



Oceanic patterns of thermal stress and coral community degradation on the island of Mauritius

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Abstract Knowing the responses of high-latitude corals to thermal impacts will be critical to predicting the possibility for range expansion of reefs provoked by climate change. We, therefore, tested how oceanographic and island geography variation and subsequent interactions between chronic and acute environmental stresses would influence the temperate corals of Mauritius (~ 20°S). Specifically, we predicted higher impacts of thermal stress due to rare events on ocean-impacted windward than leeward reefs. To test this prediction, surveys of benthic cover and corals in the shallow lagoon's perimeter reefs were repeated between 2004 and 2019—an interval with frequent warm thermal anomalies. Hard and soft coral cover declined 40% and 83%, respectively, and erect algae increased 78% over the 15-yr interval. Coral taxa were distributed along a *Montipora*-community axis dominant on the island's leeward reefs and an *Acropora*-axis dominant on the windward reefs. Nine of the 30 originally encountered subgenera were not observed in the second sampling, of which most losses were on the windward reefs and among taxa that were initially uncommon during the initial 2004 sampling. The largest declines occurred in the southeast

where rare acute stress was higher and open-ocean conditions interacted strongly with the island. The north and western corals experienced less acute stress and greater persistence of taxa. Searching an additional 15 sites in 2019 found six of the missing coral taxa, often in deeper reef edges. Screening of potential environmental variables indicated that that skewness of the degree heating weeks and thermal stress anomalies were the strongest predictor of the changes. A chronic stress metric was more difficult to identify but water flow variability and chlorophyll-a concentrations were part of the oceanographic conditions associated with attenuated responses to acute stress. Frequent acute stress was associated with lower thermal acclimation rates over the 15-yr interval and more evident for the dominant than subdominant taxa. The extra-equatorial location of Mauritius will not ensure latitudinal sanctuary, apart from the leeward reefs.

Keywords Biogeography · Climate change · Coral bleaching · Land–sea interactions · Extinction · Indian Ocean

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Introduction

Predictions of the demise of coral reefs due to climate change are dire (van Hooidonk et al. 2016). While large-scale thermal stress and associated changes in coral communities are evident (Ateweberhan et al. 2011; Donner et al. 2017; Hughes et al. 2018; Sully et al. 2019), the spatial scale and heterogeneity of these observations are complex and less understood (McClanahan et al. 2011, 2015; Heron et al. 2016). Thermal stress and its effects on specific taxa are also complicated and possibly changing as the climate warms (McClanahan et al.

2019a, 2020a, b). Moreover, making accurate predictions for an increasingly warm and stressful climate is challenged by variable resistance, mortality, acclimation, recovery, and genetic adaptation responses among taxa (Palumbi et al. 2014). Consequently, the spatial, temporal, and biological complexity of responses needs to be better understood to establish the priorities required for improved management (Darling et al. 2019).

Islands provide unique geomorphologies that are an opportunity to better understand climate impacts. For example, the circular nature of many volcanic islands and subsequent interaction with ocean currents provide a natural experiment for evaluating ocean currents and reef interactions. Ocean–land interactions are expected to create distinct thermal and stress environments and variable acclimation and resistance of corals (Golbuu et al. 2007; Couch et al. 2017). For example, ocean exposed or windward reefs generally experience stable oceanic and low-level chronic temperature variability. Low thermal variability is expected to reduce acclimation and promote lower tolerance to rare thermal anomalies (McClanahan et al. 2005; Safaie et al. 2018). Leeward reefs, in contrast, are expected to experience more variable water flow and temperature variability that may acclimate corals to acute stress created by episodic thermal anomalies (Baker et al. 2013; Cunning et al. 2015; Gove et al. 2016). The island of Mauritius is ringed by coral reefs and variable oceanographic conditions that provide an opportunity to better understand coral responses to the interactions between chronic background and acute stress conditions (Fig. 1). Mauritius is most influenced by strong ocean currents that directly impact the southeast side due to the interaction between the Indian Ocean South Equatorial Current, Mascarene Plateau, and Mascarene Islands of La Reunion and Mauritius (Pous et al. 2014).

Unusually warm thermal anomalies have been observed in Mauritius and affected corals via bleaching and subsequent mortality (Fig. 2) (Pillay et al. 2002a, b; Elliot et al. 2018). Analyses of coral cover data collected between 1998 and 2010, for example, indicated that coral mortality began around 2005, was geographically variable, and subsequently followed by periods of mortality and recovery (Elliot et al. 2018). Therefore, the conditions of repeated thermal stress and the circular island geomorphology create an opportunity to test the role of the proposed ocean–land interactions on coral resilience. Field surveys of coral taxa response to bleaching conducted during a moderate thermal stress event in 2004 found that bleaching was highest in reefs with faster water flow and low background temperature variation. These conditions were located on the eastern and southern reefs of the island where ocean currents directly impact the island (McClanahan et al. 2005; Pous et al. 2014). Consequently, it was hypothesized that

corals, usually accustomed to high water flow and stable temperatures, bleached and potentially died when these conditions changed rapidly during the 2004 summer. Therefore, doldrum conditions that reduce wind speeds, water flow, and spike water temperatures should be particularly deadly for corals on windward island locations where environmental conditions are often stable and good for coral health. The frequency of rare conditions is expected to be critical to identify environments where corals are at risk due to increasing and often extreme variability promoted by climate change.

Water flow improves coral health, growth and can reduce responses to thermal stress, such as bleaching (Nakamura and van Woessik 2001). However, when these benign conditions change rapidly, corals acclimated to high water flow and stable temperatures are expected to bleach and die more frequently (McClanahan and Maina 2003). Thus, there can be large differences in chronic and acute stress and subsequent bleaching responses when either tides or winds are the primary drivers of water flow. An interruption in wind-driven currents will create acute stress. In contrast, tidal currents are more predictable, chronic, and able to buffer episodic acute interruptions. Coral acclimation and bleaching responses should, therefore, differ when unusual inter-annual thermal stress occurs between tidal and wind-driven water flow environments. Circular islands provide natural experimental conditions to test the role of wind-driven water flow because their convex shorelines create different windward and leeward current patterns. When circular islands are also oceanic and have steep coasts, such as Mauritius, then the small and uniform tides make them ideal locations to study ocean–land interactions.

We asked how the shallow coral taxa and communities in Mauritius changed across a 15-yr interval between 2 yrs experiencing warm thermal anomalies, specifically 2004 and 2019. First, would the most severe and acute temperature extremes impact the ocean-dominated windward more than the leeward environments due to higher and more stable current speeds and low variation in background or chronic temperatures on windward locations (McClanahan et al. 2007; Côté and Darling 2010; Safaie et al. 2018)? And, second, could these patterns in land–sea interactions, predict the changes in coral cover, number of taxa, and the composition of the coral communities? The conditions of low to moderate background but larger aperiodic and rare current flow and thermal variation were predicted to be more evident on the island's south and eastern than the north and western reefs. In contrast, the island's ocean current-protected sides of the north and western were predicted to experience moderate to high background variation and less frequent extreme aperiodic thermal stress. Sea surface temperature's (SST)

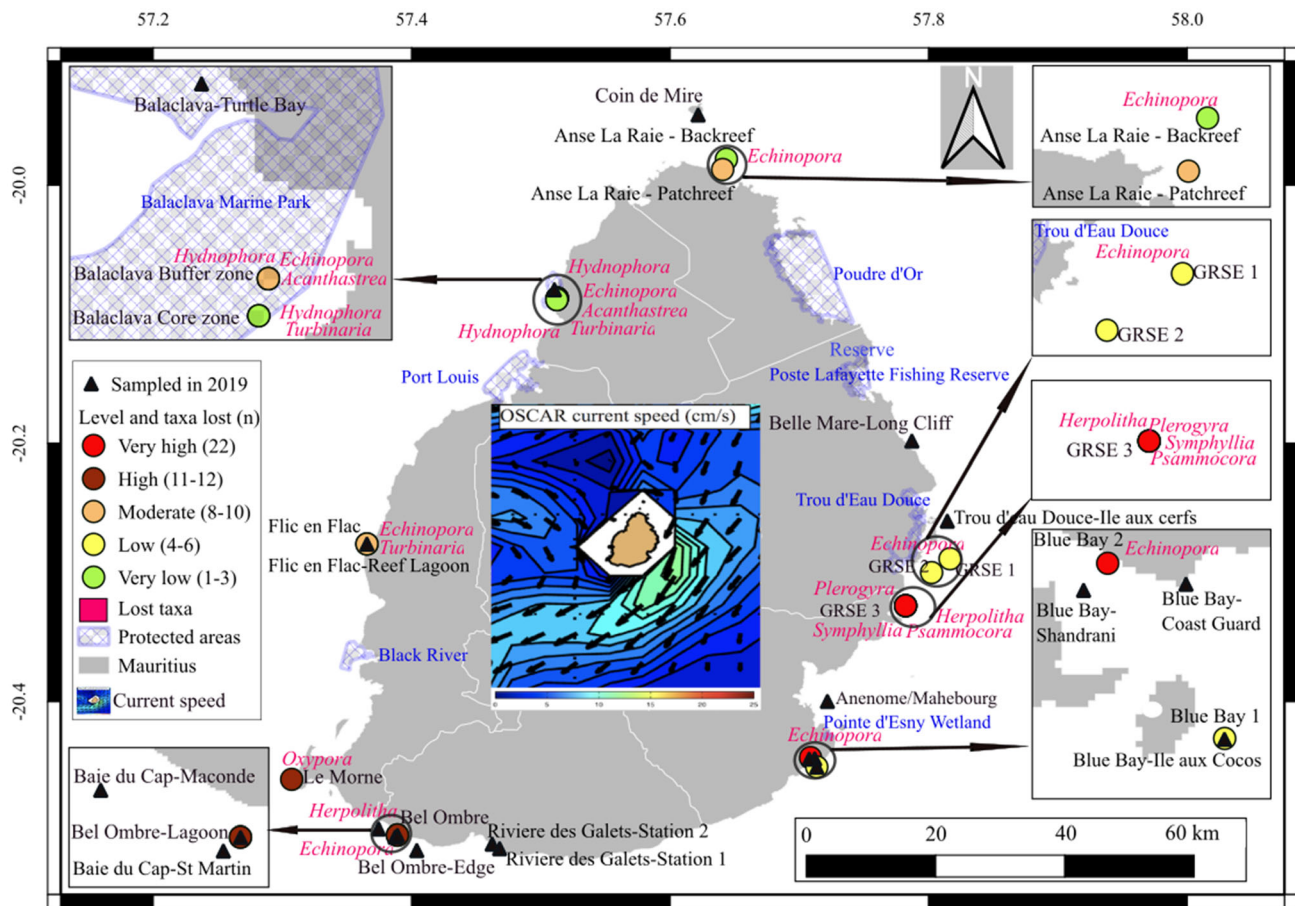


Fig. 1 Map of Mauritius, marine managed area locations, and the study sites. Site points indicate the percent changes in number of observed coral genera between 2004 and 2019. Taxa observed in 2004

but not 2019 are shown in red letters for the specific sampled sites. Colored inset shows current speeds based on the study by Pous et al. (2014)

metrics of skewness, kurtosis, and degree heating weeks (DHWs) were expected to reflect these ocean-land interactions. Further, we predicted that taxa should respond to these different environments by displaying differential bleaching, mortality, and acclimation over time. Finally, taxa that were uncommon, most susceptible to thermal stress, and acclimating the least to heat stress were predicted to be most susceptible to population declines. Assessment of these hypotheses and descriptions of change were made possible by repeating coral surveys on reefs surrounding the Mauritian island during the 2004 and 2019 warm seasons over a 15-yr period when a number of thermal anomalies and bleaching events were reported.

Materials and methods

Field methods

The primary sites we selected were shallow (< 3-m deep at low tide) coral dominated hard-bottom environments

within fringing reef lagoons protected from direct impacts of ocean currents and waves. Sites were located around the circular coastlines of the island and included some fisheries managed areas (Fig. 1). These sites were marked by GPS in the summer (January to March) of 2004 and revisited in 2019. One site marked in 2004 could not be found, and this resulted in a total of 12 repeated sites. In order to determine if taxa missing between sampling intervals were present in fore reefs and deeper water, an additional 15 sites were sampled in 2019, in variable water depths water (ranging between 0.7 and 20 m) and across the lagoon to the fore reef.

During each survey, an observer assessed coral bleaching across a series of haphazardly placed replicate (15 to 20) quadrats (~ 1.5 m²) during a 40- to 60-min swim. Within each quadrat, hard coral colonies (> 5 cm) were identified to the genus (Moothien-Pillay et al. 2002a, b) and scored for bleaching severity. Severity was scored using seven categories: c0—normal; c1—pale; c2—0–20% bleached; c3—21–50% bleached; c4—51–80% bleached, c5—81–100% bleached; c6—recently dead and using a

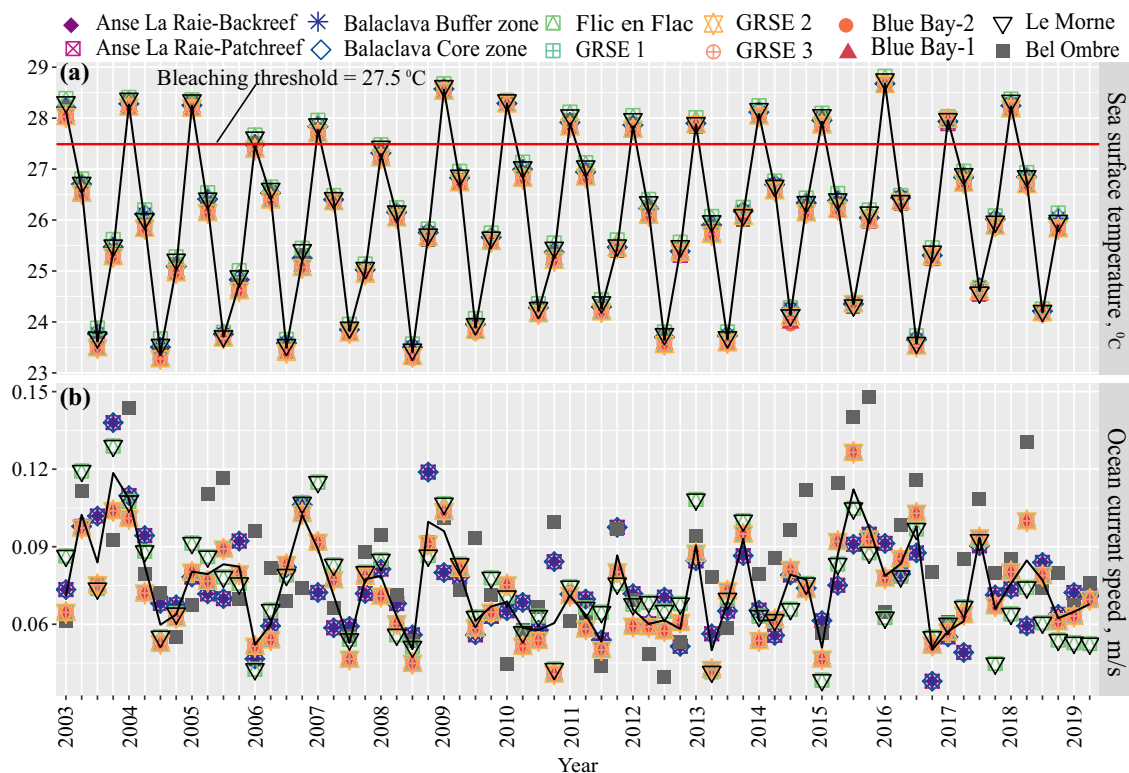


Fig. 2 Long-term time series of **a** temperature and **b** current flow data time series for the main studies sites with trend lines in black connecting averages. Sites in the legend organized from north (top) to south (bottom). Data are the quarterly values for each year

weighted formula (McClanahan et al. 2007). Within each quadrat, observers also estimated the average percent cover of live hard coral, live soft coral, and erect macroalgae to the nearest 5% (e.g., fleshy or calcareous algae in all three phyla that were taller than filamentous turf such as *Sargassum*, *Padina*, *Amphiroa*, and *Halimeda*). Samples of numbers of colonies per taxa were standardized to 40-min to make comparison sites by the same sampling effort. To evaluate coral community composition, we estimated the relative abundance of taxa from each survey as the number of observed colonies divided by the total number of colonies.

Environmental data

The National Oceanographic and Atmospheric Administration (NOAA) satellite-derived temperature data were used for our environmental analyses. Data included two related sources, namely the Coral Reef Watch Database (CRW) database Version 3.1 (<https://coralreefwatch.noaa.gov/product/5km/>) and the Coral Reef Temperature Anomaly Database (CoRTAD). The NOAA-CRW products use daily 5-km resolution readings and, at the time of our downloading (July 18, 2019), included the 1985–2018 sampling interval. At the same time, CoRTAD (<https://www.nodc.noaa.gov/SatelliteData/Cortad>) uses a daily

4-km resolution and presents thermal stress anomaly (TSA) and thermal stress anomaly-degree heating week (TSA_DHW) data for the 1982–2012 sampling interval at the time of downloading. Thus, due to a lack of the full time series, it is used as a proxy for conditions at these sites. TSA is the difference between the temperature on a given day and the maximum weekly mean climatological SST based on 52 climatological weeks averaged over 30 yr (Zinke et al. 2018). TSA_DHW is a derivative of TSA computed as the sum of temperatures $> 1 - ^\circ\text{C}$ above the climatological mean over the 12-week summer period. These metrics were summarized for each site as the mean, median, minimum, maximum, standard deviation, skewness, and kurtosis. Testing the two data sets for similarity between the overlapping years found they were strongly but not precisely correlated ($r^2 = 0.76$). The CoRTAD data used here are considered a proxy for rare anomalies at each geographic location, which was hypothesized to impact coral heat tolerance, rather than the specific cause of the changes reported here. The bleaching threshold for Mauritius has been calculated from SST satellite data from NOAA as $27.5\text{ }^\circ\text{C}$ as per the $1\text{ }^\circ\text{C}$ above the local summer baseline methods of Glynn and D’Croz (1990).

Chlorophyll-a (mg m^{-3}) was obtained from the COASTCOLOUR project (www.coastcolour.org/). The European Space Agency’s GlobColor data were used rather

than MODIS, SeaWiFS, or MERIS because it uses multiple sensors that average out errors from individual sensors. Therefore, it reduces the overall data variability and

c_0 = normal, c_1 = pale, c_2 = 0–20%, c_3 = 21–50%, c_4 = 51–80%, c_5 = 81–100%.

$$BI = \frac{((0 \times c_0) + (1 \times c_1) + (2 \times c_2) + (3 \times c_3) + (4 \times c_4) + (5 \times c_5) + (6 \times c_6))}{7}$$

uncertainties, such as those caused by bottom reflectance. These data have limited temporal and time series resolution and we, therefore, limited evaluations to the mean and median metrics as course-level indicators of water quality for each study sites.

Current data were extracted from Ocean Surface Current Analysis Real-time (OSCAR) (https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg) at a 1/3-degree grid with a five-day resolution for the period 2003 to 2019 for the 12 sites where coral data were collected. OSCAR contains near-surface ocean current estimates, derived using quasi-linear and steady flow momentum equations. The horizontal velocity is directly estimated from sea surface height, surface vector wind, and SSTs. These data were collected from the various satellites and in situ instruments. The model formulation combines geostrophic, Ekman and Stommel shear dynamics, and a complementary term from the surface buoyancy gradient (Bonjean and Lagerloef 2002). Ocean Surface Zonal and Meridional Maximum Mask currents were extracted. The two current directions were averaged for the same locations and time and the mean, median, standard deviation, skewness, and kurtosis were calculated for each site. An additional source of water flow data used in the analysis was clod card dissolution rates. Clod cards were placed next to corals in the site, and the change in weight over a 24 hrs period was used to estimate the current speed (McClanahan et al. 2005). Temperature and current data were plotted over time (Fig. 2).

Data analyses

Dependent variables

The study focused on the changes in benthic cover, coral bleaching, numbers of coral taxa, the coral community, and lost taxa across the 2004 and 2019 period. Change in benthic cover and the bleaching index were evaluated as ratios of the \log_{10} abundance and bleaching in 2019/2004. The bleaching index (BI) was evaluated at site level having weighted bleaching by the abundance of the individual genera bleaching for the two time periods using the following formula, (McClanahan et al. 2007), where

Changes in number of taxa were evaluated as square root of absolute difference in numbers of taxa in 2019–2004. The log of the ratio and square root of the absolute difference improved the data distributions to better fit statistical model assumptions (Crawley 2012).

Changes in the coral community were evaluated as changes in multivariate community axes for each site. The coral community comprised the number of individuals observed in 30 taxa (mostly genera). The communities at each site were evaluated via distance-based redundancy analysis (dbRDA) using the R package version 2.5-5 (<https://CRAN.R-project.org/package=vegan>). The site-specific values along the first and second axes in each year were used in subsequent evaluations of changes in community structure over time. The sign of the data was changed to present increases in relative abundance as positive values. Due to the high number of taxa, the dbRDA plot presented in the results includes only the 14 dominant genera, which accounts for 96% of coral cover.

Disappearance rates of taxa were evaluated at the coral genus level. For each genus, a relative cover, commonness, BI, and the change in bleaching between 2004 and 2019 responses were calculated. Relative cover is based on line transects undertaken in each of these sites in 2004 (McClanahan et al. 2005). Commonness is the frequency of observations at a site in 2004 and relativized, such that a genus seen in only one site would have a value of 0 and all sites a value of 1. The taxa's BI was also based on 2004 as a baseline, which would reduce the possible influence of changes in responses over time. Therefore, the rate of change in bleaching was the ratio of the BI in 2019/2004. Corals not observed in either year were not evaluated. An index of relative loss was calculated as 1—average of these normalized metrics. This index was compared to actual losses as coral taxa observed in 2004 but not in 2019. The number of species of each genus was summarized from a country-level compilation (Moothien-Pillay et al. 2002a, b).

Independent variables

Variables were selected for possible associations with the changes in coral communities over time. First, the 22

environmental variables described above were evaluated for their ability to be good proxies for chronic and acute stress. Then, we chose variable with low redundancy in having low variance inflation factors (VIF) but high statistical significance in the GLM models. This process reduced the 22 to 10 environmental variables for subsequent analyses (Supporting Information, Table S1). This process removed many of the standard mean and variance variables used in evaluating climate impacts, which are often highly correlated but weak indicators or proxies of chronic or acute stress (Sully et al. 2019). As an example, the GLM process found that mean TSA and DHW both had high VIF (TSA VIF = 22.4, DHW VIF = 98.0). This was due to high correlations with the standard deviations of TSA and SST, while mean DHW was highly correlated with TSA skewness. TSA and DHW skewness, however, lacked high correlations and positive skewness and therefore good indicators of rare or acute thermal stress, the focus of our impact hypotheses.

The final 10 variables were local clod-based current speed (cm s^{-1}), ocean current speed skewness (m s^{-1}), TSA_DHW skewness ($^{\circ}\text{C}$), TSA skewness ($^{\circ}\text{C}$), chlorophyll (mg m^3), TSA minimum ($^{\circ}\text{C}$), SST kurtosis ($^{\circ}\text{C}$), SST maximum ($^{\circ}\text{C}$), mean wave energy mean (kW m^{-1}), and TSA mean ($^{\circ}\text{C}$). In separate evaluations and because we were testing the effect of geographical location, latitude and longitude were included. The final twelve variables were normalized between 0–1 prior to analysis to improve the accuracy of the predictions. The final set of variables were evaluated by general linear model (GLM), stepwise regression, and boosted regression tree (BRT) analyses.

For GLM procedures, we evaluated those variables that had low VIF < 3 and model combinations of the variables selected as having $< 2\text{AIC}$ values of the 127 possible model combinations (Burnham and Anderson 1998). In the case of numbers of taxa, 3 of the 10 variables were removed because of VIF considerations, leaving 7 variables that were evaluated with the follow basic model structure:

Changes in number of coral taxa \sim Ocean.current.speed.skewness + Chlorophyll + Local clod current speed + TSA_DHW.skewness + TSA.minimum + TSA.skewness + Wave_mean energy.

Additionally, forward stepwise regressions present variables selected as significant at $p < 0.05$. Finally, the BRT regression results of the sites dbRDA Axes 1 and 2 partial plots of the 2019/2004 ratios are presented.

Results

Environmental variation

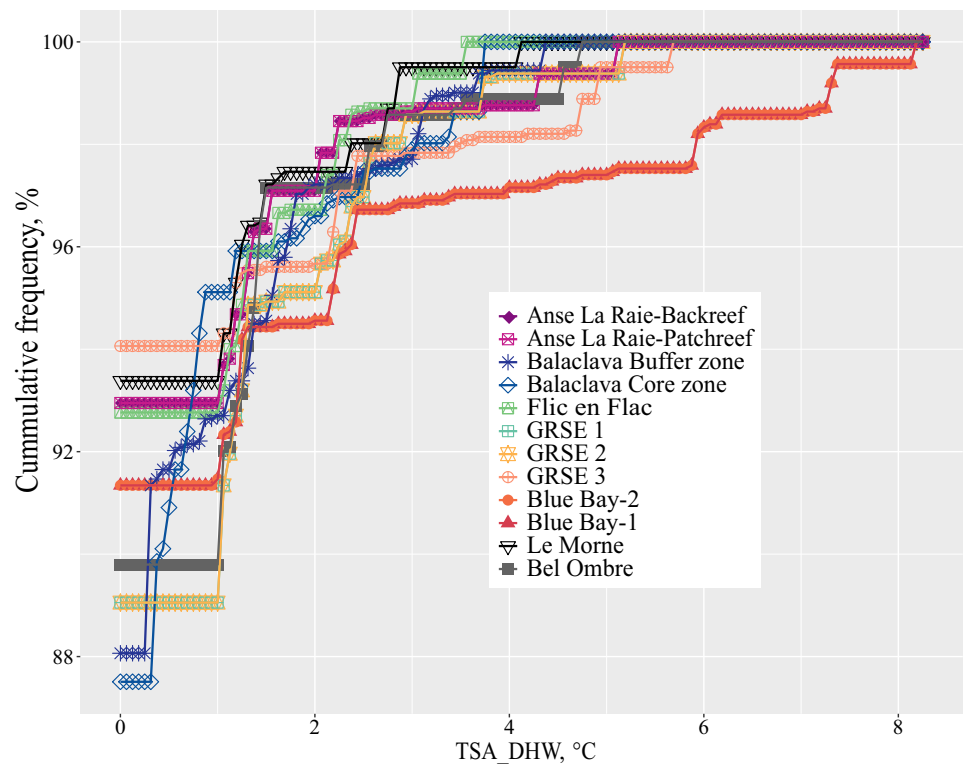
Study sites were located around the island and experienced different environmental and oceanographic forces (Fig. 1, Supporting Information). Mean temperatures display seasonal fluctuations with small differences between sites (Fig. 2a). There were, however, inter-annual differences in the maximum and minimum temperatures with many years exceeding the standard 27.5°C threshold for bleaching. Years above the bleaching threshold included the 2003 to 2005 period and most years between 2008 and 2019. The years with the highest summer temperatures over the study period were 2004, 2008, 2009, and 2016. The metrics of warm-temperatures rarity, DHW-skewness and TSA-skewness, were not highly correlated, had variance inflation factors (VIFs) of < 3 with other temperature metric and variable between sites. The skewness in the DHW metric was generally higher in the north, while TSA skewness was generally higher in the east and lowest in the north and west for the 1985–2018 period. Blue Bay and sites in the east had notably higher TSA_DHW among the most extreme anomalies when presenting the rare anomalies as cumulative frequencies (Fig. 3).

Physical energy of current speeds and wave energy had more variation in some metrics between sites than SSTs (Table S1). Intra- and inter-annual variation in current speed was complex with no clearly repeatable seasonal or inter-annual patterns (Fig. 2b). Mean offshore ocean current speeds were similar between sites but clod dissolution, which were restricted to a single sampling time, suggests that the local conditions varied more between sites than reflected in ocean current speeds. Variation in some metrics around the island reflected the island's east to southward current oceanography with stronger wave energy in the southern sites of Bel Ombre and Le Morne and Balaclava. Wave energy was low in the north and in the GRSE and Blue Bay lagoons but more variable in other locations. Ocean current speed skewness, a measure of frequency of pulses of high current speeds, was not strongly correlated with other metrics and, therefore, good for distinguishing sites and was highest in the north and northwest sites of Anse le Raie and Balaclava.

Changes in coral taxa and communities

Coral taxa and benthic communities changed in these 12 study sites over this 15-yr period with losses in hard, soft coral cover and changes in numbers of taxa and coral community structure (Table 1). The overall mean site-level loss of hard and soft coral cover was 40% and 83%,

Fig. 3 Cumulative frequencies of the rare thermal stress anomalies in the degree heating weeks (TSA_DHW) for Mauritian study sites for the years 1985 to 2018. Sites in the legend organized from north (top) to south (bottom)



respectively. Erect algae increased by an average of 78% but was unchanged and low in the two sites in the Blue Bay marine reserve. Coral cover and numbers of coral taxa were weakly negatively correlated in 2004 ($r^2 = 0.28$, $p < 0.075$) but not significantly correlated in 2019 ($r^2 = 0.10$, $p = 0.80$).

Many changes in benthic and coral cover variables were site-specific suggesting both local and larger-scale environmental influences. Losses in coral taxa were common for most sites despite more moderate changes in coral cover (Fig. 1). The Blue Bay Park site nearest the open ocean lost 22 of the original 24 taxa found in 2004. Some sites, such as GRSE 3, lost almost all coral cover and taxa and the remaining rubble was colonized by erect algae. A nearby site, GRSE 2, was the only site to gain coral cover but also lost five hard coral taxa. In contrast, a low diversity patch reef, Anse le Raie, in the north lost little coral cover and no taxa.

The dbRDA coral community axes 1 and 2 displayed some consistent patterns over time and space for the colonies found per sampling time (Table 1, Fig. 4). The taxonomic composition of Axis 1 was largely driven by *Acropora*, massive *Porites*, *Favites*, *Stylophora* and *P. rus* (*Synaraea*) whereas Axis 2 was driven by *Montipora*, *Millepora*, *Fungia*, branching *Porites*, and *Galaxea* numbers. The number of colonies associated with Axis 1 declined over time for most sites with the most pronounced losses in the east and southern sites of Blue Bay, Le Morne,

and Bel Ombre (Table 1). The Anse le Raie sites in the north and GRSE 3 had some gains in Axis 1 coral colonies. Numbers of colonies of the Axis 2 corals also declined in most sites particularly in the south but also in the Anse le Raie and Flic and Flac sites. There were some small increases in Axis 2 corals in Balaclava and GRSE 2.

Environmental and oceanographic associations with coral change

Declines in coral cover were moderately associated with the skewness of the TSA_DHW metric, or number of rare acute thermal stresses, for both the GLM ($r^2 = 0.55$) and stepwise procedures ($r^2 = 0.43$). There was no evidence for significant influence of other variables or geographic location (Table 2, Supporting Information). Declines in the number of coral taxa also increased with the skewness of TSA in the top GLM model ($r^2 = 0.61$) and stepwise regression ($r^2 = 0.40$) (Table 3). However, skewness in ocean current speed, or the frequency of rare and fast current pulses, was associated with fewer losses in coral taxa ($r^2 = 0.55$) in the second top model. When including geographic variables, latitude was picked in the top two GLM models and produced the highest fits ($r^2 = 0.69$), especially when including the clod card current speed ($r^2 = 0.79$). Losses of coral taxa were, therefore, higher in the south and associated with higher TSA skewness, or rare warm temperatures, and higher local current speeds.

Table 1 Benthic and coral community variables summarized for the 12 study sites organized from north to south

Sites	Coral cover (%)						Erect algae (%)						Soft coral (%)						Number of taxa						Bleaching index (%)						Multivariate coral community axes values						Percentage changes (%)						Change in coral community axes (2004–2019)					
	2004		2019		2004		2019		2004		2019		2004		2019		2004		2019		2004		2019		dbRDA 1		dbRDA 2		Coral cover		Soft coral		Erect algae		Change in number of taxa		dbRDA 1		dbRDA 2									
	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019	2004	2019												
Anse la Raie–Backreef	59.8	20.2	5.6	21.2	0	0	17	16	22.2	20.8	0.68	–1.3	0.68	–1.3	–66.11	73.58	0	0	–1	–1	0.68	–1.3	–1	–1	0.68	–1.3	–1	–1	0.68	–1.3	–1	–1	0.68	–1.3	–1	–1												
Anse la Raie–Patchreef	63	53.3	2.3	6.7	0.4	0	8	8	16	5.5	0.1	–0.24	0.1	–0.24	–15.37	65.67	–100	–100	0	0	0.1	–0.24	0	0	0.1	–0.24	–100	–100	0	0	0.1	–0.24	–100	–100	0	0												
Balacava Buffer zone	51.7	19.1	1.6	12	0	0.2	25	15	32.9	3.28	–0.6	–0.18	–0.6	–0.18	–62.93	86.67	100	100	–10	–10	–0.6	–0.18	–10	–10	–0.6	–0.18	–100	–100	–10	–10	–0.6	–0.18	–100	–100	–10	–10												
Balacava Core zone	49	17.4	0	2.2	0	0.2	20	17.5	27	2.4	–0.17	0.18	–0.17	0.18	–64.36	100	100	100	–2.5	–2.5	–0.17	0.18	–2.5	–2.5	–0.17	0.18	–100	–100	–2.5	–2.5	–0.17	0.18	–100	–100	–2.5	–2.5												
Flic en Flac	46.6	23.3	2.2	6.2	0	0.2	21	12.5	16.9	10.2	–0.51	–0.65	–0.51	–0.65	–49.89	64.52	100	100	–8.5	–8.5	–0.51	–0.65	–8.5	–8.5	–0.51	–0.65	–100	–100	–8.5	–8.5	–0.51	–0.65	–100	–100	–8.5	–8.5												
GRSE 1	66.4	67.3	2.4	13.3	1.4	0	12	6	36.5	53.1	–0.67	–0.1	–0.67	–0.1	1.35	81.95	–100	–100	–6	–6	–0.67	–0.1	–6	–6	–0.67	–0.1	–100	–100	–6	–6	–0.67	–0.1	–100	–100	–6	–6												
GRSE 2	43.8	84.2	7.5	20.7	0	0	12	7	24.9	56.4	–0.36	0.15	–0.36	0.15	92.03	63.77	0	0	–5	–5	–0.36	0.15	–5	–5	–0.36	0.15	0	0	–0.36	0.15	0	0	–0.36	0.15	0	0												
GRSE 3	58.5	0	13.5	63.3	0	0	22	0	18.8	0	0.29	–1.06	0.29	–1.06	–99.83	78.67	0	0	–22	–22	0.29	–1.06	–22	–22	0.29	–1.06	0	0	0.29	–1.06	0	0	0.29	–1.06	0	0												
BlueBay-2	57.5	27.3	1.3	0	1.1	0	9	5	22.3	44	–1.46	–2.16	–1.46	–2.16	–19.06	–85.71	–100	–100	–4	–4	–1.46	–2.16	–4	–4	–1.46	–2.16	–100	–100	–4	–4	–1.46	–2.16	–100	–100	–4	–4												
BlueBay-1	29.8	24.1	1.3	0.7	0.7	0	24	2	25.4	1.6	–0.52	–0.86	–0.52	–0.86	–52.43	–100	–100	–22	–22	–0.52	–0.86	–22	–22	–0.52	–0.86	–100	–100	–22	–22	–0.52	–0.86	–100	–100	–22	–22													
Le Morne	50.5	24.1	1.2	22.5	0	0	17	6	18.4	9.7	–1.66	–1.32	–1.66	–1.32	–52.17	94.67	0	0	–11	–11	–1.66	–1.32	–11	–11	–1.66	–1.32	0	0	–1.66	–1.32	0	0	–1.66	–1.32	0	0												
Bel Ombre	48.9	21.7	3.9	16	0.03	0	17	5	15.9	1.8	–1.38	–1.34	–1.38	–1.34	–55.51	75.63	–100	–100	–12	–12	–1.38	–1.34	–12	–12	–1.38	–1.34	–100	–100	–12	–12	–1.38	–1.34	–100	–100	–12	–12												
Average	52.1	31.8	3.6	15.4	0.3	0.05	17	8.3	23.1	17.4	0.52	0.74	0.52	0.74	–37.02	49.95	–16.67	–16.67	–8.67	–8.67	0.52	0.74	–8.67	–8.67	0.52	0.74	–16.67	–16.67	–8.67	–8.67	0.52	0.74	–16.67	–16.67	–8.67	–8.67												

Multivariate coral community variables are the difference of the coral community of 30 genera in the years 2019 and 2004 for the two dBRDA axes of the coral community's taxonomic structure. Percentage changes in benthic variables and changes in numbers of taxa and coral communities presented

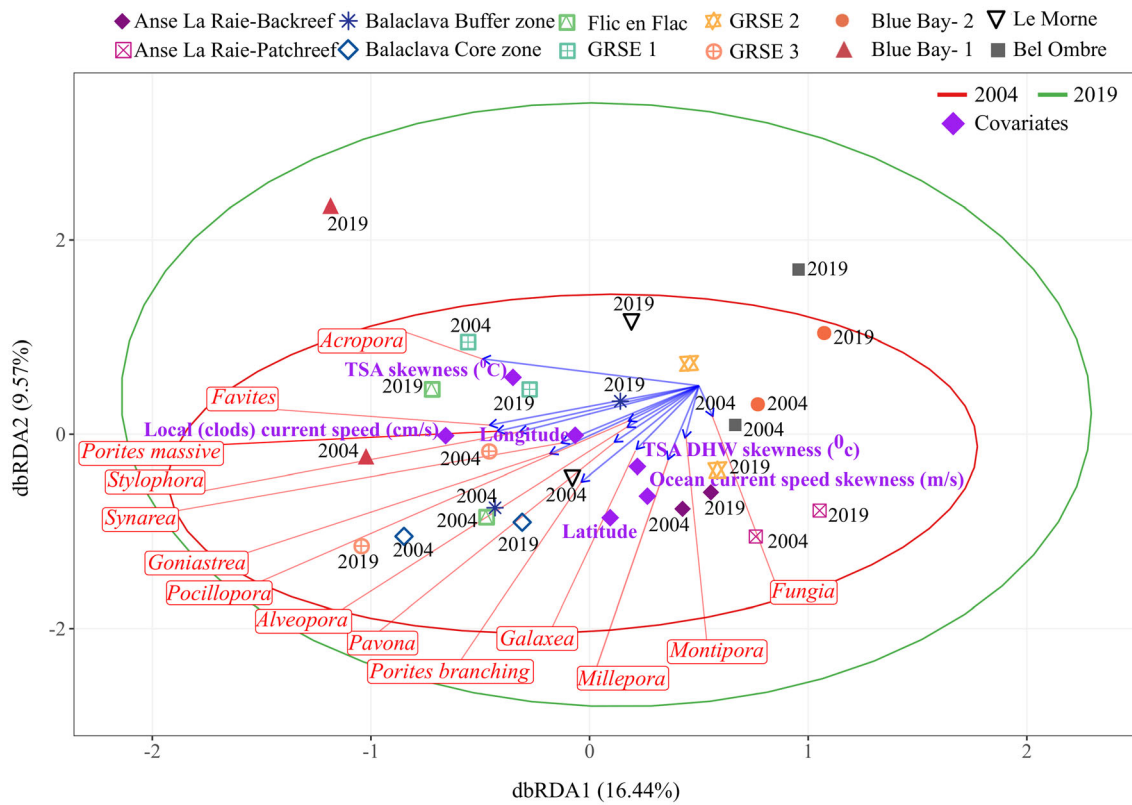


Fig. 4 Distance-based redundancy analysis (dbRDA) of 14 dominant coral communities in 2004 versus 2019 and the significant vectors (Table 2). Environmental influences of changes in sites by boosted

regression tree analysis for the two axes are presented in Fig. 5. Ellipses represent 95% Confidence Intervals

The dbRDA analyses indicates that the time period and the TSA skewness were the strongest associations with community change ($r^2 = 0.69$) in the absence of geographic location (Table 4). When geographic location was included, the latitude, local current speed, TSA skewness and TSA_DHW skewness were significant. The BRT regression evaluating changes in coral communities over the 15-yr time periods, indicate the strongest response (Relative Importance (RI) = 57%) was with water-column chlorophyll with the largest change in coral community Axis 1 associated with low chlorophyll conditions (Fig. 5a). Most of the change was associated with losses of *Acropora* (RI = 34%) with lesser effects of temperature and ocean current skewness. Most of change in Axis 2 corals over time (RI = 94.3%) was associated with declines of these corals at sites with the highest ocean current speeds with lesser effects of taxa and other environmental conditions (Fig. 5b).

The overall community-level bleaching was less in 2019 than 2004 (Table 1). Moreover, taxa-specific bleaching responses indicate that taxa responses changed between 2004 and 2019 (Fig. 6). Many taxa had lower bleaching intensity in 2019 than predicted by their responses in 2004. *Goniopora* and *Millepora* were the two exceptions in having higher than expected responses in 2019 than 2004

while *Alveopora* had similar responses between years. The single significant variable for the change in bleaching intensity was the frequency of warm acute temperature pulses (TSA_DHW skewness). While weak, this observation indicates less change in the resistance of corals to bleaching where the rare high temperature pulses were more frequent (Table 5).

Losses of taxa

Plots of the commonness of the taxa and their bleaching responses in the 2 yr indicate a number of losses of taxa as well as declines in bleaching intensity (Table 6). The most common taxa, such as *Acropora*, *Montipora*, *Pocillopora*, *Pavona*, and massive *Porites*, were lost from one or two sites each. In contrast, eight uncommon taxa, found at only one or two sites in 2004, were subsequently not seen in 2019 (Table 7). *Echinopora* was the most unusual taxa in that it was found in half the sites in 2004 but not seen again in any of the same sites in 2019. *Goniastrea*, *Leptoria*, *Favites*, *Cyphastrea*, and *Astreopora* were also moderately abundant taxa in 2004 but their numbers were reduced to one or two sites in 2019. Overall, less abundant, rare, and non-acclimating taxa were most likely to be lost from the

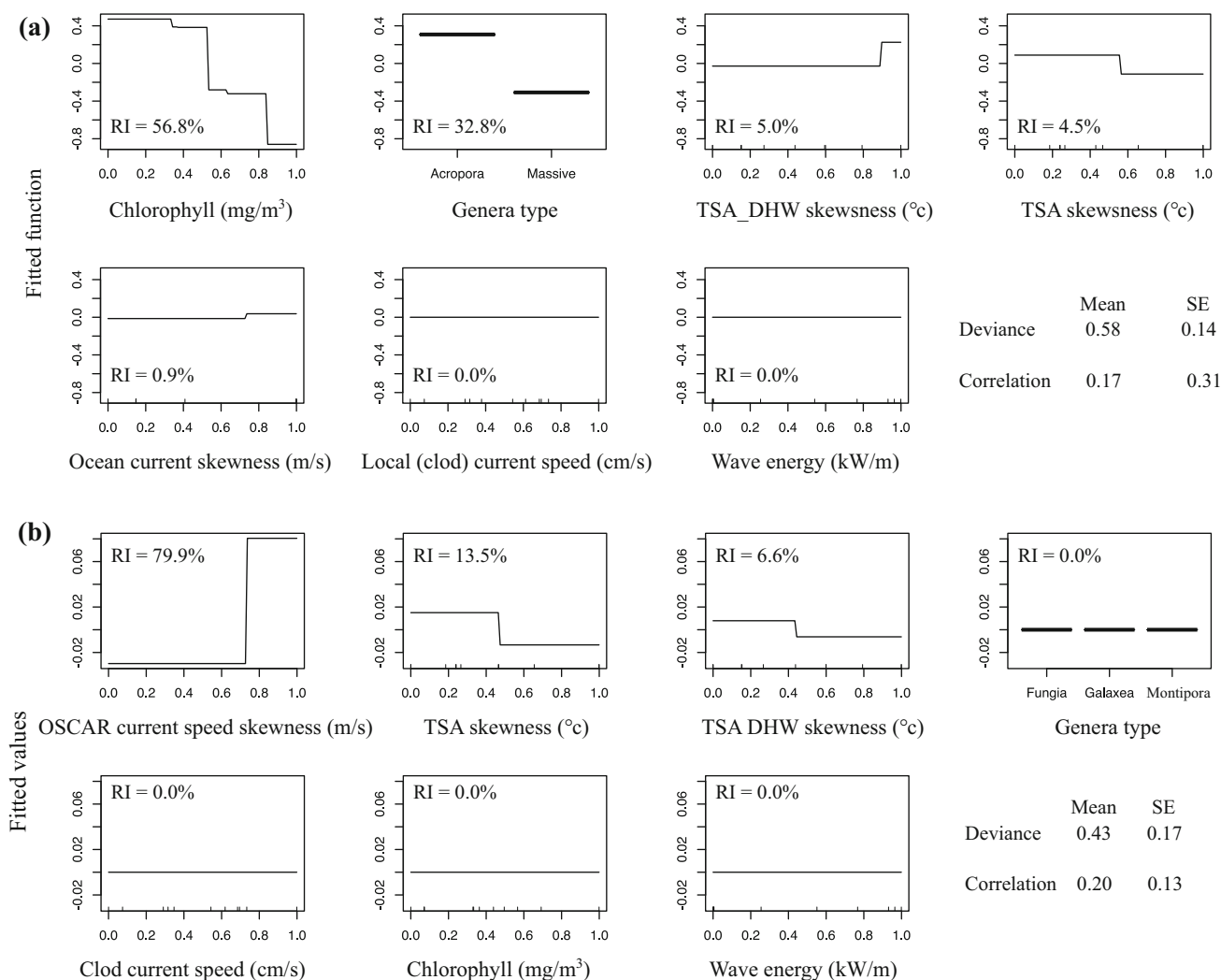


Fig. 5 Partial plots based on BRT analyses of the environmental influences on the redundancy analysis of the **a** first (x) and **b** second (y) axis for the top genera. Top genera on the first axis are *Acropora*,

massive *Porites*, *Favites*, *Stylophora* and *Porites rus* and on the second axis *Montipora*, *Millepora*, *Fungia*, and *Galaxea*

sites. Three taxa were unusual in that they were rare but still present in 2019, these were *Echinophyllia*, *Plesiastrea*, and *Lobophora*.

Surveys of an additional 15 reef sites of more variable depth in 2019 found that seven sites contained one or more of the nine coral taxa not observed in the 12 lagoon sites (Table 8). Six taxa were observed in at least one reef site. Three taxa, *Herpolitha*, *Plerogyra*, and *Psammocora*, were not observed in any of the reef sites and therefore any of the 27 sites sampled in 2019. The two sites with the most, or six of the nine lagoons missing corals, were Balaclava and Belle Mare in the north-west and north-east of the island, respectively. Consequently, three taxa may have been lost from the island while six were uncommon and mostly found in deeper water sites. Three taxa rare in 2004, namely *Plesiastrea*, *Lobophora*, and *Stylophora*, were not

seen in the additional 15 sites while three were seen, namely *Platygyra*, *Lobophyllia*, and *Echinophyllia*. *Platygyra*, and *Echinophyllia* were moderately abundant in the two northern sites of Belle Mare and Balaclava.

Discussion

Changes in coral communities over time

Mauritian coral taxa and communities changed by a number of metrics over the 15-yr interval. Large changes were observed in benthic cover with a 40% and 83% decline in total hard and soft coral, respectively, and 78% increases in erect fleshy algal cover. Community structure changed with losses of numbers of colonies in the two dominant

Table 2 Ratio of coral cover [$\log_{10}(2019/2004)$] modeled with environmental variables and (a) without latitude and longitude and (b) with latitude and longitude using (i) generalized linear models (GLM) and (ii) stepwise regression

(i) GLM model		Top model		VIF		
Predictors	Estimates \pm SE	<i>p</i> value				
(a) Ratio of coral cover modeled with environmental variables without latitude and longitude						
Intercept	0.21 \pm 0.39	Ns				
TSA_DHW skewness ($^{\circ}$ C)	– 1.86 \pm 0.68	0.02		2.78		
Observations	12					
R^2 Nagelkerke	0.55					
AIC	32.85					
Term	Estimates \pm SE	<i>t</i> Ratio	Prob > [<i>t</i>]	VIF	R^2	Whole model <i>P</i>
(ii) Stepwise regression						
Intercept	5.78 \pm 2.36	2.45	0.03		0.43	0.02
TSA_DHW skewness ($^{\circ}$ C)	– 1.36 \pm 0.50	– 2.73	0.02	4.86		
(i) GLM model		Top Model		VIF		
Predictors	Estimates \pm SE	<i>p</i> value				
(b) Ratio of coral cover modeled with environmental variables and latitude and longitude						
Intercept	0.21 \pm 0.39	Ns				
TSA_DHW skewness ($^{\circ}$ C)	– 1.86 \pm 0.68	0.02		3.63		
Observations	12					
R^2 Nagelkerke	0.55					
AIC	32.85					
Term	Estimates \pm SE	<i>t</i> Ratio	Prob > [<i>t</i>]	VIF	R^2	Whole model <i>P</i>
(ii) Stepwise regression						
Intercept	5.78 \pm 2.36	2.45	0.03		0.43	0.02
TSA_DHW skewness ($^{\circ}$ C)	– 1.36 \pm 0.50	– 2.73	0.02	4.88		

Bold *p* values indicate statistical significance

The top GLM models of < 2 AICs presented. Estimates and standard errors of the means (\pm SE), significance of models, and variance inflation factor (VIF) presented

communities *Acropora/Favites*/massive *Porites* and the *Montipora/Fungia/Galaxea*. The biggest biodiversity change, however, was the disappearance or loss of nine of the 30 coral taxa that were recorded among the 12 sites in 2004. Moreover, their distributions were very limited and numbers sparse throughout all 27 sites sampled in 2019. Therefore, reef biodiversity and possibly function were compromised over this 15-yr study period (Benkwitt et al. 2020). Many changes observed here were poorly reflected in previous coarsely-sampled studies of Mauritian reefs (Obura et al. 2017; Elliot et al. 2018). Consequently, restricting measurements to total hard coral and dominant taxa, such as *Acropora*, failed to detect many of the changes observed among subdominant and rarer taxa.

Only a few of the many examined environmental factors were not redundant, differentiated sites, and associated with considerable changes in coral cover, numbers of taxa, and bleaching responses. Environmental variables responded as expected from the land-sea interactions that arise from the east to southerly ocean current system around

Mauritius (Fig. 1; Pous et al. 2014). The main environmental metrics associated with changes in the coral communities were the thermal stress metrics but mostly notably the frequency of warm thermal acute stress periods reflected by skewness in DHWs and TSA metrics. These metrics had the strongest associations with coral cover and number of taxa changes, respectively. Metrics of acute stress, such as skewness, are found to be highly influential in reflecting the environmental conditions that allow corals to acclimate or not to thermal stress events and the subsequent state of coral communities (Zinke et al. 2018; McClanahan 2020a).

The eastern region and specifically the Blue Bay Marine Park had the highest frequency of rare DHWs (Fig. 3). Large declines in coral cover were reported between 2008 and 2009 in Blue Bay and other reefs that did not have such frequent warm temperature anomalies (Elliot et al. 2018). Water temperatures in 2008 rose above the bleaching threshold after 3 yr of cooler summer temperatures (Fig. 2). This rise was not associated with large-scale

Table 3 Absolute difference of the numbers of coral taxa [$\sqrt{\text{absolute difference (2019–2004)}}$] modeled with environmental variables and (a) without latitude and longitude and (b) with latitude and longitude using (i) generalized linear models-GLM and (ii) stepwise regression

(i) GLM	Top model 1		Top model 2		VIF		
	Estimates \pm SE	<i>p</i> value	Estimates \pm SE	<i>p</i> value			
(a) Absolute difference of numbers of coral taxa modeled with environmental variables without latitude and longitude							
Intercept	1.6 \pm 0.51	0.011	3.45 \pm 0.49	< 0.001			
TSA skewness ($^{\circ}\text{C}$)	2.6 \pm 1.00	0.026				2.8	
Ocean current speed skewness (m s^{-1})			– 1.87 \pm 0.81	0.04		4.56	
Observations	12		12				
R^2 Nagelkerke	0.61		0.55				
AIC	40.42		41.49				
Term	Estimates \pm SE	<i>t</i> Ratio	Prob > [<i>t</i>]	VIF	R^2	Whole model <i>P</i>	
(ii) Stepwise regression							
Intercept	2.63 \pm 0.32	1.77	Ns		0.40	0.03	
TSA skewness ($^{\circ}\text{C}$)	1.30 \pm 0.50	2.6	0.03	2.94			
(i) GLM	Top model 1		Top model 2		Model 3		VIF
	Estimates \pm SE	<i>p</i>	Estimates \pm SE	<i>p</i> value	Estimates \pm SE	<i>p</i> value	
(b) Absolute difference of numbers of coral taxa modeled with environmental variables and latitude and longitude							
Intercept	3.84 \pm 0.50	< 0.001	3.1 \pm 0.63	0.001	1.6 \pm 0.51	0.01	
Latitude	–2.66 \pm 0.87	0.012	–2.83 \pm 0.81	0.007			9.07
Local (clods) current speed (cm s^{-1})			1.67 \pm 1.00	ns			2.87
TSA skewness ($^{\circ}\text{C}$)					2.6 \pm 1.00	0.03	6.79
Observations	12		12		12		
R^2 Nagelkerke	0.69		0.79		0.61		
AIC	38.74		37.50		40.42		
Term	Estimates \pm SE	<i>t</i> Ratio	Prob > [<i>t</i>]	VIF	R^2	Whole model <i>P</i>	
(ii) Stepwise regression							
Intercept	2.63 \pm 0.32	– 2.97	0.01		0.48	0.01	
TSA skewness ($^{\circ}\text{C}$)	– 1.33 \pm 0.44	– 3.05	0.01	8.3			

Bold *p* values indicate statistical significance

The top GLM models of less than 2 AICs presented. Estimates and standard errors of the means (\pm SE), significance of models, and VIFs presented

oceanographic variation in the El Niño Southern Oscillation (ENSO) or Indian Ocean Dipole (IOD). Rather, the Southwest Indian Ocean (SWIO) SST Index was positive during the 2006–2008 period and more likely to be associated with the large-scale but patchy warming in the southern Indian Ocean (<https://stateoftheocean.osmc.noaa.gov/sur/ind/swio.php>). The SWIO index is frequently used to evaluate SST fluctuations from southern Madagascar and South Africa, which influence South African rainfall (Walker 1989).

Losses in coral taxa were most influenced by the geographic position with the highest losses in the east and south where open-ocean currents impinge on the coastline, such that corals experience strong and constant currents

and low chlorophyll concentrations in some lagoons. This southern region was also where the *Acropora*/*Favites*/massive *Porites* communities were common, dominant, and also the most disturbed across the study period. High water flow is expected to create good conditions for *Acropora* growth and possibly give them a competitive advantage over sub-canopy taxa like *Galaxea* and *Fungia* (Tanner 1995). If these currents are constant, such as those driven by tides, their periodic constancy may reduce warm-water acute thermal stress and subsequent coral bleaching (Nakamura and van Woesik 2001). Nevertheless, the findings suggest that warm acute thermal stresses propagated by inter-annual variation in ocean current heating is likely to have caused the high *Acropora*

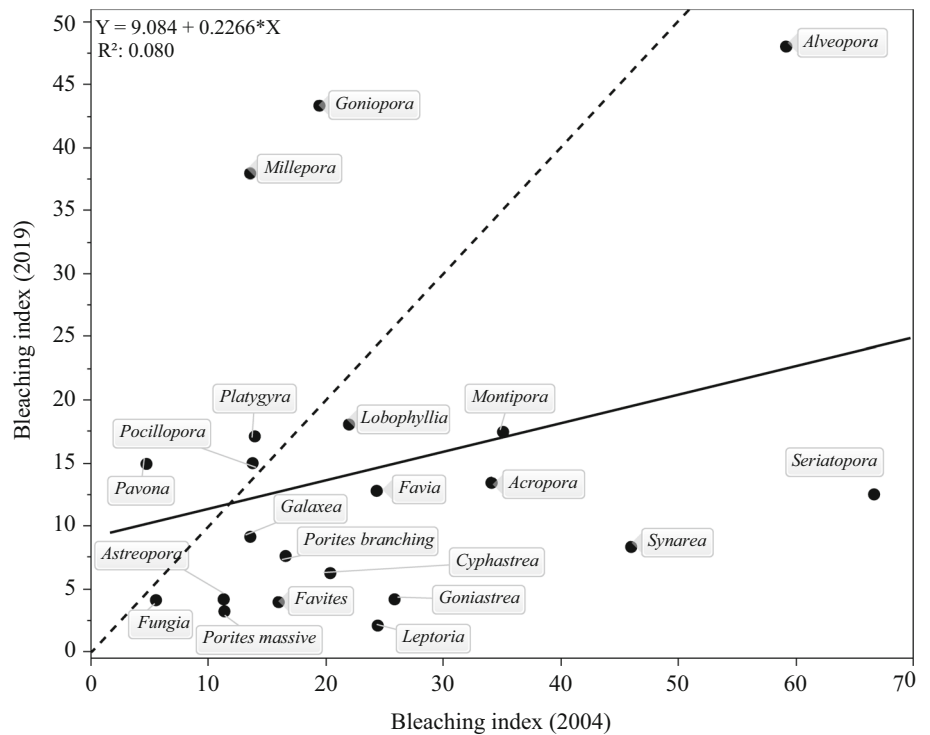
Table 4 Selected variables from multivariate dbRDA analysis of coral community (numbers of coral colonies per 40 min) with environmental variables; (i) without geographic variables and (ii) with geographic variables. Significance of the models and proportion of inertia explained presented

Category	Covariate	Sum of Squares	F Ratio	P(> F)	VIF	Whole model P	Proportion of inertia explained
<i>Numbers of colonies per 40 min search</i>							
(i) Coral community without geography	Time period	0.43	1.89	0.43	1.0	0.009	0.69
	Local (clods) current speed (cm s ⁻¹)	0.36	1.56	ns	1.44		
	TSA skewness (°C)	0.45	1.96	0.04	1.86		
	Ocean current speed skewness (m s ⁻¹)	0.33	1.42	ns	2.03		
	TSA_DHW skewness (°C)	0.33	1.45	ns	1.66		
(ii) Coral community with geography	Time period	0.43	2.07	0.04	1.0	0.002	0.45
	Longitude	0.23	1.1	ns	1.78		
	Latitude	0.48	2.27	0.02	4.59		
	Local (clods) current speed (cm s ⁻¹)	0.51	2.44	0.02	2.46		
	TSA skewness (°C)	0.47	2.23	0.02	2.44		
	Ocean current speed skewness (m s ⁻¹)	0.18	0.88	ns	3.57		
	TSA_DHW skewness (°C)	0.39	1.85	0.05	2.22		

Bold *p* values indicate statistical significance

Data based on based on number of colonies per sample

Fig. 6 Scatterplots of the bleaching responses over the 15-yr study period as a taxa-specific responses in normalized to a 40-min search. *Stylophora* was uncommon but observed in line transects but not bleaching surveys. Dashed line is the 1:1 line expected for no change in bleaching responses over time



mortality and the loss of subdominant and rare taxa. Interestingly, a higher frequency of rare episodic fast currents in the north was associated with fewer losses of coral

taxa, which suggests that extreme variation in thermal stress rather than variation in fast current drove the coral losses. Leeward but current-influenced sides of the island

Table 5 Ratio of bleaching index [$\log_{10}(2019/2004)$] modeled with environmental variables and (a) latitude and longitude and (b) without latitude and longitude using (i) generalized linear models-GLM and (ii) stepwise regression

Predictors	Top model 1		Tope model 2		VIF
	Estimates \pm SE	<i>p</i> value	Estimates \pm SE	<i>p</i> value	
(a) Ratio of bleaching index modeled with environmental variables without latitude and longitude					
Intercept	- 0.5 \pm 0.22	0.045	- 0.27 \pm 0.37	ns	
TSA_DHW skewness ($^{\circ}$ C)		- 0.51 \pm 0.66	Ns	2.71	
Observations	12		12		
R^2 Nagelkerke	0		0.07		
AIC	30.66		31.97		
(b) Ratio of bleaching index modeled with environmental variables and latitude and longitude					
Predictors	Estimates \pm SE	<i>p</i> value	Estimates \pm SE	<i>p</i> value	VIF
Intercept	- 0.5 \pm 0.22	0.045	- 0.27 \pm 0.37	ns	
TSA_DHW skewness ($^{\circ}$ C)		- 0.51 \pm 0.66	Ns	2.78	
Observations	12		12		
R^2 Nagelkerke	0		0.07		
AIC	30.66		31.97		

Bold *p* values indicate statistical significance

The top GLM models of < 2 AICs presented. Estimates and standard errors of the means (\pm SE), significance of models and VIFs presented

*No variables were significant with stepwise regression

(i.e., the north) are expected to have slower but more variable currents that appeared to promote coral acclimation over the study period. Leeward ocean gyres will be generated by this land–sea interaction and result in episodic current speed variability that is reflected in the current skewness metric.

The intensity of the bleaching response appeared to decline over the 15-yr study period, which might be expected from previous studies that measured bleaching over recent time (Guest et al. 2016; Couch et al. 2017; McClanahan 2017; Hughes et al. 2019). Increased resistance can be attributable to changes in taxa-specific acclimation, genotypic change due to differential survival, and changes in the taxonomic composition of the corals. A global summary compilation of thermal responses found evidence for acclimation or community change as the threshold for bleaching increased by 0.5 $^{\circ}$ C between 1998 and 2007 (Sully et al. 2019). Changes in Mauritius over 15 yr were, however, not large and there were differences in the timing of stress, sampling, taxonomic composition, and types of thermal stress that make direct between-year comparisons problematic. Nevertheless, the change in community-level bleaching index declined as the frequency of acute stress of the rare thermal anomalies (TSA_DHW skewness) increased. This would be expected if constant and moderate but not rare and extreme variation provokes acclimation (Ateweberhan and McClanahan 2010). Consequently, high SST skewness reflects atypical acute stresses that may prevent acclimation whereas

predictable or chronic variability should promote acclimation (Safaie et al. 2018).

The 2004 versus 2019 taxa comparison further support observations in the Indian Ocean that most, but not all taxa, have reduced their sensitivity to warm thermal stress since first measured (McClanahan and Muthiga 2014; McClanahan 2017). Moreover, the taxa that show low acclimation or even increased sensitivity appeared to vary with location, suggesting some local environment–taxa interactions. We expected that exposed and windward reefs or reefs directly exposed to more frequently stable open-ocean conditions would be least capable of resisting rare and acute SST anomalies (McClanahan et al. 2005; Louis et al. 2016). Given that the frequency of strong inter-annual SST variation is increasing with climate warming (Nakamura et al. 2011; Wang et al. 2019; Abram et al. 2020), corals in ocean-exposed sites are expected to lose more coral colonies and taxa than ocean-sheltered locations (Golbuu et al. 2007; McClanahan et al. 2007). Compilations of coral cover in near and off-shore environments support this prediction, finding lower coral cover in more offshore and ocean-exposed environments (Bruno and Valdivia 2016; McClanahan et al. 2019b).

Bleaching and patterns of community change observed at the gross community level may be less powerful when evaluating specific communities or taxa. For example, the *Acropora/Favites/massive Porites* community declined the most where oceanographic conditions promoted low chlorophyll concentrations. Consequently, some combination of light penetration or, perhaps the availability of

Table 6 Percentage means and standard errors from the mean (mean \pm SE) of bleaching index and sites containing genera in 2004 and 2019

Genera	Bleaching index 2004 (%)	Sites 2004 (%)	Bleaching index 2019 (%)	Sites 2019 (%)
<i>Seriatopora</i>	66.67 \pm 0.00	8.33 \pm 3.18	0 \pm 0	0 \pm 0
<i>Alveopora</i>	59.18 \pm 7.84	66.67 \pm 1.15	48.03 \pm 15.07	16.67 \pm 2.89
<i>Porites rus (Synaraea)</i>	45.99 \pm 0.33	16.67 \pm 2.89	8.33 \pm 0.00	8.33 \pm 3.18
<i>Plerogyra</i>	43.33 \pm 0.00	8.33 \pm 3.18	0 \pm 0	0 \pm 0
<i>Montipora</i>	35.09 \pm 4.89	100 \pm 0.00	17.46 \pm 5.03	75.00 \pm 0.87
<i>Acropora</i>	34.10 \pm 3.55	100 \pm 0.00	13.42 \pm 3.75	91.67 \pm 0.29
<i>Goniastrea</i>	25.85 \pm 3.95	50.00 \pm 1.73	4.17 \pm 0	8.33 \pm 3.18
<i>Echinopora</i>	25.00 \pm 8.35	50.00 \pm 1.73	6.25 \pm 0.85	16.67 \pm 2.89
<i>Leptoria</i>	24.41 \pm 6.66	75.00 \pm 0.87	2.08 \pm 0	8.33 \pm 3.18
<i>Favia</i>	24.32 \pm 3.32	66.67 \pm 1.15	12.78 \pm 4.18	33.33 \pm 2.31
<i>Lobopyllia</i>	21.97 \pm 4.88	41.67 \pm 2.02	14.98 \pm 3.05	75.00 \pm 0.87
<i>Cyphastrea</i>	20.37 \pm 3.34	25.00 \pm 2.60	18.06 \pm 3.97	16.67 \pm 2.89
<i>Goniopora</i>	19.44 \pm 3.67	25.00 \pm 2.60	14.92 \pm 3.85	33.33 \pm 2.31
<i>Acanthastrea</i>	16.67 \pm 0.00	8.33 \pm 3.18	4.17 \pm 0.00	8.33 \pm 3.18
<i>Oxypora</i>	16.67 \pm 0.00	8.33 \pm 3.18	0 \pm 0	0 \pm 0
<i>Turbinaria</i>	16.67 \pm 0.00	16.67 \pm 2.89	0 \pm 0	0 \pm 0
<i>Psammacora</i>	16.67 \pm 0.00	8.33 \pm 3.18	0 \pm 0	0 \pm 0
<i>Porites branching</i>	16.57 \pm 3.55	58.33 \pm 1.44	7.61 \pm 1.75	25.00 \pm 2.60
<i>Favites</i>	15.97 \pm 3.04	66.67 \pm 1.15	17.1 \pm 1.62	66.67 \pm 1.15
<i>Herpolitha</i>	14.46 \pm 4.93	16.67 \pm 2.89	0 \pm 0	0 \pm 0
<i>Platygyra</i>	13.95 \pm 1.59	75.00 \pm 0.87	37.96 \pm 8.69	16.67 \pm 2.89
<i>Pocillopora</i>	13.76 \pm 3.69	100 \pm 0.00	0 \pm 0	0 \pm 0
<i>Galaxea</i>	13.56 \pm 3.40	75.00 \pm 0.87	9.13 \pm 2.38	33.33 \pm 2.31
<i>Millepora</i>	13.55 \pm 3.83	58.33 \pm 1.44	4.11 \pm 1.11	41.67 \pm 2.02
<i>Hydnophora</i>	12.50 \pm 1.70	16.67 \pm 2.89	3.21 \pm 1.16	50.00 \pm 1.73
<i>Porites massive</i>	11.36 \pm 2.73	83.33 \pm 0.58	43.33 \pm 0.00	8.33 \pm 3.18
<i>Astreopora</i>	11.30 \pm 1.48	41.67 \pm 2.02	3.95 \pm 0.48	16.67 \pm 2.89
<i>Symphyllia</i>	11.11 \pm 0.00	8.33 \pm 3.18	0 \pm 0	0 \pm 0
<i>Fungia</i>	5.53 \pm 1.39	91.67 \pm 0.29	0 \pm 0	0 \pm 0
<i>Pavona</i>	4.73 \pm 1.13	66.67 \pm 1.15	12.5 \pm 0.00	8.33 \pm 3.18

Genera arranged from most to least bleached in 2004. The 9 lost genera in 2019 are in bold italics

planktonic food for corals that rely on heterotrophy, interact with thermal stress (Anthony et al. 2009; Mollica et al. 2019). There is considerable debate about the potential roles of nutrients, their concentrations, thresholds, ratios of nitrogen and phosphorus, plankton, and light penetration that make it difficult to conclude about the mechanisms producing these observations (DeAngelo and Wiedenmann 2014). In contrast, the more diverse *Montipora/Fungia/Galaxea* community changed the least in low current environments common to the north and west of the island. Thus, changes in communities to thermal responses are likely to be modified by interactions between taxa and their responses to currents and associated light and nutrient conditions.

We found that the *Acropora/Favites/massive Porites* community dominant in the high-water flow conditions was the most susceptible to acute thermal stress. Nevertheless, *Acropora* in Mauritius has some species or genotypes that are resistant to thermal stress in some habitats. For example, a study of one of the most common corals on the windward side, *Acropora muricatum*, found differences in susceptibilities to thermal stress between colonies living near and further from shore (Louis et al. 2016). This study found that colonies living near the coast in the northeast site of Belle Mar exhibited enhanced photo-physiological responses, antioxidant activities, and increased total phenolic contents compared to offshore colonies. These conditions appeared to provide greater resistance to thermal stress. Up-regulating of stress-response genes has been

Table 7 Metrics used to evaluate coral genera probabilities of disappearance where genera are arranged from highest to lowest disappearance rate

Genera	Number of species	Relative coral cover	Relative commonness, site frequency	Relative bleaching index	Bleaching adaptation	Relative disappearance rate	Disappeared in 2019
<i>Echinophyllia</i>	2	0.0001	0.00	Nd	Nd	0.99	No
<i>Plesiastrea</i>	2	0.02	0.00	Nd	Nd	0.99	No
<i>Lobophora</i>	ND	0.01	0.00	Nd	Nd	0.99	No
<i>Symphyllia</i>	1	0.0000	0.00	0.12	Nd	0.96	Yes
<i>Hydnophora</i>	2	0.001	0.00	0.14	Nd	0.95	Yes
<i>Herpolitha</i>	1	0.01	0.00	0.18	Nd	0.94	Yes
<i>Acanthastrea</i>	3	0.004	0.00	0.22	Nd	0.93	Yes
<i>Oxypora</i>	?	0.0000	0.00	0.22	Nd	0.93	Yes
<i>Psammocora</i>	1	0.0000	0.00	0.22	Nd	0.93	Yes
<i>Stylophora</i>	?	0.04	0.09	Nd	Nd	0.93	No
<i>Turbinaria</i>	3	0.0000	0.09	0.22	Nd	0.90	Yes
<i>Lobophyllia</i>	3	0.01	0.00	0.32	0.05	0.90	No
<i>Platygyra</i>	4	0.004	0.27	0.17	0.05	0.88	No
<i>Echinopora</i>	2	0.04	0.00	0.37	Nd	0.86	Yes
<i>Millepora</i>	1	0.04	0.09	0.16	0.40	0.83	No
<i>Cyphastrea</i>	3	0.0000	0.00	0.29	0.46	0.81	No
<i>Galaxea</i>	1	0.07	0.45	0.16	0.13	0.80	No
<i>Fungia</i>	5	0.06	0.64	0.01	0.09	0.80	No
<i>Favites</i>	7	0.03	0.09	0.21	0.55	0.78	No
<i>Plerogyra</i>	1	0.0000	0.00	0.71	ND	0.76	Yes
<i>Porites</i> branching	7	0.07	0.36	0.22	0.29	0.76	No
<i>Pocillopora</i>	4	0.04	0.73	0.17	0.00	0.76	No
<i>Favia</i>	7	0.01	0.36	0.36	0.24	0.76	No
<i>Goniastrea</i>	5	0.04	0.00	0.39	0.73	0.71	No
<i>Alveopora</i>	3	0.14	0.09	1.00	0.05	0.68	No
<i>Porites</i> massive	5	0.13	0.55	0.12	0.50	0.67	No
<i>Pavona</i>	8	0.13	0.82	0.00	0.45	0.65	No
<i>Leptoria</i>	1	0.01	0.18	0.36	1.00	0.61	No
<i>Porites rus</i> (<i>Synaraea</i>)	Nd	0.05	0.09	0.76	0.68	0.60	No
<i>Montipora</i>	18	0.30	0.91	0.56	0.26	0.49	No
<i>Acropora</i>	31	1.00	1.00	0.54	0.36	0.27	No

Bold *p* values indicate statistical significance

Factors included are the relative coral cover, the frequency of sites observation (commonness), relative bleaching index, and bleaching adaptation. Adaption is the ratio the bleaching in 2019 and 2004 and therefore not available for taxa not observed in 2019. The column for disappearances is based on the observations of taxa seen in 2004 but not seen in 2019. Relative commonness of 0 means taxa seen at only 1 site. ND = no observational data. Number of species is the whole country count based on surveys of Moothien-Pillay et al. (2002a, b)

observed for *Acropora* and specifically for *A. muricata* in Japan (Palumbi et al. 2014; Lee et al. 2018). Thus, *Acropora* in Mauritius appears to have persisted over time more than recorded in other more equatorial Indian and Pacific Ocean reefs (McClanahan et al. 2014; Darling et al. 2019). Exploring the variance in these metrics within and between

taxa on windward and leeward positions and other larger geographic gradients could further uncover phenotypic and physiological acclimation mechanisms. Findings here on leeward-windward differences add to observations that bleaching and mortality can be reduced in reefs adjacent deep-water lagoons, up-welling regions, and those

Table 8 Numbers of coral colonies (per 40 min) that were observed in 15 study sites sampled in 2019 but not in 2004

Lost genera	Belle Mare-Long cliff	Balacava-Turtle Bay Hotel	Coin de Mire	Bel Ombre-Edge	Flic en Flac-Reef Lagoon	Trou d'eau Dou-Ille aux Cerf	Riviere des Galets-Station 2	Blu Bay-Ille Cocos	Baie du Cap-St. Martin	Baie du Cap-Maconde	Blue Bay-Coast Guard
Water depth (m)	15.5	5.0	14.5	20	1.5	1.5	1.0	1.5	0.7	0.8	5
Missing taxa											
<i>Echinopora</i>	27	5	4	4	0	4	0	0	0	0	0
<i>Acanthastrea</i>	10	7	3	1	10	0	0	0	0	0	0
<i>Turbinaria</i>	4	3	4	1	0	0	0	0	0	0	0
<i>Oxypora</i>	3	10	0	0	0	0	0	0	0	0	0
<i>Symphyllia</i>	2	3	0	0	0	0	0	0	0	0	0
<i>Hydnophora</i>	2	1	0	0	0	0	2	0	0	0	0
<i>Plerogyra</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Herpolitha</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Psammocora</i>	0	0	0	0	0	0	0	0	0	0	0
Rare taxa sighted from the 15 sites surveyed in 2019											
<i>Platygyra</i>	64	45	4	2	0	2	0	6	3	1	0
<i>Lobophyllia</i>	1	9	0	1	0	0	0	0	0	0	2
<i>Echinophyllia</i>	2	6	0	5	0	0	0	0	0	0	0
<i>Plesiastrea</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Lobophora</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Stylophora</i>	0	0	0	0	0	0	0	0	0	0	0

(Top) colonies of taxa that disappeared and (bottom) rare taxa based on repeated surveys in 12 lagoon sites sampled in 2004 and 2019. Seven of the 15 sites surveyed in 2019 had missing taxa while 11 of the 15 sites had rare taxa. Reef water depths (m) at time of survey presented

The other 4 reefs sampled but without lost and rare taxa included: Blue Bay-Shandrani (7 m), Riviere des Galets-Station 1 (1 m), Mahebourg-Anemone (4 m) and Bel Ombre-Lagoon (1 m)

experiencing internal tidal waves (Riegl et al. 2012; Tkachenko and Song 2017; Randell et al. 2019). Thus, a variety of recent findings indicate the potential for a number of moderate-scale geographic features to provide coral sanctuary, which may be useful knowledge for prioritizing climate-adaptation planning and management.

Potential causes of environmental stress

Evaluations and selection of the initial 22 environmental metrics indicate complexities in discovering the potential causes of environmental stress. Environmental data from satellite have coarse spatial and temporal resolution, which is expected to limit the capacity to predict patterns at the more spatially limited scale influencing corals. Coarse sampling of the ocean environment is likely to be most problematic for leeward reefs where smaller-scale environmental conditions created by aperiodic eddies and upwelling will not be well resolved by coarse-resolution satellite data. A study of the leeward islands of northern Tanzania, for example, found satellite data were notably

poor at measuring temperature distribution metrics, such as kurtosis and skewness, compared to in situ data (McClanahan 2020a). Moreover, high covariation among common heat stress metrics and weak differentiation among sites challenged efforts to evaluate specific stresses. We did, however, predict that background chronic variation interacting with acute stress would be the main drivers of coral responses to stress. Variation around mean values or the standard deviations and flatness of SST distributions (i.e., kurtosis) may provide some acclimation to corals (Safaie et al. 2018). But, here we found little SST variation among sites for the frequency distributions of chronic variables using coarse-scale satellite data. Thus, with these data, we have little evidence that SST variation was the source of acclimation and differences between sites in their responses to acute thermal stresses. There was more evidence that water flow variation and light penetration were contributing to the acclimation or resistance to acute thermal stress. In contrast, the degree of right skew in thermal stress anomalies (TSA) and DHW better differentiated sites. Therefore, skewness should represent acute

and rare warm temperature variation outside of acclimatable ranges.

The screening procedure may have eliminated some potential impactful variables. This seems unlikely, however, given that excluded variables had low between-site variation and were arguably theoretically poor to modest proxies of either chronic or acute stresses. For example, high correlation between mean and standard deviations of SSTs is a challenging problem for distinguishing chronic and acute stress as both can act as stresses and acclimation mechanisms. In this case, skewness was the better metric of acute stress while chronic stress was problematic—appearing more evident in the geographic outcomes or the site's position on the coastline rather than specific satellite-derived environmental variables. Nevertheless, the findings suggest some combination of water flow variability and reduced light promoted increased acclimation or resistance to acute thermal stresses.

Corals may acclimate to mean conditions given moderate and predictable variation but are less likely to acclimate to extremes reflected by frequent anomalous temperature extremes. Mauritius provided a good example of this local adaptation, as it has a low bleaching threshold of 27.5 °C due to its low-latitude (20°S). Bleaching thresholds are generally > 30 °C for many shallow tropical and equatorial reefs (Liu et al. 2014; Heron et al. 2016) but also decline with depth (Venegas et al. 2019). While the frequency of rare environmental events (i.e., skewness) is not commonly used to evaluate coral bleaching (Eakin et al. 2010; Sully et al. 2019), it is theoretically robust and has been a useful predictor for various coral abundance, life history, and diversity metrics (McClanahan and Muthiga 2016; Zinke et al. 2018; McClanahan 2020a). Here, we see that acclimation over 15 yr was higher in the absence of rare acute thermal stress.

There are a number of possible alternative explanations for the observed patterns including severe storms, outbreaks of coral predators, and human development. To be viable hypotheses, these forces would need to be more destructive on the island's windward than leeward reefs. Human population development in watersheds, for example, is an alternative driver of changes that has been associated with losses of coral cover (Elliot et al. 2018). Human development and thermal disturbances are increasing simultaneously, which makes it difficult to separate their effects using correlation methods. Nevertheless, there may be additive and synergistic effects contributing to the observed changes, as found globally (Darling et al. 2019). Human settlements, tourism, and agricultural developments in Mauritius and elsewhere are frequently located on leeward side of large islands. Thus, the expectation is that human impacts will be greatest on the leeward rather than the windward reefs. A study of the

Micronesian Island of Kosrae, for example, lacked a history of thermal disturbances, showed the greatest impacts of overfishing were on the wave-protected leeward reefs, affecting both fish and benthic communities (McLean et al. 2017). Thus, because the greatest changes and losses of taxa in Mauritius were in the more sparsely populated windward island regions, it is more plausible that the patterns we observed arose from large-scale thermal stress. Storms and coral predator outbreaks remain as alternative drivers, but these are more frequently observed to damage corals on smaller scales than the large-scale coral demise patterns observed here.

Conservation and management implications

One hypothesized consequence of climate change is that coral distributions will expand and find sanctuary in high-latitude locations where cooler environmental conditions are conducive to coral survival (Precht and Aronson 2004). The historical presence of reefs at high latitudes is a proxy indicator for this potential climate-driven expansion (Greenstein and Pandolfi 2008; Couce et al. 2013). This possibility has stimulated conservation and spatial planning (Maina et al. 2008; Freeman et al. 2013; Makino et al. 2014; Beyer et al. 2018). However, the current causes of coral mortality and resilience and the taxa-specific responses are too poorly known to be confident about the potential for large-scale latitudinal coral sanctuary and expansion (McClanahan et al. 2012, 2014; Madin et al. 2016).

This short 15-yr study indicates that a number of Mauritian coral taxa are threatened and some may already be locally extinct. Rarity in 2004 was the strongest correlate of taxa disappearance in the lagoons as many of the lost taxa, with the exception of *Plerogyra*, did not have notably high bleaching responses. Bleaching and mortality are not always well correlated (McClanahan 2004; Buddemeier et al. 2004), and the losses observed here support that observation. For example, eight of the lost taxa were in one or two sites in 2004. The one exception was *Echinopora*, which had moderate bleaching responses and was originally found in six or half the sites. *Echinopora* was, however, observed in five of the additional 15 sampled sites, some in deeper water and therefore probably mostly lost in shallow water. There is no compelling reason why *Echinopora* would be particularly sensitive to disappearance in Mauritius. *Echinopora* is generally robust to various environmental disturbances, including river sediments, and also observed to colonize some reefs after bleaching disturbances (McClanahan and Obura 1997; McClanahan 2014). Mauritius has two species, *E. gemmacea* and *E. hirsutissima*, and therefore knowing which of these species was most affected would require a study that evaluates

their presence and distribution. Currently, it is unclear whether or not both species have persisted and in which habitats.

No new coral genera were observed, which suggests that these losses were not compensated for by gains, and we recorded directional net losses rather than both immigration and extinction processes that would be expected across disturbance events (McClanahan 2020b). Additionally, not all rare taxa disappeared, even those that are susceptible, such as *Seriatopora*, *Porites rus*, and *Stylophora*. These taxa and other rare taxa including *Echinophyllia*, *Plesiatrea*, and *Lobophora* are likely to be susceptible to future losses due to their rarity and susceptibility to stress. Consequently, perhaps more than half the coral genera in Mauritius are susceptible to local extinction in the lagoons and more broadly in the coming decades.

The number of species lost and susceptible to extirpation is difficult to determine as the species per genus among the taxa is variable (Table 8). This is particularly true for the dominant genera, *Montipora*, and *Acropora*, which are listed in Mauritius as having 18 and 31 species, respectively (Moothien-Pillay et al. 2002a, b). Another example is *Porites*, which has seven species of which many are branching forms that are highly susceptible to thermal stress in many locations (McClanahan et al. 2001; Cacciapaglia and van Woesik 2018). There are also taxa identification problems that require genetic analysis to resolve. For example, *Stylophora pistillata*, which was not listed in the 2002 country-level compilation of Moothien-Pillay et al. (2002a, b), is present and has a complex morphology. This makes it difficult to classify and the current classification may contain hidden species that have been given a single name (Bhagooli et al. 2017).

The three missing taxa, *Plerogyra*, *Herpolitha*, and *Psammocora*, were only listed as having one species per genus in Mauritius and therefore among the least species-diverse genera. Low numbers of species in a genus appear to be a proxy for susceptibility to stress and extinction (McClanahan et al. 2007). Nevertheless, it is likely that many species are susceptible, if not already gone from locations across the whole islands, possibly among the more diverse genera. More research is needed to determine if threatened taxa still persist in deeper water. The research here suggests threatened taxa may be mostly present in the west and north or leeward side of the island.

The study indicates the importance of evaluating the status of reefs at some genus to sub-genus level of taxonomic resolution, as opposed to evaluations that report cover of dominant taxa (i.e. *Acropora*). Here, coral cover is not a proxy for diversity but is greatly influenced by the more resilient *Acropora* and *Montipora* species, such as *A. muricata* (Louis et al. 2016). Thus, cover is expected to produce poor or false conclusions about the status of these

reefs. Reefs may be functional, in terms of maintaining cover and reef growth, but losses of taxa are expected to reduce the long-term resilience of these reefs (Hooper et al. 2005) and possibly threaten the high species endemism found in Mauritius (Roberts et al. 2002). In order to protect Mauritian reef diversity, there is a need to determine the locations of the susceptible taxa, the threats to their populations, and reduce these threats, which are likely to include fishing, river sedimentation, and eutrophication (Elliot et al. 2018).

The predictions of land–sea oceanographic interactions and the results here suggest that corals are likely to endure climate changes better in the leeward and more heavily human populated areas of the north and west. Thus, a major recommendation is to increase efforts to reduce the human impacts and engage people in protection of threatened taxa. Management efforts will require a mixture of watershed and water quality management as well as restricted fishing in the least thermally impacted sites. We found here that the Blue Bay Marine Park was able to reduce the possible adverse effects of increased algal abundance but not climatic impacts. Protected areas on the north and west are few and also of low compliance (McClanahan, T. personal observation). Consequently, efforts to develop and implement functional fisheries management systems are a high priority recommendation for maintaining the resilience of Mauritian reefs. Failure to engage in management and protect these species is likely to lead to losses of possibly half the Mauritian coral fauna and undermine the island's potential as a future sanctuary for corals.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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