

Coral conservation in a warming world must harness evolutionary adaptation

To facilitate evolutionary adaptation to climate change, we must protect networks of coral reefs that span a range of environmental conditions — not just apparent ‘refugia’.

Madhavi A. Colton, Lisa C. McManus, Daniel E. Schindler, Peter J. Mumby, Stephen R. Palumbi, Michael M. Webster, Timothy E. Essington, Helen E. Fox, Daniel L. Forrest, Steven R. Schill, F. Joseph Pollock, Lukas B. DeFilippo, E. W. Tekwa, Timothy E. Walsworth and Malin L. Pinsky

Evolution plays a crucial role in determining how populations respond to climatic changes^{1–3}, and evidence is growing that evolutionary adaptation to contemporary warming can occur when sufficient genetic variation for climate-related traits is present⁴. In fact, evolutionary adaptation will be essential for the persistence of many species that inhabit narrow geographic ranges and/or habitat zones, such as reef-building corals.

We can develop conservation strategies that promote evolutionary adaptation by understanding the ecological mechanisms that underpin it. The pathways by which adaptation occurs in any population depend on existing environmental mosaics, dispersal, additive genetic variation⁵ and the pace of environmental change^{6–8}. In most species, evolutionary adaptation that keeps pace with climate change needs to act on existing genetic variation — through changes in the relative frequency of alleles and their associated phenotypes already present in the population^{7,8}. We argue that carefully considered conservation policy and implementation can enhance, suppress or modify the genetic and phenotypic diversity required for successful adaptation.

Despite the increasing appreciation of evolutionary capacity, contemporary conservation strategies may fail to protect the diversity required to facilitate adaptation. We suggest that this is particularly true of conservation planning that prioritizes the protection of refugia — locations where the climate is predicted to be more stable over time⁹. Such planning has been applied to terrestrial¹⁰, freshwater¹¹ and marine systems¹². However, a narrow focus on refugia may fail to address other threats to biodiversity¹³ and may not protect a key source of adaptive capacity: individuals in more stressful locations that may be better adapted to future conditions. Furthermore,

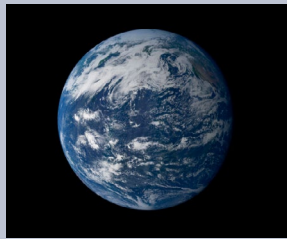
	Local	Regional	Global
Spatial scale			
Goals	Increase: • Reproduction • Recruitment and settlement • Survival	Facilitate: • Ecological reorganization • Evolutionary rescue • Demographic rescue	Lower rate of change in: • Temperature • pH
Actions	Reduce local stressors by: • Sustainably managing fisheries • Wastewater and run-off control • Preventing and treating disease Augment natural demographic processes: • Restoration and assisted gene flow	Implement spatial management for: • Environmental diversity, including thermal diversity • Connectivity and gene flow Artificially increase connectivity: • Translocate genotypes/species/larvae	Reduce emissions through: • International agreements • National and sub-national targets

Fig. 1 | Goals and actions for evolutionarily informed coral conservation. Recommended goals and actions for management and policy at local, regional and global scales to enhance the eco-evolutionary processes and genetic and phenotypic diversity required for successful adaptation of corals to climate change. Local image credit: Travel Pix/Alamy; regional image credit: NASA/World History Archive and ARPL/Alamy; global image credit: Stocktrek Images, Inc./Alamy.

the identification of refugia involves substantial uncertainty, which makes such approaches risky to implement and evaluate¹⁴.

Corals occupy wide ranges of environmental conditions and exhibit high levels of local genetic diversity and genetic variation in heat resistance¹⁵. As a result, corals have been highlighted as a potential target for management and interventions to increase climate resilience¹⁶. Thermal tolerance is closely linked to environmental conditions, with corals in warmer waters displaying higher thermal tolerance than those in cooler areas¹⁷. This means that adaptation in different environments will likely follow different pathways. In cooler environments, coral adaptation will rely heavily on genetic connectivity to warmer

areas, whereas corals in warmer areas will adapt primarily by local selection^{6,18,19}. Furthermore, strong selective pressure in warmer areas may drive more rapid evolutionary responses⁸. Understanding these pathways helps to elucidate the conservation strategies and policies at multiple scales that can facilitate successful evolutionary adaptation.

While understanding of — and evidence for — rapid adaptation has grown, implementation of evolutionarily enlightened management² has lagged. Here, we describe actions at three spatial scales — local, regional and global — that, when conducted together, harness existing eco-evolutionary processes to help coral reefs adapt to the effects of climate change (Fig. 1).

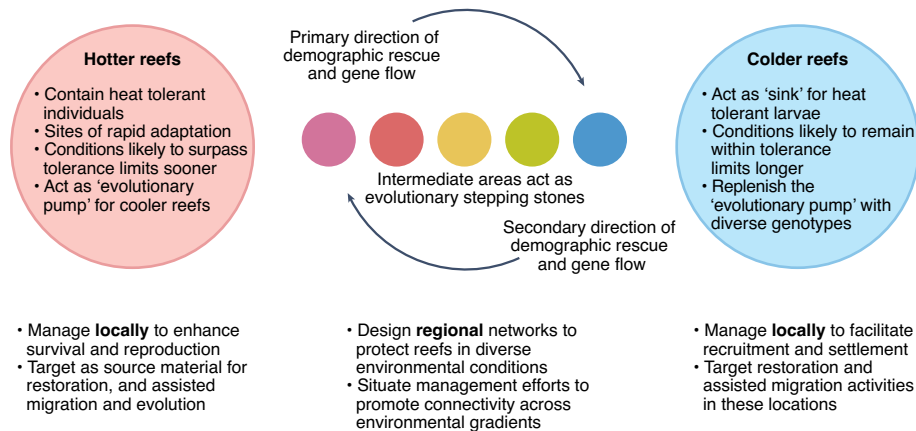


Fig. 2 | Managing across thermal gradients to facilitate evolutionary adaptation. Characteristics of hotter and colder reefs. Arrows indicate demographic rescue and gene flow.

Conservation actions at local scales

Local stressors to coral reefs include water pollution, habitat destruction and overfishing, which increase coral mortality, impede sexual reproduction and exacerbate the adverse effects of marine heatwaves²⁰. Local management actions, such as marine protected areas to control fishing rates and land-based efforts to reduce wastewater and run-off, can improve reef health and resilience, and can support coral adaptation and persistence²⁰. However, there is rising concern that reducing local stressors alone will be insufficient to avert the rapid decline of coral reefs, owing to the overwhelming effects of climate change²¹. Consequently, more proactive interventions to augment existing populations are gaining popularity. Examples include supplementing coral populations by outplanting corals or seeding reefs with larvae²² and engineering or selectively breeding heat-tolerant corals²³. In order to be successful, these proactive interventions need to occur in places where the local causes of reef decline have been controlled, and where coral population size and diversity are maintained. Furthermore, proactive interventions may provide only localized benefits and make limited contributions to evolutionary adaptation²⁴.

Understanding eco-evolutionary processes at regional scales can help identify which local-scale interventions are most likely to promote adaptation. To facilitate local adaptation and ensure that warm and cool reefs contribute to regional-scale adaptation, local management activities should focus on keeping corals alive and reproducing across all thermal regimes (Fig. 1)²⁰. For reefs in warmer waters, actions should focus on assisting natural selection and promoting gene flow by protecting population size and reproductive output

through management of local stressors (Fig. 2). Conservation actions in cooler areas should focus on ensuring that conditions support coral larval recruitment, settlement and growth. For example, improving water quality and maintaining herbivore biomass can reduce excessive algal growth that inhibits larval settlement²⁵. Proactive interventions could focus on outplanting more heat tolerant corals in cooler locations or assisting migration of corals from warmer to cooler areas. These proactive efforts are most likely to be successful in areas where local stressors have been reduced and if scale and cost challenges can be overcome^{22,24}. Augmenting populations in warmer locations is unlikely to be effective unless the new individuals are tolerant of even more extreme temperatures²⁴.

Proactive interventions should be evaluated for their risks and benefits. For example, coral transplantation over long distances increases the danger of introducing exogenous microbes, viruses, algae and invertebrates that could have negative effects as invasive species. Genetically engineering or selectively breeding more heat-tolerant corals may incur negative trade-offs in growth and disease susceptibility, and a reduction in genetic diversity¹⁵. Furthermore, proactive interventions face significant scaling issues^{22,24} and are currently prohibitively expensive at scale²². Finally, because proactive interventions will only be successful if local stressors are reduced, they should be seen as a supplement to local management actions rather than a replacement for them.

Regional planning for evolutionary adaptation

At regional scales, genetic variation and gene flow are the main determinants of

contemporary evolutionary capacity. Genetic variation is often linked to environmental heterogeneity^{17–19,26}, such that corals inhabiting different temperature regimes display different thermal tolerances¹⁷. Gene flow among habitats is largely driven by larval dispersal, which in turn is governed by dynamic oceanographic features and the spatial mosaic of environmental conditions. While these conditions are beyond the control of conservation interventions, some conservation actions — such as the selection of sites for protection and for proactive interventions such as assisted migration — can act to strengthen or weaken both genetic variation and gene flow. Regional conservation strategies, therefore, can be designed to promote adaptation by protecting genetic diversity and facilitating connectivity (Figs. 1, 2).

Eco-evolutionary processes act across networks of interconnected reefs that span a range of environmental conditions. Within warmer areas, corals have adapted primarily by local natural selection, and these sites often already contain larger numbers of heat-resistant corals^{15,17,26}. Corals on warm reefs can therefore play a central role in regional-scale adaptation by seeding connected reefs with heat-tolerant larvae (Fig. 1)^{27,28}. For corals in cooler areas, where there are likely to be fewer heat-tolerant colonies¹⁵, models have shown that adaptation will rely heavily on an influx of heat-tolerant larvae. Indeed, cooler areas that receive larvae from warmer areas have been shown to be more likely to persist through time^{27,28}, resist bleaching^{19,28} and have higher coral cover¹⁸ (Fig. 1). In contrast, there is some evidence that dispersal from cool to warm reefs may lead to maladaptive gene swamping, though the demographic benefits of larval input from any reef environment are likely to outweigh any negative impacts^{27,29}. Finally, areas with intermediate temperatures may act as stepping stones for adaptive alleles produced in warm areas of a network (Fig. 2)²⁹.

While many conservation strategies focus on picking climate change winners in terms of habitats, sites, species, phenotypes or genotypes, such approaches can be detrimental to long-term persistence because they reduce the diversity required for adaptive responses^{13,27,30}. For example, a strategy that is gaining popularity in conservation is to identify and protect potential refugia^{9–12}. However, we argue that protecting diverse portfolios of habitats and populations is necessary to support long-term species persistence and community stability, and that these approaches reduce the risk of catastrophic population collapse¹⁴. Recent research also

shows that portfolio-based approaches more effectively facilitate evolutionary adaptation than refugia-based strategies^{27,30}. One of the main reasons that refugia-based strategies underperform in eco-evolutionary models is that they fail to protect warmer water reefs, which contain more thermally tolerant corals^{1,18}. Reefs in these warmer areas distribute heat-tolerant larvae to other sites, facilitating adaptation^{6,28}.

Policies guiding conservation planning at regional scales should explicitly focus on protecting a diversity of environmental conditions. The growing movement to protect 30% of our lands and oceans by 2030 provides an opportunity to expand existing protections in ways that maximize evolutionary adaptive capacity, but only if this goal is deliberately pursued. For coral reefs, this could be accomplished by designing marine protected area networks to achieve representation and replication goals for both habitats and thermal diversity, and by situating local efforts in close enough proximity to allow effective larval exchange.

Global emissions control

Even with optimistic assumptions about adaptive capacity, models show that corals struggle to cope under future climates at higher emissions scenarios^{1,27}. In fact, under a high emissions scenario, coral cover is predicted to decline to zero before the end of this century^{1,27,30}. However, the difference in outcomes between high and medium emissions scenarios is noteworthy. With a more aggressive strategy to reduce emissions, declines in coral cover can be reversed over time through evolutionary adaptation, suggesting that if humanity takes rapid and effective action to address climate change, coral reef ecosystems may recover on decadal or centennial timeframes and thrive in the future^{1,27}.

For coral reefs — and all other ecosystems — global action to combat climate change is essential. It is not too late for coral reefs and other ecosystems if we take swift and effective global action in tandem with strategic local and regional-scale management actions that harness evolutionary adaptive capacity. □

Madhavi A. Colton¹✉, Lisa C. McManus^{2,3}, Daniel E. Schindler⁴, Peter J. Mumby⁵, Stephen R. Palumbi⁶, Michael M. Webster^{1,7}, Timothy E. Essington⁴, Helen E. Fox¹, Daniel L. Forrest^{3,8}, Steven R. Schill⁹, F. Joseph Pollock^{10,11}, Lukas B. DeFilippo^{4,12}, E. W. Tekwa¹³, Timothy E. Walsworth^{4,14} and Malin L. Pinsky¹³

¹Coral Reef Alliance, San Francisco, CA, USA.

²Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kane'ohe, HI, USA.

³Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA. ⁴School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA. ⁵School of Biological Sciences, University of Queensland, Brisbane, QLD, Australia. ⁶Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, CA, USA. ⁷Department of Environmental Studies, New York University, New York, NY, USA. ⁸Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC, Canada. ⁹The Nature Conservancy, Caribbean Division, Coral Gables, FL, USA. ¹⁰The Nature Conservancy, Hawai'i & Palmyra Program, Honolulu, HI, USA. ¹¹Pennsylvania State University, Department of Biology, University Park, PA, USA.

¹²Resource Assessment and Conservation Engineering Division, NOAA Alaska Fisheries Science Center, Seattle, WA, USA. ¹³Department of Zoology, University of British Columbia, Vancouver, BC, Canada. ¹⁴Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, UT, USA.

✉e-mail: madhavi.colton@gmail.com

Published online: 16 September 2022
<https://doi.org/10.1038/s41559-022-01854-4>

References

- Logan, C. A., Dunne, J. P., Ryan, J. S., Baskett, M. L. & Donner, S. D. *Nat. Clim. Chang.* **11**, 537–542 (2021).
- Cook, C. N. & Sgrò, C. M. *Conserv. Biol.* **31**, 501–512 (2017).
- Gonzalez, A., Ronce, O., Ferriere, R. & Hochberg, M. E. *Phil. Trans. R. Soc. Lond. B* **368**, 1–8 (2013).
- Kovach, R. P., Gharrett, A. J. & Tallmon, D. A. *Proc. R. Soc. Lond. B* **279**, 3870–3878 (2012).
- Bonnet, T. et al. *Science* **376**, 1012–1016 (2022).
- Norberg, J. et al. *Nat. Clim. Chang.* **2**, 747–751 (2012).
- Torda, G. et al. *Nat. Clim. Chang.* **7**, 627–636 (2017).
- Catullo, R. A., Llewellyn, J., Phillips, B. L. & Moritz, C. C. *Curr. Biol.* **29**, R996–R1007 (2019).
- Keppel, G. et al. *Glob. Ecol. Biogeogr.* **21**, 393–404 (2012).
- Vos, C. C. et al. *J. Appl. Ecol.* **45**, 1722–1731 (2008).
- Isaak, D. J. et al. *Glob. Change Biol.* **21**, 2540–2553 (2015).
- Beyer, H. L. et al. *Conserv. Lett.* **11**, e12587 (2018).
- Tingley, M. W., Estes, L. D. & Wilcove, D. S. *Nature* **500**, 271–272 (2013).
- Schindler, D. E., Armstrong, J. B. & Reed, T. E. *Front. Ecol. Environ.* **13**, 257–263 (2015).
- Cornwell, B. et al. *eLife* **10**, e64790 (2021).
- National Academies. of Sciences Engineering & Medicine. *A Decision Framework for Interventions to Increase the Persistence and Resilience of Coral Reefs*. (The National Academies Press, 2019).
- Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N. & Bay, R. A. *Science* **344**, 895–898 (2014).
- Matz, M. V., Tremblay, E. A. & Haller, B. C. *Glob. Change Biol.* **26**, 3473–3481 (2020).
- Bay, R. A. & Palumbi, S. R. *Curr. Biol.* **24**, 2952–2956 (2014).
- Donovan, M. K. et al. *Science* **372**, 977–980 (2021).
- Anthony, K. et al. *Nat. Ecol. Evol.* **1**, 1420–1422 (2017).
- Morrison, T. H. et al. *Nature* **573**, 333–336 (2019).
- van Oppen, M. J. H., Oliver, J. K., Putnam, H. M. & Gates, R. D. *Proc. Natl Acad. Sci. USA* **112**, 2307–2313 (2015).
- DeFilippo, L. B. et al. *Ecol. Appl.* <https://doi.org/10.1002/eap.2650> (2022).
- Steneck, R. S. et al. *Front. Mar. Sci.* **6**, 265 (2019).
- Dixon, G. B. et al. *Science* **348**, 1460–1462 (2015).
- McManus, L. C. et al. *Glob. Change Biol.* **27**, 4307–4321 (2021).
- Kleypas, J. A. et al. *Glob. Change Biol.* **22**, 3539–3549 (2016).
- McManus, L. C. et al. *Ecology* **102**, e03381 (2021).
- Walsworth, T. E. et al. *Nat. Clim. Chang.* **9**, 632–636 (2019).

Acknowledgements

This research was made possible by funding from the Gordon and Betty Moore Foundation and The Nature Conservancy.

Author contributions

M.C. conceptualized and wrote the manuscript, with input from all authors. All authors edited the manuscript.

Competing interests

All authors declare no competing interests.