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Coral Reef Population Genomics in an Age of Global Change

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Abstract

Coral reefs are both exceptionally biodiverse and threatened by climate change and other human activities. Here, we review population genomic processes in coral reef taxa and their importance for understanding responses to global change. Many taxa on coral reefs are characterized by weak genetic drift, extensive gene flow, and strong selection from complex biotic and abiotic environments, which together present a fascinating test of microevolutionary theory. Selection, gene flow, and hybridization have played and will continue to play an important role in the adaptation or extinction of coral reef taxa in the face of rapid environmental change, but research remains exceptionally limited compared to the urgent needs. Critical areas for future investigation include understanding evolutionary potential and the mechanisms of local adaptation, developing historical baselines, and building greater research capacity in the countries where most reef diversity is concentrated.

INTRODUCTION

Coral reefs fringe one-sixth of the coastlines on Earth, support a quarter of all marine species alive today, enable productive fisheries that benefit hundreds of millions of people, reduce flooding and storm risks for 100 million people or more, and are at the core of tourism economies around the world (20, 47, 69, 100, 146, 189). However, coral cover has declined by 14% globally, owing to climate change, destructive fishing, disease, and other aspects of global change (210**)**. Coral reef species are especially vulnerable to climate change because they have evolved in a relatively stable thermal environment and live particularly close to their upper thermal limits (194). Rising temperatures and marine heatwaves have already been linked to dramatic coral bleaching and mortality around the world (76, 108–110).

In response to rapid environmental change, populations and species have three primary responses: move, adapt, or die. All three are mediated by and affect population genomic processes, including drift, migration, and selection. Adaptive evolutionary responses are expected to be particularly important at the low latitudes occupied by reefs because climate change is driving the appearance of new environmental niches without a coincident influx of preadapted competitors (158). Population genomic processes will determine whether and for which taxa evolutionary responses to climate and other stressors will be possible. Understanding the genomics of adaptation on coral reefs has taken on particular urgency because many corals appear to have limited ability to shift to higher latitudes (150, 222).

At the same time, as the urgency of this research has increased, rapid declines in DNA sequencing costs have greatly improved the feasibility of genomic research on nonmodel organisms, a category that includes nearly all reef species. As a result, population genetic research on coral reefs has expanded substantially over the last two decades, and population genomic study is increasing as well (**Figure 1**). Whereas population genetic research examines one or a handful of genetic loci across many individuals, population genomic studies examine the whole genome or substantial fractions of the genome. Existential concerns for coral reefs have also sparked interest in genetic engineering, controlled breeding, assisted migration, and other radical interventions that use population genomic insights (101, 227).

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Figure 1 Growth of coral reef population genetics and genomics research. Papers were identified from the Web of Science on 18 October 2022, with either “population genetics” and “coral” or “population genomics” and “coral” in the Topic field.

Coral reefs are built primarily by scleractinian (stony) corals, but corals themselves are considered holobionts to reflect the critical role of interactions among the coral host, endosymbiotic algae in the family Symbiodiniaceae (zooxanthellae), and the coral microbiome (49). Beyond corals, the three-dimensional structure and function of reefs support an immense diversity of fishes, invertebrates, macroalgae, and other organisms across at least 12 phyla (177, 181, 189) in dozens of countries across the Pacific, Indian, and Atlantic Oceans (215). These organisms share similar environmental challenges (including climate change), spatial population structures defined by the patchiness and extent of reefs, and physical environments characterized by tropical and subtropical marine climates, shallow depths, low seasonality, and generally clear waters. Population genomic patterns and processes therefore share a number of similarities across this impressively wide diversity of taxa, making them amenable to a unified review.

Population genomic patterns and processes are dynamic through time as they respond to environmental change. The need to understand these dynamics is especially urgent now given accelerating climate change and other global change from anthropogenic activity. This article focuses on what is known about population genomic changes in coral reef organisms as a result of global change, and particularly climate change. To explore this topic effectively, we also review the unique features of microevolutionary processes in coral reef environments, address the implications of population genomics for species survival on reefs, and highlight key research opportunities in this growing field. For related questions outside the scope of this article, we refer readers to excellent reviews on the evolutionary history of coral reefs (12, 167, 235, 236), corals and climate change (102, 109), interventions for coral conservation (157), seascape genomics more broadly (133), molecular tools for studying coral reefs (121, 168), bioinformatics of coral holobionts (49), and epigenetics in marine organisms (62).

POPULATION GENOMIC PROCESSES ON CORAL REEFS

We begin our review by highlighting some of the population genetic patterns and processes that are common across many coral reef organisms and yet distinct from those in many other ecosystems. Given the extraordinary diversity of organisms on coral reefs, we also note up front that there are exceptions to every rule, but these general patterns provide a useful starting point for understanding reef genomics.

Pervasive Gene Flow

Dispersal is a fundamental genetic process affecting gene flow between habitat patches, but most dispersal in coral reef taxa occurs during the larval phase, which is difficult to observe. Partly for this reason, our understanding of dispersal has benefited immensely from applications of population genetic techniques, including parentage studies that match postdispersal offspring to their parents and isolation-by-distance analyses that convert spatial genetic patterns into estimates of the spatial scale of gene flow (200). Parentage methods provide direct observations of dispersal distances at a given moment in time, while isolation-by-distance analyses provide indirect estimates of the multigenerational average scale of dispersal (15, 176). The greater buoyancy of water compared to air means that passive dispersal is easier in marine than terrestrial systems, requiring a low energy investment to travel long distances (22). Accordingly, marine species often disperse widely, perhaps one to two orders of magnitude further than on land (118). Moreover, the Indo-Pacific Ocean basin where most coral reefs are found lacks hard barriers to dispersal (50). Such widespread dispersal has helped create low levels of genetic differentiation for many coral reef species (200) (**Figure 2**).

Isolation by distance: a spatial pattern of genetic variation in which genetic differentiation increases with geographic distance between sampling sites

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Figure 2 Conceptual diagram of population genomic processes on coral reefs. Their inherent patchiness, extensive but irregular gene flow among habitat patches, strong selective gradients at both broad and microgeographic scales, and large effective population sizes create a unique mix of microevolutionary patterns and processes. Colors in the environmental variation arrow represent changes in environmental (and selective) pressures across spatial scales of meters (m) and kilometers (km), such as temperature variation.

Gene flow between far-flung reefs prevents the strong spatial genetic differentiation historically assumed to drive diversification in terrestrial systems (51). Major biogeographic barriers, such as the mid-Pacific and the Amazon River outflow, more commonly act as filters to dispersal rather than impermeable obstacles (99). However, coral reefs are also not globally continuous: Tropical coral reefs cover only a tiny, highly discontinuous fraction of ocean area (132), and fluctuations in sea level and plate tectonics can isolate ocean regions (7, 161). Even in contiguous oceans, gene flow commonly involves intermediate reefs as stepping stones (58, 206). This stepping-stone mode of dispersal appears as an isolation-by-distance population genetic pattern for many coral reef taxa, in which genetic differentiation increases with geographic distance between sampling sites (200).

The spatial scales of dispersal and gene flow for many reef taxa are determined by the physiology, development, and behavior of their larvae. Genetic parentage and isolation-by-distance analyses have begun to reveal substantial differences among taxa, though more widespread applications are needed to understand how and why dispersal differs among species and to understand the evolutionary forces shaping dispersal-relevant traits (137). Key traits appear to include pelagic larval duration and swimming speeds (137, 204). For example, reef groupers (*Plectropomus* spp.) with strong larval swimming and weeks-long pelagic stages exhibit median dispersal distances of over 100 km (234), while marine sponges (with weak swimming and larval durations of hours to days) appear to primarily disperse under 200 m (11). Among fishes, dispersal distances vary among species from neon gobies (*Elacatinus lori*), with a median distance of 1.7 km (56), to Clark's anemonefish (*Amphiprion clarkii*) at 5 to 12 km (30) and vagabond butterflyfish (*Chaetodon vagabundus*) at 43 to 64 km (2). Among corals, broadcast spawners generally disperse further than brooding corals (159), though mean dispersal distances also differ between closely related species (58). For example, most dispersal in the brooding coral *Seriatopora hystrix* is within 100 m of the natal site, but rare long-distance dispersal of 9 km or more is possible (225). In addition, dispersal distances within species can differ substantially between locations because of variations in ocean currents, with stronger currents driving more widespread gene flow (48, 74).

Gene flow for coral reef taxa, however, is far from stable (**Figure 2**). Nearshore ocean currents are chaotic (205), and their temporal variation can cause dispersal to differ as widely across years for the same population as it does across species (30). Many coral reef species experience sweepstakes reproductive success, producing large, dispersing broods with probabilities of survival that differ substantially between them (8). When combined with wide interannual variation in dispersal distances, these processes can create chaotic genetic patchiness, a condition in which genetic differentiation varies irregularly across a landscape, including at small spatial scales below the scale of dispersal (63). Chaotic genetic patchiness has been documented in a variety of reef taxa, including among gobies in Belize (202) and *Acropora hyacinthus* corals on Palau (52). Together, this widespread but temporally variable gene flow on coral reefs sets the stage and determines the potential for local adaptation, speciation, and the spread of beneficial alleles during rapid environmental change.

Local adaptation: the pattern (and evolutionary process leading to it) in which resident genotypes have higher fitness in their local environment than do genotypes originating from other environments

Local Adaptation Despite Gene Flow

With extensive gene flow across wide distances that tends to nearly homogenize allele frequencies, coral reef taxa would seem to have little potential for local adaptation. However, population genomic studies have revealed that signals of local adaptation are surprisingly common, including allele frequencies at loci under selection that are more strongly diverged among populations than would be expected from drift and migration across the rest of the genome (i.e., outlier loci) and genotypes that have higher fitness in their local environments than genotypes from elsewhere (9, 14, 55, 114, 165). Local adaptation can produce strong differences in environmental tolerances and can exist in traits under selection even when neutral loci show little divergence between populations (14, 55). These patterns suggest that spatially divergent selection in reef environments is often strong enough to counteract the homogenizing effects of gene flow (113) (**Figure 2**), producing a fascinating study system for the interplay of natural selection and gene flow. While understudied in reef systems, the genetic architecture of local adaptation with gene flow is expected to result in a few alleles of large effect, including those packaged within chromosomal inversions or other tightly linked genomic islands (241). However, if dispersal completely mixes the gene pool and selection acts independently on each generation through strong environmental filtering, genomic architecture from spatially divergent selection can be highly polygenic and lack tight linkage among selected loci (219). Such cases of independent selection on each generation may not be considered local adaptation per se because they lack genetic differentiation among local demes (113), but in practice, there is likely to be a fascinating and poorly understood gradation between weak differentiation of local demes and complete panmixia.

Outlier loci: genomic loci or markers (e.g., single nucleotide polymorphisms) whose allele frequencies are much more diverged among populations than those of the rest of the genome

Environmental filtering: the process in which the environment allows certain genotypes to survive and persist in a particular location; also applies to species

Local adaptation has been documented in a wide variety of species and across a wide range of environmental gradients. These include corals adapted to high salinity and low pH, as well as reef-dwelling sea urchins adapted to low pH from natural CO_2 vents (57, 122, 226). Local adaptation to temperature has been demonstrated in multiple reef taxa, including reef fishes along latitudinal gradients (80), but appears particularly common in sessile taxa since they have fewer behavioral mechanisms with which to regulate their thermal environment (147, 154). Broad evidence supports the local adaptation of corals to higher temperatures both between and within reefs (59, 218). Most notably, this includes adaptation to extremely high temperatures in the Red Sea and Persian Gulf, where some genera of stony corals exhibit bleaching tolerances several degrees higher than do their conspecifics in cooler environments (106). Also in the Persian Gulf, strong selective sweeps were associated with rapid thermal adaptation in populations of *Platygyra daedalea* (207).

Local adaptation in reef species can exist on scales well below the range of dispersal, which has been called microgeographic adaptation (94, 185, 195). Habitat choice by individuals, including settlement choices by larvae, can favor the maintenance of local adaptation at fine spatial scales (141, 185, 209). Coral and fish larvae, for example, possess a complex set of searching and sensing behaviors to choose their settlement locations (125, 187). Individuals with different genotypes may possess behavioral mechanisms to encounter preferred habitat (180), including settling on preferred hosts in case of parasitic or mutualistic organisms (60). Alternatively, local adaptation can be maintained through strong postsettlement elimination of maladaptive genotypes through environmental filtering, as appears to occur in corals across depth gradients (129, 178). Local genetic adaptation to habitat type at spatial scales below the range of dispersal exists in octocorals (*Plexaura flexuosa*) in Florida, marine sponges (*Chondrilla nucula*) in the Caribbean, and banded coral shrimp (*Stenopus hispidus*) in Indonesia (61, 117, 232). Evidence for hyperlocal adaptation (within a few dozen meters) to differing temperatures within reefs exists for several species of stony corals, including phenotypic differences, genetic outlier loci, and genotype–environment associations (9, 29, 165, 220). However, it remains unclear whether gene pools are sufficiently differentiated for these examples to be called local adaptation, or whether selection instead acts independently each generation on a well-mixed gene pool (113). These distinctions have important implications for the scale of gene flow and the potential for beneficial alleles to spread to new areas during environmental change.

Microgeographic adaptation: local adaptation of a population occurring at less than the typical spatial scale of dispersal

Speciation with Gene Flow

The existence of occasional gene flow between even distant reef patches makes true allopatric speciation difficult in reef taxa, yet reefs host an incredible wealth of species (18). Multiple explanations exist for this apparent paradox. First, lower sea levels in the Pleistocene fragmented reef habitat and led to divergence among some sister taxa (126, 136). In a similar fashion, plate tectonics created the Isthmus of Panama and split species into Caribbean and Pacific sister taxa (161). Second, speciation can occur even without complete genetic isolation. Parapatric speciation describes divergence of adjacent populations experiencing differential selection as well as some gene flow, which may be especially common on coral reefs (190). Many reef taxa have diverged during partial geographic separation, including several species of *Dascyllus* reef fishes in the Indo-Pacific with varying levels of population overlap and *Calcinus* hermit crabs in the Indo-Pacific with both overlapping and nonoverlapping species distributions (127, 139). In *Orbicella* (formerly *Montastraea*) corals in the Caribbean, genetic and morphologic novelty is concentrated near the edge of the genus's range despite incomplete genetic isolation, suggesting that geographic distance plays an important role in speciation even without total genetic separation (19). Speciation due to divergent environmental selection in adjacent populations can be driven by the same forces underlying local adaptation. Both local adaptation and early-stage speciation can also share the same genomic signatures, including the presence of a small proportion of outlier loci within an otherwise undifferentiated genome (172).

Parapatric speciation: occurs with restricted gene flow among populations, but without a hard barrier that prevents gene flow, in contrast to allopatric speciation (in which new species occupy separate locations without gene flow) or sympatric speciation

Sympatric speciation is thought to be globally rare because reproductive isolation is difficult when gene flow and recombination break up the association between coadapted alleles (75). Similarly to local adaptation with gene flow, sympatric speciation is aided by the evolution of tightly clustered loci, haplotype blocks, and large-effect loci (75). However, evidence nonetheless suggests the occurrence of sympatric speciation in multiple coral reef taxa. This process can be triggered by host specificity and shifts in host preference, which have been documented in coral-feeding nudibranchs (*Phestilla* spp.), coral-dwelling barnacles (*Wanella* spp.), and coral-dwelling gobies (*Gobiodon* spp.) (66, 153, 224). Alternatively, sympatric gobies (*Elacatinus* spp.) and hamlets (*Hypoplectrus* spp.) may have speciated primarily due to assortative mating by color, and Caribbean grunts (*Haemulon* spp.) due to assortative mating by vocalization (97, 191, 214). Comparative genomics of the hamlets suggests that speciation occurred through a few loci of large effect that control color patterns and vision, which in turn was facilitated by the hamlets' large effective population sizes (N_e) (97). Large effective population size allowed for the accumulation of novel mutations and the retention of ancestral variation while also promoting high rates of recombination that inhibited the formation of genomic islands of divergence. Other mechanisms include divergence in depth and spawn timing (178).

Sympatric speciation: occurs while both new species continue to occupy the same geographic area

Effective population size (N_e): the size of an idealized population that loses heterozygosity at the same rate as the focal population

Species boundaries are not always obvious from morphology, and recent advances in population genetics have revealed that coral reefs host an impressive variety of cryptic species. Cryptic coral reef species discovered with population genetics include polychaete worms (Nereididae spp.), cleaner shrimps (*Saron* spp.), hydrozoans (*Pteroclava* spp.), octocorals (*Carijoa* spp.), several genera of fishes, and multiple stony corals (5, 42, 82, 84, 107, 149). Similarly to locally adapted populations within species, cryptic species may exhibit distinct environmental tolerances. Differing environmental stress tolerance has been identified in cryptic *Pocillopora* corals in French Polynesia and the *A. hyacinthus* species complex in American Samoa, highlighting the susceptibility of unique evolutionary lineages to continued global change (23, 192, 193). The origins, maintenance, and evolutionary trajectories of cryptic species remain largely unknown.

Hybridization

The converse of speciation with gene flow is that closely related species also have opportunities for hybridization. Population genetics has been critical for identifying hybrid species and understanding their relationships, and hybridization is common in both coral reef fishes (91, 148,

237) and corals (**Figure 2**). In reef fishes, persistent hybridization can lead either to a decrease in lineage diversity or the endurance of distinct hybrid lineages (98). Hybridization has played an important role in the evolution of coral diversity, including the generation of diversity within species and the emergence of new species (140, 235). Of particular interest is evidence that hybrid corals have been able to expand into novel habitats, suggesting that the generation of genomic diversity through hybridization has relevance to survival in the face of global change (235). Widespread hybridization in some genera such as *Acropora* (branching corals) has led to the formation of syngameons, which are species complexes with multiple hybrid forms that sometimes include cryptic species (184). The same assemblages of cryptic and hybridizing species can sometimes be found across many distinct reefs and thousands of kilometers (124). The conditions under which hybridization generates new species, facilitates the adaptation of existing species, or leads to the dissolution of species boundaries on coral reefs remain an area of active investigation (140).

Weak Genetic Drift

Many marine populations contain millions to billions of individuals, and coral reef taxa are no exception (43, 133). One square meter of coral reef may have $>10^{10}$ symbiotic dinoflagellates, for example (46). N_e quantifies the strength of genetic drift—with more drift in smaller populations—(34), and evolutionary theory suggests that N_e is generally between 10% and 50% of census population sizes (160, 233).

Some features of marine populations—including large numbers of offspring, high variance in reproductive success among individuals, and skewed sex ratios—have been proposed to reduce N_e by many orders of magnitude below census population size, but whether these or other factors actually create N_e values this low remains hotly debated (95, 164, 233). N_e is roughly the number of parents who contribute to the next generation (233), so an N_e of 1,000 in a population of 1,000,000 would imply that approximately 1 in every 1,000 individuals successfully reproduces (and contributes to the next generation) over its lifetime. Drift is weak even with an N_e of 1,000, suggesting that, overall, drift does not play a strong role shaping population genetic patterns on coral reefs (**Figure 2**). N_e for staghorn coral in the Florida Keys, for example, was estimated at roughly 40,000 to 115,000 individuals (96), and five reef fishes on the Mesoamerican Barrier Reef have N_e estimates ranging from nearly 1,000 to nearly 100,000 individuals (179). Weak drift contributes to low levels of genetic divergence among populations and creates a relatively stronger role for selection in population genomic processes.

However, drift cannot be entirely discounted. Patchy habitats such as coral reefs tend to incur more genetic drift than do uniform habitats such as open ocean, and coral reef species generally experience more genetic drift than widespread and well-mixed pelagic species (134, 200). Evidence for the influence of drift includes lower genetic diversity on smaller coral reef patches (201) and at range edges (37). In addition, a surprisingly large fraction of reef animals—including many corals—are clonal, suggesting an important role for somatic mutations and somatic genetic drift in addition to multigenerational genetic drift (183, 229). Further research will be needed to understand the broader range of conditions and taxa for which drift is a strong force.

OBSERVED GENOMIC CHANGE ON CORAL REEFS

Over the past two decades, there has been substantial interest in the ecological and evolutionary repercussions of increased anthropogenic pressure on coral reefs. Coral reefs evolved under thermal regimes without high-frequency variability (194) but are now experiencing accelerated rates of warming and carbonate chemistry change (81). Human populations have grown particularly fast along coastlines, exposing reefs to overfishing, coastal habitat degradation, and localized pollution. All of these dramatic environmental changes may have strong evolutionary consequences, but most attention has instead been on demographic and ecological responses. While widespread evolutionary changes are almost certainly occurring as well, understanding these changes is at a nascent state. Below, we review the population genomic impacts of global change that have been observed on coral reefs to date (**Figure 3**; **Table 1**). More widespread application of population genomic methods to coral reef taxa will almost certainly expand this list.

<COMP: PLEASE INSERT TABLE 1 HERE>

<COMP: PLEASE INSERT FIGURE 3 HERE>

Figure 3 Map of observed genomic changes on coral reefs due to anthropogenic forces. Colors represent the driver of the observed change, while icon shapes (coral or fish) indicate the taxa the change was observed in. Numbers correspond to **Table 1**, which contains more information about the findings in each individual study.

Bottlenecks and Genetic Diversity Change

Overexploitation and habitat degradation reduce genetic diversity by decreasing N_e and limiting the number of individuals contributing genomic variation to future generations (53, 112). This decrease in N_e drives the erosion of heterozygosity at the rate of $1/(2N_e)$ while also depleting the number of rare alleles in a population and increasing the chance that any given allele is lost due to drift (1). Rare alleles are lost faster than the reduction in expected heterozygosity, which results in a temporary excess of heterozygous individuals (44). Coral reefs have a deep history of genetic bottlenecks due to environmental change. During the Holocene, large fluctuations in sea level spurred dramatic reductions in population size of many reef fish species (68, 136). Drops in sea level resulted in large-scale habitat fragmentation, barriers to gene flow, and, in some instances, new speciation events that shaped modern-day reef species assemblages.

Evidence for contemporary bottlenecks is substantially more mixed, however. Mass bleaching events in populations of *Acropora millepora* and *Acropora pulchra* resulted in altered genetic composition but no detectable reductions in genetic diversity (211, 228). Strong but quickly disappearing genetic differentiation in damselfish (*Stegastes partitus*) populations after an extreme hurricane event suggested that there had been a genetic bottleneck in at least one population (123). In a field experiment, short-term heat stress increased the mortality rates of juvenile damselfish (*Dascyllus aruanus*) and reduced allelic richness, indicating that unfavorable environmental conditions have the potential to result in widespread genetic diversity loss (173). Nassau grouper (*Epinephelus striatus*) were heavily overfished in the Caribbean throughout the 1970s and 1980s, but only a weak bottleneck signal of excess heterozygosity in the US Virgin Islands was detected when sampling was done in 2008–2010 following some population recovery (13). Gene flow from other populations appeared to help reduce the bottleneck signature.

The emerging picture is one of weak and difficult-to-detect bottlenecks on coral reefs, likely because even collapsed populations have remained relatively large (and drift therefore not particularly strong), bottlenecks have not lasted long enough to have a large impact, and because gene flow has helped offset diversity loss. However, difficulty detecting bottlenecks may obscure a more widespread loss of standing genetic variation through the elimination of rare but functionally important haplotypes (175). More widespread application of whole-genome sequencing and testing for the loss of rare haplotypes will be needed to evaluate these ideas.

Adaptation to Changing Environments

Reef populations are adapting in response to novel selective pressures, but evidence for these responses is only starting to appear in the scientific literature. Traits involved in adaptation to climate change, such as bleaching response and growth, often have high heritability (6), suggesting in situ adaptation may be a common response to rapid selective events. Such adaptation can be challenging to detect, however, as it may manifest as slight shifts at many loci of small effect (21, 240) and involve different genes in different populations (240). For example, a genome-wide association study (GWAS) across 213 individuals of *A. millepora* did not identify any single locus that was significantly associated with individual bleaching response during a 2017 marine heatwave, but a polygenic score constructed from the GWAS mildly improved prediction of bleaching (78). Similarly, signatures of selection at many loci were apparent between populations of *A. hyacinthus* that inhabit differing thermal environments in American Samoa, suggesting that mild selection across many loci helped to maintain extensive reservoirs of adaptive polymorphisms (9). Controlled crosses of Red Sea and Indian Ocean *P. daedalea* brain coral also identified hundreds of loci related to heat tolerance (105).

In other cases, selection can involve large shifts in allele frequency at a few loci of large effect. For example, artificial selection experiments on *A. millepora* coral larvae produced allele frequency changes up to 40% over a single generation and implicated mitochondrial transporter genes (59). However, evidence of contemporary adaptive evolution on coral reefs is rare. While not tropical, there is evidence of rapid adaptation to cold temperatures along the northern expansion front of the invasive coral *Oculina patagonica* in the Mediterranean (131). Allele frequencies at three anonymous loci were associated with temperature along this expansion front. Similarly, lobe coral (*Porites lobata*) populations in Hawaii inhabiting heavily polluted nearshore sites were strongly differentiated at three genetic loci from nearby but less-polluted offshore sites, and reciprocal transplant experiments revealed local adaptation, providing evidence of contemporary adaptation to poor water quality and pollution (220).

Changes in Gene Flow

Global change has the potential to directly alter patterns and dynamics of dispersal, and therefore, of gene flow (152). Warming ocean temperatures could disrupt current patterns (152), but the largest effects appear to be through reducing larval dispersal distances due to shortened pelagic larval durations and lowered larval survival (72, 135). For an example beyond coral reefs, variation in sea surface temperatures drove fluctuation in pelagic larval duration and genetic patchiness in populations of black-faced blennies (198). Juveniles dispersing at the end of the recruitment season (under high temperatures) tended to have shorter pelagic larval durations than those dispersing at the beginning of the season in cooler conditions (198).

Short-term events, including hurricanes, also have the capacity to alter gene flow corridors, such as in 2005 when storm surge from Hurricane Dennis redistributed estuarine sailfin molly (*Poecilia latipinna*) individuals across long distances, erasing previously established isolation-by-distance patterns (3). Although brief, such occurrences may have lasting evolutionary implications because of their ability to enable rare long-distance dispersal events. Larvae of the brooding coral *S. hystrix*, for example, typically recruit within 100 m of their parents, producing strong genetic differentiation at kilometer scales (225). After bleaching in 2017 drove substantial declines in coral cover on the Scott Reefs, Australia, an influx of larvae and distinct genotypes from a healthier site 9 km away appears to have allowed coral recovery (225). Isolated reefs are less likely to receive beneficial gene flow after catastrophic disturbance from bleaching or other events (4, 217).

Genomic Consequences of Range Shifts and Invasions

At a global scale, changing environments are causing shifts and expansions of entire species ranges. For example, coral species have expanded poleward since the mid-1900s (238), while tropical species increasingly dominate temperate fish assemblages (71, 156). Such rapid, large-scale dispersal events can leave lasting genomic signatures. Serial founder events during range expansions can allow low-frequency, potentially deleterious alleles to surf to high frequency along the expansion wave (65, 90), resulting in lower genetic diversity (213) and higher mutation load (170) at the range edge. Studies tracking the range expansion of *A. hyacinthus* coral in Japan found evidence for such signatures, including higher clonality and lower diversity in edge populations (70, 155). Notably, six genes were near outlier loci in comparisons of edge versus core populations, which provided evidence of local adaptation to lower winter temperatures at the range edge (70).

Invasion events are another pathway by which species can expand their ranges, and they often share the same genomic consequences as range shifts, including allele surfing, postestablishment adaptation, and bottleneck events (17). For example, in one of the most famous examples of a human-mediated marine invasion event, lionfish (*Pterois volitans*) first became established in the western Atlantic in the early 2000s due to aquarium releases (203) and have subsequently shown evidence of allele surfing in their introduced range (16). Signatures of selection (F_{ST} outliers) between native and introduced lionfish populations are also apparent, particularly near genes that may help facilitate such rapid expansion and dispersal events (182). Furthermore, while yet to be seen on reefs, marine invaders have the potential to hybridize with native congeners, when available (231), which can help provide the expanding species with new sources of genetic diversity to supplement the diversity lost during the invasion wave and subsequent founder events (17). Such hybridization may also lead to the eventual replacement or extirpation of the native species and the opening up of new evolutionary pathways (17).

Allele surfing: the neutral eco-evolutionary process by which some alleles can drift to high frequencies during the extension of a population range edge

Elevated Hybridization Rates

Genomic responses to global change can also have repercussions at the species level, disrupting macroevolutionary processes via hybridization with newly introduced species or secondary contact between formerly isolated populations. Environmental disturbance can mediate hybridization (86), as evidenced by extensive hybridization among damselfish (*Stegastes* spp.) and the blurring of species boundaries in Jamaica but not in Barbados (151). The higher hybridization rates appear to result from habitat degradation in Jamaica that reduced the differences among habitats and therefore reduced the ecological isolation among species (151).

This positive relationship between hybridization and disturbance rates has been seen elsewhere as well. Hybridization levels were higher among damselfish congeners (*Abudefduf* spp.) in the heavily human-perturbed southern Hawaiian islands than in the more pristine northwestern part of the archipelago (38). While the mechanism driving these elevated rates remains unclear, it is likely that one of the hybridizing species is a marine invader that recently arrived to the Hawaiian archipelago via hitchhiking with marine debris (38).

THE EVOLUTIONARY FUTURE FOR CORAL REEF TAXA

Ongoing and accelerating rates of environmental change and human impacts suggest that coral reefs will continue to evolve in the coming years, decades, and centuries. Of the many anthropogenic pressures driving long-term changes to coral reef ecosystems, climate change looms preeminent (212). While possible climate change trajectories range from 1°C to 5°C warming over the next century, the most likely scenarios project between 2°C and 3°C warming above preindustrial levels by 2100 (93). The 2022 Intergovernmental Panel on Climate Change (IPCC) report (111) predicts substantial loss of tropical coral reefs even under a relatively low 1.5°C of warming, though other authors are more optimistic (143, 144, 166). In addition, even pessimistic scenarios do not preclude the possibility of adaptation to future change by at least some taxa in some locations.

Evolutionary rescue is the process by which adaptive evolutionary change allows a population to reverse its decline and survive environmental change (25, 85). For evolutionary rescue to be successful, the rate of evolution needs to be sufficiently fast, which in turn depends on the amount of standing genetic variation in the evolving population measured as the additive genetic variance (10, 25, 28, 119, 169). Reef-building corals and their symbionts will continue to adapt genetically to the Anthropocene, though both the pace and magnitude of the potential adaptation remain controversial (102, 166).

Evolutionary rescue: a process in which a population with declining abundance instead evolves to tolerate its current conditions and survives

Models that integrate knowledge of coral genomics and dispersal have been helpful for understanding if and where adaptation will be sufficient to rescue corals. For example, a coral evolutionary metapopulation model for the Central Indo-West Pacific suggested that reefs vary widely in their capacity for persistence, with the majority collapsing within the coming century under a high (but not a low) greenhouse gas emissions scenario (143). However, reefs with substantial larval input from warmer areas persisted in all simulated warming scenarios, since immigrants were, in effect, preadapted to future conditions (143). Likewise, eco-evolutionary simulations across reef networks in the Caribbean, Southwest Pacific, and Coral Triangle suggested that the likelihood of coral species persistence increases with both larval input and genetic variance (144, 145). Both models agreed that adaptive evolution was critical for coral survival. Coral metapopulations in the former model required the existence of both migration and selection to avoid coral collapse, and corals in the latter model required at least some genetic variance (**Figure 4**). Similar nonevolutionary models reinforce the conclusion that naturally cooler reefs (often called climate refugia) alone are not sufficient for coral persistence, suggesting that reef refugia will be unable to produce sufficient coral larvae to reseed even half of present-day reef areas (88). Strong selection for heat-tolerant corals and the loss of more sensitive corals are also expected to drive reductions in genetic diversity (230).

<COMP: PLEASE INSERT FIGURE 4 HERE>

Figure 4 Predicted evolutionary trait change on coral reefs (*colored lines*) under high [representative concentration pathway (RCP) 8.5; *dashed lines*] or lower (RCP 4.5; *solid lines*) greenhouse gas emissions scenarios. The trait in this eco-evolutionary model is thermal tolerance. The colors indicate scenarios with no (*purple*), limited (*turquoise*), or sufficient (*lime green*) additive genetic variance (V) to evolve in response to temperature change (*gray*). Figure adapted with permission from Reference 144 (CC BY-NC 4.0).

Even with adaptation, some reef species will certainly vanish. While documented marine extinctions in the Anthropocene are few (188), tropical seas are already experiencing disproportionate extirpations (35). Among fishes, the small, coral-dependent species may be at particular risk of extinction, as are endemic species (152). For zooxanthellate stony corals, more than 30% of the 704 species assessed by the International Union for Conservation of Nature (IUCN) are listed as vulnerable, endangered, or critically endangered, highlighting the possibility of increased coral extinctions over the next century (26). These losses, combined with predicted mass bleaching and loss of coral cover accompanying future climate change may lead to a domino effect resulting in loss of diversity and mass extinctions in reef-associated taxa (230). Likewise, a recent projection of extinction risks in marine species predicts catastrophic mass extinction across marine ecosystems by 2300 under strong warming scenarios of climate change, highlighting the tropical Indo-Pacific as an area of particular risk (171). Other, more localized human impacts such as sedimentation, disease, overfishing, and pollution also threaten coral reef taxa and impede adaptation to climate change by reducing population sizes and adaptive potential.

These troubling predictions have convinced some stakeholders to pursue more radical methods of reef conservation, especially to bolster heat tolerance in hard corals. If successful, these efforts would have long-lasting effects on the genetics of future coral populations. Multiple research groups have proposed moving heat-tolerant coral larvae or fragments from warmer to cooler reefs as an implementation of assisted migration (186, 197). Successful assisted migration would produce many of the same genomic changes as natural migration, while incurring the ecological risks of transporting nontarget organisms such as pathogens and the evolutionary risks of outbreeding depression (157a).

More direct genetic interventions may target either coral animals or algal symbionts. Selective breeding of coral animals shows theoretical promise for increasing coral resilience to climate change (227). In particular, hybridization of some congeneric coral species has successfully increased coral survival under heat stress in laboratory conditions (33). Laboratory breeding can also be used to enhance the heat tolerance of algal symbionts, which have the advantage of short generation times that enable potentially faster evolution (32). Laboratory selection of heat-tolerant algal symbionts successfully raised the in vitro heat tolerance of the population over just two years, though it showed much weaker effects on the heat tolerance of coral holobionts hosting the novel symbionts (31). Researchers have also proposed direct editing of symbiont genomes to enhance heat tolerance using CRISPR-Cas9 and have identified genes of interest, though this research remains mostly hypothetical (130). If laboratory-bred or -altered coral lineages have increased heat tolerance and do not suffer from decreased competitive abilities in other areas, their outplanting might narrow overall coral genetic diversity by outcompeting wild types (157a). These effects have already been observed in salmon supplementation programs (36). There is active debate over whether the risk of negative side effects is worth the potential reduction in risk of losing coral reef taxa from climate change (40, 157a).

FUTURE CHALLENGES AND OPPORTUNITIES

The urgency of climate change and other threats to coral reefs drives a need for the substantial expansion of population genomic research in this ecosystem. Tropical ecosystems are understudied across ecological and evolutionary research fields (54), and population genomics is particularly important given the substantial role of evolution in tropical responses to climate change (158). Genomic research on coral reefs faces particular challenges, however, including the remoteness and logistical challenges of accessing many of the most biodiverse reefs, the large fraction of undescribed species and the potential for cryptic species, and the relatively few genomic resources for tropical species. Here, we highlight a few of the particularly urgent research topics and opportunities for progress.

Evolutionary Potential and Trade-offs

Whether evolutionary rescue can avert extinction for vulnerable coral reef taxa is a critical question, and yet key factors that contribute to the likelihood of evolutionary rescue remain unknown. For example, the additive genetic variance for most conservation-relevant traits is unknown (92). Efforts to measure additive genetic variance for coral thermal tolerance have, to date, been underpowered and had confidence intervals spanning almost the entire range of possibilities (78). Because controlled breeding in most coral reef organisms is difficult or impossible given current knowledge, whole-genome methods for measuring additive genetic variance are particularly promising (174, 239). These methods are a subset of GWAS approaches and typically require sample sizes above 1,000 phenotyped and genotyped individuals. Sample sizes this large remain higher than most coral reef studies, and high-throughput phenotyping remains one of the more substantial bottlenecks. Advances in imagery analysis and automated phenotyping show promise for overcoming this challenge (104). Tolerance for disease, pollution, warming, acidification, fishing, and other stressors are all traits that are important and likely of interest.

Beyond measurement, however, predicting more broadly the potential for evolutionary rescue requires understanding how and why standing genetic variation of pertinent phenotypes differs among species. Measurement of adaptively relevant genetic variation is time consuming and expensive, so finding species traits that are appropriate proxies of standing variation on coral reefs is important. Population size, for example, is a common constraint, with lower adaptive potential in small populations (233a), but even population size is poorly known for most coral reef taxa. Neutral genetic diversity is another common proxy, but its relevance for predicting extinction risk and adaptively relevant diversity remains debated (79, 216). Growing evidence suggests microgeographic adaptation on reefs (185, 217), implicating environmental heterogeneity as likely important for maintaining adaptive variation (129). Environmental heterogeneity, such as the variability of microclimates on reefs, may therefore be a useful proxy for functional genetic variation.

Antagonistic genetic correlations also provide key constraints on evolutionary potential (64). There are thermal tolerance versus growth trade-offs among zooxanthellae in corals (128), and a similar trade-off may exist in coral hosts that is mediated by their symbiont density (45). Applying population genomic methods more broadly to understand trade-offs in global change–relevant traits is an important area for further research.

Mechanisms of Local Adaptation and Eco-Evolutionary Feedback

Despite increasing recognition that coral reef organisms are adapted to fine-grained environmental variation, including at spatial scales substantially smaller than the scales of dispersal, the mechanisms and environmental drivers behind this adaptation remain largely unknown. With a well-mixed gene pool, sorting of adaptive genotypes into separate habitats can occur each generation through strong environmental filters and high postsettlement mortality of maladapted individuals, but only under fairly restrictive conditions on the relative fitness of genotypes across different environments (129). Do coral reef species, including corals, fit these conditions? Perhaps the exceptionally large number of offspring produced by most coral reef organisms allows them to absorb the high cost of strong selection each generation. Or does settlement behavior favor microgeographic adaptation to an extent not yet appreciated, reducing the importance of postsettlement filtering? As yet another possibility, reproduction and dispersal may occur on sufficiently fine spatial scales that cause effective gene flow among fine-scale habitats to be relatively weak.

One prediction of strong environmental filtering would be the presence of within-cohort allele frequency shifts at adaptive loci, from an undifferentiated pelagic larval cohort up through locally adapted adults. New genomic tools and the ability to resequence whole genomes at the population genomic scale could make this kind of investigation possible, particularly if coupled with interdisciplinary investigations of larval behavior in the lab and field. New underwater video technologies and the ability to automate the image annotation will likely assist these studies (138).

Another key area for investigation will be to understand the ecological consequences of gene flow across the environmental mosaic, particularly in the context of rapid environmental change. Gene flow can import alleles that are beneficial in a new environment, or bring maladapted alleles, depending on the scale of local adaptation, the scale and directionality of gene flow, and the grain of environmental variation (120, 142). Recent eco-evolutionary models for corals predict that gene flow will favor rapid adaptation to warming and persistence in some locations while driving maladaptation and extirpation in others (143, 144), but field tests are needed to identify whether these evolutionary processes actually matter for demography. Such questions sit at the boundary of population genomics and ecology and will be facilitated by integrated research across fluid dynamics, demography, and genomics.

Genomic Resources for Reef Species

Many of the most pressing population genomic questions for coral reef organisms rely on the availability of high-quality genomes, including questions about demographic history, natural selection, local adaptation, genetic load, and structural variation. Theory, for example, predicts that local adaptation in the face of gene flow will often occur through inversions and linkage blocks (241), but initial evidence in corals suggests that local adaptation of thermal tolerance involves many genes of small effect (9). Whether large linkage blocks also play an important role in local adaptation on reefs remains unclear, and the high rates of gene flow for most coral reef taxa and the potential for independent selection on each generation may mean the patterns and mechanisms differ from those appearing on land (89, 221).

Genetic load: reduced fitness (survival or reproduction) of a population because of deleterious genes or genotypes

Linkage block: an area of the genome in which alleles are likely to be inherited together because of reduced rates of recombination

Chromosome-scale genomes are now being generated for coral reef organisms (**Figure 5**), costs are dropping under $5,000 for sequencing new genomes (67), and complete and error-free genome assemblies for both maternal and paternal haplotypes are becoming possible (162). The availability of assembled genomes, however, is completely dwarfed by the diversity of coral reef organisms, including microbes. Most attention to date has focused on fishes and stony corals (**Figure 5**), mirroring their ecological and economic importance as fishery targets and foundation species. The ability to bring long-read DNA sequencers to the field provides a novel opportunity to rapidly expand the availability of genomic resources for coral reef taxa (27, 39) by expediting sequencing timelines, involving local scientists, and simplifying permit logistics.

<COMP: PLEASE INSERT FIGURE 5 HERE>

Figure 5 Genome assemblies available from the National Center for Biotechnology Information (NCBI) for eukaryotic organisms identified as coral reef–associated by FishBase and SeaLifeBase as of November 2022 (77, 163, 196). Non-chordates are organized by phylum, and chordates are organized by class. Phyla and classes are shown according to the current FishBase and SeaLifeBase taxonomies, which are not necessarily up to date. Only one genome was counted when multiple assemblies were available for the same species. Missing taxa reflect database gaps and lack of taxonomic harmonization across databases, including at least 14 missing zooxanthellae genomes (phylum Dinophyta or Myzozoa, depending on taxonomic system) (49).

Historical Samples and Baselines

Understanding the population genomic changes occurring on coral reefs relies in part on having accurate baselines. Genomic time series provide insight into processes such as drift, gene flow, and selection that cannot be disentangled from contemporary samples (208). While time series can be collected specifically for research, understanding longer processes over decades or centuries often relies on the availability of historical or ancient samples (24). DNA from tropical environments degrades quickly, greatly limiting but not eliminating the availability of ancient samples from coral reefs (103). Metabarcoding ancient DNA from coral reef cores, sediments, and middens has become possible (83, 87, 199), however, and preserved museum samples provide an underexplored resource. The US National Museum of Natural History, for example, houses one of the largest collections of tropical fishes, many collected in the 1907–1909 Albatross expedition and suitable for DNA sequencing (115).

Democratization of Population Genomics Infrastructure

As population genomic research on coral reefs expands, there remains a striking disparity between the location of reefs and the location of researchers and resources for population genomics. This disparity means that much of the population genomic research is concentrated in Hawaii, on the Great Barrier Reef, and in Florida, rather than in species-rich regions of the Coral Triangle and East Africa (73, 116). Overcoming this geographic bias will require the further development of close collaborations between researchers in high- and low-income countries, with particular attention to local and Indigenous consent, benefit sharing, local priorities, and capacity building rather than exclusionary and colonial approaches to science (223). Groups such as the Western Indian Ocean Marine Science Association (WIOMSA) and the Coastal Oceans Research and Development—Indian Ocean (CORDIO) are organized in part to address these issues. Workshops on and access to funding for population genomic lab techniques, bioinformatics, and data analysis can also help build capacity.

SUMMARY

Coral reefs present a fascinating combination of microevolutionary processes—including weak drift, strong biotic and abiotic gradients, and extensive gene flow—that contrast with more deeply studied terrestrial systems. At the same time, these ecosystems are exceptionally important to human well-being and highly threatened by environmental change. Research to date has revealed surprisingly few evolutionary impacts of global change, but this likely reflects a lack of attention and limited application of population genomic tools at wide enough scales rather than a paucity of impacts. Rapid evolutionary adaptation facilitated by high standing genetic variation has the potential to play an important role in the future of coral reef taxa, and the extent and limits of evolutionary rescue on coral reefs present an urgent research topic. The confluence of basic science questions and applied science needs provides critical research opportunities at the nexus of population genomics, conservation biology, and global change.

SUMMARY POINTS

1. Coral reefs are among the most biodiverse and threatened ecosystems on the planet, sparking rapid growth in population genetic research over the last 20 years.
2. Many coral reef taxa are characterized by extensive gene flow, large effective population sizes, patchy habitats, and strongly divergent selection across fine-grained environmental variation, setting up a unique mix of microevolutionary processes.
3. Global change, such as climate change, is already altering the course of evolution on coral reefs, including population bottlenecks, evolutionary adaptation to novel environments, changes in gene flow, and increased rates of hybridization among coral reef taxa.
4. Models and limited empirical data suggest that corals possess some capacity for evolutionary rescue from climate change and other forms of global change, but the effectiveness of this process for maintaining populations and species depends on the rate of environmental change, evolutionary trade-offs, and the amount of standing genetic variation.

FUTURE ISSUES

1. As coral reef taxa continue to face rapid climate change and anthropogenic impacts, a key question concerns their evolutionary potential and potential for evolutionary rescue, including trade-offs that may impede evolutionary rescue.
2. Coral reef taxa exhibit genomic evidence of strong, spatially divergent selection and

phenotypic evidence of local adaptation, but given their potential for well-mixed gene pools, the genomic architecture for these evolutionary patterns and the relative roles of multigenerational inheritance versus independent selection on each generation remain unclear.

3. New research is needed to understand the amount of standing genetic variation in coral reef taxa for global change–relevant traits, the genomic architecture of such traits, the mechanisms maintaining such variation, and the best proxies for this variation across species.
4. Progress on understanding demographic history, natural selection, local adaptation, genetic load, and standing genetic variation will rely on expanding the availability and quality of genomic resources for coral reef taxa, including genomic sampling through time from natural history or contemporary scientific collections.
5. Close collaborations and capacity building in coral-rich, low-income countries are needed to overcome biases in the location and focus of existing coral reef research.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Table 1 Summary of research on observed genomic changes on tropical coral reefs

Evolutionary process	**Number**[a]	**Study**	**Organism**	**Driver of change**	**Summary**
Bottlenecks and change in diversity	1	Lacson & Morizot (1991) (123)	Damselfish (*Stegastes partitus*)	Hurricane	Temporary genetic differentiation was observed after a hurricane.
	2	Fifer et al. (2022) (70)	Coral (*Acropora hyacinthus*)	Range expansion	Reduced diversity and signatures of local adaptation to lower winter temperatures were found at the expansion front.
	3	Nakabayashi et al. (2019) (155)	Coral (*A. hyacinthus*)	Range expansion	Lower genetic diversity was observed in marginal habitats along the expansion front.
	4	Bors et al. (2019) (16)	Lionfish (*Pterois volitans*)	Range expansion	Allele surfing was observed in the introduced Atlantic range.
	5	Souter et al. (2010) (211)	Coral (*Acropora millepora*, *Acropora pulchra*)	Bleaching	No loss of genetic diversity, but a change in genetic composition was found following a severe bleaching event.

	6	Bernard et al. (2016) (13)	Nassau grouper (*Epinephelus striatus*)	Overfishing	Temporary heterozygote excess was observed after overfishing.
Adaptation	7	Reiskind et al. (2019) (182)	Lionfish (*Pterois volitans*)	Range expansion	Local adaptation to introduced Atlantic range was observed.
	8	Tisthammer et al. (2021) (220)	Coral (*Porites lobata*)	Pollution	Genetic differentiation was observed between coral in heavily polluted nearshore and higher-quality offshore environments.
Gene flow	9	Underwood et al. (2007) (225)	Coral (*Seriatopora hystrix*)	Bleaching	Population declined at some but not all sites, and this facilitated rare long-distance gene flow.
Hybridization and secondary contact	10	Coleman et al. (2014) (38)	Damselfish (*Abudefduf vaigiensis*, *Abudefduf abdominalis*)	Pollution	Observed hybridization levels were higher in parts of the Hawaiian archipelago with heavy human habitation; introduced species arrived to the island chain via hitchhiking with marine debris.
	11	Mullen et al. (2012) (151)	Damselfish (*Stegastes adustus*,	Hurricane	Extensive hybridization was observed due to reef substrate destruction by

			Stegastes diencaeus)		frequent hurricanes.

[a]Numbers in the table correspond with numbers in **Figure 3**.

TERMS AND DEFINITIONS