Global coral genomic vulnerability explains recent reef losses

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The dramatic decline of reef-building corals calls for a better understanding of coral adaptation to ocean warming. Here, we characterized genetic diversity of the widespread genus *Acropora* by building a genomic database of 547 coral samples from different oceanic regions—from the Great Barrier Reef to the Persian Gulf. Through genome-environment associations, we found that different *Acropora* species showed evolutionary signals of heat-adaptation in the same genomic regions, pointing to genes associated with molecular heat shock responses and symbiosis. These adaptive signals were uncommon in *Acropora* populations exposed to less than two heatwaves, indicating a potential genomic vulnerability to future heat exposure. We showed that genomic vulnerability estimates corroborate local and global patterns of coral decline, and used these estimates to reassess global coral reef conservation risks and priorities.

Climate change-induced heat waves and subsequent coral bleaching have reduced reef-building corals worldwide by ~14% just over the 2009–2018 decade (*1*). As corals form the physical scaffold of the reef ecosystem, their decline also threatens the persistence of dependent wildlife—estimated to one quarter of all known marine species (*2*). Despite this mass mortality, several lines of research indicated that coral populations are evolutionarily adapted to local environments [*e.g.*, cross-breeding experiments (*3*, *4*), colony genotyping from thermally contrasted reefs (*5–10*), and experiments exposing corals to controlled thermal conditions (*8*, *11*)], suggesting that evolutionary adaptation is a possible escape route from heat vulnerability. However, global efforts in reef conservation monitoring and risk assessments are still lacking integrated indicators on coral evolution. Here, we build a multi-species coral genomic dataset to identify evolutionary signals of adaptation to recent heatwave exposure, use these signals to explain recent coral loss, and build the first map of corals' genomic vulnerability to global heatwaves.

To generate a broad picture of coral genomic diversity, we compiled genomic sequencing datasets from over one thousand corals, of which 547 samples passed our quality controls (**Text S1**). These samples include five species of the genus *Acropora sp.*: *A. downingi* from the Persian Gulf (*12*), *A. digitifera* from the Ryukyu Archipelago (Japan) (*13*), *A. cervicornis* from the Florida Reef Tract (*14*), *A. tenuis* from the Australian Great Barrier Reef (GBR) (*10*), and *A. millepora* from the GBR (*15*) and New Caledonia (*5*) (**Fig. 1A, Table S1,** see **Text S1**). For every dataset, researchers sampled coral colonies from multiple sampling sites (5–22 sites) across a large spatial scale (> 100 km), and genotyped each colony with whole genome or restriction–site-associated DNA sequencing. For comparisons between species, we assembled a consolidated genotype matrix by mapping reads from each dataset against the chromosome-level assembly of *A. millepora* (*9*) because it is currently the most complete reference genome of the genus. To map reads from different *Acropora* species to the *A. millepora* reference, we used a read mapping method allowing for sequence divergence (*16*) that achieved high mapping rates in all datasets (mean percentage of mapped reads in each dataset were between 89% and 95%; **Fig. S2B, Text S2**). Next, we called biallelic single nucleotide polymorphisms (SNPs) after accounting for uncertainty due to low sequencing coverage (**Text S3**) (*17*). The resulting multi-species genotype matrix was analyzed using three methods summarizing genetic diversity patterns across datasets. First, a Principal Coordinate Analysis (PCoA) revealed genetics patterns coherent with taxonomy and geography between the *Acropora sp.* worldwide (**Fig. 1A**, **Fig. S7**). Specifically, the first PCoA axis separated Atlantic corals from Indo-Pacific corals [*i.e.*, Florida Reef Tract *A. cervicornis* separated from the other samples, percentage of variance explained (PVE) = 42%]. The second PCoA axis separated Coral Sea corals (*A. millepora* and *A. tenuis* from New Caledonia and GBR) from those in the Northern Indo-Pacific (*A. digitifera* from Japan and *A. downingi* from the Persian Gulf, PVE = 28%). Second, the mean nucleotide genetic diversity of *Acropora sp.* was π/bp = 0.37% (dataset averages ranging 0.14–0.97%; **Table S1A**), which was consistent with previous *A. millepora* estimates (*9*). Third, genetic diversity within datasets followed a scaling relationship with area (*18*) that confirmed decreasing gene flow with increasing geographic distance, as observed in other *Acropora* populations (**Fig. S24**) (*19*, *20*).

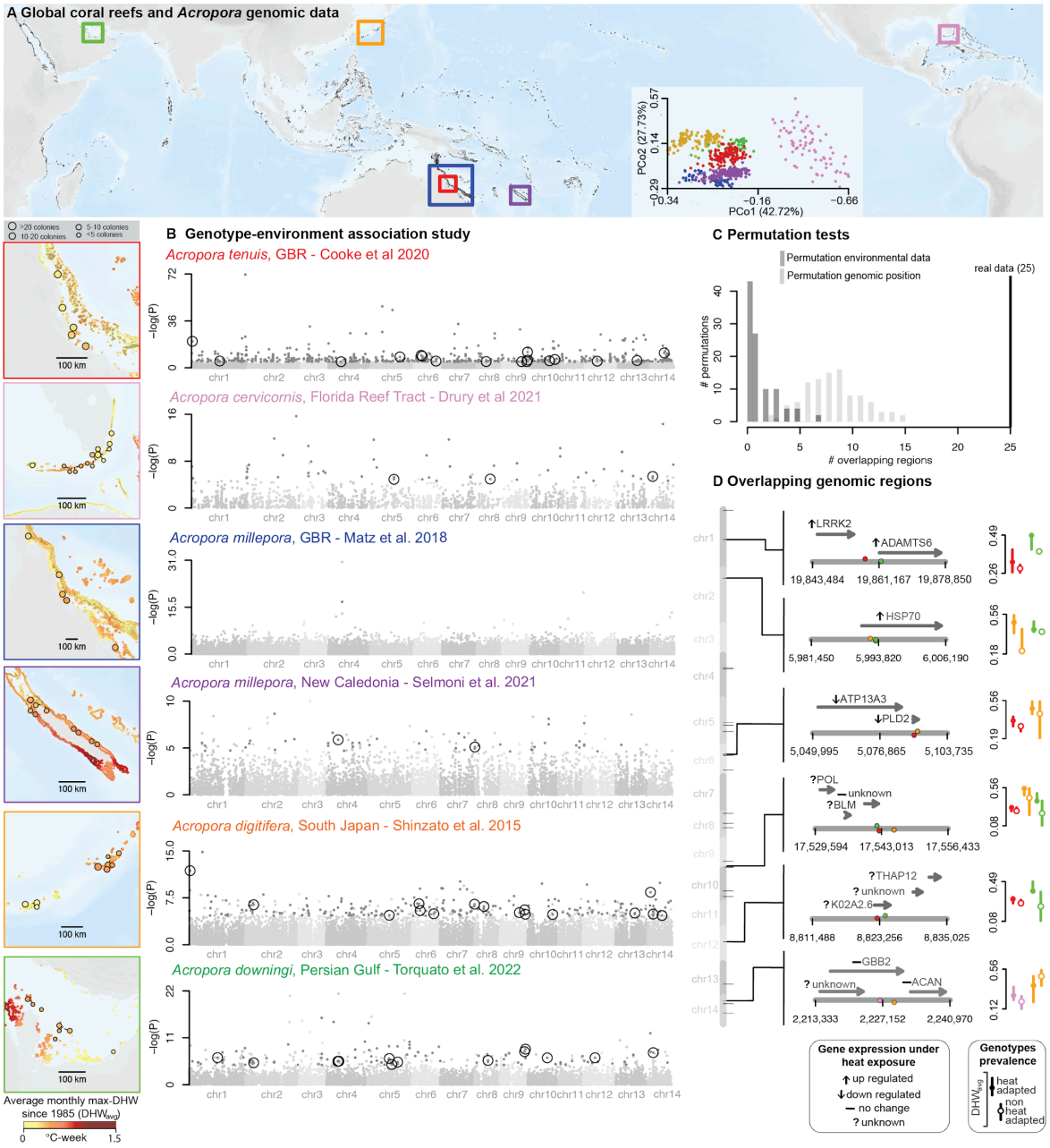

Fig. 1 | Genome-wide scans of evolutionary signals in 547 *Acropora sp.* identifies overlapping signals of heat adaptation.

(**A**) Distribution of global coral reefs and DNA sequencing data from six *Acropora sp.* populations (squares). For every population, shown are the sampling locations across reefs exposed to contrasting thermal history [*i.e.*, average of monthly maxima Degree Heating Week (DHW_{avg}) since 1985 (maps on the left)]. The inset shows the two main principal coordinate axes summarizing the genetic distances between the six *Acropora* populations. (**B**) Genotype-environment association analyses identifying genetic variants significantly associated with thermal history (dark points) ($P_{permutations} < 0.1$). Circles show significant variants overlapping in the same genomic region (within a 5 kb distance) in two or more *Acropora* populations. (**C**) Results of 100 permutation tests showing the expected number of overlapping genomic regions with randomized environmental variables and randomized genomic position of genetic variants. (**D**) Six of the overlapping genomic regions, showing the genomic position of significant genetic variants (circles, colored by *Acropora* population) and annotated genes (arrows). Whether the annotated genes are known to change expression during heat stress from a meta-analysis of RNAseq of various *Acropora* species is shown next to the gene name (*21*). For every significant genetic variant, shown on the right is the prevalence of heat-adapted and non-heat-adapted genotypes by DHW_{avg} across *Acropora* populations (colors). Background maps were produced using the Global Relief Model from NOAA [ETOPO 2022 (*22*)] and the Global Distribution Map of Coral Reefs from the UNEP World Conservation Monitoring Center (*23*).

Given that controlled experiments exposing different *Acropora* individuals to heat show heritable differences in heat tolerance (*3*, *4*, *8*, *11*), we reason that surviving colonies from reefs that recently suffered repeated heatwaves would be enriched in genotypes enabling their survival. To test this hypothesis with the compiled datasets, we conducted genotype-environment associations (GEA) along the genome using a latent factor mixed model (LFMM2) (*24*). First, we characterized past heatwaves across reefs as a proxy for the environmental selection using Degree Heating Week (DHW), a variable describing the accumulation of thermal stress over a 12-week period (**Fig. 1A**) (*25*). A DHW above 4°C-week is associated with significant coral bleaching, and a DHW above 8°C-week with severe, widespread bleaching (*25*). We extracted the maximal DHW for every month from 1985 to the year of sampling from remote–sensing-derived datasets, and calculated the overall average (DHW_{avg}) (*26*) (**Text S4**). Next, using GEA analysis, we uncovered several SNPs significantly associated with historical heat stress, after proper correction for confounding population structure and multiple testing, ranging from two significant SNPs in GBR *A. millepora* to 750 SNPs in *A. tenuis* (**Fig. 1B, Table S1C, Text S5**). We found 25 genomic regions with overlapping heat-associated SNPs (*i.e.*, within 5 kb of each other) from at least two species. This overlap is significantly more than expected by chance based on two permutation approaches——one that randomizes environmental values across reefs and the other that randomizes genomic positions of significant SNPs (**Fig 1B**; **Table S2**; $P < 0.01$ using 100 permutations in both approaches). While genotype-environment association studies conducted on a single species are prone to false discoveries (*27*), the overlap of adaptive signals across species implies these are indeed important adaptive genotypes and there may be molecular convergence underlying heat adaptation across species (*28*).

To identify genes potentially impacted by these heat-associated SNPs, we searched within ±10 kbs of the 25 genomic regions with overlapping adaptive signals and found 34 annotated genes (**Fig. 1D, Table S2, Text S6**). We also retrieved the transcriptomic expression changes during heat stress from a meta-analysis of different *Acropora sp.* experiments (*21*), and found that 12 of the annotated genes were differentially expressed under heat exposure (**Table S2**). One of the annotated genes encoded a Heat Shock 70 kDa protein (HSP70), a molecular chaperone that refolds proteins misfolded by heat stress (*29*). This gene is up-regulated in heat-exposed *Acropora sp.*, and higher levels of a heat shock protein 70 were found associated with bleaching resistance in field experiments (*30*). Another annotated gene encoded p58IPK-interacting protein (THAP12), which is also implicated in the misfolded protein response as p58IPK (DnaJ homolog subfamily C member 3) is a molecular chaperone located in the endoplasmic reticulum (*31*). As heat-associated bleaching causes corals to lose the symbiotic algae living inside their tissue and that are essential for their survival, it seems plausible this symbiosis would be a target of selection during heatwave exposure (*32*). Consistent with this hypothesis, we also identified an annotated gene encoding for protein containing a thrombospondin-type-1 repeat domain (ADAMTS6), which has been proposed to mediate the early establishment of symbiosis and regulate symbiont specificity in the coral model system *Aiptasia sp.* (*33*, *34*). In addition, we identified another annotated gene, Phospholipase D2 (PLD2), that may mediate the cnidarian-algal symbiosis as the Phospholipase D signaling pathway was reported as the most prominent target for post-translational modification in symbiotic Aiptasia (*35*). Intriguingly, another Phospholipase (Phospholipase A2) has been shown to be upregulated in symbiotic versus aposymbiotic Aiptasia and is quickly downregulated during heat stress before bleaching (*36*). Finally, one annotated gene encoded for an aggrecan core protein (ACAN), an extracellular matrix component, that has also been found to be differentially expressed during heat in symbiotic versus aposymbiotic Aiptasia, suggesting an important role in symbiosis (*36*). Given their association with molecular heat responses and symbiosis, these genes should be prioritized in molecular and genetic studies to determine their roles in heat tolerance, symbiosis, and bleaching (*37*).

We then investigated how the prevalence of adaptive genotypes varied between *Acropora* populations exposed to different patterns of historical heatwaves. Focusing on SNPs from the 25 genomic regions with overlapping signals, we modeled the occurrence of putative heat-adaptive genotypes by DHW_{avg} values (**Fig. 3A**) through a Bayesian logistic mixed model with random factors controlling for variation across datasets, sampling sites, and genomic regions (*38*) (**Text S7, Fig. S15A)**. The resulting environmental genomic model indicated that *Acropora* from reefs exposed to a threshold DHW_{avg} value of 0.37°C-week have a 50% probability of adaptive genotype occurrence [95% confidence interval (CI) = 0.21–0.53; **Fig. 2A**]. Within our datasets, this threshold value of DHW_{avg} was typically observed with reefs exposed to 2 significant heatwaves (IQR = 1) since 1985 and was exceeded in sampling sites from the Florida Reef Tract, Japan, New Caledonia, and the Persian Gulf (**Fig. 2B, Fig. S8**). The environmental genomic model can be used to predict the distribution of heat-adapted genotypes in new unsampled regions with a mean absolute error of 20% (SD = ±10%, in a leave-one-population-out cross validation; **Fig. 2C**, **Fig. S15B**). As coral sampling and sequencing efforts expand (*39*), this environmental genomic model could be updated with data from new coral taxa to improve its predictive power.

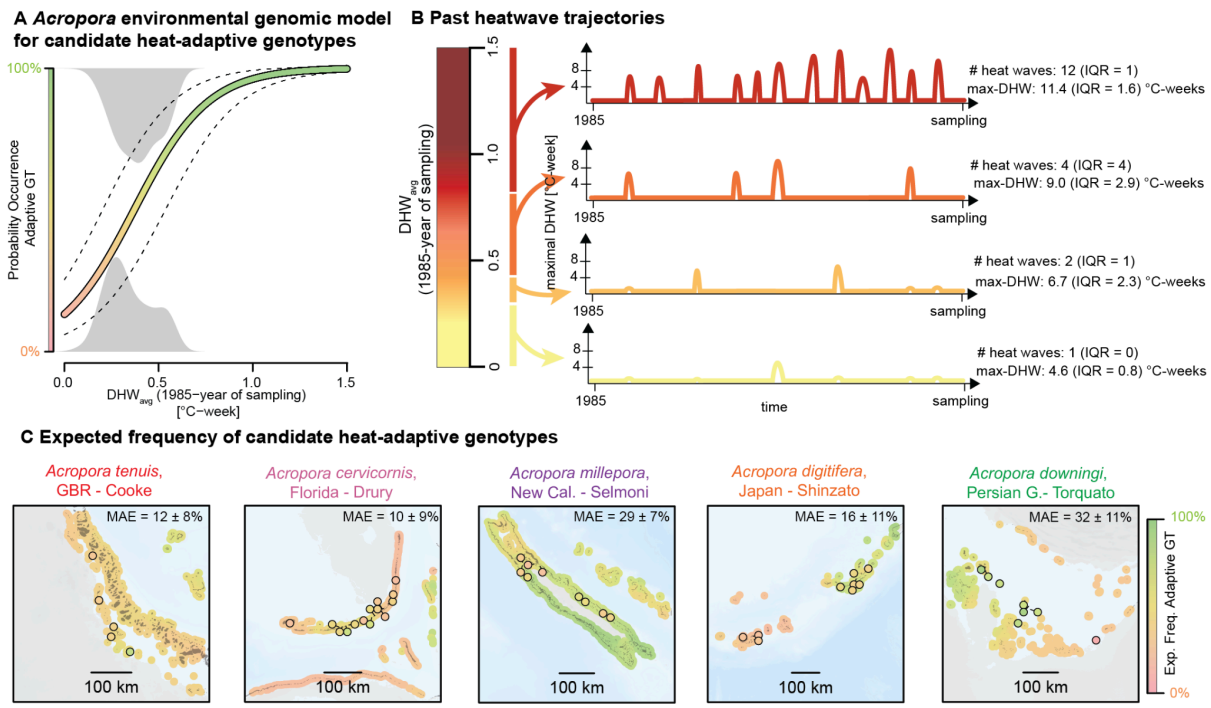

Fig. 2 | *Acropora* environmental genomic model for candidate heat-adaptive genotypes.
(A) Environmental genomic model showing the probability of occurrence of heat-adaptive genotypes as a function of thermal history—*i.e.*, average monthly maximal Degree Heating Week (DHW_{avg}) since 1985. The model was derived from frequencies of candidate heat-adaptive genotypes in five *Acropora* populations (histogram on the bottom: prevalence of non heat-adaptive genotypes along DHW_{avg}, histogram on top prevalence of heat-adaptive genotypes). Dashed line represents the confidence interval. **(B)** Exemplary thermal trajectories—defined by number of heatwaves above 4°C-week and maximal intensity—by range of DHW_{avg}, as observed across the reefs of the *Acropora* populations. **(C)** Spatial predictions of the frequency of heat-adaptive genotypes across the reefs of the five *Acropora* populations. For every population, predictions were made using the environmental genomic model trained on data from the other four populations (*i.e.*, leave-one-out cross validation). The mean absolute error (MAE) of the predicted genotype frequencies is shown in the top right corner of each map. Circles represent real genotype frequencies at sampling sites. Background maps were produced using the Global Relief Model from NOAA [ETOPO 2022 (*22*)] and the Global Distribution Map of Coral Reefs from the UNEP World Conservation Monitoring Center (*23*).

Although there is considerable interest in monitoring the conservation status of reefs, the observed variation in recent coral cover losses is notoriously challenging to interpret with heatwave data alone (*40*, *41*). We thus asked whether predictions from our environmental genomic model could help explain local *Acropora* decline (*40*, *41*). For this proof-of-concept analysis, we focused on one of the best surveyed reef areas in the world—the northern GBR—leveraging *in situ* survey data (*42*) covering the marine heatwaves of 2016 (23 surveyed reefs; **Fig. 3A**) and 2017 (29 surveyed reefs; **Fig. 3B**). To explain the relative change in *Acropora* cover given the heatwave intensity, we first built a linear mixed model (*43*) using random factors to control the unbalanced geographical and temporal distribution (**Text S8**). Built under the null hypothesis that *Acropora* cover change is driven only by heat exposure, this model estimated a 6% cover decline per °C-week of heat exposure (95% CI = [2%, 10%]; $P = 5x10^{-3}$; **Table S4A**) and explained 8% of the *Acropora* cover variation [*i.e.,* marginal R^2=0.08, (*44*); **Fig. 3C**]. We then used our environmental genomic model to group survey sites by the expected frequency of heat-adaptive genotypes (low: <50% and high: ≥50%). By including this adapted/non-adapted reef categories, our alternative hypothesis model significantly improved the goodness of fit by $\Delta mR^2 = +0.20$ [difference in the marginal coefficient of determination; $P < 2.2 \times 10^{-16}$ under a Mann-Whitney-Wilcoxon test of jackknife resampled mR^2]. The separation of *Acropora* decline rates between adapted and non-adapted reefs explains the increase in the model fit; while there was a nonsignificant ~1% cover decline for reefs with high frequencies of heat-adaptive genotypes, there was a significant ~5% *Acropora* cover decline per °C-week for reefs with a low expected frequency of heat-adaptive genotypes (95% CI = [2%, 8%]; $P = 1.5 \times 10^{-6}$; **Fig. 4D; Table S4B**). In comparison, the predictive power of another alternative model based on past heat exposure alone (*i.e.,* without using the environmental genomic model) was significantly lower ($\Delta mR^2 = -0.1$, $P < 2.2 \times 10^{-16}$ under a Mann-Whitney-Wilcoxon test; **Fig. 3C, Text S8**). These results suggest that better predictions of the vulnerability of reefs to future heatwaves could be generated by including genetic information from a few coral colonies projected at large scales.

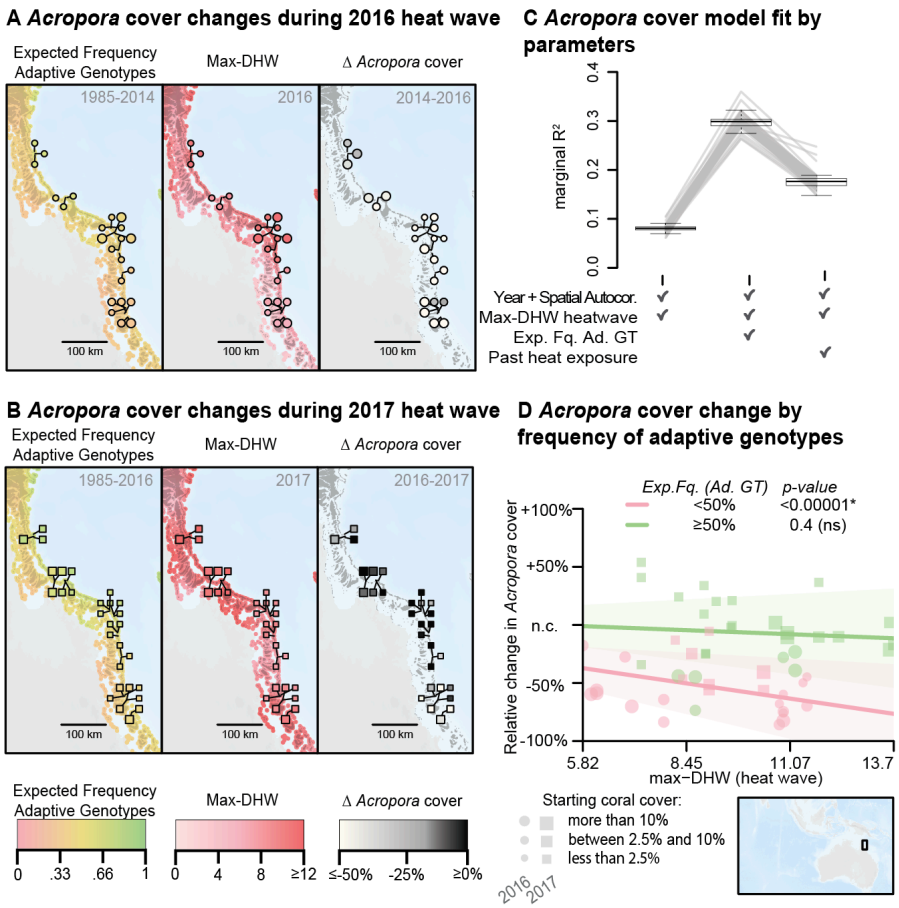

Fig. 3 | Adaptive genotype predictions explain local *Acropora* decline by heat exposure in the Great Barrier Reef

Shown are genomic, environmental, and ecological indicators for the northern Australian Great Barrier Reef during the **(A)** 2016 and **(B)** 2017 heatwaves. The left map shows the expected frequency of heat-adaptive genotypes across the region (pink to green; circles are survey sites of *Acropora* cover), derived from the average monthly maxima Degree Heating Week (DHW_{avg}) since 1985 using the environmental genomic model. The central map displays the distribution of heat stress intensity during the heatwave as maximal DHW (red). The map on the right displays the relative changes in *Acropora* cover (greyscale) before and after the heatwave (*42*). **(C)** The distributions of marginal coefficients of determination (marginal R^2) for models explaining change in *Acropora* cover using different explanatory variables. Gray lines represent marginal R^2 estimations from distinct jackknife subsamples. **(D)** The model with the highest marginal R^2 from (C): the relative change in *Acropora* cover is represented as a function of heatwave intensity for reefs predicted with high (>50%, green) or low (<50%, red) expected frequency of heat-adaptive genotypes. The shaded areas show the confidence intervals of the regression lines. Background maps were produced using the Global Relief Model from NOAA [ETOPO 2022 (*22*)] and the Global Distribution Map of Coral Reefs from the UNEP World Conservation Monitoring Center (*23*).

Global predictive models of coral decline and real-time detection of coral bleaching are primarily guided by remote sensing of sea surface temperature (*45*), and do not yet account for the evolutionary and genetic differences between corals from different reefs. As *Acropora* is a geographically widespread reef-building coral taxa (**Fig. S18**) (*46*), we used our environmental genomic model to predict the spatial distribution of heat-adapted genotypes at worldwide scale, and to study if this distribution aligned with global patterns of coral decline (**Text S9**). We first retrieved broad-scale coral decline estimates during the 2009–2018 decade for eight oceanic regions from the 2020 Status of Coral Reefs of the World report (*1*) (**Table S5**). Next, we compiled DHW data over the same period to categorize reefs worldwide by the degree of heatwave exposure: low (maximal DHW <4°C-week), significant (4–8°C-week), and severe (>8°C-week). (**Fig. 4A**, **Fig. S21**, **Table S5**). In addition, we compiled global DHW_{avg} between 1985 and 2008 (**Fig. S19**) and categorized the world's reefs by the expected frequency of heat-adaptive genotypes (low: <50% and high: ≥50%) using our *Acropora* environmental genomic model (**Fig. S20**). Genomic vulnerability was detected when reefs were exposed to severe heat waves while having low frequency of heat-adaptive genotypes (**Fig. 4A, Table S5**) (*47*). We found a weak correlation between regional coral loss and the fraction of reefs exposed to severe heatwaves among the eight oceanic regions [weighted Pearson correlation by reef area of every region, wR= –0.48; **Fig. 4B**; using the R package wCorr (*48*)]. Remarkably, the regional fractions of reefs under genomic vulnerability correlated strongly with regional coral decline (wR= –0.86; **Fig. 4B**). Furthermore, the global fraction of genomically vulnerable reefs (18%) aligned with the worldwide coral decline reported during the 2009–2018 period (14%; **Table S5**). Running the same analysis without genetic information (*i.e.,* adaptive thresholds arbitrarily set from past heatwave exposure) resulted in weak correlations with coral cover decline (**Fig. S22C**, **Fig. S23**). Together, these results strongly suggest that accounting for genomic vulnerability can improve the predictability of coral decline at a global scale.

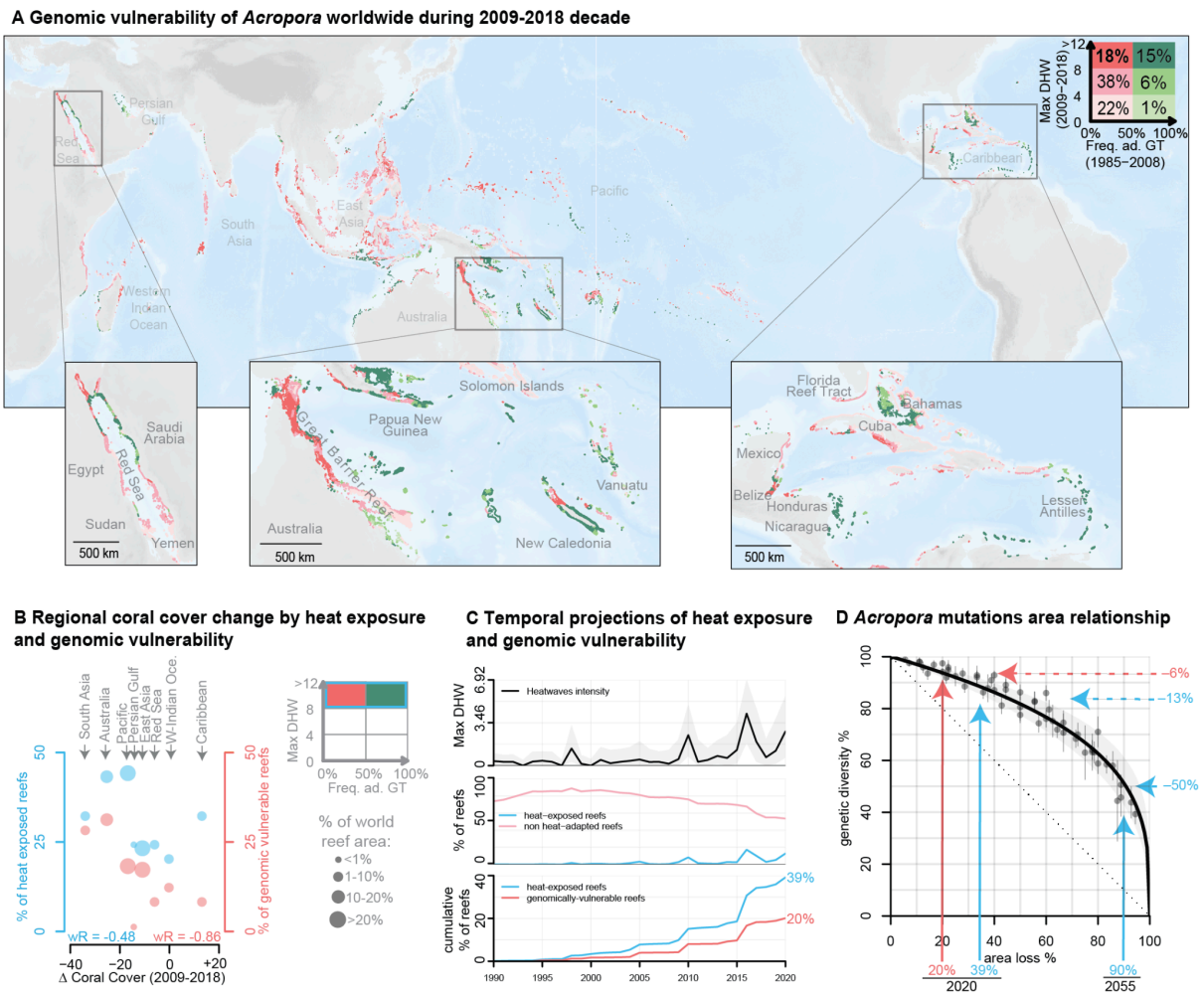

Fig. 4 | Genomic vulnerability and ongoing genetic diversity loss across global reefs.
(**A**) Global map of coral reefs colored by expected frequency of heat-adaptive genotypes based on heat stress from 1985–2008 (<50%: red, ≥50% green). The intensity of colors represents the intensity of heat stress (maximal DHW) during the 2009–2018 decade (low: <4°C-week, significant: ≥4 and <8°C-week, severe: ≥8°C-week). Genomically vulnerable reefs (dark pink) are categorized as those with a low expected frequency of adaptive genotypes by 2008 and exposed to severe heat stress between 2009–2018. **(B)** Coral declines during the 2009–2018 decade across eight oceanic regions (*1*), and weighted correlation (wR) of regional declines with the fraction of reefs exposed to severe heat stress (blue) and with the fraction of genomically vulnerable reefs (pink). Correlation scores are weighted by regional reef area, displayed by points size. **(C)** For the 1990–2020 period, shown are the year-by-year global trends of heatwave intensity (top graph), fraction of heat-exposed and non-heat-adapted reefs (middle graph), and cumulative fraction of heat-exposed and genomically vulnerable reefs (bottom graph). **(D)** Estimated mutations-area relationship (MAR) of the *Acropora* populations (black line, shaded area as interval of confidence). Points represent the genetic diversity loss by area loss, as observed in stochastic simulations of extinction. Blue arrows represent the potential 2020 and 2055 reef loss (solid line) due to heat-exposure, and the corresponding genetic loss (dashed line). Pink line represents the potential 2020 reef loss (solid line) due to genomic vulnerability, and the corresponding genetic loss (dashed line). Background map was produced using the Global Relief Model from NOAA [ETOPO 2022 (*22*)] and the Global Distribution Map of Coral Reefs from the UNEP World Conservation Monitoring Center (*23*).

Over the past three decades, we have witnessed consistent ocean warming resulting in three global heatwaves (1998, 2010, 2016) that jeopardizes the future of coral reef ecosystems (*49*, *50*). To simulate how coral heat exposure, adaptation, and genomic vulnerability may have changed over time worldwide, we combined year-by-year thermal trajectories during 1990–2020 with our environmental genomic model (**Text S11**). Despite the global fraction of heat-adapted reefs increased by ~30% during the projected period (**Fig. 4C**, center plot), the fraction of reefs experiencing genomic vulnerability to heatwaves approximately doubled in concomitance to each of the three global heatwaves (**Fig. 4C**, bottom plot). The potential coral decline driven by heat exposure and genomic vulnerability has likely caused the loss of entire *Acropora* populations and of the associated genetic diversity. Even if reefs recover from this widespread decline, the erosion of genetic diversity reduces the adaptive capacity of the new coral populations, which might be more sensitive to future environmental stressors (*51*). To estimate the amount of *Acropora* genetic diversity at risk by reef area loss, we used the mutations-area relationship (MAR) framework (*18*), which characterizes the scaling relationship between the number of genetic variants (SNPs) and geographical range across the six *Acropora* datasets (**Text S10**). Validated through stochastic simulations under different extinction scenarios (**Fig. S28**), this scaling relationship was summarized in an *Acropora* z_{MAR} parameter of 0.31 that can be used to predict the percentage of *Acropora* genetic diversity at risk by reef loss (95% CI = [0.24, 0.37]) (**Fig. S24, Fig. S25**). For example, 39% of the world's reefs had been exposed to at least one severe heatwave between 1990–2020, corresponding to the potential loss of 14% of the genetic diversity in *Acropora* corals. By 2055, 90% of the world's reefs might be exposed to severe heatwaves (*52*), resulting in a potential loss of ~50% of the global *Acropora* genetic diversity (**Fig. 4D**). Accounting for genomic vulnerability, the worldwide fraction of at-risk reefs is reduced to 20%, corresponding to a potential *Acropora* genetic loss of ~6%. These results suggest that quantifying the spread of heat-adapted corals under future heat will be key for accurately anticipating long-term coral decline.

Though our temporal reconstruction shows that 46% of the world's reefs have a high probability (>50%) of hosting heat-adapted coral genotypes (**Fig. 4C**, central plot), it is not known whether this will allow corals to withstand the hotter and more frequent heatwaves of the future (*52*). Furthermore, our estimation suggests that approximately half of these heat-adapted reefs originate from heatwave selection events experienced after 2010 and may still be recovering reef cover after the recent loss of unadapted corals. This recovery however might be hampered by local stressors [e.g., destructive fishing or coastal development (*53*, *54*)]. When we compare the predicted global distribution of heat-adapted reefs (**Fig. S29**) with worldwide proxies of human pressure on reefs—such as the Human Pressure Index (HPI) (*53*) and maps of marine protected areas (*55*)—heat-adapted reefs are slightly less exposed to local human stressors than non-heat-adapted ones (ΔHPI = –0.070, 95% CI = [–0.073, –0.066], $P < 2.2 \times 10^{-16}$ under an Analysis of Variance; **Fig. S30A**), although their extents are significantly less protected in some regions, including the Red Sea, the Persian Gulf, and the Pacific ($P < 2.2 \times 10^{-16}$ under a Chi-square test) (**Fig. S30B**). Heat-adapted reefs may be the most likely to survive future climate change and thus should be a priority for protection from human impacts by global reef conservation efforts. Recent research proposed that coral conservation efforts should focus on a portfolio of climate refugia (*i.e.,* reef regions escaping heatwaves and cyclones, and with a strong potential for larval dispersal) (*56*). As these refugia are by definition regions not impacted by climate change, heat-adapted coral reefs are drastically underrepresented in the climate refugia portfolio (12% heat-adapted reefs in refugia compared to 56% of non-heat-adapted reefs; **Fig. S30C**). Our results solidify the notion that evolutionary adaptation is a key component to understanding global change-driven risks and reef losses. We thus advocate that reef conservation priorities should include indicators of coral genomic vulnerability.

REFERENCES AND NOTES

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Competing interests. The authors declare no competing financial interests.

Data availability. The analyzed datasets are publicly available (see Supplemental Materials for data links). Code and processed data are available at Zenodo (*57*).

REFERENCES

1. D. Souter, S. Planes, J. Wicquart, M. Logan, D. Obura, F. Staub, *Status of Coral Reefs of the World: 2020* (Australian Government, United Nation Environment Program (UNEP), 2021).

2. M. Spalding, C. Ravilious, E. Green, *World Atlas of Coral Reefs* (University of California Press, Berkley, USA, 2001).

3. G. B. Dixon, S. W. Davies, G. A. Aglyamova, E. Meyer, L. K. Bay, M. V. Matz, Genomic determinants of coral heat tolerance across latitudes. *Science* **348**, 1460–1462 (2015).

4. E. J. Howells, D. Abrego, E. Meyer, N. L. Kirk, J. A. Burt, Host adaptation and unexpected symbiont partners enable reef-building corals to tolerate extreme temperatures. *Glob. Chang. Biol.* **22**, 2702–2714 (2016).

5. O. Selmoni, G. Lecellier, H. Magalon, L. Vigliola, N. Oury, F. Benzoni, C. Peignon, S. Joost, V. Berteaux-Lecellier, Seascape genomics reveals candidate molecular targets of heat stress adaptation in three coral species. *Mol. Ecol.* **30**, 1892–1906 (2021).

6. L. Thomas, J. N. Underwood, N. H. Rose, Z. L. Fuller, Z. T. Richards, L. Dugal, C. M. Grimaldi, I. R. Cooke, S. R. Palumbi, J. P. Gilmour, Spatially varying selection between habitats drives physiological shifts and local adaptation in a broadcast spawning coral on a remote atoll in Western Australia. *Sci Adv* **8**, eabl9185 (2022).

7. O. Selmoni, E. Rochat, G. Lecellier, V. Berteaux-Lecellier, S. Joost, Seascape genomics as a new tool to empower coral reef conservation strategies: An example on north-western Pacific Acropora digitifera. *Evol. Appl.* **13**, 1923–1938 (2020).

8. R. A. Bay, S. R. Palumbi, Multilocus adaptation associated with heat resistance in reef-building corals. *Curr. Biol.* **24**, 2952–2956 (2014).

9. Z. L. Fuller, V. J. L. Mocellin, L. A. Morris, N. Cantin, J. Shepherd, L. Sarre, J. Peng, Y. Liao, J. Pickrell, P. Andolfatto, M. Matz, L. K. Bay, M. Przeworski, Population genetics of the coral Acropora millepora: Toward genomic prediction of bleaching. *Science* **369** (2020).

10. I. Cooke, H. Ying, S. Forêt, P. Bongaerts, J. M. Strugnell, O. Simakov, J. Zhang, M. A. Field, M. Rodriguez-Lanetty, S. C. Bell, D. G. Bourne, M. J. van Oppen, M. A. Ragan, D. J. Miller, Genomic signatures in the coral holobiont reveal host adaptations driven by Holocene climate change and reef specific symbionts. *Sci Adv* **6** (2020).

11. Y. K. Jin, P. Lundgren, A. Lutz, J.-B. Raina, E. J. Howells, A. S. Paley, B. L. Willis, M. J. H. van Oppen, Genetic markers for antioxidant capacity in a reef-building coral. *Sci Adv* **2**, e1500842 (2016).

12. F. Torquato, J. Bouwmeester, P. Range, A. Marshell, M. A. Priest, J. A. Burt, P. R. Møller, R. Ben-Hamadou, Population genetic structure of a major reef-building coral species Acropora downingi in northeastern Arabian Peninsula. *Coral Reefs* **41**, 743–752 (2022).

13. C. Shinzato, S. Mungpakdee, N. Arakaki, N. Satoh, Genome-wide SNP analysis explains coral diversity and recovery in the Ryukyu Archipelago. *Sci. Rep.* **5**, 18211 (2015).

14. C. Drury, D. Lirman, Genotype by environment interactions in coral bleaching. *Proc. Biol. Sci.* **288**, 20210177 (2021).

15. M. V. Matz, E. A. Treml, G. V. Aglyamova, L. K. Bay, Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. *PLoS Genet.* **14**, e1007220 (2018).

16. F. J. Sedlazeck, P. Rescheneder, A. von Haeseler, NextGenMap: fast and accurate read mapping in highly polymorphic genomes. *Bioinformatics* **29**, 2790–2791 (2013).

17. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of Next Generation Sequencing Data. *BMC Bioinformatics 2014 15:1* **15**, 1–13 (2014).

18. M. Exposito-Alonso, T. R. Booker, L. Czech, L. Gillespie, S. Hateley, C. C. Kyriazis, P. L. M. Lang, L. Leventhal, D. Nogues-Bravo, V. Pagowski, M. Ruffley, J. P. Spence, S. E. Toro Arana, C. L. Weiß, E. Zess, Genetic diversity loss in the Anthropocene. *Science* **377**, 1431–1435 (2022).

19. R. García-Urueña, S. A. Kitchen, N. V. Schizas, Fine scale population structure of Acropora palmata and Acropora cervicornis in the Colombian Caribbean. *PeerJ* **10**, e13854 (2022).

20. R. M. van der Ven, H. A. Ratsimbazafy, M. Kochzius, Large-scale biogeographic patterns are reflected in the genetic structure of a broadcast spawning stony coral. *Coral Reefs* **41**, 611–624 (2022).

21. G. Dixon, E. Abbott, M. Matz, Meta-analysis of the coral environmental stress response: Acropora corals show opposing responses depending on stress intensity. *Mol. Ecol.* **29**, 2855–2870 (2020).

22. NOAA National Centers for Environmental Information, ETOPO 2022 15 Arc-Second Global Relief Model, (2022); https://doi.org/10.25921/fd45-gt74.

23. Unep-Wcmc, WorldFish-Center, Wri, Tnc, Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 4.1 (2021). http://data.unep-wcmc.org/datasets/1.

24. K. Caye, B. Jumentier, J. Lepeule, O. François, LFMM 2: Fast and Accurate Inference of Gene-Environment Associations in Genome-Wide Studies. *Mol. Biol. Evol.* **36**, 852–860 (2019).

25. G. Liu, A. E. Strong, W. Skirving, Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *Eos Trans. Amer. Geophys. Union* **84**, 137–141 (2003).

26. O. Selmoni, G. Lecellier, V. Berteaux-Lecellier, S. Joost, The Reef Environment Centralized InFormation System (RECIFS) : An integrated geo‐environmental database for coral reef research and conservation. *Glob. Ecol. Biogeogr.* **32**, 622–632 (2023).

27. O. Selmoni, E. Vajana, A. Guillaume, E. Rochat, S. Joost, Sampling strategy optimization to increase statistical power in landscape genomics: A simulation-based approach. *Mol. Ecol. Resour.* **20**, 154–169 (2020).

28. T. R. Booker, S. Yeaman, M. C. Whitlock, Using genome scans to identify genes used repeatedly for adaptation. *Evolution* **77**, 801–811 (2023).

29. R. Rosenzweig, N. B. Nillegoda, M. P. Mayer, B. Bukau, The Hsp70 chaperone network. *Nat. Rev. Mol. Cell Biol.* **20**, 665–680 (2019).

30. Y. D. Louis, R. Bhagooli, D. Seveso, D. Maggioni, P. Galli, M. Vai, S. D. Dyall, Local acclimatisation-driven differential gene and protein expression patterns of Hsp70 in Acropora muricata: Implications for coral tolerance to bleaching. *Mol. Ecol.* **29**, 4382–4394 (2020).

31. R. van Huizen, J. L. Martindale, M. Gorospe, N. J. Holbrook, P58IPK, a novel endoplasmic reticulum stress-inducible protein and potential negative regulator of eIF2α signaling. *J. Biol. Chem.* **278**, 15558–15564 (2003).

32. M. J. H. van Oppen, J. M. Lough, "Synthesis: Coral Bleaching — Patterns, Processes, Causes and Consequences" in *Coral Bleaching: Patterns, Processes, Causes and Consequences*, M. J. H. van Oppen, J. M. Lough, Eds. (Springer Berlin Heidelberg, Berlin, Heidelberg, 2009; https://doi.org/10.1007/978-3-540-69775-6_11), pp. 175–176.

33. E.-F. Neubauer, A. Z. Poole, P. Neubauer, O. Detournay, K. Tan, S. K. Davy, V. M. Weis, A diverse host thrombospondin-type-1 repeat protein repertoire promotes symbiont colonization during establishment of cnidarian-dinoflagellate symbiosis. *Elife* **6** (2017).

34. E. S. Bellis, R. B. Edlund, H. K. Berrios, H. A. Lessios, D. R. Denver, Molecular signatures of host specificity linked to habitat specialization in Exaiptasia sea anemones. *Ecol. Evol.* **8**, 5413–5426 (2018).

35. F. Simona, H. Zhang, C. R. Voolstra, Evidence for a role of protein phosphorylation in the maintenance of the cnidarian-algal symbiosis. *Mol. Ecol.* **28**, 5373–5386 (2019).

36. P. A. Cleves, C. J. Krediet, E. M. Lehnert, M. Onishi, J. R. Pringle, Insights into coral bleaching under heat stress from analysis of gene expression in a sea anemone model system. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 28906–28917 (2020).

37. O. Selmoni, L. K. Bay, M. Exposito-Alonso, P. A. Cleves, Finding genes and pathways that underlie coral adaptation. *Trends Genet.* **40**, 213–227 (2024).

38. J. D. Hadfield, MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *J. Stat. Softw.* **33**, 1–22 (2010).

39. M. L. Pinsky, R. D. Clark, J. T. Bos, Coral Reef Population Genomics in an Age of Global Change. *Annu. Rev. Genet.* **57**, 87–115 (2023).

40. T. R. McClanahan, E. S. Darling, J. M. Maina, N. A. Muthiga, S. D'agata, J. Leblond, R. Arthur, S. D. Jupiter, S. K. Wilson, S. Mangubhai, A. M. Ussi, M. M. M. Guillaume, A. T. Humphries, V. Patankar, G. Shedrawi, J. Pagu, G. Grimsditch, Highly variable taxa-specific coral bleaching responses to thermal stresses. *Mar. Ecol. Prog. Ser.* **648**, 135–151 (2020).

41. T. R. McClanahan, J. M. Maina, E. S. Darling, M. M. M. Guillaume, N. A. Muthiga, S. D'agata, J. Leblond, R. Arthur, S. D. Jupiter, S. K. Wilson, S. Mangubhai, A. M. Ussi, A. T. Humphries, V. Patankar, G. Shedrawi, P. Julius, J. Ndagala, G. Grimsditch, Large geographic variability in the resistance of corals to thermal stress. *Glob. Ecol. Biogeogr.* **29**, 2229–2247 (2020).

42. M. González-Rivero, P. Bongaerts, O. Beijbom, O. Pizarro, A. Friedman, A. Rodriguez-Ramirez, B. Upcroft, D. Laffoley, D. Kline, C. Bailhache, R. Vevers, O. Hoegh-Guldberg, The Catlin Seaview Survey - kilometre-scale seascape assessment, and monitoring of coral reef ecosystems. *Aquat. Conserv.* **24**, 184–198 (2014).

43. M. E. Brooks, K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, B. M. Bolker, glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400 (2017).

44. S. Nakagawa, P. C. D. Johnson, H. Schielzeth, The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* **14** (2017).

45. W. Skirving, B. Marsh, J. De La Cour, G. Liu, A. Harris, E. Maturi, E. Geiger, C. M. Eakin, CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1. *Remote Sensing* **12**, 3856 (2020).

46. W. Renema, J. M. Pandolfi, W. Kiessling, F. R. Bosellini, J. S. Klaus, C. Korpanty, B. R. Rosen, N. Santodomingo, C. C. Wallace, J. M. Webster, K. G. Johnson, Are coral reefs victims of their own past success? *Sci Adv* **2**, e1500850 (2016).

47. K. E. Lotterhos, Interpretation issues with "genomic vulnerability" arise from conceptual issues in local adaptation and maladaptation. *Evol Lett*, qrae004 (2024).

48. A. Emad, P. Bailey, *wCorr: Weighted Correlations* (2023; https://american-institutes-for-research.github.io/wCorr/).

49. T. P. Hughes, J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J. P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Y. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, S. K. Wilson, Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).

50. T. P. Hughes, M. L. Barnes, D. R. Bellwood, J. E. Cinner, G. S. Cumming, J. B. C. Jackson, J. Kleypas, I. A. van de Leemput, J. M. Lough, T. H. Morrison, S. R. Palumbi, E. H. van Nes, M. Scheffer, Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).

51. W. F. Fagan, E. E. Holmes, Quantifying the extinction vortex. *Ecol. Lett.* **9**, 51–60 (2006).

52. R. van Hooidonk, J. A. Maynard, D. Manzello, S. Planes, Opposite latitudinal gradients in

projected ocean acidification and bleaching impacts on coral reefs. *Glob. Chang. Biol.* **20**, 103–112 (2014).

53. M. Andrello, E. S. Darling, A. Wenger, A. F. Suárez-Castro, S. Gelfand, G. N. Ahmadia, A global map of human pressures on tropical coral reefs. *Conserv. Lett.* **15** (2022).

54. D. C. Claar, S. Starko, K. L. Tietjen, H. E. Epstein, R. Cunning, K. M. Cobb, A. C. Baker, R. D. Gates, J. K. Baum, Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nat. Commun.* **11**, 6097 (2020).

55. UNEP-WCMC, IUCN, The World Database on Protected Areas (WDPA), (2020); www.protectedplanet.net.

56. H. L. Beyer, E. V. Kennedy, M. Beger, C. A. Chen, J. E. Cinner, E. S. Darling, C. M. Eakin, R. D. Gates, S. F. Heron, N. Knowlton, D. O. Obura, S. R. Palumbi, H. P. Possingham, M. Puotinen, R. K. Runting, W. J. Skirving, M. Spalding, K. A. Wilson, S. Wood, J. E. Veron, O. Hoegh-Guldberg, Risk‐sensitive planning for conserving coral reefs under rapid climate change. *Conserv. Lett.* **11**, e12587 (2018).

57. O. Selmoni, P. Cleves, M. Exposito-Alonso, Scripts and data from "Global coral genomic vulnerability explains recent reef losses," (2024); https://doi.org/10.5281/zenodo.10838948.