
1194 10.1139/f76-129
- 1195 Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof,  
1196 K. X., et al. (2015). Advances in restoration ecology: rising to the challenges of  
1197 the coming decades. *Ecosphere* 6:art131. doi: 10.1890/es15-00121.1
- 1198 Phillips, J. A. (2001). Marine macroalgal biodiversity hotspots: why is there high  
1199 species richness and endemism in southern Australian marine benthic flora?  
1200 *Biodivers. Conserv.* 10, 1555–1577.
- 1201 Piaggio, A. J., Segelbacher, G., Seddon, P. J., Alphey, L., Bennett, E. L., Carlson,  
1202 R. H., et al. (2017). Is it time for synthetic biodiversity conservation? *Trends*  
1203 *Ecol. Evol.* 32, 97–107.
- 1204 Popkin, G. (2018). Can a transgenic chestnut restore a forest icon? *Science* 361,  
1205 830–831. doi: 10.1126/science.361.6405.830
- 1206 Potts, B. M., Barbour, R. C., Hingston, A. B., and Vaillancourt, R. E. (2003). Genetic  
1207 pollution of native eucalypt gene pools-identifying the risks. *Austr. J. Bot.* 51,  
1208 1–25.
- 1209 Powers, R. P., and Jetz, W. (2019). Global habitat loss and extinction risk  
1210 of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim.*  
1211 *Change* 9, 323–329. doi: 10.1038/s41558-019-0406-z
- 1212 Pretorius, I. S. (2017). Synthetic genome engineering forging new frontiers for wine  
1213 yeast. *Crit. Rev. Biotechnol.* 37, 112–136. doi: 10.1080/07388551.2016.1214945
- 1214 Ralls, K., Ballou, J. D., Dudash, M. R., Eldridge, M. D. B., Fenster, C. B., Lacy, R. C.,  
1215 et al. (2018). Call for a paradigm shift in the genetic management of fragmented  
1216 populations. *Conserv. Lett.* 11:e12412. doi: 10.1111/cons.12412
- 1217 Razgour, O., Forester, B., Taggart, J. B., Bekaert, M., Juste, J., Ibáñez, C., et al.  
1218 (2019). Considering adaptive genetic variation in climate change vulnerability  
1219 assessment reduces species range loss projections. *Proc. Natl. Acad. Sci. U.S.A.*  
1220 116, 10418–10423. doi: 10.1073/pnas.1820663116
- 1221 Reynolds, L. K., Mcglathery, K. J., and Waycott, M. (2012). Genetic diversity  
1222 enhances restoration success by augmenting ecosystem services. *PLoS ONE*  
1223 7:e38397. doi: 10.1371/journal.pone.0038397
- 1224 Rinkevich, B. (2014). Rebuilding coral reefs: does active reef restoration lead to  
1225 sustainable reefs? *Curr. Opin. Environ. Sustain.* 7, 28–36. doi: 10.1016/j.cosust.  
1226 2013.11.018
- 1227 Rinkevich, B. (2019). Coral chimerism as an evolutionary rescue mechanism to  
1228 mitigate global climate change impacts. *Global Change Biol.* 25, 1198–1206.  
1229 doi: 10.1111/gcb.14576
- 1230 Robinson, N., Winberg, P., and Kirkendale, L. (2013). Genetic improvement of  
1231 macroalgae: status to date and needs for the future. *J. Appl. Phycol.* 25, 703–716.  
1232 doi: 10.1007/s10811-012-9950-x
- 1233 Rossetto, M., Bragg, J., Kilian, A., Mcpherson, H., Van Der Merwe, M., and  
1234 Wilson, P. D. (2019). Restore and Renew: a genomics-era framework for species  
1235 provenance delimitation. *Restor. Ecol.* 27, 538–548. doi: 10.1111/rec.12898
- 1236 Sanderson, J. C., Ling, S. D., Dominguez, J. G., and Johnson, C. R. (2015). Limited  
1237 effectiveness of divers to mitigate 'barrens' formation by culling sea urchins  
1238 while fishing for abalone. *Mar. Freshw. Res.* 67, 84–95.
- 1239 Sandler, R. L. (2013). "Environmental virtue ethics," in *International Encyclopedia of*  
1240 *Ethics*, ed. H. LaFollette (Oxford: Blackwell Publishing).
- 1241 Schroeter, S. C., Reed, D. C., and Raimondi, P. (2018). Artificial reefs to mitigate  
1242 human impacts in the marine environment: the Wheeler North Reef as a test  
1243 case. *Am. Fish. Soc. Symp.* 86, 197–213.
- 1244 Segan, D., Murray, K., and Watson, J. (2016). A global assessment of current and  
1245 future biodiversity vulnerability to habitat loss–climate change interactions.  
1246 *Glob. Ecol. Conserv.* 5, 12–21. doi: 10.1016/j.gecco.2015.11.002
- 1247 Sera. (2017). *National Standards for the Practice of Ecological Restoration in*  
1248 *Australia*, Second Edn. New South Wales: Society for Ecological Restoration  
1249 Australasia.
- 1250 Sexton, J. P., Strauss, S. Y., and Rice, K. J. (2011). Gene flow increases fitness at the  
1251 warm edge of a species' range. *Proc. Natl. Acad. Sci. U.S.A.* 108, 11704–11709.  
1252 doi: 10.1073/pnas.1100404108
- 1253 Sgrò, C. M., Lowe, A. J., and Hoffmann, A. A. (2011). Building evolutionary  
1254 resilience for conserving biodiversity under climate change. *Evol. Appl.* 4,  
1255 326–337. doi: 10.1111/j.1752-4571.2010.00157.x
- 1256 Shih, P. M., Vuu, K., Mansoori, N., Ayad, L., Louie, K. B., Bowen, B. P., et al. (2016).  
1257 A robust gene-stacking method utilizing yeast assembly for plant synthetic  
1258 biology. *Nat. Commun.* 7:13215.
- 1259 Torda, G., Donelson, J. M., Aranda, M., Barshis, D. J., Bay, L., Berumen, M. L., et al.  
1260 (2017). Rapid adaptive responses to climate change in corals. *Nat. Clim. Change*  
1261 7, 627–636. doi: 10.1038/nclimate3374
- 1262 Van Ommen, M. J. H., Gates, R. D., Blackall, L. L., Cantin, N., Chakravarti, L. J.,  
1263 Clancy, W. Y., et al. (2017). Shifting paradigms in restoration of the world's coral  
1264 reefs. *Glob. Change Biol.* 23, 3437–3448.
- 1265 Van Oppen, M. J. H., Oliver, J. K., Putnam, H. M., and Gates, R. D. (2015). Building  
1266 coral reef resilience through assisted evolution. *Proc. Natl. Acad. Sci. U.S.A.* 112,  
1267 2307–2313. doi: 10.1073/pnas.1422301112
- 1268 Venter, O., Sanderson, E. W., Magrath, A., Allan, J. R., Beher, J., Jones, K. R., et al.  
1269 (2016). Sixteen years of change in the global terrestrial human footprint and  
1270 implications for biodiversity conservation. *Nat. Commun.* 7:12558.
- 1271 Verdura, J., Sales, M., Ballesteros, E., Cefali, M. E., and Cebrian, E. (2018).  
1272 Restoration of a canopy-forming alga based on recruitment enhancement:  
1273 methods and long-term success assessment. *Front. Plant Sci.* 9:1832. doi: 10.  
1274 3389/fpls.2018.01832
- 1275 Vergés, A., Doropoulos, C., Malcolm, H. A., Skye, M., Garcia-Pizá, M., Marzinelli,  
1276 E. M., et al. (2016). Long-term empirical evidence of ocean warming leading  
1277

- 1255 to tropicalization of fish communities, increased herbivory, and loss of kelp. 1312  
 1256 *Proc. Natl. Acad. Sci. U.S.A.* 113, 13791–13796. doi: 10.1073/pnas.161072 1313  
 5113
- 1257 Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., 1314  
 1258 Ballesteros, E., et al. (2014). The tropicalization of temperate marine 1315  
 1259 ecosystems: climate-mediated changes in herbivory and community phase 1316  
 1260 shifts. *Proc. R. Soc. B-Biol. Sci.* 281.\* 1317
- 1261 Wang, H., La Russa, M., and Qi, L. S. (2016). Crispr/Cas9 in genome editing and 1318  
 1262 beyond. *Annu. Rev. Biochem.* 85, 227–264. 1319
- 1263 Webster, M. S., Colton, M. A., Darling, E. S., Armstrong, J., Pinsky, M. L., 1320  
 1264 Knowlton, N., et al. (2017). Who should pick the winners of climate change? 1321  
 1265 *Trends Ecol. Evol.* 32, 167–173. doi: 10.1016/j.tree.2016.12.007 1322
- 1266 Weeks, A. R., Sgro, C. M., Young, A. G., Frankham, R., Mitchell, N. J., Miller, 1323  
 1267 K. A., et al. (2011). Assessing the benefits and risks of translocations in changing 1324  
 1268 environments: a genetic perspective. *Evol. Appl.* 4, 709–725. doi: 10.1111/j.1752- 1325  
 4571.2011.00192.x 1326
- 1269 Wernberg, T., Bennett, S., Babcock, R. C., De Bettignies, T., Cure, K., Depczynski, 1327  
 1270 M., et al. (2016). Climate-driven regime shift of a temperate marine ecosystem. 1328  
 1271 *Science* 353, 169–172. doi: 10.1126/science.aad8745 1329
- 1272 Wernberg, T., Coleman, M., Babcock, R. B., Sy, Bolton, J., Connell, S., et al. 1330  
 1273 (2019a). “Biology and ecology of the globally significant kelp *Ecklonia radiata*,” 1331  
 1274 in *Oceanography and Marine Biology: An Annual Review*, eds M. Barnes, R. N. 1332  
 1275 Gibson, and R. N. Gibson (Boca Raton, FL: CRC Press). 1333
- 1276 Wernberg, T., Krumhansl, K. A., Filbee-Dexter, K., and Pedersen, M. (2019b). 1334  
 1277 “Status and trends for the world’s kelp forests,” in *World Seas: An Environmental 1335  
 1278 Evaluation*, ed. C. Sheppard (London: Elsevier). 1336
- 1279 Wernberg, T., Coleman, M. A., Bennett, S., Thomsen, M. S., Tuya, F., and Kelaher, 1337  
 1280 B. P. (2018). Genetic diversity and kelp forest vulnerability to climatic stress. *Sci. 1338  
 1281 Rep.* 8:1851. 1339
- 1282 1340  
 1283 1341  
 1284 1342  
 1285 1343  
 1286 1344  
 1287 1345  
 1288 1346  
 1289 1347  
 1290 1348  
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 1303 1361  
 1304 1362  
 1305 1363  
 1306 1364  
 1307 1365  
 1308 1366  
 1309 1367  
 1310 1368  
 1311
- Wernberg, T., and Filbee-Dexter, K. (2019). Missing the marine forest for the trees. 1312  
*Mar. Ecol. Prog. Ser.* 612, 209–215. doi: 10.3354/meps12867 1313
- Williams, S. L. (2001). Reduced genetic diversity in eelgrass transplantations affects 1314  
 both population growth and individual fitness. *Ecol. Appl.* 11, 1472–1488. doi: 1315  
 10.1890/1051-0761(2001)011%5B1472:rgdiet%5D2.0.co;2 1316
- Williams, T. C., Xu, X., Ostrowski, M., Pretorius, I. S., and Paulsen, I. T. (2017). 1317  
 Positive-feedback, ratiometric biosensor expression improves high-throughput 1318  
 metabolite-producer screening efficiency in yeast. *Synth. Biol.* 2:ysw002. 1319
- Wood, G., Marzinelli, E., Vergés, A., Connell, A., Steinberg, P., and Coleman, M. 1320  
 (in press). Using genetics to test provenance effects and to optimise seaweed 1321  
 restoration. *J. Appl. Ecol.* 1322
- Wood, G., Marzinelli, E. M., Coleman, M. A., Campbell, A. H., Santini, N. S., 1323  
 Kajlich, L., et al. (2019). Restoring subtidal marine macrophytes in the 1324  
 Anthropocene: trajectories and future-proofing. *Mar. Freshw. Res.* 70, 936–951. 1325
- Zhang, B.-L., Yan, X.-H., and Huang, L.-B. (2011). Evaluation of an improved strain 1326  
 of *Porphyra yezoensis* Ueda (Bangiales, Rhodophyta) with high-temperature 1327  
 tolerance. *J. Appl. Phycol.* 23, 841–847. doi: 10.1007/s10811-010-9587-6 1328
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