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Current Biology

Marine Heatwave Drives Cryptic Loss of Genetic Diversity in Underwater Forests

Highlights

- A marine heatwave caused massive loss of genetic diversity in underwater forests
- Between 30% and 65% of average genetic diversity was lost across 800 km of coastline
- Loss of genetic diversity was cryptic and not reflected in measures of forest cover
- Marine heatwaves may compromise ability to respond to future climatic change

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In Brief

Extreme events have profound ecological impacts, but knowledge of how they affect underlying genetic diversity is scant. Gurgel et al. use rare empirical data from before a marine heatwave to demonstrate massive and cryptic loss of genetic diversity in underwater forests, which may compromise their ability to respond to future climatic change.

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Marine Heatwave Drives Cryptic Loss of Genetic Diversity in Underwater Forests

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SUMMARY

Extreme events have profound ecological impacts on species and ecosystems, including range contractions and collapse of entire ecosystems. Although theory predicts that extreme events cause loss of genetic diversity, empirical demonstrations are rare, obscuring implications for future adaptive capacity of species and populations. Here, we use rare genetic data from before an extreme event to empirically demonstrate massive and cryptic loss of genetic diversity across ~800 km of underwater forests following the most severe marine heatwave on record. Two forest-forming seaweeds (*Sargassum fallax* and *Scytothalia dorycarpa*) lost ~30%–65% of average genetic diversity within the 800-km footprint of the heatwave and up to 100% of diversity at some sites. Populations became dominated by single haplotypes that were often not dominant or present prior to the heatwave. Strikingly, these impacts were cryptic and not reflected in measures of forest cover used to determine ecological impact of the heatwave. Our results show that marine heatwaves can drive strong loss of genetic diversity, which may compromise adaptability to future climatic change.

INTRODUCTION

Extreme events have precipitated significant impacts to species and ecosystems over both evolutionary and contemporary timescales [1]. Events, such as floods, bushfires, heatwaves, and cold spells, shape both the contemporary response and future adaptability of species to change [2–7]. With extreme events predicted to increase in frequency and intensity [8], understanding impacts at all levels of biological organization, from genes to ecosystems, is critical for assessing species adaptive capacity under future scenarios of climatic change.

Although the ecological impacts of extreme climatic events are often obvious and well documented, little is known about how these events impact underlying patterns of genetic diversity and adaptability [1, 5, 7, 9]. Theory predicts that genetic diversity is lost following extreme events due to mortality and population bottlenecks driven by strong directional selection that promotes the survival and persistence of stress-tolerant genotypes [10]. Indeed, selection within natural populations may generally be weak, except during extreme events [11]. This is because, by definition, extreme events are characterized by conditions that are beyond the range normally experienced by organisms and often exceed physiological thresholds, thus promoting non-random mortality that can drive directional selection [7, 11].

Empirical demonstration of loss of genetic diversity following extreme events is, however, scant and heavily biased toward terrestrial ecosystems [1]. For example, genetic diversity of frogs and lizards has been shown to decline following bushfires [6, 12], and rapid diversity loss and directional selection for cold tolerance occurred in lizards following a severe cold snap [4]. In contrast, extreme flooding had variable effects on trajectories of insect genetic diversity that were dependent on taxa and their respective traits [7]. The impact of extreme events on genetic diversity in marine environments is, however, almost completely unstudied. This is likely because extreme events are largely spatially and temporally unpredictable [1, 13, 14], making the timely collection of *a priori* genetic data difficult, especially on the large spatial scales over which such events often occur. Although a few studies have shown the "option value" of genetic diversity for marine population persistence, whereby greater diversity confers fitness or survival following extreme events [9, 15], the impact of such events on subsequent genetic diversity and adaptability remains a critical knowledge gap.

Marine heatwaves are discrete, anomalously warm water events that exceed historical norms [16] and are increasing in frequency globally [17] with significant consequences for coastal marine species, communities, and the ecosystem services they provide [3, 18, 19]. An unprecedented marine heatwave impacted ~2,000 km of coast off Western Australia in 2011, where sea temperatures increased 2.5°C–5°C above normal for several weeks [20] (Figure 1). The heatwave precipitated

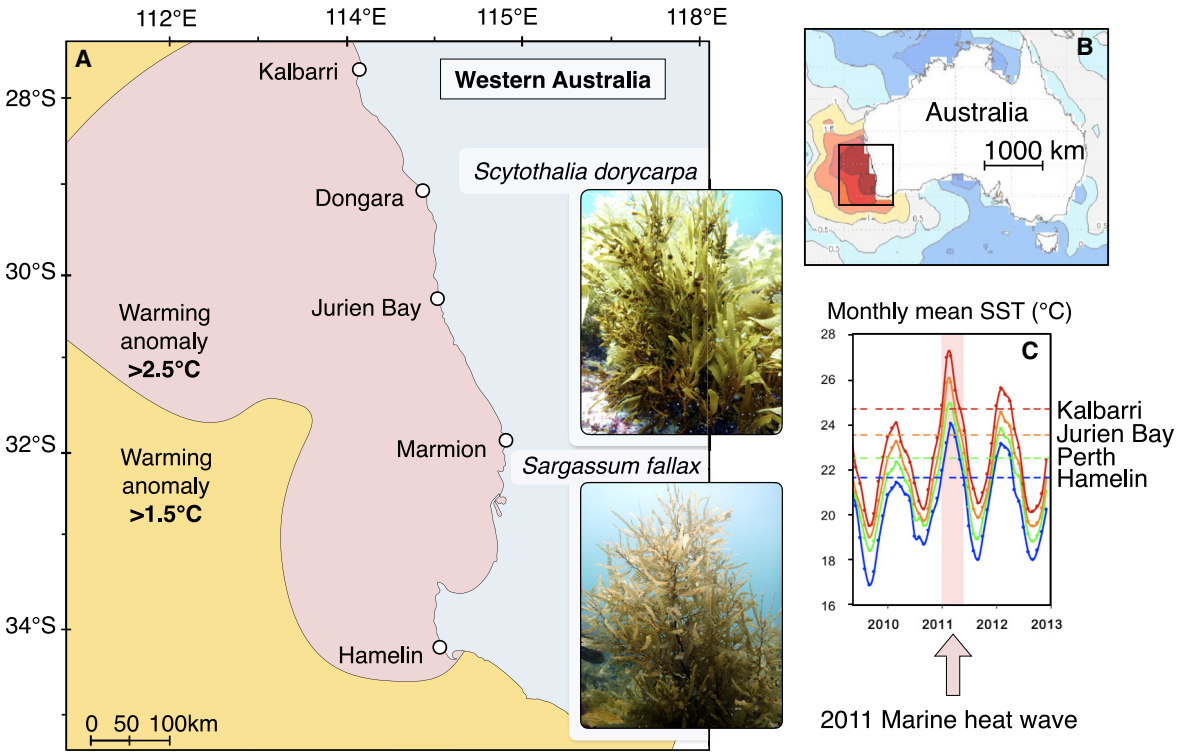

Figure 1. Sampling Locations within the Footprint of the Marine Heat Wave and Regional Evolution of the Heatwave

Sampling locations (A) and details of the regional evolution (B) of the temperature anomaly [9] based on surface temperature anomaly (C) reported from March 2011 compared to 1971–2000 surface temperature records [20]. Images of the species are also shown.

widespread and significant local extinction and range contraction of entire marine communities [3, 20, 21] and shifts in ecological structure [3, 22] and impacted fisheries [23]. Most heavily impacted were marine seaweed forests that underpin biodiversity throughout temperate regions [24–26].

The ecological response of marine seaweed forests to the heatwave varied among species and distributional position relative to the footprint of the heatwave. For example, the common foundation species, *Scytothalia dorycarpa* (Seirococcaceae, Fucales), contracted its range ~100 km at its low-latitude-range edge, losing 5% of its global distribution [20, 27], but suffered little discernible ecological impact at higher latitudes, where temperature anomalies largely remained within the species' 2.5°C thermal safety margin [28]. Other species, such as the dominant kelp, *Ecklonia radiata* (Lessoniaceae, Laminariales), showed ecological impacts that correlated with latitude as well as *a priori* standing genetic diversity [9, 29]. In contrast, abundances of other marine taxa proliferated following the heatwave due to competitive release [30, 31]. However, although the ecological impacts of the heatwave were well documented, there is no knowledge of how the heatwave impacted underlying genetic diversity of marine seaweed forests. Such knowledge may help unravel whether ecological changes are underpinned by directional loss of diversity driven by strong selection for heat-tolerant genotypes or random loss of diversity that confers greater vulnerability to future change. Such information is critical for predicting the adaptability of populations to future extreme events as well as designing management interventions [32].

Here, we provide a unique empirical demonstration of the impacts of an extreme climatic event (marine heatwave) on genetic diversity in seaweed forests. We utilize the rare occurrence of "before" genetic data on two marine forest species, *Scytothalia dorycarpa* (Seirococcaceae, Fucales) and *Sargassum fallax* (Sargassaceae, Fucales; hereafter referred to as *Scytothalia* and *Sargassum*) to characterize their genetic response to the strongest marine heatwave on record and the implications for future adaptability to climatic change.

RESULTS

The marine heatwave was associated with widespread loss of haplotype and nucleotide diversity over the 800 km sampled (Figure 2). Within the footprint of the heatwave, *Scytothalia* lost an average of 53%–65% of nucleotide diversity and 27%–66% of haplotype diversity (Figure 2A; Table S1). Similarly, *Sargassum* lost an average of 28%–29% of nucleotide diversity and 24%–33% of haplotype diversity following the heatwave (Figure 2B; Table S2). In particular, variation in haplotype diversity for *Sargassum* (among sites) was markedly greater after the heatwave (Figure 2B) because some sites were reduced to only a single haplotype (Figure 5). There was a significant increase in genetic differentiation among *Sargassum* populations after the heatwave (t tests $p < 0.05$) with average G_{ST} estimates increasing 339% for *rbc*L and 195% for *cox*3 (Table S3). Moreover, there was a loss of spatial genetic structure (north-south groupings) after the heatwave, with all sites genetically diverging in contrasting ways (Figure 3).

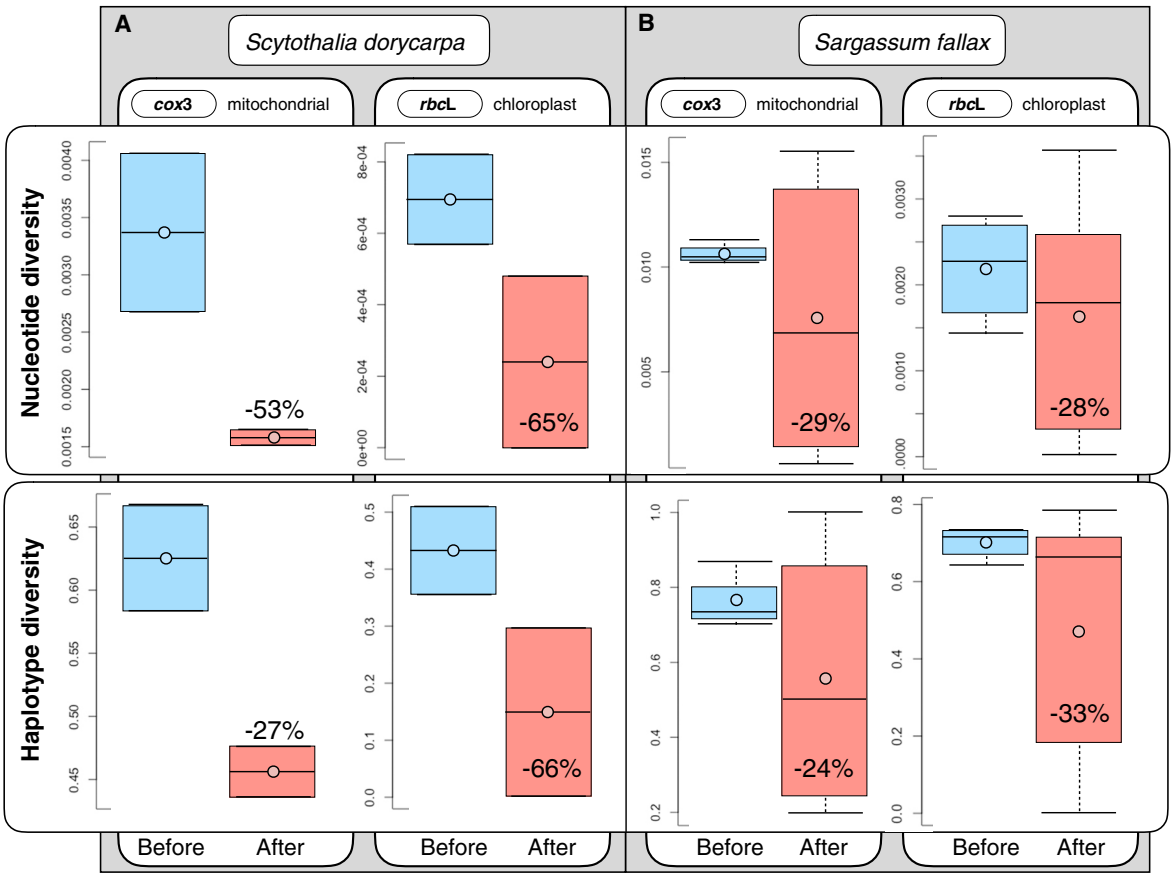

Figure 2. Boxplots Showing Decline in Genetic Diversity Metrics from Before and After the Heatwave

Nucleotide and haplotype diversity (averaged over sites) before and after the marine heatwave for *Scytothalia* (A) and *Sargassum* (B) for both the *cox*3 and *rbc*L genes. Overall percentage loss in genetic diversity is also presented. Whiskers represent upper and lower quartiles. There are no whiskers for *Scytothalia* because there were only 2 sites. See also Tables S1 and S2 for values within sites.

For both species, the declines in genetic diversity were mirrored at all sites across the 800 km sampled (Figures 4 and 5; Tables S1 and S2). For example, haplotype diversity declined at Kalbarri (−9% for *rbc*L for *Sargassum*), Jurien (−59% and −100% for *cox*3 and *rbc*L for *Sargassum*), Marmion (−12% and −100% for *Scytothalia* for cox3 and *rbc*L), and Hamelin (−77% and −74% for *Sargassum* and −46% and −28% for *Scytothalia* for *cox*3 and *rbc*L, respectively). The number of haplotypes tended to decline after the heatwave at each site, even with greater sampling effort (e.g., *Sargassum* at Hamelin; Figure 5). Often, low-frequency haplotypes were completely lost from sites after the heatwave (e.g., *cox3* and *Scytothalia*; Figure 4). The exception was *Sargassum* at Marmion, where there was an 85% and 22% increase in relative genetic diversity (nucleotide and haplotype diversity, respectively, for the *rbc*L gene) after the heatwave. A number of new *cox3* haplotypes that were not previously sampled were also found for *Sargassum* after the heatwave (Figure 5).

There was little detectable change in percent cover of these two seaweeds attributable to the heatwave between our sampling periods (genetic samples collected in 2008 and 2012; blue and red arrows in Figures 4 and 5), although, over longer timescales, increases in cover have occurred (e.g., Marmion and Jurien for *Sargassum* in 2013 and 2014).

DISCUSSION

Extreme events can have profound ecological impacts on species and ecosystems, but empirical demonstrations of how they impact underlying genetic diversity are rare, obscuring implications for future adaptive capacity. We use rare genetic data from before and after the most severe marine heatwave on record to empirically demonstrate massive and cryptic loss of genetic diversity in underwater forests.

Heatwave Drives Cryptic Loss of Genetic Diversity in Marine Forests

The marine heatwave was associated with widespread loss of haplotype and nucleotide diversity over the 800 km sampled. Overall, within the footprint of the heatwave, *Scytothalia* lost up to 66% of genetic diversity and *Sargassum* lost up to 33% of genetic diversity following the heatwave, which far exceeds losses of genetic diversity documented following extreme events in terrestrial species (e.g., 10%–14% average loss) [2, 7]. Moreover, for both species, these overall declines in genetic diversity were mirrored at most sites for which before and after samples were available. For example, loss of haplotype diversity at the rbcL gene ranged from 100% loss (*Sargassum* at Jurien and

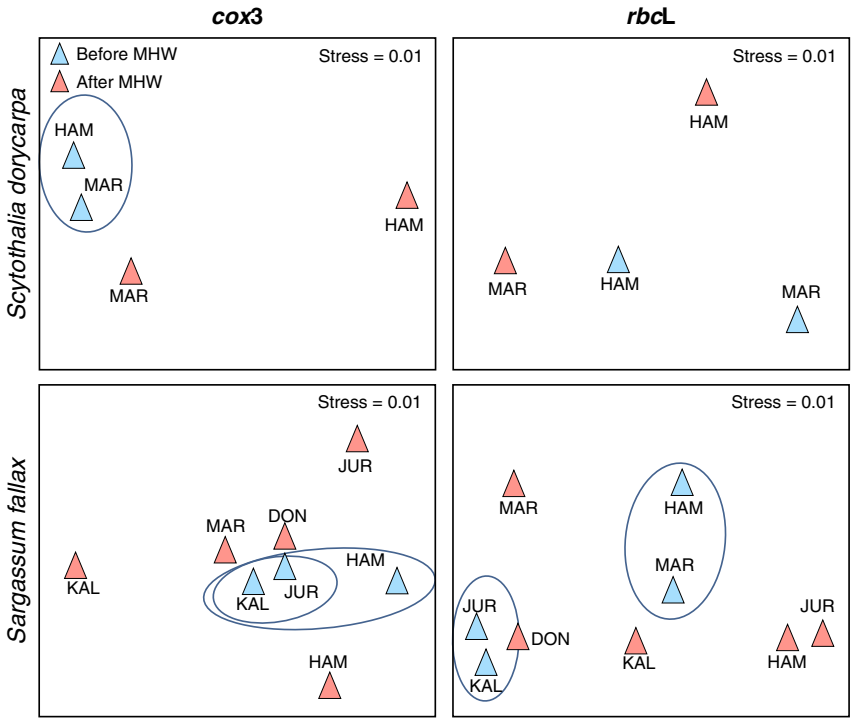

Figure 3. Overall Change in Population Genetic Structure from Before to After the Heatwave

Significant change in population genetic structure (non-metric multidimensional scaling; nMDS plots) of *Sargassum* and *Scytothalia* from before (blue symbols) to after (red symbols) the heatwave. Stress = 0.01 in all plots. Symbols show site centroids based on haplotype frequencies. KAL, Kalbarri; JUR, Jurien; DON, Dongara; MAR, Marmion; HAM, Hamelin. Ellipses represent north/south groupings before the heatwave. See also Table S3 for estimates of differentiation between pairs of sites.

Scytothalia at Marmion) to 9% loss at Kalbarri (*Sargassum*). Similarly, loss of haplotype diversity at the cox gene ranged from 100% (*Sargassum* at Kalbarri) to 12% (*Scytothalia* at Marmion). In particular, variation in haplotype diversity among sites for *Sargassum* was markedly greater after the heatwave because some sites were reduced to only a single haplotype. Although this largely precluded meaningful statistical tests, an increase in among-site variation is considered symptomatic of impacts [33]. These pronounced declines in diversity likely occurred because the heatwave was associated with increases in sea temperatures that were up to 5°C above normal for several weeks and exceeded or approached physiological thresholds of these species [28]. Indeed, *Scytothalia* suffered the most pronounced declines in diversity, consistent with the heatwave approaching its upper temperature thresholds [28] and exceeding them at lower latitudes (Jurien), where this species was completely extirpated from over 100 km of reef [27].

What is striking is that declines in genetic diversity were largely "cryptic," occurring in the absence of detectable change in percent cover of seaweeds attributable to the heatwave over our sampling periods (2008 and 2012; arrows in Figures 4 and 5). Given that it is unlikely that such declines in diversity occurred without significant mortality, we suggest that percent cover rapidly recovered following the heatwave, disguising the impacts on genetic diversity. Unlike corals that show obvious and lasting signs of mortality after thermal stress (skeletal bleaching) and continue to occupy space, seaweeds rapidly die, degrade, and disappear from the substratum, creating space for rapid recolonization. For example, cover of *Scytothalia* most likely rapidly recovered during its winter reproductive window a few months following the heatwave [34]. However, such a reproductive event would have involved a relatively small pool of surviving genotypes and, combined with the lack of dispersal ability in this species, would have propagated genetic diversity loss. Rapid reproduction and recruitment into newly available space may therefore have masked the striking genetic impact of the heatwave on this species. Such cryptic loss of diversity belies the true impact of the heatwave and suggests that measuring the response of organisms to extreme events via percent cover or abundance data only may underestimate true impacts and subsequent ability of populations to respond to future change. Instead, for fast-growing species, such as seaweeds, genetic diversity may be a sentinel indicator of impacts of extreme events and vulnerability and provides support for global initiatives to monitor genetic metrics as essential biodiversity variables (e.g., GEOBON [Group on Earth Observations Biodiversity Observation Network]; https://geobon.org/ebvs/working-groups/genetic-composition/).

Understanding Trajectories of Genetic Diversity Change

Despite an overall loss of genetic diversity in *Sargassum* within the footprint of the heatwave, the magnitude of loss varied among locations, highlighting the importance of ancillary demographic information to properly interpret impacts of extreme events. Although loss of genetic diversity was cryptic at most of the sites for which cover data were available, at Marmion, there was a 85% and 22% increase in relative genetic diversity (nucleotide and haplotype diversity, respectively, for the *rbc*L gene), which corresponded to a rapid ~50% increase in percent cover at the time genetic samples were taken after the heatwave (2012). Such an increase in cover and diversity is indicative of rapid population expansion. This is likely to have occurred via competitive release as other co-occurring species perished and space was liberated [35]. For example, the kelp (*Ecklonia radiata*) suffered ~25% cover loss at Marmion and 100% cover loss at Kalbarri [3] that would have created space for expansion and proliferation of *Sargassum* populations. Indeed, experimental canopy thinning in *E. radiata* forests has been shown to promote rapid *Sargassum* recruitment [35]. The influx of new *cox3* haplotypes that were not previously sampled suggests that the source of *Sargassum* propagules was likely external to local populations. Given this species has gas-filled vesicles and can float, dispersal and gene flow from distant populations is likely. Interestingly, populations of *Sargassum* at Jurien (which lost genetic diversity after the

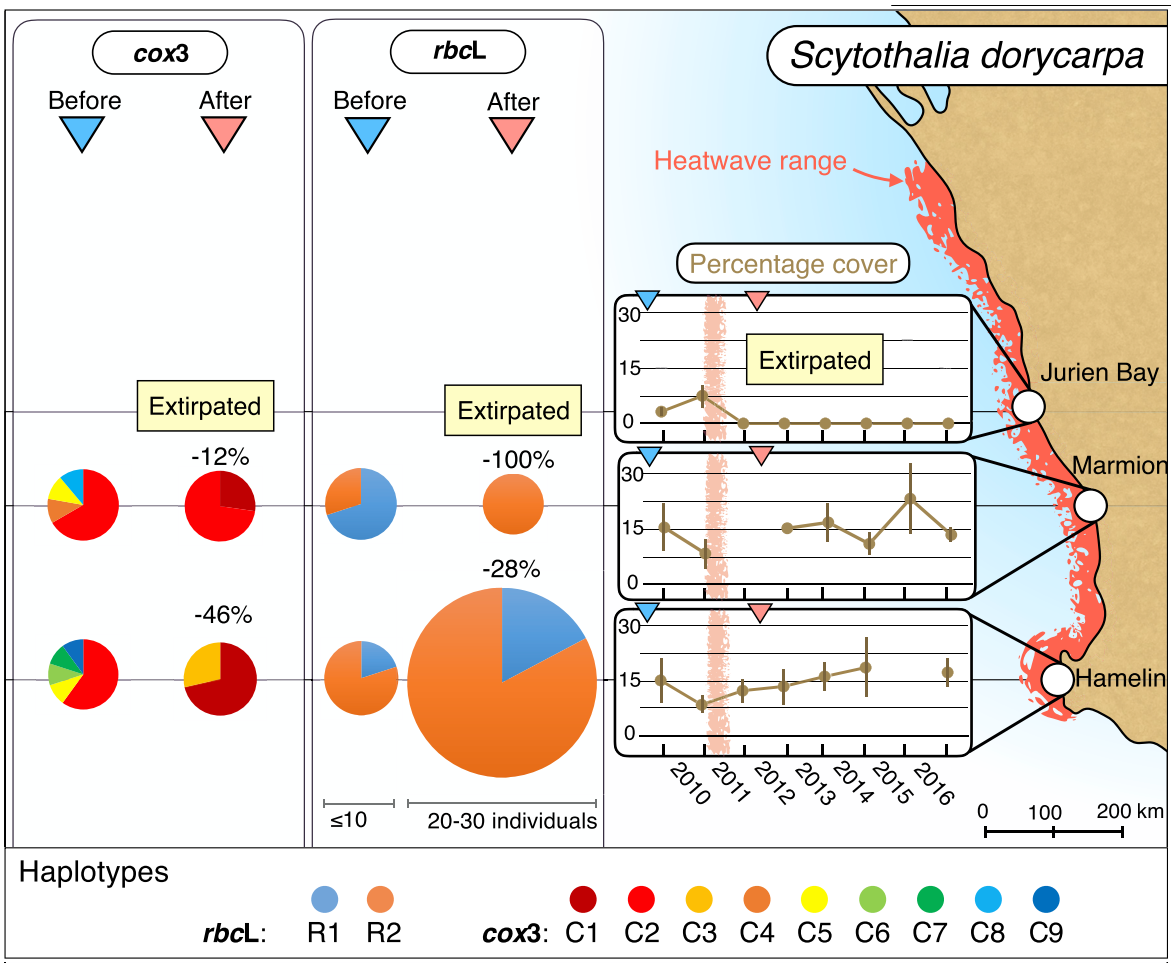

Figure 4. Change in Haplotype Frequencies, Loss of Diversity, and Cover of *Scytothalia*

Haplotype frequencies, loss of haplotype diversity, and percent cover (±SE) of *Scytothalia* before and after the heatwave at each site sampled in Western Australia. *Scytothalia* was completely extirpated at Jurien after the heatwave. Percent loss in relative loss of haplotype diversity at each site is also shown. Blue (before the heatwave) and red (after the heatwave) arrows on percentage cover graphs correspond to times of genetic sampling. See also Table S1 for estimates of diversity metrics.

heatwave) also underwent a rapid increase in cover 2 years following the heatwave (but after the time of our genetic sampling; Figure 5), concomitant with competitive release following 100% loss of *Scytothalia* [21] and ~50% loss of *Ecklonia radiata* [20]. Although this increase in cover occurred after our genetic sampling, we hypothesize that genetic diversity may have since recovered at this site, and contemporary sampling would show similar increases in diversity and population structure as for Marmion. These results highlight that spatial variation in trajectories of change in genetic diversity following extreme events can only be truly understood in the context of factors such as fluctuations in population abundance, dispersal capabilities, and competitive interactions. Thus, proper interpretation of mechanisms of genetic change after extreme events requires multifaceted knowledge from populations through to ecosystem dynamics.

Loss of Diversity and Future Adaptive Capacity

Such significant loss of genetic diversity may confer reduced adaptive capacity due to loss of latent adaptive responses [9, 15] or increased adaptive capacity to thermal change through directional selection for thermally tolerant genotypes. Although impacts can often result in a general loss of genetic diversity within populations, directional selection may manifest as a loss of diversity through dominance of certain genotypes and loss of low-frequency genotypes. Although a hypothesis of directional selection can only be robustly tested through experimentation and/or functional markers, there is some support here for selection in *Sargassum*, where haplotype R3 of the *rbc*L gene dominated after the heatwave in most sites. Mitochondrial *cox* genes have been shown to be involved in the evolution of thermal tolerance [36], and although we observed declines in diversity of *cox* haplotypes, we saw no consistent response in the dominance of certain *cox*3 haplotypes after the heatwave that would suggest selection. We suggest that the use of more variable markers with greater genome coverage (e.g., single-nucleotide polymorphisms through genotyping by sequencing, e.g., restriction-site-associated DNA sequencing [RAD-seq]) would help unravel these alternate

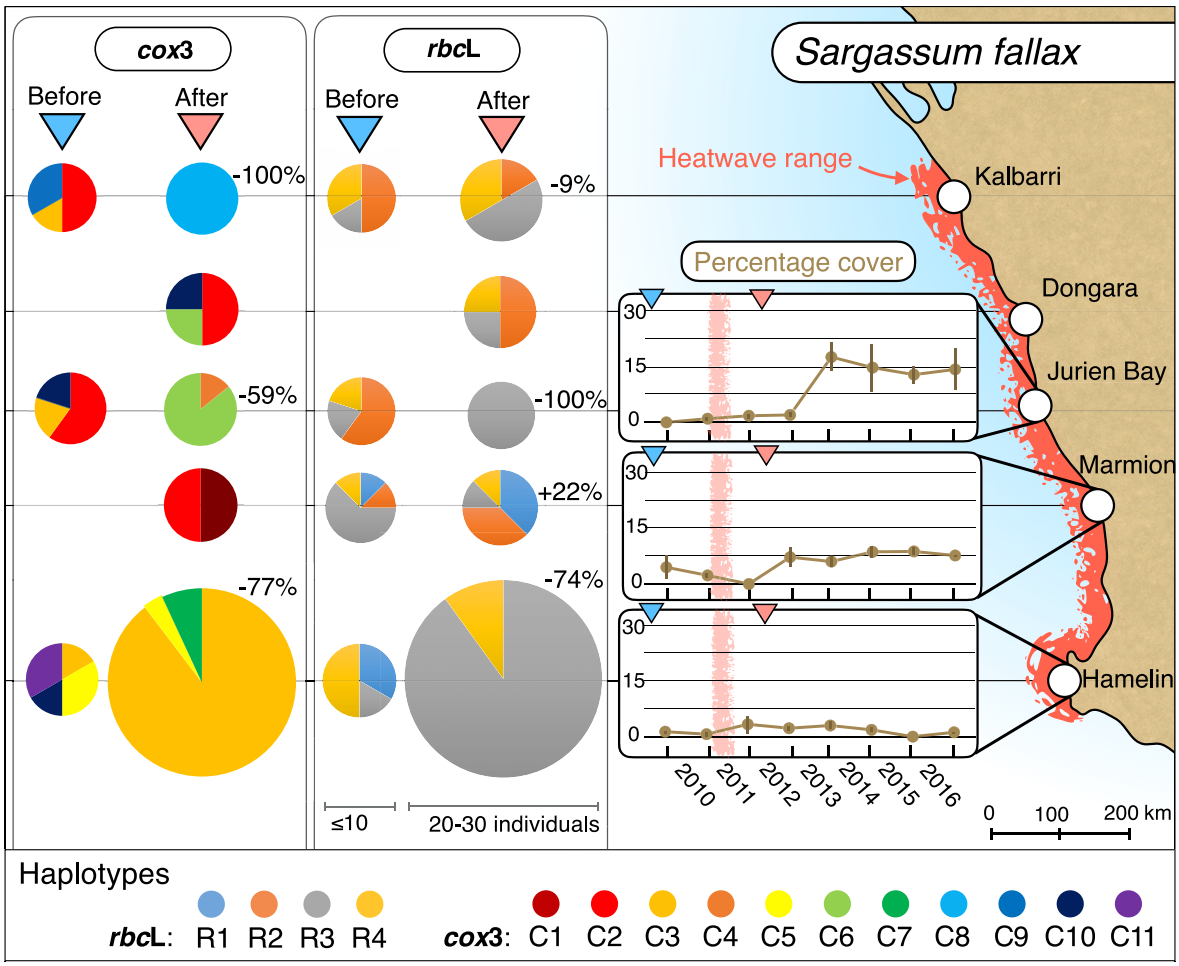

Figure 5. Change in Haplotype Frequencies and Haplotype Diversity and Cover of *Sargassum*

Haplotype frequencies, chance in haplotype diversity, and percent cover (±SE) of *Sargassum* before and after the heatwave at each site sampled in Western Australia. There were no percent cover data for Kalbarri or Dongara. Percent loss in relative haplotype diversity at each site is also shown. Blue (before the heatwave) and red (after the heatwave) arrows on percentage cover graphs correspond to times of genetic sampling. n = 1 for Kalbarri (cox) after the heatwave, and change should be interpreted with caution. See also Table S2 for estimates of diversity metrics.

hypotheses. Experimental manipulations using selected *cox*3 and *rbc*L (R3) haplotypes could also be performed to induce selection and test thermal tolerance, providing a pathway for causation. Regardless of whether selection has occurred, it is likely that a reduction in genetic diversity per se, as seen here across species and genes, will confer a reduced ability to respond to future stressors that characterize modern multi-stressor seascapes. Further, contemporary sampling will be key for unravelling the temporal persistence of heatwave impacts on genetic diversity and the subsequent adaptive capacity of these seaweed populations.

Conclusions

Although experimental studies are beginning to unravel how extreme events and environmental conditions impact genetic diversity [37, 38], empirical demonstrations from natural settings remain rare [39]. This is because *a priori* data on genetic diversity are often unavailable because extreme events are largely unpredictable in time and space [1, 13, 14]. We provide a rare empirical demonstration of the impact of an extreme event on genetic diversity across broad spatial scales and using multiple species and genes. Discrepancies between population estimates (e.g., percent cover data) and genetic diversity following events, as seen here and in other studies [6], suggests that genetic data may be a more sensitive estimate of impact and subsequent population adaptability [40, 41], especially for fast growing species that do not leave lasting visual signatures of impacts. We also highlight the importance of ancillary data to properly interpret change in genetic diversity following extreme events and demonstrate the role of competitive release and dispersal in structuring trajectories of genetic change. Population demography and ecological interactions are important factors to consider, as they can mask full impacts of extreme events. Integrated sampling is required across multiple levels of biological organization (from genes to ecosystems) and across long temporal scales to properly understand the impacts of extreme events [42] and predict subsequent adaptability of species to future climatic change.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- LEAD CONTACT AND MATERIALS AVAILABILITY
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND CODE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2020.01.051.

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AUTHOR CONTRIBUTIONS

T.W. and C.F.D.G. designed the study, and T.W. collected the samples; C.F.D.G. and O.C. analyzed the genetic samples; T.W. and M.A.C. analyzed the ecological data; M.A.C. and C.F.D.G. wrote the paper; and M.A.C., C.F.D.G., and A.J.P.M. produced all figures. All authors edited the paper and contributed to interpretation.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Oligonucleotides		
CAF4A (ATGTTTACTTGGTGRA GRGA)	Life Technologies	[43]
CAR4A (CCCCACCARTAWATNGTNAG)	Life Technologies	[43]
*rbc*L3F (CAGGTGCTACAGCTAACCGTGT)	Life Technologies	[43]
RSPR (AATAAAGGAAGACCCCATAATTCCCA)	Life Technologies	[43]
Software and Algorithms		
Geneious v. 5.5.9	Genious, New Zealand	[44]
PhyML 3.0	http://www.atgc-montpellier.fr/phyml/	[45]
DNAsp 6.11.1	http://www.ub.edu/dnasp/	[46]
Arlequin 3.5.2.2	http://cmpg.unibe.ch/software/arlequin35/	[47]
Deposited Data		
MN882363 to MN882366	*S. fallax*	rbcL
MN882369 to MN882379	*S. fallax*	cox3
MN882367 to MN882368	*S. dorycarpa*	rbcL
MN882380 to MN882388	*S. dorycarpa*	cox3
Other		
NucleoSpin® 96 Plant II kit	MACHEREY-NAGEL, Germany	740669
ExoSAP-IT	GE Healthcare	78201.1.ML
Big Dye Terminator chemistry (Applied Biosystems, Carlsbad, CA, USA)	Applied Biosystems, Carlsbad, CA, USA	4337455
Millipore Multiscreen Sequencing plates	Millipore, Ireland	MSBVN1210

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources or reagents should be directed to and will be fulfilled by the lead contact, Melinda A. Coleman (Melinda.coleman@gmail.com). This study did not generate new resources or reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Samples of each species were collected for genetic analysis before (2008) and after (2012) the 2011 heatwave event (Figure 1; Tables S1 and S2) from the same sites and reefs. While we recognize that this represents only 2 points in time, and without more temporal replication within before and after periods, the rarity of "before" genetic data in studies that seek to examine impacts of unpredictable extreme events warrants this sampling design (see [4, 7, 48, 49] for examples of similar designs with 2 time points for genetic data). Moreover, given that temporal replication of genetic data in any study is rare, our data is a critical first step in assessing genetic impacts of climatic change on natural systems. Despite the strong weight of evidence for heatwave impacts presented here across species, genes and sites, we still stress, however, that more contemporary genetic sampling would be required to assess longer-term impact and adaptability of these populations. Sampling effort was increased after the heatwave to ensure we adequately captured any change (up to n = 30 individuals per site; Tables S1 and S2) but rarefaction analyses revealed that ~8 samples were sufficient to capture diversity. Given uneven sample sizes, haplotype diversity (Figure 2) rather than the number of haplotypes was used as a measure of change. *Sargassum* samples were collected at 5 to 8 m depth across 5 populations from Kalbarri to Hamelin Bay and *Scytothalia* samples were collected from Hamelin and Marmion (Figure 1). These populations observed significant thermal anomalies during the 2011 heatwave [20] (Figure 1). Collected samples were free from epiphytes and were preserved in silica gel desiccant.

The two molecular genes chosen in this study to demonstrate change in genetic diversity were the ribulose-bisphosphate carboxylase (*rbc*L) chloroplast gene and the cytochrome *c* oxidase subunit 3 (*cox*3) mitochondrial gene. These genes code for proteins involved in carbon fixation (photosynthesis) and cytochrome *c* oxidase enzymes. They also have functional significance for populations because they are coding parts of the genome. In particular, evolution of differences in thermal tolerance have been shown to be linked to mitochondrial genes, including cox genes [36], and activity of the Rubisco enzyme is temperature sensitive. Moreover, a plethora of previous studies demonstrated that *cox*3 and *rbc*L present extensive amounts of inter- and intra-population levels genetic diversity in natural brown algal populations (e.g., [50]).

DNA was extracted using NucleoSpin® 96 Plant II kit (MACHEREY-NAGEL, Germany) following the manufacturer's protocol. We targeted the mtDNA *cox*3 region with primers CAF4A and CAR4A and the partial *rbc*L gene region with primers *rbc*L3F and RSPR (see Key Resources Table for primer sequences). Primer sequences and PCR protocols are also described in [43]. PCR products were cleaned with ExoSAP-IT (GE Healthcare) following manufacturer's instructions. Sequencing reactions were conducted in both forward and reverse directions, producing 2-fold contigs, using the same PCR primers mentioned above and the Big Dye Terminator chemistry (Applied Biosystems, Carlsbad, CA, USA). Sequences were cleaned with Millipore Multiscreen Sequencing plates (Millipore, Ireland) and capillary separation was outsourced to the Australian Genome Research Facility (AGRF), Adelaide node, South Australia. Raw sequence data were edited, aligned and proof read in Geneious v. 5.5.9 [44].

As part of a long-term study, seaweed abundance before (2009 to 2011) and after (2012-2018) the marine heatwave was sampled annually in the first half of summer (Nov-Dec) at Hamelin Bay, Marmion, Jurien Bay and Kalbarri [27]. Thus, this sampling captured percentage of *Scytothalia* and *Sargassum* populations cover immediately before and approximately 10 months after the heatwave event. Within each region, three 8-10 m deep sites were sampled 2-15 km apart. At each site a scuba diver sampled six haphazardly placed 0.25 m^2 quadrats and visually estimated the percent cover of all sessile organisms.

METHOD DETAILS

In the Austral summer of 2010/11 the west coast of Australia experienced an unprecedented marine heatwave with temperature anomalies higher than anything seen in at least 140 years of recorded history [20] (Figure 1). The heatwave engulfed ~2,000 km of coastline including the southwest coast, where this study was focused. The coastal region experienced temperature anomalies 2-5°C above the long-term maxima for more than 10 weeks [20] (Figure 1). *Scytothalia dorycarpa* and *Sargassum fallax* are two common, conspicuous and forest-forming species in Western Australia, where they support substantial biodiversity [25]. These species occur as mixed forests with kelp (*E. radiata*) throughout southwestern Australia, and together they account for up to 60% of reef cover in some places [25]. In some places, they can also form dense monospecific stands. *Scytothalia* is a perennial, monecious fucoid that releases eggs and sperm simultaneously in winter [34]. It lacks gas-filled vesicles and does not float. In contrast, *Sargassum* has perennial holdfasts and upright branches but produces annual, monecious reproductive fronds with gas-filled vesicles that float and disperse long distances [51].

QUANTIFICATION AND STATISTICAL ANALYSIS

Sargassum species identity is traditionally difficult to identify at the species level due to a wide range of phenotypic plasticity and rampant homoplasies among vegetative characters. In Australia there are at least 15 morpho-species [52], but the extent of cryptic diversity has not yet been explored. To confirm species identification for analyses, we compared newly generated *Sargassum* sequences to all *Sargassum* sequences from GenBank available on April 15th 2018 (791 and 66 *cox*3 and *rbc*L DNA sequences, respectively) via phylogenetic analyses based on the maximum likelihood method implemented in the online version of PhyML [45] using the NNI tree improvement algorithm, a BioNJ starting tree and bootstrap values based on 1000 resamplings. Model selection for both gene alignments used the PhyML 3.0 automatic smart model selection tool [53] under the Bayesian information criterion. In the case of *Scytothalia* identity, there is only one species in the genus therefore easier to identify and which was molecularly characterized for the first time in this study. A total of 9 and 2 *Scytothalia* haplotypes and 11 and 4 *Sargassum* haplotypes were obtained in the *cox*3 and *rbc*L alignments, respectively.

For each site and overall, indices of genetic diversity (K, Pi, Hd), neutrality tests (Tajima's D, Fu & Li's F and D) and population differentiation (G_{ST}) were calculated via DNAsp 6.11.1 [46] and Arlequin 3.5.2.2 [47]. Shannon-Weiner diversity index using log base 2.7182 was calculated for each species from haplotype frequency data pooling all populations sampled either before or after the heatwave. Haplotype sequences were deposited in GenBank. Population information, sample size and results from intra-population genetic diversity and neutrality tests can be found Tables S1 and S2. Statistical significance was based on $p < 0.05$.

DATA AND CODE AVAILABILITY

Sargassum and Scytothalia DNA sequences generated in this study are publically available in GenBank under accession numbers GenBank: MN882363 to GenBank: MN882366, and GenBank: MN882369 to GenBank: MN882379 for S. fallax rbcL and cox3 haplotypes, respectively; and GenBank: MN882367- GenBank: MN882368 and GenBank: MN882380- GenBank: MN882388 for Scytothalia dorycarpa rbcL and cox3 haplotypes, respectively.