REPORT

Decadal turnover of thermally stressed coral taxa support a risk-spreading approach to marine reserve design

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Abstract Coral reef communities exposed to rapid temperature rises and frequent thermal anomalies were evaluated for taxonomic turnover via presence/absence information over a 27-year period experiencing large changes in the dominant taxa. Temporal turnover of the taxa within sites was consistently high ($\sim 40\%$) due to both inter-annual episodic and directional changes. Turnover with time displayed a rapid increase and slow decline after sequential cool and warm thermal anomalies between 1996 and 1998. Subsequent warm temperature anomalies caused fewer broad-scale changes. Directional change for all sites combined indicated three overall gains and losses in taxa—*Montipora* being the only dominant taxon that declined in both abundance and presence/absence. The studied marine reserves had higher local but lower between-site taxonomic richness than fished reefs. Despite similar mean turnover, there were fewer gains than losses in marine reserves (7 gains and 20 losses in 5 sites) than fished sites (16 gains and 15 losses in 7 sites). Changes in taxonomic cover and presence/absence turnover data were not correlated, indicating that turnover detects finer scale taxonomic change likely to be missed when the cover of the dominant taxa is evaluated—especially in the higher richness marine reserves. High spatial richness, community change, and thermal acclimation in these shallow reef lagoons may have prevented higher net losses of taxa. Consequently, the probabilities of reducing local extirpations of taxa may be best achieved by planning and management that promotes spreading more evenly-spread access restrictions to reef areas with high between-site diversity rather than focusing restrictions to sites with high within-site diversity.

Introduction

The possibility of losing coral diversity is increasing with the accelerating threats to coral reefs (Carpenter et al. 2008). Dominant corals are declining or changing rapidly with increasing thermal disturbance, but the impacts on subdominant and rare corals are less understood (McClanahan et al. 2007, 2014; Edmunds et al. 2014; Hughes et al. 2017, 2018). Dominant taxa drive the state of ecological processes and services, such as reef calcification (Price et al. 2012; Perry et al. 2018). Nevertheless, dominance can be a poor indicator of more subtle and difficult-to-detect changes that influence subdominants and the long-term resilience of ecosystems (Hooper et al. 2005). Some studies indicate that thermal tolerance and recovery rates interact with other disturbances, coral life histories, and trans-generational plasticity to influence community composition (Darling et al. 2013, 2019; Torda et al. 2017). Yet, detecting some changes can be difficult when sampling favors evaluations of abundant, coarse-taxonomic resolution, and low-spatial variation taxa (Ceccarelli et al. 2016).

Ecological studies require appropriate methods to evaluate disturbances in temporal turnover in subordinate, spatially and temporally variable, and rare taxa. Studies of

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changes in the presence and absence of taxa may provide this opportunity. Turnover in presence/absence data is conservative in evaluating community stability, and hypothesized to detect change only when changes are large (Rahel 1990). Nevertheless, detection can be problematic for rare taxa when only a few sites and within-site (alpha) diversity are evaluated. Increasing the number of within habitat sites over time and evaluating between-site (beta) diversity and turnover may, however, reduce detection under-sampling problems, and associated conclusions (MacKenzie 2005; Mellin et al. 2014). Alpha- and beta-diversity and associated temporal and spatial turnover metrics can help to detect changes in subordinate and rare taxa and their responses to disturbances (Daskalova et al. 2020). Knowledge of taxonomic turnover should improve understanding of large disturbances, such as climate-impacts, and thereby improve management responses to mitigate these disturbances (Ateweberhan and McClanahan 2016).

The responses of coral reefs to climate change and the possible influences of fisheries management remains a controversial subject (Bellwood et al. 2004; Bruno et al. 2019). The potential for marine reserves to increase the ecological stability of diverse reef systems is a viable hypothesis but needs more testing of the elements of reserve design (Selig and Bruno 2010; Graham et al. 2011; Mellin et al. 2016). A concern is that thermal stress, interacting with other human disturbances, will cause rapid change and local extirpation of taxa (McClanahan et al. 2014). Alternatively, fishing and other stresses could pre-condition corals to disturbances and attenuate the effects of thermal disturbances (Côté and Darling 2010). Moreover, spatial diversity and subsequent colonization after disturbances may influence community stability (Mellin et al. 2014). Protected area planning decisions may implicitly or explicitly incorporate spatial diversity, thereby influencing large-scale outcomes of disturbances (Mellin et al. 2016). Here, the presence/absence of coral taxa from 12 uniformly sampled shallow reef sites was studied to evaluate temporal and spatial change of coral taxa in two management systems exposed to thermal disturbances. The above hypotheses of the impacts of taxonomic turnover on corals and potential local extirpation were tested using a 27-year time series in shallow reefs experiencing episodic thermal anomalies (McClanahan 2017).

Materials and methods

Study sites

The study sites and benthic sampling methods have previously been described in detail (McClanahan 2014).

Briefly, Kenya's fringing reef extends $\sim$ 250 km, experiences a 4-m tidal range, and studied sites vary in depths of 0.3–1.5 m at low tide and other water quality, erosion, and temperature variables (Carreiro-Silva and McClanahan 2012). There were seven reefs of which five sites were in three fully protected high compliance marine reserves. Sampled sites were the Malindi (2 sites), Watamu (1 site), and Mombasa (2 sites), which are 3 of the 4 National Parks with permanent fishing closures in Kenya. Seven sites were in reefs with high fishing intensity (i.e. > 5 fishers km^{-2}) (McClanahan and Azali 2020). In total, the 12 studied sites ($\sim$ 30 $\times$ 30 m) were permanently georeferenced locations. All sites were shallow back-reef lagoons composed of a mixture of living and dead hard corals, sand, algae, and seagrass.

The warmest anomalies are observed in the southern hemisphere summer months of October–April with peak bleaching occurring in March and April (McClanahan et al. 2001). This warm season frequently has two distinct periods associated with changing monsoonal wind speeds and direction (McClanahan 1988). This includes a cool period from January to February with moderate wind speeds from the northeast and a warm doldrum period from March to April with low wind speeds. These two periods can have considerable inter-annual variation depending on the intensity of the Indian Ocean Dipole and other oceanographic factors (McClanahan 2017). Coral bleaching occurs during this second warm period but may be influenced by temperatures prior to the March–April doldrums (McClanahan 2017).

Field sampling

The 12 sites were sampled 19 times for coral community and benthic cover during the summer months (December–March) between 1991 and 2018. The same line-intercept transect method was used where nine replicate 10-m draped lines were haphazardly laid in each of the 12 sites. Allen et al. (2017) evaluated the variability in coral cover in the transects and sites and found reasonable accuracy, variance, and repeatability that led to accurate models of change over time. The contour of the seafloor and draping and measurement method resulted in some differences in the length covered but linear coverage was between $\sim$ 100 and 130 m per site per sampling period. Plots of length of transects versus numbers of taxa observed produced near saturation of new taxa at this level of sampling (McClanahan and Mutere 1994; McClanahan unpublished data). Transects were consistently completed by two experienced observers (McClanahan and Muthiga) who also closely supervised the taxonomic decisions occasionally made by less experienced observers.

Corals beneath the transect line that were > 3-cm were identified and measured to the nearest centimeter. Genus was the resolution of identification with the exceptions that *Porites* was separated into branching and massive forms and *Porites rus* (*Synaraea*), while *Galaxea* was separated into *Galaxea fascicularis* and *G. astreata*. These decisions were made because of the different life histories and ecological importance of these taxa in these reefs. For example, the 3 taxa of *Porites* above respond very differently to thermal and other disturbances (McClanahan et al. 2001). *G. astreata* is a large-colony and dominant reef builder that forms isolated patch reefs whereas *G. fascicularis* is a small-colony subdominant occupying the tops of shallow and disturbed fringing and patch reefs. Most genera represent one or a few related species. However, the more diverse genera were the 14 species of *Acropora*, 8 species of *Pavona*, and 6 species of *Montipora* that were not easily distinguished in field situations (Lemmens 1993; McClanahan and Mutere 1994). The dominant *Acropora* are plating while *Montipora* are encrusting forms. The sampling and identification method resulted in 37 sampled coral taxa, including the soft coral *Tubipora*.

Temperature time series

I extracted sea surface temperature (SST) daily time series data for the 1993–2018 period from Coral Reef Watch (https://coralreefwatch.noaa.gov/product/5km/index_5km_sst.php) for each of the 7 reefs and summarized into mean monthly data (Maturi et al. 2017) using package data.table in R (R package version 1.12.2; https://CRAN.R-project.org/package=data.table) (Dowle and Srinivasan 2019) and visualized using ggplot2 version 3.6.3 (Wickham 2016). I summarized annual and seasonal mean temperature using the function 'stat_summary_bin{ggplot2}and ggplot2 version 3.6.3 (Wickham 2016). I tested for inter-annual differences in annual cool (January–February) and warm (March–April) summer periods by the Dunnett's method of a One-way ANOVA.

Changes in taxa

I described the community structure of the 14 dominant taxa in the 12 reef sites over time and by management by Distance-based Redundancy Analysis (dbRDA) using the R package version 2.5.5; https://CRAN.R-project.org/package=vegan (Oksanen et al. 2019). Prior to evaluating these changes, I logit transformed the percentage cover of each taxon. To test if changes in community structure were reflected in changes in turnover, I regressed the slope of the logit transformed coral cover against sampling date. I then correlated these by-taxa slopes against the same by-taxa

slopes of the temporal turnover data to test for significance. I undertook these tests and presented them for all 37 and the dominant 14 taxa, which constituted 95.2% of the total coral cover. I, thereby, tested the hypotheses that community change and temporal turnover were correlated and possibly redundant. The alternative hypothesis is that these two metrics of change were not correlated and measured different aspects and mechanisms of community change.

I used the presences/absences of taxa at a site to calculate temporal and spatial turnover as per the methods used in many previous studies of the biogeography of taxonomic change (Baselga 2010). I calculated the turnover of taxa using the 'R package codyn v 2.0.2' (Hallett et al. 2019) and mean and variance of turnover using R package version 4.6-2; https://CRAN.R-project.org/package=doBy (Højsgaard and Halekoh 2020). I calculated the temporal turnover using the following formula:

1   Temporal turnover = (taxa gained + taxa lost)/total taxa observed in both timepoints

Total beta diversity used the Sorensen' Index to calculate spatial turnover between sites calculated using R packages 'vegan 2.5-5' (Oksanen et al. 2019) and 'betapart version 1.5.1' using the following formula (Baselga 2010):

2.   Total beta diversity = $\frac{b+c}{2a+b+c}$

where a is number of taxa common to both surveys, b is the number of taxa that occur in the first but not in the second site and, c is the number of taxa that occur in the second but not the first site.

I tested presence/absence data for significant change between site, management, and time using nominal logistic tests in JMP software (version 14) (Sall et al. 2001) and visualized using the R package version 3.6.3; https://CRAN.R-project.org/package=ggplot2 (Wickham 2016).

Results and discussion

Temperature patterns

These reefs experienced similarly strong seasonality in temperatures and a trend of increasing mean annual temperature rise of 0.022 °C per year over the 1993–2018 study period (Fig. 1). Rates of temperature rise during this period were, therefore, higher than typical rates for tropical oceans of 0.012–0.016 °C per year evaluated over the past century prior to 2008 (Deser et al. 2010). The intensity of the two warm summer periods changed with statistical differences between years was apparent for both periods (Fig. 2). For example, the cooler January–February summer period had statistically warmer periods in 1996, 1998, 2004, and 2011 and cooler years in 1997, 2000–2002, and
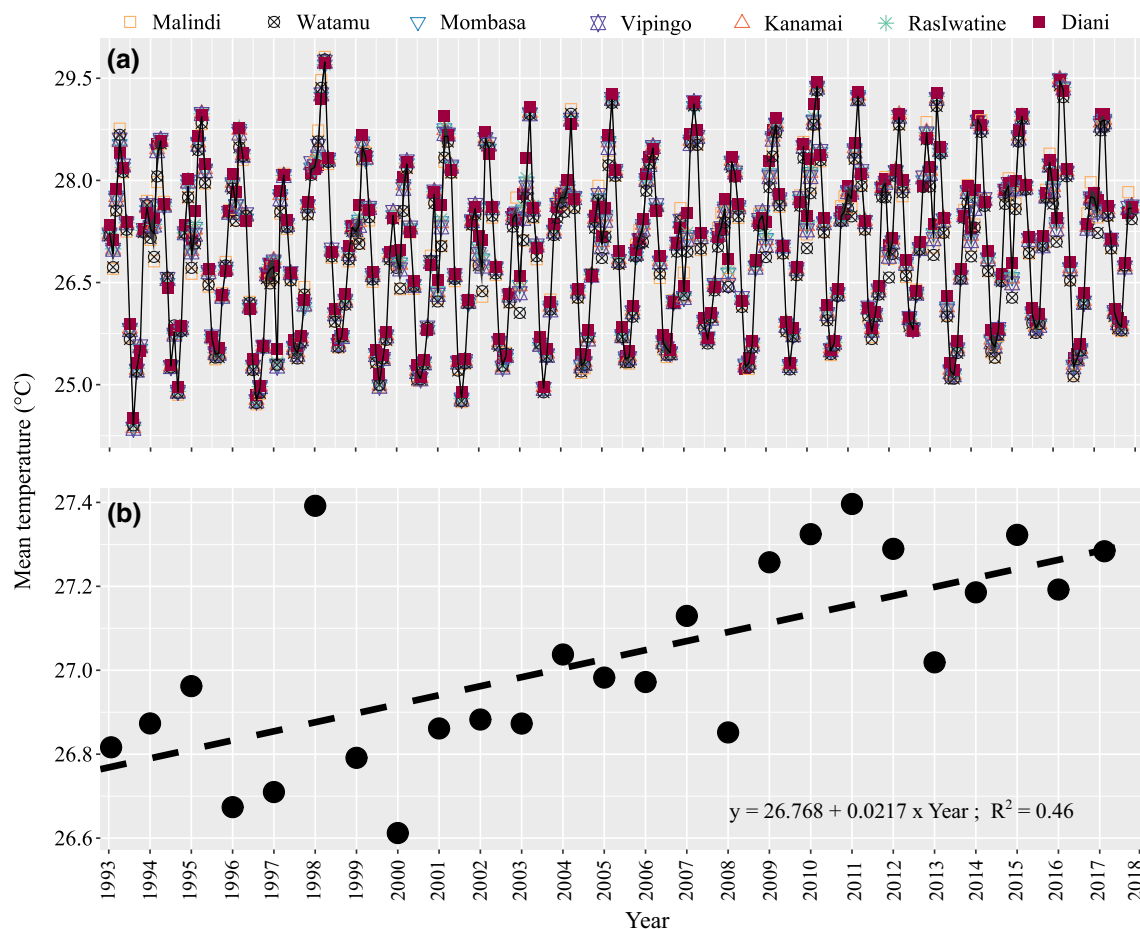
Fig. 1 Changes in **a** quarterly seawater temperatures in the seven separate reef locations and **b** annual mean temperatures from 1993 to 2018. Best-fit linear equation provided for this study period. Seawater temperatures include all studied reef areas where satellite data were available but some study sites were located within the same 5-km satellite pixel

2007 (Fig. 2a). The warmer March–April summer period had statistically warmer years in 1998, 2010, and 2016 and cool years in 1993, 1997, 2000, and 2008 (Fig. 2b). The 1997–1998 period was unusual in having one of the coolest years followed by one of the warmest years in this record. The warm years generally follow the years in which coral bleaching was observed in Kenya and throughout the WIO region and more broadly (McClanahan 2017; Hughes et al. 2018). However, at the country-scale, distinguish bleaching from non-bleaching years is challenged by the considerable spatial (i.e. reef, habitat, and depth) and taxonomic variability in bleaching responses.

Community change

Coral cover declined, on average, from ∼ 30 to 10% after the 1998 thermal anomaly and recovered to ∼ 25% by 2007 (Fig. 3a). After 2007, there were some slight declines until 2013 before rising and falling again to 22% by the end of the record. The loss in *Acropora* and *Montipora* after

1998 was largely permanent to the end of the time series whereas some loss in massive *Porites* was regained by 2003, followed by some fluctuations and a decline in 2016. The cover of other subdominant taxa that changed in their presence/absence (see below) fluctuated throughout the time series with some episodic changes in *P. rus* and *Seriatopora* (Fig. 3b). Lesser impacts on cover and greater relative dominance were reported for stress-resilient and opportunistic taxa, such as *Pavona, Platygyra, Echinopora*, and *Pocillopora* (McClanahan 2014).

The coral communities described by the dbRDA plot indicates scatter among sites by place and time and considerable segregation of the sites based on the two management categories (Fig. 4). Branching and massive *Porites* separated sites the most along the x and y axes. Fished reefs contained relatively more branching *Porites, Stylophora,* and *Pavona* while reserves contained more *Acropora, Echinopora, Montipora* and massive *Porites*. Based on past studies, the fished reef taxa probably represent an environment more disturbed by shallow water
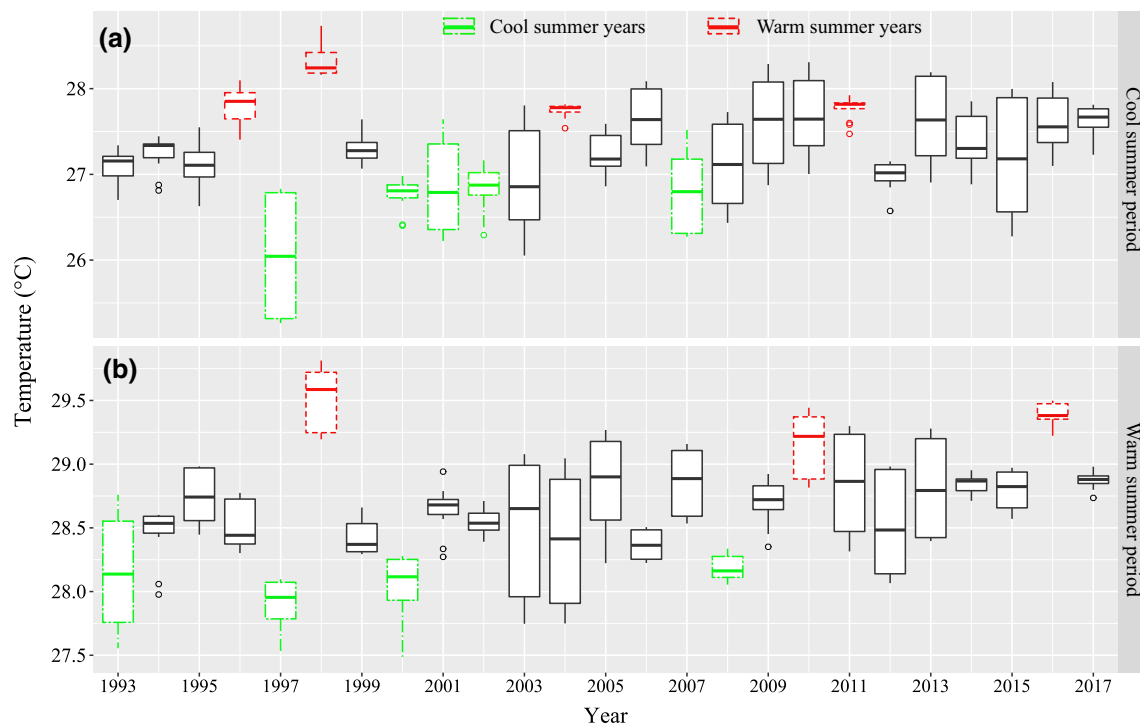
Fig. 2 Boxplot distribution of **a** cool (January and February) and; **b** warm (March and April) summer periods over the 1993–2018 study period. Boxes: upper and lower interquartile range (IQR), thick bar: medians, black circles: outliers, wiskers: min/max values $< 1.5 \times$ IQR. Green color: significant cool summer period, red color: significant warm summer period based on One-way ANOVA comparison of means using Dunnett's method

and frequent thermal and human physical disturbances while the slightly deeper reserves were more influenced by sediments, diseases, and less frequent but damaging interannual thermal disturbances (McClanahan 2014).

Change in the cover of the dominant taxa was not correlated with change in the temporal turnover of taxa for comparisons of all sites, marine reserves, and fish sites (Table 1). Consequently, taxonomic turnover is measuring a unique aspect of the coral community and cannot be inferred from changes in cover. Change in temporal turnover should be more sensitive to both larger changes stimulated by environmental disturbances but also detecting change in subdominant and rare taxa. Thus, standard community change methods should often fail to detect change in rare and cryptic taxa.

Taxonomic change

Marine reserves consistently had a higher number of taxa (14.8 ± 3.4 per site) than fished reefs (9.9 ± 3.6) (Table 2). Temporal turnover of taxa was high and quite variable on a site basis across the time series but had a mean value of 0.42 ± 0.14 (SD) with no statistical differences between marine reserves and fished sites (Fig. 5). Beginning in 1997 and peaking in 1999, turnover increased rapidly to 0.60 ± 0.14 in 1999 before subsiding to a

baseline in 2005. A number of the shallow fished sites, such as Vipingo 1 and 2, Diani 1 and 2, and Kanamai 1, displayed increases in turnover early, in 1997. Most of the remaining sites displayed peak turnovers in 1999 while a few sites, Kanamai 2 and Mombasa 2, did not appreciably increase their turnover over this time period. Consequently, the main pattern among all sites was a pulsed increase in turnover between 1997 and 2005 but not all sites responded with the same intensity or at the same time.

In contrast to temporal turnover, spatial (beta) diversity was statistically lower in marine reserves (0.20 ± 0.05) than fished reefs (0.24 ± 0.03). Additionally, spatial diversity in fished reefs fluctuated without sustained high or lows while showing considerable fluctuations in marine reserves (Fig. 6). Spatial diversity was low (~ 0.08) in marine reserves at the beginning of the time series in 1993 but increased rapidly to 0.31 by 2000, where it was temporarily higher than fished reefs. Subsequently, beta values declined to 0.16 in 2009 and rose again to 0.26 in 2018. The mean beta diversity value for all sites combined was 0.28 ± 0.03 and showed a peak of ~ 0.35 in 2000 but returned to a possible baseline of ~ 0.27 toward the end of the time series. Findings suggest the higher within-site diversity marine reserve reefs were the least stable reefs and the 1997/1998 thermal anomaly produced higher spatial diversity. It is likely that these patterns represent
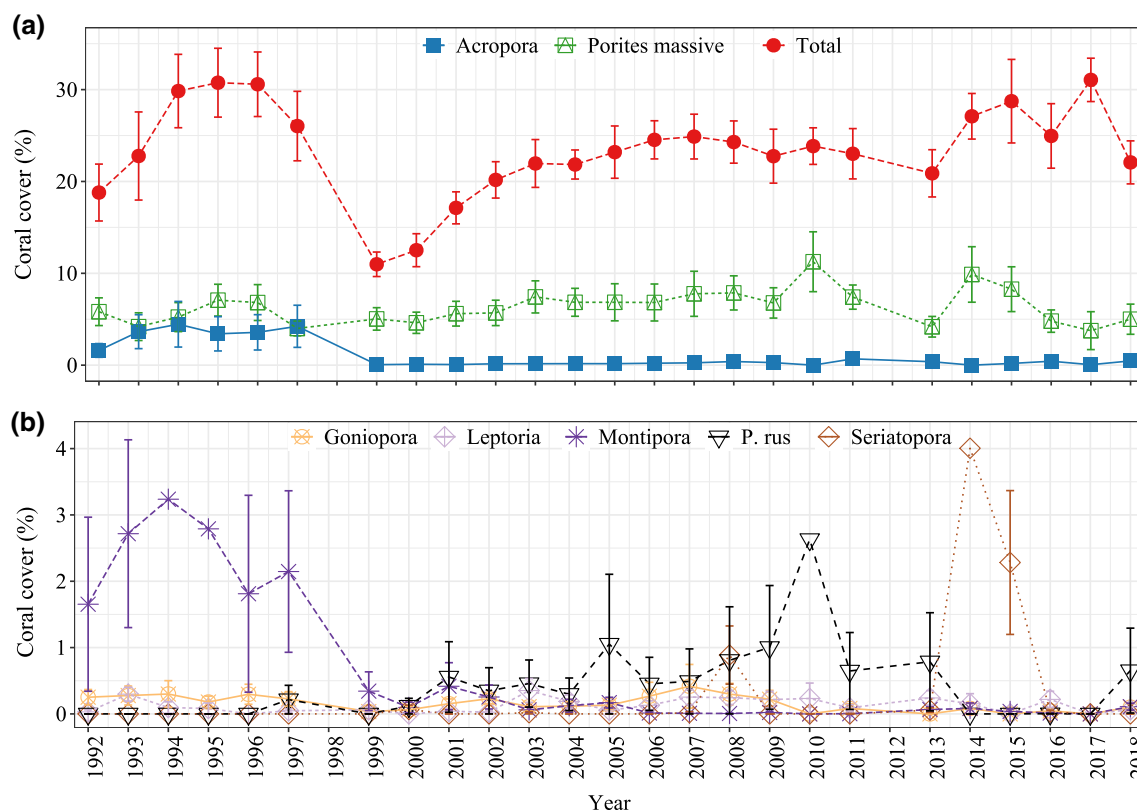
Fig. 3 Changes in percent coral cover between 1992 and 2018. **a** Total coral cover and the two dominant corals, *Acropora* and massive *Porites*, and **b** the 5 taxa that had significant changes in their presence/absence, namely *Goniopora, Leptoria, Montipora, P. rus*, and *Seriatopora*. Whiskers represent standard errors of the mean

changes in the dominance of high cover taxa, such as *Acropora* and *Montipora*, that can outcompete subordinate taxa but died due to bleaching and diseases disturbances between 1998 and 2000 and thereafter failed to recover.

The 1997/1998 period had a number of unique temperature conditions that may have combined to produce the pulsed turnover. These were the low winter and summer temperatures in 1996/1997 followed by high cold and warm summer temperatures in early 1998. The lack of a cool summer break between January and February 1998 suggests the duration of warm water may have been one of the most influential stresses in 1998 and more broadly in 2016 (McClanahan et al. 2001, 2019). More unexpected was the lack of well synchronized multiple-site increases in turnover in subsequent warms years. Some warm years, such as 2005 and 2016, showed single site responses as observed for Malindi 2. Thus, the unusual 1996–1998 temperature period was the main force reorganizing the spatial and temporal turnover of these communities.

Changes in turnover for specific taxa indicate considerable variability in the taxonomic gains and losses at specific sites and management systems (Table 3; Fig. 7). For all sites combined, there were three significant losses in the presence of taxa, namely *Goniopora (minus G.*

stelligera which was included in the *Dipsastraea* genus), *Montipora*, and *Tubipora*. *Goniopora* was a common coral often found in up to 80% of the sites but its presence fluctuated, with two periods of decline from 1997 to 2000 and 2009 and 2013 largely driven by losses within three fished sites. *Montipora* was present in > 50% of the sites prior to 1998. Nevertheless, its presence declined to ∼ 20% of the sites after 1998, followed by some recovery until 2005, declined again to ∼ 10% of the sites by 2011, and finally increased to 35% of the sites by 2013–2018. *Montipora* experienced high bleaching-induced mortality in 1998 followed by a widespread disease that killed *Montipora* but also some other taxa in 2002 (McClanahan et al. 2004). *Tubipora*'s presence was variable but also appeared to decline after 1998 and was largely absent by the final sampling period in 2018. *Tubipora* is a soft coral in the Alcyonacea order, but contains symbiotic dinoflagellates (LaJeunesse et al. 2004) and therefore susceptible to thermal conditions that appeared detrimental to their populations.

The above losses, when evaluated for all reefs, were compensated for by three significant gains in the presence of taxa, namely *Leptoria, P. rus*, and *Seriatopora*. Prior to 2003, the presence of *Leptoria* was low and fluctuating but
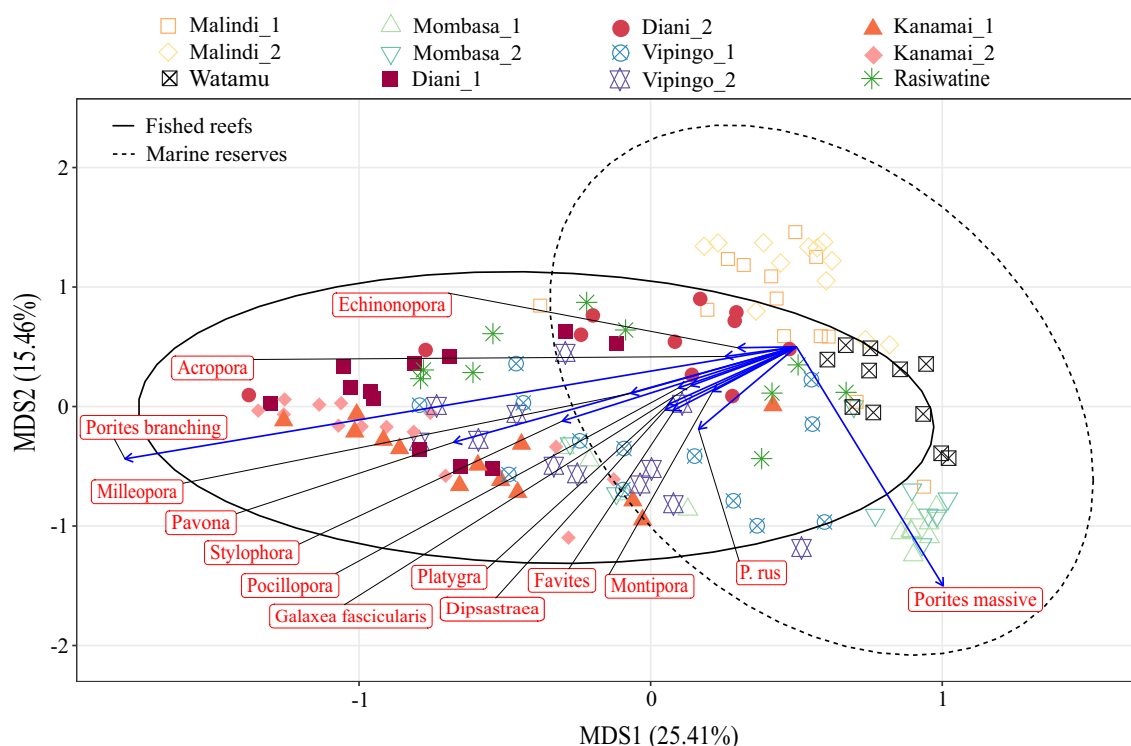
Fig. 4 Multivariate analysis of the coral community structure (dbRDA) in Kenya's southern fringing reef showing states and changes in marine reserves and fished reefs over the 1993–2018 sampling period

Table 1 Tests for correlations between change in coral cover (logit transformed) and coral turnover for (a) all 37 and (b) the 14 dominant taxa for all. Marine reserves, and fished reefs tested separately

	Category	Slope estimate	t ratio	F ratio	Prob > F
(a) All taxa	All sites	0.26 ± 0.23	1.14	1.30	NS
	Marine reserves	0.37 ± 0.19	0.19	3.96	NS
	Fished reefs	-0.09 ± 0.16	-0.52	0.27	NS
(b) Dominant taxa	All sites	0.05 ± 0.37	0.15	0.02	NS
	Marine reserves	-0.26 ± 0.41	-0.63	0.40	NS
	Fished reefs	0.05 ± 0.25	0.2	0.04	NS

*NS denotes relationship is not significant

after 2003 it was consistently found in > 25% of the reefs. *P. rus* was absent to uncommon prior to 2000 but began to appear thereafter and was present in 20% of the reefs by 2018. *Seriatopora* was also uncommon throughout most of the study but was recorded, albeit variably, in a few sites after 2000. These taxa were frequently patchily distributed or did not occupy large amounts of space, so chance could have played a role in their sampling detection. Nevertheless, the number of species encountered saturated at the level of sampling and sampling was constant over time. Because of this saturation assumption, confidence intervals are not typically used in biogeographic analyses of presence/absence data (Baselga 2010; Baselga et al. 2018). Therefore, statistically significant changes should seldom have arisen from insufficient or uneven sampling. Therefore, the patterns observed here probably arose from actual

changes in taxa that were sampled sufficiently to detect statistical change. *Leptoria* and *P. rus* may have warm temperature tolerance where as *Seriatopora* may be more opportunistic and colonize disturbed reefs, which suggests a link between life histories and observed change (Darling et al. 2012; Donner and Carilli 2019). These findings are consistent with patterns observed on broader scales near the equator where stress-tolerant and opportunistic corals appear to be replacing taxa with competitive life-histories (Darling et al. 2019).

At the pooled management levels, temporal turnover evaluations indicated three significant gains and six losses of taxa in marine reserves compared to four gains and three losses of taxa in fished reefs. *Leptoria* was gained and *Montipora* lost in both management systems but the other taxonomic changes were specific to the management. For

Table 2 Changes in the turnover of taxa and mean number of taxa at sites sampled 19 times between 1991 and 2018 in Kenya's southern fringing reef lagoons presented for marine reserves, fished reefs, and all sites combined

	Marine reserves	Fished reefs	All sites
Temporal turnover (alpha diversity)	0.40 ± 0.14	0.44 ± 0.14	0.42 ± 0.14
Spatial turnover (beta diversity)	0.20 ± 0.06	0.25 ± 0.03	0.28 ± 0.03

	Marine reserves						Fished reefs								All sites
	Malindi_1	Malindi_2	Watamu	Mombasa_1	Mombasa_2	All reserves	Vipingo_1	Vipingo_2	Kanami_1	Kanami_2	Ras Iwatine	Diani_1	Diani_2	All fished	All sites
Number of taxa per site	13.5 ± 3.5	15.2 ± 2.8	14.6 ± 3.1	15.5 ± 2.4	15.1 ± 4.6	14.8 ± 3.4	10.6 ± 3.5	10.6 ± 3.5	7.7 ± 1.6	9.1 ± 1.1	11.6 ± 3.9	6.9 ± 3.0	13.0 ± 4.1	9.9 ± 3.6	12.0 ± 4.3

example, *Acanthastrea, Astreopora, Echinopora, G. fascicularis,* and *Hydnophora* presences declined in marine reserves, whereas *Goniopora* and *Tubipora* presences declined only in fished reefs. *Pocillopora* and *P. rus* presence increases were specific to reserves while *G. astreata, Goniastrea,* and *Seriatopora* presences increased in fished reefs. These changes are likely to represent interactions between the total diversity, higher in reserves than fished reefs, and interactions with the environments, less frequent anomalies in reserves than fished reefs (Carreiro-Silva and McClanahan 2012). For example, gains in the presence of *Pocillopora* were associated with a rapid colonization in marine reserves after 1998 (McClanahan 2014). Here, the grazing environment in marine reserves appears important for promoting coralline algal cover and *Pocillopora* recruitment (O'Leary et al. 2012).

Changes in taxa turnover were even more pronounced within management categories (Table 3). For example, marine reserves experienced seven significant gains but 20 losses in five sites. Fished reefs had a more equal balance of gains and losses with 16 and 15 in seven sites. While these patterns were associated with management categorization, there were surely a number of site-specific ecological differences that account for the turnover. Differences in water quality, depth, temperature variation, substrate type, and bioeroding organisms have been found in previous studies (Carreiro-Silva and McClanahan 2012). Coral richness in the region and management systems is likely to be influenced by these environmental and ecological patterns (Ateweberhan and McClanahan 2016). Moreover, a non-random selection of reserves favoring selection of low environmental variation-high species richness is evident for Kenyan reserves. This low-environmental variation—high species richness placement is a common decision uncovered by a global evaluation of reef-scale temperature variation in reserves and non-reserve sites (Selig et al. 2012). Thus, the selective nature of reserve placement decisions in Kenya makes it difficult to conclude about the role of protection from fishing on the turnover of coral taxa. Rather, these findings combined with similar studies of Australia's Great Barrier Reef (Mellin et al. 2014, 2016) indicate that selecting reserves based on spatial heterogeneity and representativeness as well as local diversity should promote stability. Therefore, marine reserves selected for high alpha diversity will not be immune to a net loss of taxa simply by eliminating fishing and restricting human access.

Turnover of taxa was complex and likely influenced by factors such as the diversity of the genus, environmental change, and population fluctuations. *Acropora* is a diverse genus where less change in turnover was observed than other thermally sensitive taxa, such as *Montipora*. Less
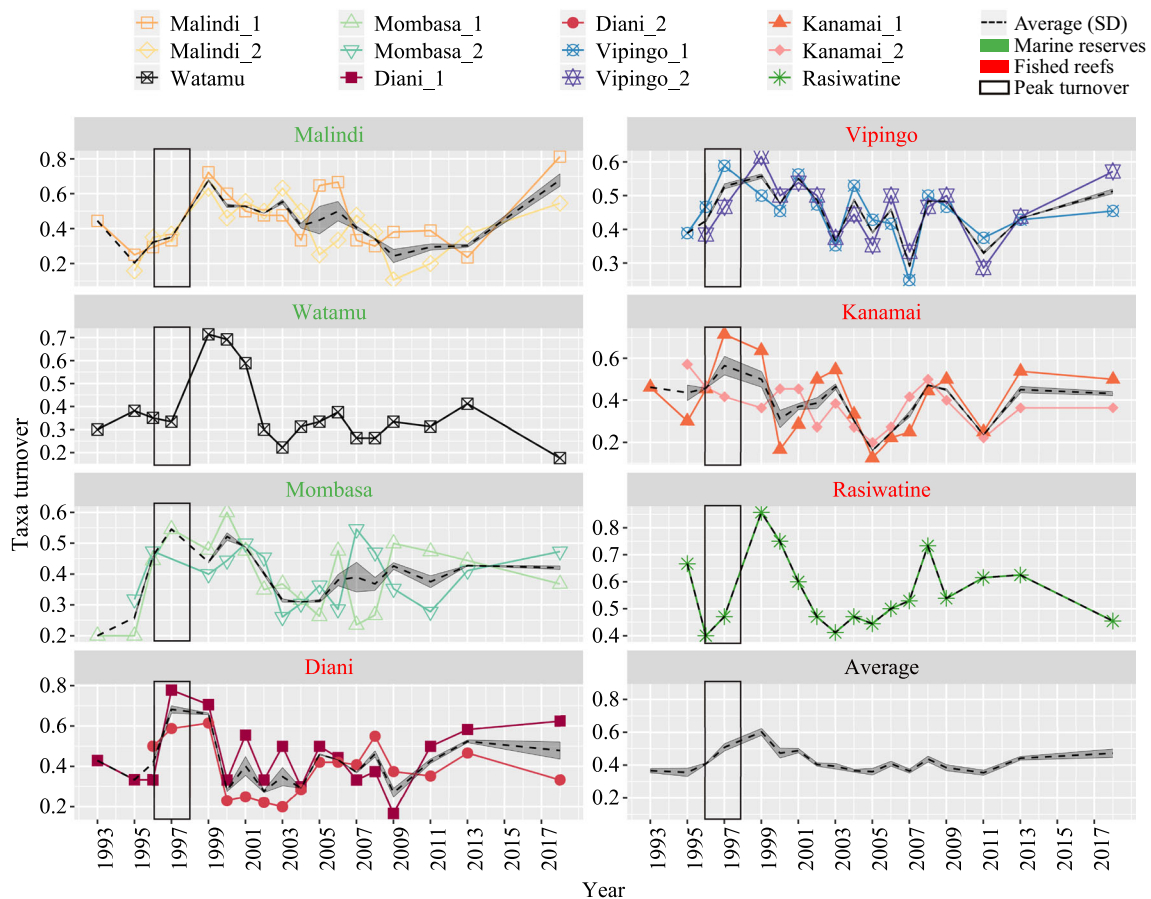
Fig. 5 Temporal taxonomic turnover of the coral communities over the 1993–2018 study period for the 7 reef locations and the average of all locations

change may have resulted from the high number of species per genus (~ 14 species) and species- and morphology-specific responses to thermal stresses (van Woesik et al. 2012). In contrast, *Montipora* had an intermediate to high number of taxa and declined due to both bleaching and a subsequent disease (McClanahan et al. 2004). Perhaps most of the decline was associated with the loss of the dominant species, *M. aequituberculata,* rather than subdominant taxa. In contrast to changes in *Acropora* and *Montipora*, the single species taxa *P. rus* displayed modest gains in presence after 1998. Pacific studies suggest that *P. rus* is a weedy or thermally resistant life history that benefits from thermal disturbances (Donner and Carilli 2019). Yet, some changes in subdominant taxa were not always clearly associated with specific thermal events. Some changes may be associated with fluctuations in population abundances above or below detection levels. For example, Baird and Marshall (2002) found taxa-specific differences in partial versus whole-colony mortality after thermal stresses that could cause variability in cover and detection. Clearly, there is a need to examine the contributions of these and

other factors to turnover if the impact of climate change on corals is to be well understood.

Turnover findings reported here using gains and losses of taxa add new insights into recent impacts of climate change that are less evident from coral cover evaluations (Gilmour et al. 2013; McClanahan 2014; Zinke et al. 2018). Cover evaluations detect changes in dominant taxa well and the associated life histories and functions (Darling et al. 2013; Perry et al. 2018). Yet, they can fail to detect changes in the fauna that are driven by local immigration and extinction rates, with consequences for assemblage stability. Rare or subordinate taxa that are part of the community portfolio provide the diversity of traits needed to support resilience across disturbances (Hooper et al. 2005; Thibaut and Connolly 2013). Kenya's southern fringing reef has been classified as low alpha but high beta diversity. Therefore, it makes sense for managers to prioritize protecting a diversity of representative sites that capture this high beta diversity within marine reserves (Ateweberhan and McClanahan 2016). The current selection system prioritizes high alpha diversity, which could
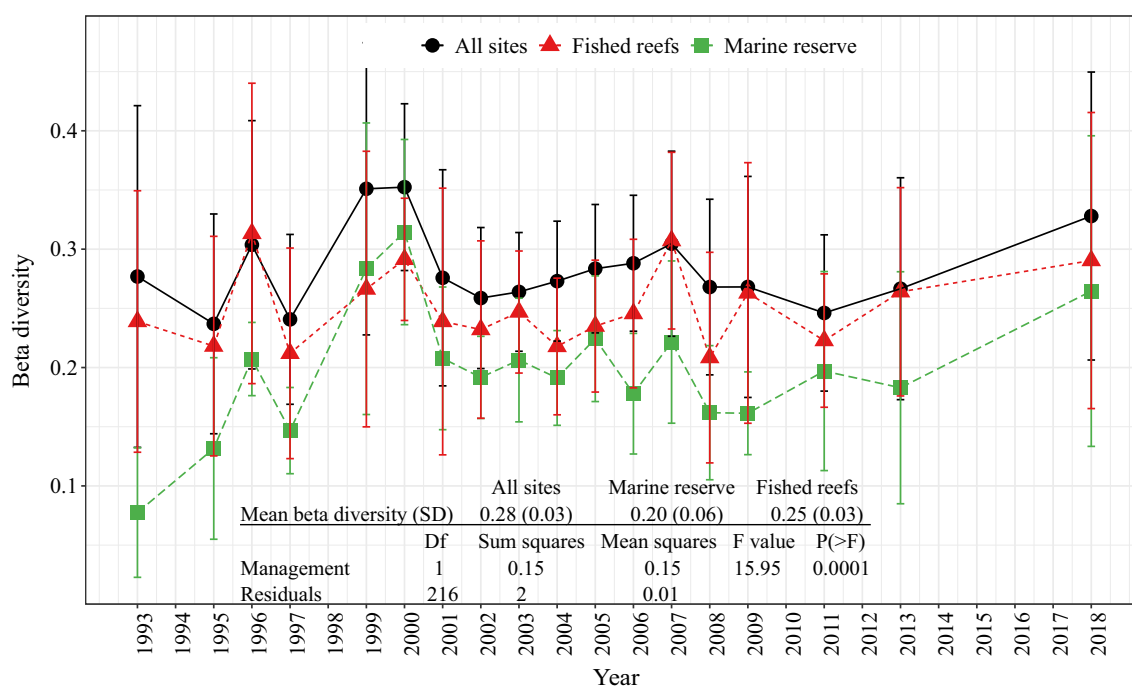
Fig. 6 Spatial turnover of the coral communities over the 1993–2018 study period evaluated for all sites and pooled as marine reserves and fished reefs. Whiskers represent standard errors of the mean

make the protected fauna susceptible to disturbances. Thus, high beta diversity outside of Kenya's marine reserves appeared to provide the risk-spreading portfolio insurance provided by subdominant taxa.

The 1996–1998 cool-warm thermal disturbances created a unique disequilibrium in the fauna that persisted for a number of years. However, it was followed by greater stability despite a number of subsequent warm thermal anomalies. One explanation is that the assemblage reorganization after 1998 led to community of more resilient taxa. Another explanation is that the 1996–1998 years were highly unusual and the unusual dual cool and warm stress combined was never replicated. Therefore, subsequent warm-only events were less stressful and influenced fewer

sites. Comparison of the 1998 and 2016 summer thermal anomalies indicated a number of thermal similarities but also qualitative differences in timing that prevent direct comparison of outcomes (McClanahan 2017). For example, 2016 was not preceded by an unusually cool year, unlike the 1997/1998 summer. Thus, subsequent faunal changes were less widespread and more site restricted. Overall, community change toward resilient taxa and taxa-specific acclimation to thermal change have been recorded (McClanahan 2014, 2017). Community and acclimation changes interacting with the high beta diversity of this reef system appeared to provide the resilience not provided by no-take marine reserve protection alone.

Table 3 Mean number of taxa at sites sampled and tests of changes in turnover of the studied taxa sampled 19 times between 1991 and 2018 in Kenya's southern fringing reef lagoons

	Marine reserves					
	Malindi_1	Malindi_2	Watamu	Mombasa_1	Mombasa_2	All reserves
Number of taxa per site	13.5 ± 3.5	15.2 ± 2.8	14.6 ± 3.1	15.5 ± 2.4	15.1 ± 4.6	14.8 ± 3.4
Acropora	ns	ns	ns	**0.04**	ns	ns
Alveopora	ns	ns	ns	ns	ns	ns
Acanthastrea	ns	ns	ns	**0.04**	**0.03**	**0.02**
Astreopora	ns	ns	**< .0001**	**0.02**	ns	**0.003**
Coscinaraea	ns	ns	ns	ns	ns	ns
Cyphastrea	ns	ns	ns	ns	ns	ns
Echinonopora	ns		ns	**0.01**	ns	**0.02**
Echinophyllia			ns			ns
Dipsastraea	ns	ns	ns	ns	ns	ns
Favites	ns	ns	ns			ns
Fungia	ns	ns	ns	ns	ns	ns
Galaxea fascicularis	**0.01**	ns		ns	ns	**0.01**
Galaxea astreata	ns		ns		ns	ns
Gardineroseris	ns					ns
Goniastrea	ns	**0.005**	ns	ns	ns	ns
Goniopora	ns	ns	ns	ns	ns	ns
Herpolitha						
Hydnophora	ns	ns	ns	**0.001**	ns	**0.04**
Leptastrea	ns	ns	ns	ns	ns	ns
Leptoria	ns	ns	ns	*0.02*	*0.04*	*0.03*
Lobophyllia			ns	ns	ns	ns
Millepora	ns	ns	ns	ns	ns	ns
Paramontastrea	ns		ns			ns
Montipora	**0.01**	ns	**0.04**	ns	ns	**0.01**
Pavona	ns	ns	ns	ns	ns	ns
Platygyra	ns	ns	ns	ns	ns	ns
Plesiastrea		ns	ns	ns		ns
Pocillopora	ns	ns	ns	ns	*0.049*	*0.02*
Porites branching		ns	**0.04**	ns	ns	ns
Porites massive						
Porites rus				*< .0001*	ns	*0.02*
Psammocora						
Seriatopora		ns				ns
Stylophora	ns	ns		**0.01**	**< .0001**	ns
Tubastraea						
Tubipora	ns	ns		ns	ns	ns
Turbinaria			ns	ns	ns	ns
All genera	ns	ns	ns	ns	ns	ns

	Fished reefs								All
	Vipingo_1	Vipingo_2	Kanami_1	Kanamai_2	Ras Iwatine	Diani_1	Diani_2	All fished	All sites
Number of taxa per site	10.6 ± 3.5	10.6 ± 3.5	7.7 ± 1.6	9.1 ± 1.1	11.6 ± 3.9	6.9 ± 3.0	13.0 ± 4.1	9.9 ± 3.6	12.0 ± 4.3
Acropora	**0.04**	ns	ns	ns	ns	ns	ns	ns	ns
Alveopora	ns	ns	ns	ns	ns	ns	ns	ns	ns
Acanthastrea					*0.03*		ns	ns	ns

Table 3 continued

	Fished reefs								All
	Vipingo_1	Vipingo_2	Kanami_1	Kanamai_2	Ras Iwatine	Diani_1	Diani_2	All fished	All sites
Astreopora			ns		ns		ns	ns	ns
Coscinaraea	**0.01**		**0.01**		ns		ns	ns	ns
Cyphastrea	ns	ns		ns	ns	ns	ns	ns	ns
Echinonopora	ns	ns		ns	ns	ns	*0.001*	ns	ns
Echinophyllia									ns
Dipsastraea	ns		ns	ns	ns	ns	*0.004*	ns	ns
Favites	ns	ns	ns	ns	ns	ns	ns	ns	ns
Fungia	ns	ns	ns	ns		ns	ns	ns	ns
Galaxea fascicularis	ns	ns	ns	0.01	ns	ns	*0.004*	ns	ns
Galaxea astreata	ns					*0.01*		*0.01*	ns
Gardineroseris					ns			ns	ns
Goniastrea	ns	ns			ns	ns	ns	*0.04*	ns
Goniopora	**0.049**	ns	ns	**0.01**	ns	ns	ns	**0.0002**	**0.01**
Herpolitha	ns							ns	ns
Hydnophora	ns	ns			ns	ns	ns	ns	ns
Leptastrea	**0.01**	ns	ns		ns	ns	ns	ns	ns
Leptoria	ns	ns		ns	*0.01*	ns	ns	*0.03*	*0.01*
Lobophyllia		ns			ns	ns		ns	ns
Millepora	ns	ns	ns	0.01	ns	ns		ns	ns
Paramontastrea						ns	**0.0004**	ns	ns
Montipora		ns	ns		ns	ns		**0.02**	**0.003**
Pavona	ns				ns	**0.01**		ns	ns
Platygyra	ns	ns	ns	ns	ns	ns	ns	ns	ns
Plesiastrea									ns
Pocillopora	ns	*0.03*	ns	ns	ns	ns	**0.002**	ns	ns
Porites branching									ns
Porites massive				ns				ns	ns
Porites rus	ns				*0.0004*		ns	ns	*0.01*
Psammocora	ns	ns	**0.01**		*0.01*	ns		ns	ns
Seriatopora	ns	ns	ns	ns			ns	*0.02*	*0.03*
Stylophora	ns	ns	ns	ns	ns		ns	ns	ns
Tubastraea		ns						ns	ns
Tubipora	ns	ns	ns	**0.02**	ns	**0.049**	ns	**0.01**	**0.03**
Turbinaria	ns				**0.01**			ns	ns
All genera	ns	ns	ns	ns	*0.03*	ns	ns	ns	

Nominal logistic tests of changes in taxa over time presented and emphasized when changes were statistically significant evaluated for marine reserves, fished reefs, and all sites combined. Bold and italics represent significant declines and increases, respectively. *Dipsastraea* includes *Goniopora stelligera*
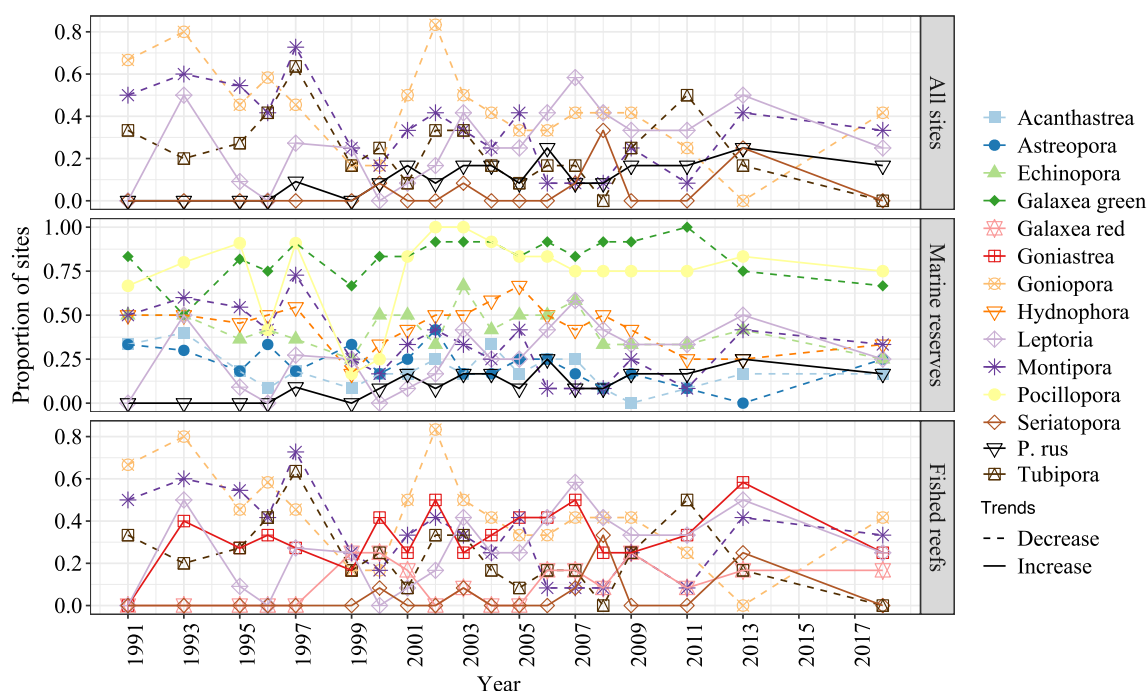
Fig. 7 Time-series plots of taxa exhibiting statistically significant presence/absence changes over time when evaluated for **a** all sites, **b** marine reserves and **c** fished sites

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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