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Documenting decadal disturbance dynamics reveals archipelago-specific recovery and compositional change on Polynesian reefs

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Abstract :

Coral reefs are declining at an unprecedented rate as a consequence of local and global stressors. Using a 26-year monitoring database, we analyzed the loss and recovery dynamics of coral communities across seven islands and three archipelagos in French Polynesia. Reefs in the Society Islands recovered relatively quickly after disturbances, which was driven by the recovery of corals in the genus *Pocillopora* (84% of the total recovery). In contrast, reefs in the Tuamotu and Austral archipelagos recovered poorly or not at all. Across archipelagos, predation by crown-of-thorns starfish and destruction by cyclones outweighed the effects of heat stress events on coral mortality. Despite the apparently limited effect of temperature-mediated stressors, the homogenization of coral communities towards dominance of *Pocillopora* in the Society Archipelago and the failure to fully recover from disturbances in the other two archipelagos concern the resilience of Polynesian coral communities in the face of intensifying climate-driven stressors.

Highlights

► Long-term monitoring allows tracking coral communities through space and time ► Crown-of-thorns outbreaks and cyclones heavily impacted corals in French Polynesia ► Recovery dynamics in cover and compositional changes vary among archipelagos ► Homogenization of genus *Pocillopora* may compromise the future resilience of reefs

Keywords : Coral cover, Disturbances, Recovery, Community shift, Pocillopora

Introduction

Coral reefs are rapidly changing as a consequence of natural and anthropogenic stressors (Hughes et al., 2018). Human-induced climate change and ocean acidification are commonly identified as the most existential threats to coral reefs (Walther et al., 2002; Hoegh-Guldberg et al., 2007; Foden et al., 2013). Global warming, for instance, can reshape entire coral reefs at a regional scale through Mass Coral Bleaching Events (MCBE), which result in large-scale mortality of corals to produce fundamentally different ecosystem dynamics that can be difficult to reverse (Heron et al., 2016; Hughes et al., 2017). In addition, there are various natural (e.g., cyclones, crown-of-thorn starfish [COTS] outbreaks) and anthropogenic (e.g., fishing, pollution and sedimentation) local stressors that affect coral reef communities (Roberts 1995; Fabricius 2005; Bégin et al., 2016). The presence of several different stressors at various scales and their complex interactive effects suggest that reefs face an uncertain future (Darling et al., 2013). Already, many coral reefs across the globe have undergone ecosystem transitions to less-desirable states (Graham et al., 2015) and with global warming predicted to surpass 1.5 °C by 2100 (IPCC, 2018), even more severe and larger-scale shifts stand to occur.

Understanding, predicting, and counteracting consequences of disturbances caused by cyclones, COTS, and temperature-mediated stress requires a thorough grasp on their isolated and combined effects on organisms, communities, and ecological processes on coral reefs (Brandl et al., 2019). By recording biotic and abiotic parameters over time, long-term monitoring programs permit the documentation of reef community dynamics and their drivers at a large temporal and spatial scale. This documentation is particularly relevant for scleractinian corals, which, as the primary reef builders, hold a dominant role in determining the status of coral reef ecosystems. Monitoring changes in coral communities as well as their potential causes over extended time periods is,

therefore, useful to identify the main drivers of coral mortality and their role for shifts in community-wide properties following disturbances (Bjornstad and Grenfell, 2001; Gardner et al., 2003; Pandolfi et al., 2003; De'ath et al., 2012). In this study, we will consider resilience as the capacity of an ecosystem to return to its original state after a disturbance in terms of coral cover and composition (Holling, 1973), while we will consider recovery as the rate at which coral cover (in particular) returns to its pre-disturbance levels. The recovery of a coral reef after disturbances depends on the settlement of new larval recruits, their growth, and the survival of established coral colonies (Gilmour et al., 2013; Adjerdoud et al., 2018). Mortality events usually create unoccupied space in the benthic community, after which recovery hinges on the dynamics between newly recruited corals and their algal competitors (Diaz-Pulido et al., 2009). However, these are often relatively slow processes that require long-term monitoring datasets that can trace the respective representation of benthic taxa before, throughout, and after disturbances.

Beyond the island of Mo'orea (Galzin et al., 2016), coral reefs in French Polynesia are relatively poorly studied. Yet, Polynesian reefs represent an excellent opportunity to assess how reefs may change as a consequence of physical and/or biological impacts and temperature-mediated stressors. Because they are remote islands in various geomorphological settings (i.e., from high volcanic islands to atolls), many Polynesian reefs are subject to relatively low local anthropogenic pressures (Cinner et al., 2018). Indeed, beyond the heavily populated island of Tahiti (189,500 inhabitants, INSEE-ISPFF), most Polynesian islands are sparsely or not inhabited, creating a seascape of coral reefs with varying conditions, where most disturbances can be attributed to acute events such as physical storm and cyclones or COTS outbreaks (Adjerdoud et al., 2009). Nevertheless, the global footprint of anthropogenic warming also affects reefs across

French Polynesia, creating a second group of stressors of fundamentally different scale and nature (Donovan et al., 2020). Since 1993, the Center of Insular Research and Observatory of the Environment (CRIOBE) has monitored coral reefs across seven islands in French Polynesia (SO CORAIL, [Polynesia Mana](#)). During this time, the studied coral reefs have experienced three main types of disturbances: (i) predation by COTS (*Acanthaster planci*) in 2007–2009; (ii) tropical cyclones Martin and Osea in 1997 and cyclone Oli in 2010, and (iii) various heat stress periods. The effects of these disturbances are documented in detail for reefs surrounding the island of Mo’orea in the Society Archipelago (Adjeroud et al., 2009; Lamy et al., 2016), where reefs have shown a remarkable capacity to recover from disturbances in terms of overall live coral cover (Berumen and Pratchett, 2006; Edmunds et al., 2018, 2016). This suggests that, in certain environmental settings, a lack of strong local anthropogenic impacts may facilitate resilience and recovery from natural and climate-induced degradation. Yet, it is unknown whether this island-level trend can be extended to other islands in the Society Archipelago or different Polynesian archipelagos (i.e., Tuamotu, Marquesas, Gambier and Austral).

In the present study, we aimed to understand disturbance and recovery dynamics in coral communities across a range of Polynesian reefs. Specifically, using a long-term monitoring database across three archipelagos, our goals were to (1) document decadal disturbance and recovery dynamics across three different archipelagos, (2) examine how compositional patterns differ across space and time, and (3) evaluate the comparative impacts of acute disturbances (cyclones, COTS and thermal stress).

Materials and Methods

Locations and coral monitoring

Permanent monitoring sites were located at 10m depth on the forereefs of seven islands from three archipelagos in French Polynesia. In the Society Archipelago, we studied the high-volcanic islands Mo'orea (17.479°W, 149.852°S), Tahiti (17.5425°W, 149.619°S) and Raiatea (16.732°W, 151.504°S) and the atoll Tetiaroa (17.031°W, 149.563°S). In the Tuamotu Archipelago, we surveyed the atolls Tikehau (15.014°W, 148.285°S) and Nengo Nengo (18.707°W, 141.867°S). In the Austral Archipelago, we surveyed the high-volcanic island Tubuai (23.344°W, 149.404°S) (Fig. 1).

Overall, 87 surveys were performed over the past 26 years (1993 – 2019) by the SO Corail Monitoring Program ([Polynesia Mana](#)). Each site was monitored every two years. This biannual survey method was set as a rule since 1997, after the beginning of the time series. Surveys in Nengo Nengo were stopped after 2015 because of administrative problems. All sites were outside protected areas and chosen according to fieldwork logistics (i.e., away from passes between the forereef and lagoon to minimize their effect, navigation time, wave exposure, and a compromise between deep and shallow diving constraints, etc.).

Surveys were performed using permanent photo-quadrats. Each survey consisted of the identification of points defined by a superimposed grid (10 × 10 cm mesh) placed on each photo-quadrat (1 m², n=20 per survey), aligned consecutively along a 20m transect laid parallel to the reef crest (Hill and Wilkinson 2004). In order to analyse these data, we used an approach similar to that used by other authors working with the same dataset (see Adjeroud et al., 2005; Vercelloni et al., 2019). The approach consists of measuring coral cover at the genus level and pooling observations over 5m² of reef area, thus obtaining four replicates of 5m² for each 20m² transect. However, contrary to

previous studies, we applied a permutational approach where we randomly select five non-contiguous quadrats for each transect and repeated this random selection 1000 times. The statistical tests (either t-tests or pairwise PERMANOVA, see below) are calculated at each permutation and significance is calculated on the basis of the full distribution of the statistics obtained by the random draw. We grouped corals into five main genera (*Acropora*, *Astreopora*, *Montipora*, *Pocillopora* and *Porites*) and an “*Other*” category that included all remaining genera of lower abundance (<5%, Fig. 2 & 1 SD).

Environmental context

We collated information concerning the occurrence of COTS outbreaks and cyclones over the studied period through different sources. First, we gathered COTS occurrence data from field observations over the 26-year monitoring period and supplemented these data with COTS population dynamics described in the literature (Vieux et al., 2004; Chin et al., 2011). We extracted occurrences of cyclones from records published by Météo France (Laurent and Varney 2010), the European Centre for Medium-Range Weather Forecasts (ECMWF), and the Global Forecast Systems (GFS) from the National Oceanic and Atmospheric Administration (NOAA). We compared the resulting data with the available information from published sources (Canavesio, 2019; Duvat and Pillet, 2017) (Fig. 2).

To establish thermal context and calculate heat stress, we extracted daily satellite-derived sea surface temperature (SST) recordings from the NOAA Coral Reef Watch from 1985 to 2018, with a 5 km spatial resolution (0.05 degrees) (Maturi et al., 2016; Roberts-Jones et al., 2012). We compared the accuracy of satellite observations with *in situ* recorded temperatures from 56 temperature sensors (SeaBird thermometer) deployed at the depth of the coral monitoring (i.e., ~ 10 m) using direct comparisons. From the matched daily temperatures, we calculated root mean square errors (RMSE) and biases

(i.e., average of satellite - logger) (DeCarlo and Harrison, 2019). In light of consistently low RMSE < 0.33 and bias < 0.08 between remotely-sensed and empirically-derived temperature, we preferentially used satellite SST observations because (1) several gaps existed in the *in situ* temperature database due to technical or logistical issues, and (2) standard heat stress calculations are primarily based on satellite observations. We computed heat stress using the Degree Heating Weeks (DHWs) index (Glynn, 1996; Eakin et al., 2010; Liu et al., 2018, 2013). To do so, we first calculated the Monthly Maximum Mean (MMM) for each location over the climatological period suggested by NOAA (i.e., from 1985 to 1993 – excluding 1991 and 1992 because of bias caused by the volcano Mt. Pinatubo). Then, we calculated heat stress as the weekly sea surface temperatures that exceeded the MMM by more than one-degree °C. This temperature (MMM + 1°C) is generally considered as the bleaching threshold. DHWs represent the accumulation of heat stress and time of exposure over the bleaching threshold for the twelve preceding weeks. When DHWs were above 4 (generally termed “bleaching alert level 1” (Liu et al., 2018)), we considered the event as major thermal stress and as a main disturbance independently of changes in coral cover. When DHWs were below 4, we considered them as a minor disturbance. More details on the DHW calculation and its values are available in the Supplemental Information (Fig. 2 SD).

Statistical analysis

We defined main disturbances as the occurrence of an environmental perturbation or a major thermal stress event causing abrupt changes in coral cover. We analyzed the effects of each of these main disturbances in isolation, assessing the change of coral cover before and just after the particular perturbation for each island (Δ coral cover - Fig. 3). In addition, we studied changes in coral cover and community composition after recovery

of main disturbances in the affected islands. For each disturbance that caused an abrupt change in coral cover, we defined two periods, denominated as ‘before’ and ‘after recovery’. The period defined as ‘before’ corresponded to the survey immediately before the identified abrupt change in coral cover caused by the disturbance. The period defined as ‘after recovery’ corresponded to the maximum value of coral cover after disturbance. Because of the biannual survey method, we analyzed some disturbances as a combined effect of two disturbances, and the defined periods for ‘before’ and ‘after recovery’ were specific for each island.

We used parametric Student’s t-tests for paired samples to examine changes in total coral cover caused by each specific main disturbance and to assess the periods ‘before’ and ‘after recovery’ of disturbances at each location. We selected t-tests depending on the assumptions of normality in the response and the homogeneity of the variance, which we assessed using Shapiro-Wilk test (for normality) and F-tests (for variance). Furthermore, we assessed changes in coral cover (Δ coral cover) as a function of the different disturbance types, i.e. ‘cyclone’, ‘COTS’, ‘COTS and cyclones simultaneously’, and ‘thermal stress’. Δ coral cover was fitted using ANOVAs across disturbance types. To examine shifts in the community composition of coral genera (i.e., the relative abundance of each genus), we used a PERMANOVA on the Bray-Curtis distance matrix of the data with pairwise comparisons (Martinez, 2019), with each island and time period specified as fixed effects.

We also computed coral recovery rate ($\% \text{ coral cover} \cdot \text{year}^{-1}$) after disturbance with a modification of the geometric rate of change (Côté et al., 2005) using equation (1). Specifically, $\text{Post.Dist.cover} (\%)$ was the maximal coral cover value recorded during the ‘after recovery’ period of a given disturbance event, corresponding to a specific year. $\text{Min.cover} (\%)$ was the lowest coral cover observed in a particular year just after the focal

disturbance. Time (years) was the number of years necessary for coral cover to transition from its lowest (Min.cover) to highest (Post.Dist.cover) value. In the case of multiple main disturbances, we separately calculated recovery for each transition event (Table 1). The contribution of each genus to the total coral recovery rate was calculated using linear regressions.

$$\text{Coral recovery rate} = \frac{\text{Post.Dist.cover} - \text{Min.cover}}{\text{Time}} \quad (1)$$

To investigate overall compositional changes in the coral community across the seven islands and over the monitored period, we performed a non-metric multi-dimensional scaling (nMDS) ordination on a Bray-Curtis dissimilarity matrix (Kruskal, 1964; Shepard, 1962). Percent cover estimates of the most abundant coral genera were square root transformed to adjust for unequal representation of the genera (Edmunds et al., 2016). We validated the convergence of the ordination by examining stress values. Furthermore, we applied a permutational multivariate analysis of variance (PERMANOVA) to the distance matrix to test for the effects of temporal (i.e., year) and spatial (i.e., island) differences on coral community dissimilarities. All analyses were conducted using R and the ‘vegan’ package (Oksanen et al., 2013).

Results

Disturbance effects on coral cover

Overall, coral cover on observed Polynesian reefs ranged from 2% to 55% across the examined time period and was affected by tropical cyclones, COTS and heat stress anomalies (Fig. 2). The islands of the present study were not equally impacted by these disturbances.

In the Society Archipelago, cyclones Martin and Osea affected only the island of Raiatea. Coral cover fell from 8.27% (Standard Deviation = 0.55) to 2.16% (0.39) causing a significant decline (Student t-test, $t = -5.13$, $p = 0.01$). After the cyclones, the recovery rate in Raiatea was 4.8% coral cover·year⁻¹ and in 2005-2006 (the ‘after recovery’ time point for Martin and Osea), coral cover was significantly higher than before the disturbance ($t = 8.43$, $p < 0.005$). On the other hand, the COTS outbreak from 2007 to 2009 heavily impacted Mo’orea ($t = -18.7$, $p < 0.005$) and Raiatea ($t = -10.53$, $p < 0.005$), and together with cyclone Oli was particularly strong in Tahiti ($t = -9.32$, $p < 0.005$), but also affected Tetiaroa ($t = -4.08$, $p = 0.03$). While maximum pre-disturbance coral cover ranged from 25.7% to 36.1%, coral cover declined to less than 2% in 2010–2012 (a 99% loss). Reefs in Tetiaroa differed from Mo’orea, Tahiti and Raiatea by continuously declining from 45.9% (0.8) in 1994 to 18.92% (0.68) in 2009, but also exhibited a steep decline in 2010. After these disturbances, reefs in Mo’orea, Tahiti, Raiatea, and Tetiaroa showed recovery trajectories of 6.8%, 5.9%, 3.1 and 5.4% increases in coral cover·year⁻¹, respectively. In 2017–2019 (the ‘after recovery’ time point for these disturbances), estimates of coral cover did not significantly differ from ‘before’ disturbance values in Tahiti (from 27.4% to 37.3% [$t = 2.14$, p -value = 0.14]), Tetiaroa (from 25.6% to 32.7%; [$t = 1.65$, $p = 0.24$]) or Raiatea (from 31.8% to 25.25% [$t = -1.56$, $p = 0.25$]), despite the slower recovery. However, a significant difference was present for Mo’orea (36.01% to 54.63% [$t = 5.79$, $p = 0.006$]). In contrast to the effects of physical and biological disturbances associated with the two perturbation events, the minor temperature-mediated stress events recorded in Mo’orea, Tahiti, and Tetiaroa had no visible effect on coral communities. While major temperature-mediated stress events (above 4 DHW) occurred in Raiatea, coral cover did not significantly change following this event ($t = 2.23$, $p = 0.13$).

In the Tuamotu Archipelago, the two islands differed markedly in how they were affected. Tikehau was impacted by two cyclones and temperature stress. First, the cyclones Martin and Osea (1997) reduced coral cover from 39.5% (1.1) to 4.1% (0.3), causing a significant decline ($t = -19.48$, $p < 0.005$). Then, a recovery rate of 4.1% coral cover·year⁻¹ returned the reef to its pre-disturbance value ($t = -1.04$, $p = 0.44$). Second, cyclone Oli (2010) caused a less extreme, but still significant ($t = -5.79$, $p = 0.007$) decrease, from 39.57% (1.1) to 14.27 % (0.95), followed by a slower recovery rate of 0.9% coral cover·year⁻¹. Consequently, coral cover ‘after recovery’ remained significantly lower in 2018 than before the disturbance in 2006 (from 36.72% to 19.6% [$t = -5.29$, $p = 0.01$]). Conversely, Nengo Nengo was the only undisturbed reef. Being spared by major disturbances, its reefs exhibited a relatively stable trajectory over the past 25 years, with a slight but significant increase in coral cover from 15.3% (0.53) in 1994 to 26.9% (1.6) in 2015 ($t = 3.92$, $p = 0.036$). As for the island of Raiatea, thermal stress events occurred for Tikehau and Nengo Nengo (DHW = 6.7 °C-weeks and DHW = 4.2 °C-weeks, respectively) but these events did not cause a clear decrease in coral cover ($p > 0.05$). The contribution of the minor thermal anomaly of 1998 in Tikehau might have affected simultaneously to the coral decrease after the cyclone.

Finally, reefs in the Austral Archipelago (island of Tubuai) reached 25% (1.8) coral cover in 2005, but the 2006 bleaching event (DHW = 14.1°C-weeks) led to a 20 % loss of coral cover (from 25.2 % [1.8] to 20.4 % [1.4]). After this, the impact of cyclone Oli in 2010 further caused a 97% loss of coral cover ($t = -8.65$, $p = 0.006$). Here, the recovery rate after the disturbance was the lowest across all islands and disturbance events (0.65% coral cover·year⁻¹) and resulted in a coral cover after recovery (2019, 4.4%) that was significantly lower than before (2005, 25.4%, $t = -7.29$, $p = 0.01$). Reefs around Tubuai suffered from multiple heat stress events (7 total, Fig. 2 SD & Fig. 3 SD) ranging

from 1 up to 16.3°C-weeks in 2017 that did not cause further significant declines in coral cover ($p > 0.05$) but potentially compromised recovery.

Overall, disturbance type had a significant effect on Δ coral cover ($F = 13.93$, $p = 0.007$; linear model: $se = 7.23$, R-squared: 0.92 , p-value: 0.03) (Fig. 3), with Δ coral cover showing more pronounced declines following COTS outbreaks ($t = [-18.7$ to $-10.5]$, and $p < 0.005$), COTS & cyclones simultaneously ($t = [-9.32$ to $-4.08]$, and $p = [0.002$ to $0.03]$) and cyclones alone ($t = [-19.48$ to $-2.11]$, and $p = [0.0004$ to $0.16]$) than when compared to heat stress ($t = [-1.17$ to $6.4]$, and $p = [0.009$ to $0.566]$), which did not cause universal declines (Fig. 3).

Disturbance effects on coral community composition

Following cyclones Martin and Osea of 1997, the community composition of Raiatea changed (PERMANOVA: $F_{\text{statistic}} = 9.336$, $p = 0.034$) but remained similar in Tikehau (PERMANOVA: $F_{\text{statistic}} = 3.803$, $p = 0.066$). The dominant genera in Raiatea switched from *Acropora* to *Pocillopora*. Their contribution changed from 43% and 16% to 33% and 56%, respectively. In Tikehau, the relative contribution of *Pocillopora* decreased from 83% to 75% but the genus remained dominant (Fig. 4A).

Following the COTS episodes and cyclone Oli in the 2000s, all islands exhibited shifts in coral community composition (PERMANOVA: $F_{\text{statistic}} = [94.05$ to 5.62 , $p < 0.05$) (Fig. 4B). In the four islands of the Society Archipelago, the relative contribution of *Pocillopora* was consistently higher in 2017-2019 (78.4%, 71.1%, 59.8% and 72.1%, respectively) compared to 2004-2005 (36.3%, 46.3%, 7.43% and 48.2%, respectively). Mo'orea showed a particularly strong shift towards new domination of *Pocillopora* ($F = 94.05$, $p = 0.03$). The same occurred in Tetiaroa, driven by the near-complete loss of *Astreopora* ($F = 74.04$, $p = 0.03$), which was also replaced by *Pocillopora*. In contrast, in

the Tuamotu Archipelago, Tikehau showed a considerable decrease in *Pocillopora* after the impact of cyclone Oli, from 75.6% in 2006 to 46.6% in 2018 ($F = 5.62$, $p = 0.04$). Notably, even in the relatively disturbance-free reefs of Nengo Nengo, where coral cover was stable, significant shifts in community composition occurred, mostly due to increases in the *Other* category ($F = 16.06$, $p = 0.029$). Finally, in the Austral Archipelago, which was also unaffected by COTS, Tubuai experienced a significant shift towards a more pronounced dominance of *Acropora* corals than before the cyclonic disturbance ($F = 25.149$, $p = 0.03$).

In accordance with the observed genus-specific dynamics, the nMDS ordination revealed considerable temporal and spatial differences in coral communities (PERMANOVA $F = 3.27$, $p = 0.002$ for year; $F = 7.91$, $p = 0.001$ for island). Only Mo'orea and Tahiti showed similarities in coral community composition (PERMANOVA-pairwise comparisons; $F = 2.38$, $p = 0.059$). As expected, Nengo Nengo reefs and Tikehau showed the least pronounced compositional changes over time, while temporal trajectories were particularly expansive for Tubuai, Tetiaroa, and Mo'orea. Aside from reefs in Tubuai, all surveyed islands converged towards coral communities dominated by *Pocillopora* colonies, which had high recovery rates (e.g., 5.38 and 4.41 *Pocillopora* cover·year⁻¹, contributing up to 78.4% to 71.1% of the total recovery, respectively, in Mo'orea and Tahiti) (Fig. 5). Consequently, *Pocillopora* increased the contribution after recovery because the genus accounted for between 7.4-48.2% of cover before the COTS and cyclone disturbances in 2007-2010 and between 59.8-78.4% of cover after recovery across all islands, with the exception of Tikehau and Tubuai. *Pocillopora* represented between 57% and 84% of the overall recovery rate for all studied islands, except for Tubuai (Fig. 4 SD). This strong recovery of *Pocillopora* offset the very

low recovery rates of *Acropora* (<0.6% *Acropora* cover·year⁻¹) and *Porites* (<0.3% *Porites* cover·year⁻¹).

Discussion

Disturbances of fundamentally different nature and magnitude can severely influence coral reef ecosystems by restructuring scleractinian coral assemblages. By analyzing long-term monitoring data on coral assemblages across French Polynesia, we reveal distinct causes of coral mortality and recovery dynamics over 26 years. Of the seven studied reefs, six were severely impacted by COTS predation and cyclones, which appear to represent the major drivers of coral mortality over the surveyed period from 1993 to 2018. In contrast, heat stress had limited impacts on the studied reefs during the survey period, except for reefs in Tubuai, especially during La Niña events. Furthermore, heat stress events may have compromised ongoing recovery across different islands. While coral cover showed distinct pulse dynamics in synchrony with disturbances, coral community composition exhibited more linear dynamics with a relatively consistent (five out of seven islands) convergence towards communities dominated by *Pocillopora* colonies.

Spatially divergent recovery dynamics

Our study revealed distinct temporal dynamics in coral cover across the seven islands. Specifically, while Mo'orea, Tahiti, Tetiaroa and Raiatea exhibited good recovery after disturbances, and values of coral cover in 2018 were close to the maximum observed since 1993, Tikehau and Tubuai fell significantly short of these values. Given the comparable nature and intensity of disturbances, these results suggest that reefs in

different archipelagos are subject to fundamentally divergent ecological processes pertaining to the recovery of coral populations.

One explanation for the differences in coral recovery may lie in different connectivity and/or distinct local environmental conditions resulting in diverse coral settlement and recruit survival patterns. The fast and extensive recovery in the four Society islands mirrors previous results from Mo'orea (Adjeroud et al., 2009; Bramanti and Edmunds 2016; Trapon et al., 2011; Lamy et al., 2016), and might be facilitated by strong connectivity within the Society Archipelago and a resulting supply of larvae from neighboring islands and/or deeper reefs (Bongaerts et al., 2010; Tsounis and Edmunds, 2016). Genetic evidence suggests the Society Archipelago as the most likely source of larvae after the disturbances, since *Pocillopora meandrina*, for example, exhibits a strong spatially clustered genetic structure within the Society Archipelago (Magalon et al., 2005). Thus, recovery from natural pulse disturbances appears to be swift in the well-connected Society Archipelago (3.1% to 6.8% coral cover·year⁻¹), supporting the previously suggested high potential for recovery of Indo-Pacific reefs (3% to 9.5% coral cover·year⁻¹; Done et al., 1991; Baker et al., 2008; Graham et al., 2011; Gilmour et al., 2013).

In contrast, more remote islands such as Tubuai (Austral) and Tikehau (Tuamotu) were much slower to recover or failed to do so entirely, which may suggest an important role for seascape configurations in governing recovery dynamics. The distance between reefs in our study generally ranged from 17 km (Tahiti-Mo'orea) to 607 km (Tahiti-Tubuai), thus lying well below the 850 km dispersal distance reported for scleractinian corals (Robitzch et al., 2015). However, given the largely passive dispersal of coral larvae, oceanographic currents are key determinants of dispersal dynamics (Pineda et al., 2007). In French Polynesia, surface currents flow in average southwestward north of 20°S

(South Equatorial Current; Rougerie and Ranchert 1994), and eastward in the south (South Tropical Counter Current; Martinez et al., 2009). Thus, surface waters are unlikely to transport larvae from the Society and Austral archipelagos to the Tuamotu, potentially limiting the scope for replenishment of the reefs studied in the Tuamotu from the Society. The recovery dynamics in Tikehau lend some support to this hypothesis. The drastic decline in recovery rate from 4.08 to 0.89% coral cover·year⁻¹ between the cyclones of 1997 and 2010 in Tikehau suggests that, while a large enough regional pool of larvae may have been present to boost recovery after the first event, a resulting lack of recruitment may have stymied recovery after the second event. This insufficient recovery might be associated with inhospitable environmental conditions mediated by heat stress (i.e., DHW = 6.7 °C-weeks), which can impede the survival of coral larvae and recruits while not affecting adult coral cover. The lack of recovery after the cyclone of 2010 in Tikehau deserves further studies to identify whether coral recovery potential has been permanently altered (i.e. reef source of larvae) by changes in larval connectivity, or whether local degradation of environmental conditions is responsible for the lack of recovery.

Conversely, larvae from the Society Archipelago might be advected to the Austral Archipelago, since the average surface currents in the region (Martinez et al., 2009; Tomczak and Godfrey, 2013) can connect the two archipelagos (Martinez et al., 2007). Yet, the potential influx of larvae does not seem sufficient to counterbalance the heat stress suffered by coral larvae and explain the slow recovery. Indeed, since cyclone Oli in 2010, coral communities in Tubuai experienced intense heat stress (e.g., DHW = 16.3°C-weeks in 2017). While this had limited effects on the already limited coral cover (less than 2% in 2017), these thermal anomalies may have compromised the survival of local coral larvae and recruits during and after the critical settlement phase (Randall and Szmant, 2009). In addition, as the southernmost island in our dataset, corals in Tubuai are

exposed to the lowest Polynesian SSTs during winter, which approach the lower coral temperature limits (Kleypass et al., 1999). These cold temperatures may reduce coral growth and recovery capacity after disturbances (Rodolfo-Metalpa et al., 2008; Anderson et al., 2017), but also alter the survival of coral larvae arriving from the Society Archipelago that are less adapted to such a wide range of temperatures. Thus, beyond dispersal, environmental context is critical for the interpretation of the observed recovery dynamics.

Compositional changes

The compositional changes in coral communities showed similar spatial dynamics as the overall recovery trajectories, with Tikehau and Tubuai being the only islands that were not characterized by a shift toward *Pocillopora* colonies. In contrast, in the Society Archipelago, the loss of corals in the Acroporidae family (*Acropora*, *Astreopora*) was compensated by a stark increase in the already dominant genus *Pocillopora*. *Pocillopora* is one of the primary reef-building genera on Indo-Pacific reefs (e.g. Carriquiry et al., 2001; Glynn et al., 1972; Veron and Pichon, 1976) and has been dominant in French Polynesia for decades. However, historically, *Acropora* colonies have contributed more substantially to recovery than in the present study (e.g., recovery in 1991; Adjeroud et al., 2009). Our study emphasized this contribution in Raiatea, where the recovery rate of *Acropora* was 1.56% coral cover·year⁻¹ after the cyclone of 1997 but only 0.18% after the COTS of 2007 and cyclone 2010. This dwindling contribution of *Acropora* in recent years in French Polynesia may be driven by a combination of the life-history of acroporid corals and recent developments on Polynesian reefs.

While *Acropora* and *Pocillopora* share similar competitive life-history strategies (Darling et al., 2017), the prevalence of *Pocillopora* on Polynesian reefs is likely

attributable to several ecological traits. First, while *Acropora* larvae require specific substrata for settlement (e.g., crustose coralline algae, CCA) to induce metamorphosis (Baird and Hughes 2000; Baird and Morse 2004), *Pocillopora* larvae can settle on fairly unconditioned surfaces (Atoda, 1951, 1947a, 1947b; Harrigan, 1972). Since reef colonization by CCA can be slow (Klumpp and McKinnon 1992), weedy *Pocillopora* corals may enjoy early colonization success in open space and on barren or poorly conditioned reef substrata following disturbances (Connell, 1973; Grigg and Maragos, 1974; Loya, 1976), especially in comparison with other genera (Darling et al., 2012). In fact, after 2010, the loss of corals in Mo'orea was followed by the rapid establishment of turf algae (Diaz-Pulido et al., 2009; Diaz-Pulido and McCook, 2002). While herbivorous grazing on reefs around Mo'orea is seen as sufficient to prevent the establishment of macroalgae following disturbances (Holbrook et al., 2016), species-specific effects of herbivore grazers on benthic successional dynamics (Burkepile and Hay, 2010) suggest that even nuanced shifts in herbivore composition (Han et al., 2016) could hamper the establishment of CCA. This would likely favor colonization of *Pocillopora* over *Acropora* larvae in the Society Archipelago. Second, *Pocillopora* propagules have the ability to travel long-distances (up to 850 km for *P. verrucosa*; Robitzch et al., 2015). As such, *Pocillopora* species may boast higher levels of connectivity compared to acroporids across the scattered islands of the Society Archipelago (Magalon et al., 2005). Continental reefs in the Indo-Pacific (Wood et al., 2014), where recovery dynamics do not customarily result in the dominance of *Pocillopora*, are likely to be less prone to the dispersal-driven effects that may underpin *Pocillopora* dominance in French Polynesia.

Cyclones and COTS impacts vs. temperature-mediated stress effects

Across the studied islands, COTS outbreaks and cyclones appeared to have a more significant impact on coral cover and community composition than heat stress events. While this may suggest a capacity for local management to enhance reef resilience in the face of climate change, our findings need to be interpreted with caution. Chronic stressors, such as warming SSTs may affect recovery processes even under excellent local management. Non-lethal, chronic thermal stress increased during the past 26 years in all sites (even Nengo Nengo, which did not show clear acute disturbances). Across locations, there was an evident decline in mounding and plating corals such as *Astreopora* and *Acropora*. In contrast, branching/weedy corals such as *Pocillopora* increased in their contribution to coral cover. Thus, similar to the Caribbean, chronic stressors that were not considered in this study may play a role in shifting community composition (Alvarez-Filip et al., 2009). In French Polynesia, this shift is clearly going towards a monoculture of *Pocillopora*, which raises critical questions concerning the functioning and resilience of the newly formed assemblages (McWilliam et al., 2020; Pratchett et al., 2015).

Decades of research have revealed strong effects of both species identity and diversity on ecosystem functioning (Cardinale et al., 2012; Duffy et al., 2017). On coral reefs, the relationship between diversity and functioning is relatively poorly explored (Brandl et al., 2019), but emerging evidence suggests that coral growth is, in fact, promoted by species richness (Clements and Hay, 2019; McWilliam et al., 2018). The observed recovery dynamics on Polynesian reefs suggest a strong contribution of *Pocillopora* corals to functioning (i.e., coral cover); yet, care must be taken not to conflate coral cover with rates of calcification that underpin reef scale functioning (Brandl et al., 2019). At this stage, we are unable to resolve whether the revealed shifts towards *Pocillopora* represent a permanent, stable community shift or a temporary successional shift that will soon give way to a more diverse community. In the latter case, it appears

that intervals between disturbances provide insufficient time for the re-establishment of the previous community.

Regardless of the mechanism that has caused the current emergence of *Pocillopora*-dominated reefs, the concept of response diversity suggests a higher vulnerability of monocultures to disturbances such as heat-stress events in the future (Dalin et al., 2009; Lin, 2011). Reefs dominated by a single genus have a more limited range of traits and functions to persist and survive under challenging conditions than those with more diverse reef ecosystems (Aronson and Precht, 1995; Palumbi et al., 2009). Therefore, despite the apparent resilience of Polynesian reefs to climate change to date, the recent shift toward *Pocillopora* dominated states on Polynesian reefs may severely compromise their capacity to cope with future global changes. In fact, recent large-scale bleaching throughout the Society Archipelago in 2019 (pers. obs.) suggests that climatic disturbances will have more dramatic effects than previously observed. This observation highlights the importance of examining the historical context of coral communities to understand future responses to disturbances.

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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.

Author contribution Conceptualization: GP-R, LH; Data curation: YC, GS, EM; Formal analysis: GP-R, VP; Writing – original draft: GP-R; Writing – review & editing: GP-R, SB, EM, VP, LH

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Figure legends

Figure 1. Map of French Polynesia, with the studied islands indicated. Color palettes

indicate different archipelagos: Red = Society Archipelago; Blue = Tuamotu Archipelago; Green = Austral Archipelago.

Figure 2. Cumulative plots per genus highlighting coral cover dynamics and main

disturbance events across the seven islands. Points indicate years of sampling and total coral cover. Disturbances are included as cyclones, COTS outbreaks, and DHWs (arrows with numbers).

Figure 3. Effects of disturbance types on the change in coral cover (Δ) across the studied

islands. Boxplots show interquartile ranges (IQRs), while external points are statistical outliers. An ANOVA revealed a significant effect of the type of disturbance ($F = 13.93$, $p = 0.007$) in coral cover. The t-test results of particular disturbance types in the change of coral cover are displayed for each island, with ‘*’ when the change was significant and with ‘NS’ when not significant.

Figure 4. Changes in peak coral cover and coral community composition ‘before’ and

‘after recovery’ from disturbances that affected French Polynesia during our study. Panel (A) refers to the period between 1995 and 2005; panel (B) refers to the time between 2006-07 and 2017-2019). Colours in the coral community represent each coral genus. * = significant, NS = not significant.

Figure 5. nMDS ordination on the Bray-Curtis dissimilarity matrix of coral community

composition across space and time. Symbols display the different disturbances. The disturbances correspond to the first survey after the disturbances, not the year the disturbance occurred. Coral genera are displayed in black inside labels.

French Polynesia

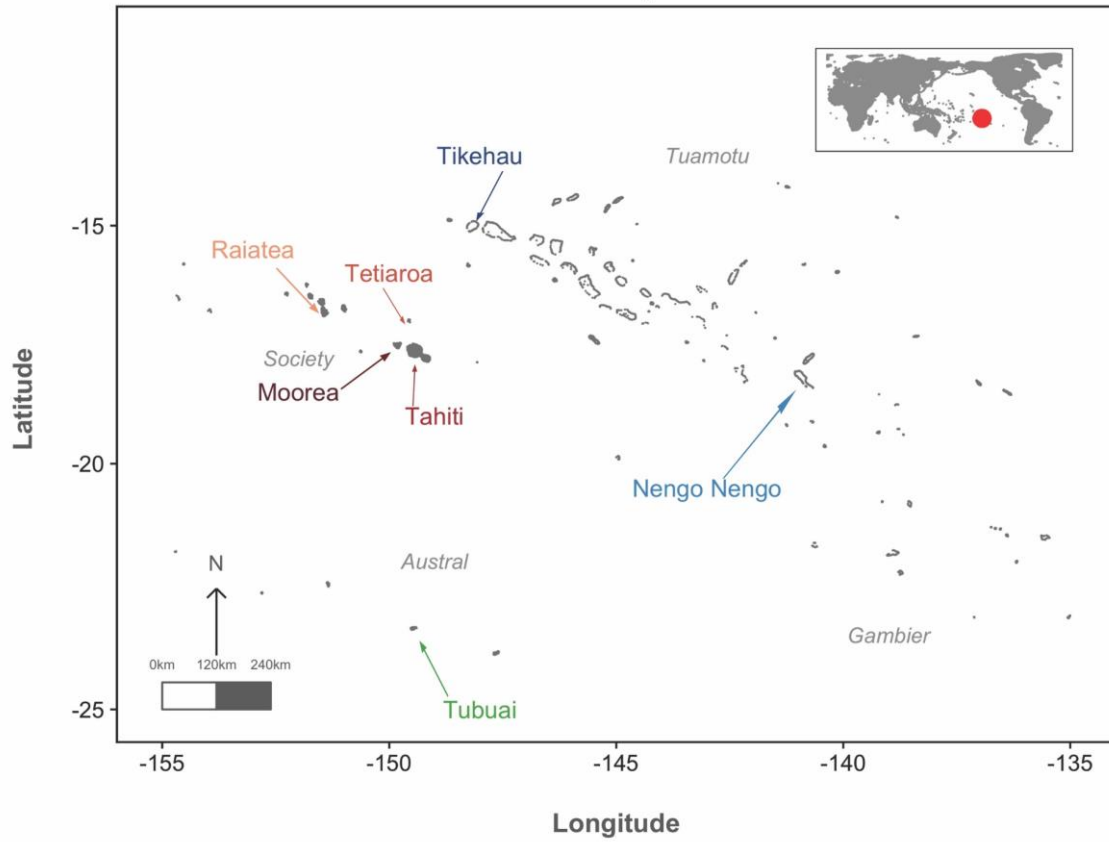


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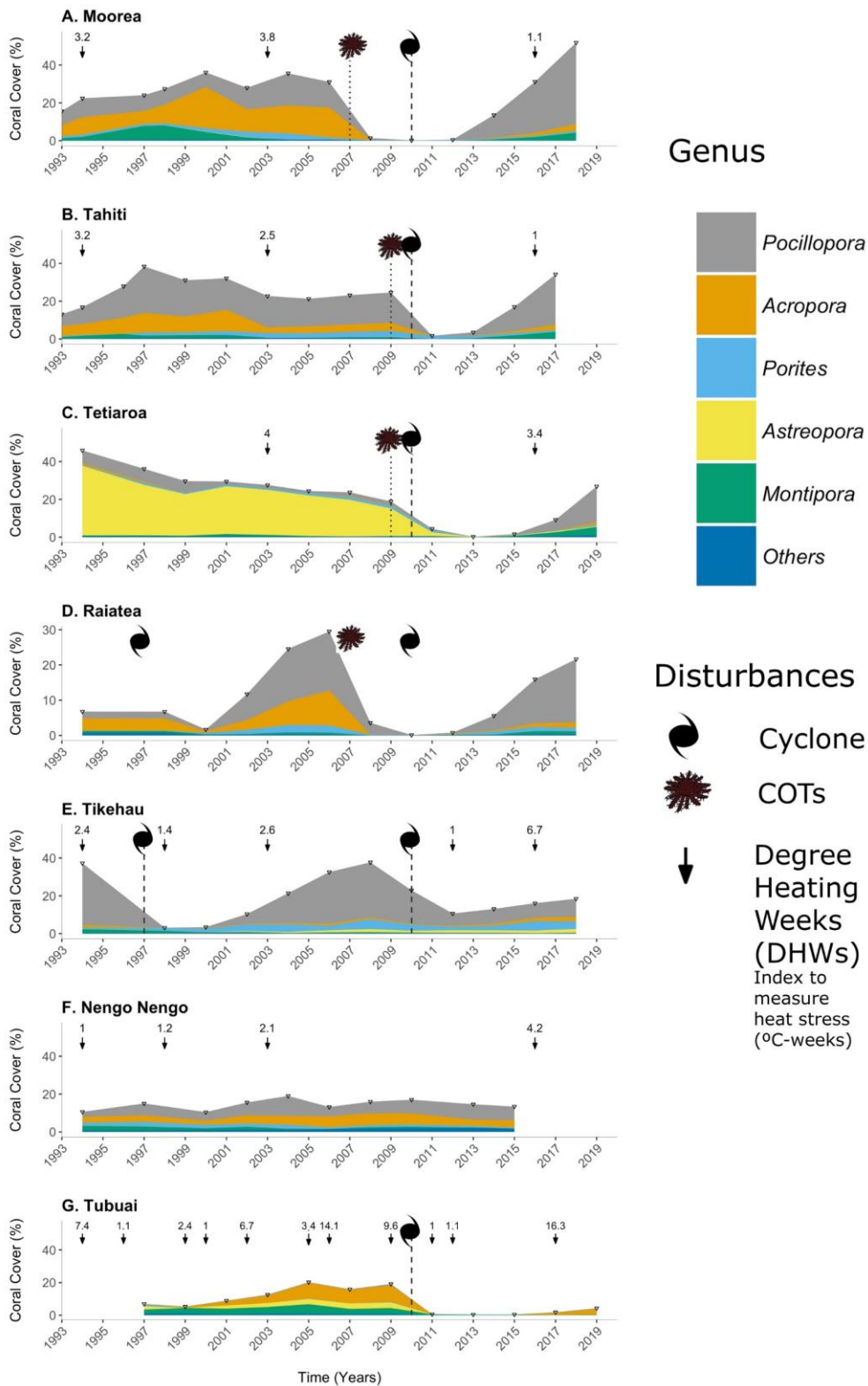


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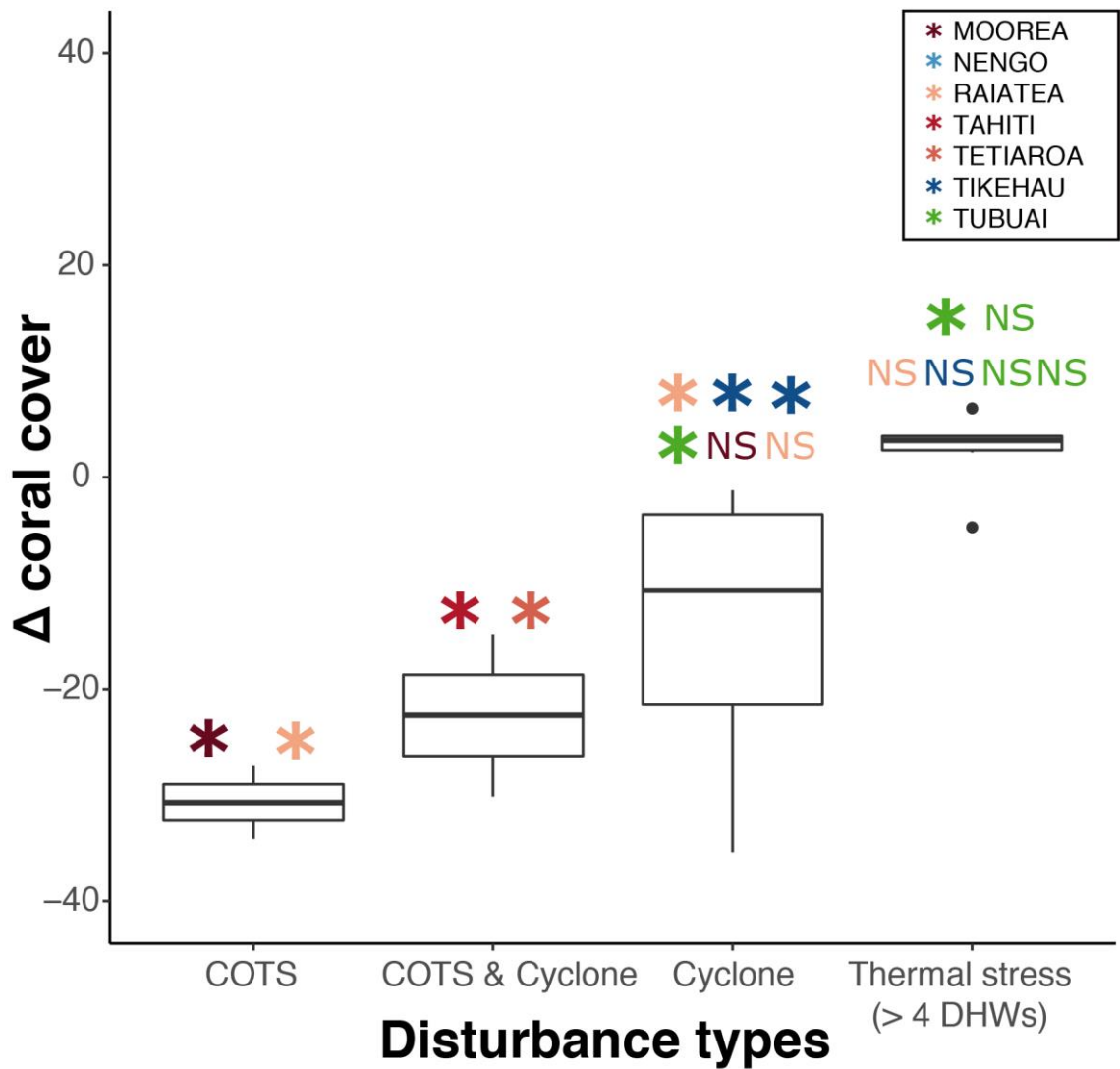
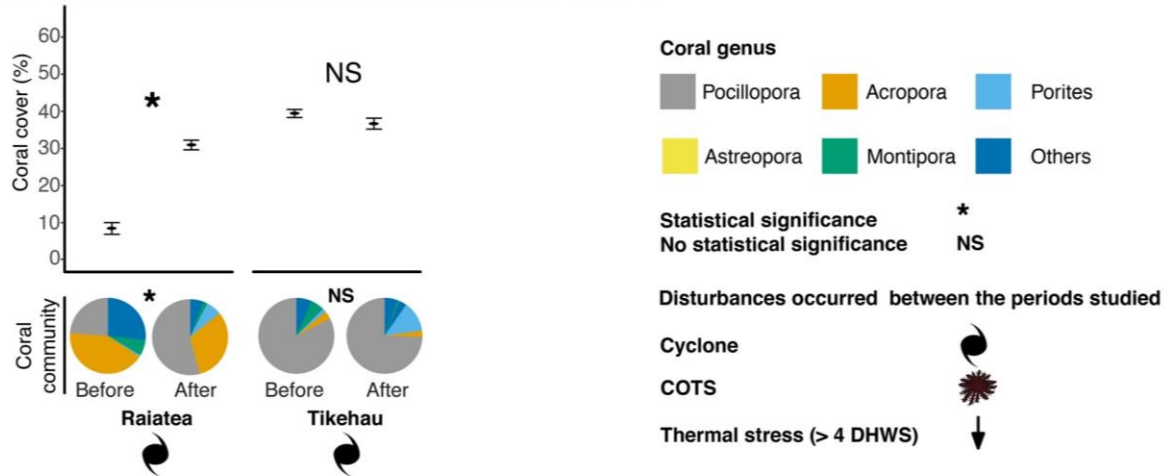


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A. Changes from Before (1994-1995) & After recovery (2005-2006) of Disturbances



B. Changes from Before (2005-2006) & After recovery (2017-2019) of Disturbances

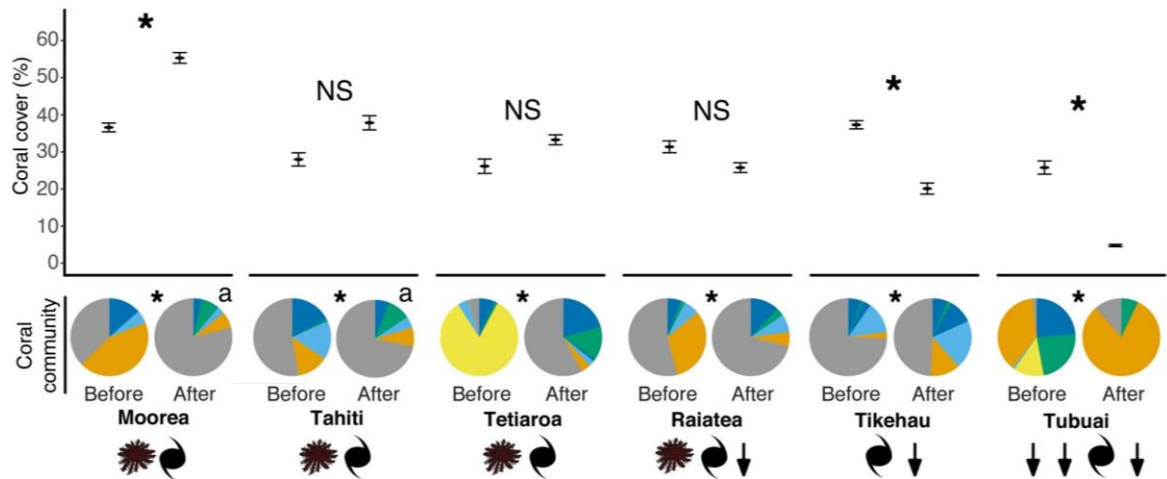


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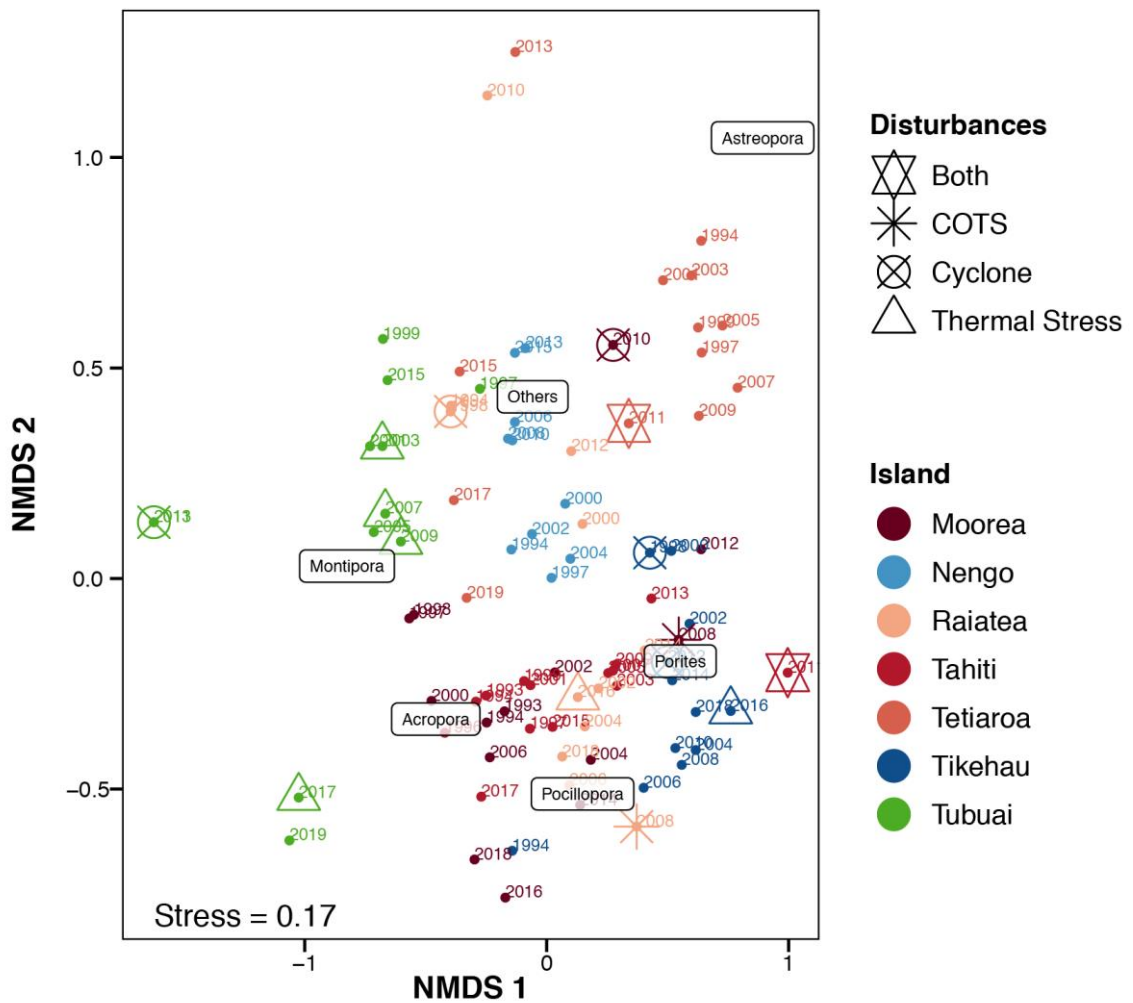


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Table 1 Summary of coral cover values and recovery dynamics ‘before’ and ‘after recovery’ the main disturbances.

Island	Disturbance type (year)	Type (Genus)	Pre-disturbance cover (%) and (year)	Min. cover after disturbances (%) and (year)	Max. Post-disturbance cover (%) and (year)	Minimum below 1% time (years)	Recovery (coral * year ⁻¹) (mean ± se)
Mo'orea	COTS (2007, 2008) & Cyclone (2010)	All genera	36.01 (2006)	0.18 (2010)	54.63(2018)	4	6.8 ± 0.31
		<i>Pocillopora</i>	13.52 (2006)	0 (2010)	43.02 (2018)	6	5.38 ± 0.3
		<i>Acropora</i>	15.8 (2006)	0 (2010)	3.64 (2018)	8	0.45 ± 0.1
		<i>Porites</i>	1.97 (2006)	0.12 (2010)	1.726 (2018)	6	0.2 ± 0
Tahiti	COTS (2008, 2009) & Cyclone (2010)	All genera	27.4 (2005)	1.85 (2011)	37.3 (2017)	0	5.91 ± 0.8
		<i>Pocillopora</i>	14.63 (2005)	0.06(2011)	26.54 (2017)	1	4.41 ± 0.5
		<i>Acropora</i>	3.58 (2005)	0 (2011)	2.9 (2017)	4	0.48 ± 0.1
		<i>Porites</i>	4.44 (2005)	1.48(2011)	1.79 (2017)	0	0.05 ± 0.2
Tetiara	COTS (2009) & Cyclone (2010)	All genera	25.63 (2005)	0.31 (2013)	32.70 (2019)	1	5.39 ± 0.43
		<i>Pocillopora</i>	1.17 (2005)	0 (2013)	18.95 (2019)	6	3.16 ± 0.3
		<i>Acropora</i>	0.06 (2005)	0 (2013)	1.29 (2019)	8	0.21 ± 0
		<i>Porites</i>	1.11 (2005)	0 (2013)	0.8 (2019)	5	0.13 ± 0
		<i>Astreopora</i>	21.48 (2005)	0.18 (2013)	0.37 (2019)	6	0.03 ± 0
Raiatea	Cyclone (1997)	All genera	8.27 (1994)	2.16 (2000)	30.84 (2006)	0	4.77 ± 0.6
		<i>Pocillopora</i>	1.97 (1994)	0.43(2000)	16.79(2006)	1	2.72 ± 0.5
		<i>Acropora</i>	3.46 (1994)	0.49(2000)	9.87 (2006)	1	1.56 ± 0.2
		<i>Porites</i>	0.06 (1994)	0.43(2000)	2.03 (2006)	6	0.27 ± 0.1
	COTS (2007, 2008) & Cyclone (2010)	All genera	31.81 (2006)	0.12(2010)	25.25 (2018)	4	3.14 ± 0.3
		<i>Pocillopora</i>	16.790 (2006)	0.06(2010)	18.02 (2018)	4	2.25 ± 0.2
		<i>Acropora</i>	9.87 (2006)	0 (2010)	1.48 (2018)	8	0.18 ± 0.1
		<i>Porites</i>	2.03 (2006)	0 (2010)	1.91 (2018)	8	0.24 ± 0
Tikehau	Cyclone (1997) & Bleaching (1998)	All genera	39.51 (1994)	4.13 (1998)	36.73 (2006)	0	4.08 ± 0.3
		<i>Pocillopora</i>	32.65 (1994)	0.06(1998)	27.40 (2006)	4	3.42 ± 0.2
		<i>Acropora</i>	1.35 (1994)	0.06(1998)	0.98 (2006)	12	0.11 (0.1)
		<i>Porites</i>	0.67 (1994)	1.54(1998)	4.81 (2006)	0	0.4 ± 0.1
	Cyclone (2010)	All genera	36.72 (2006)	14.24 (2012)	19.62 (2018)	0	0.89 ± 0.4
		<i>Pocillopora</i>	27.4 (2006)	6.48(2012)	9.63 (2018)	0	0.52 ± 0.3
		<i>Acropora</i>	0.99 (2006)	0.49 (2012)	2.4 (2018)	8	0.32 ± 0.2
		<i>Porites</i>	4.81 (2006)	3.70 (2012)	3.94 (2018)	0	0.04 ± 0.1
Tubuai	Cyclone (2010)	All genera	25.26 (6.5)	0.43 (2013)	4.37 (2019)	6	0.65 ± 0.1
		<i>Pocillopora</i>	0.37 (2005)	0 (2013)	0.49 (2019)	12	0.08 ± 0
		<i>Acropora</i>	9.63 (2005)	0 (2013)	3.52 (2019)	6	0.59 ± 0.1