



# Long-term monitoring of benthic communities reveals spatial determinants of disturbance and recovery dynamics on coral reefs

Charlotte Moritz<sup>1,2,3,\*</sup>, Simon J. Brandl<sup>1,2,4,5</sup>, H elo ise Rouz e<sup>1,2,5</sup>, Jason Vii<sup>1,2,5,6</sup>, Gonzalo P erez-Rosales<sup>1,2,5</sup>, Pauline Bosserelle<sup>1,2,7</sup>, Yannick Chancerelle<sup>1,2,5</sup>, Ren e Galzin<sup>1,2,5</sup>, Vetea Liao<sup>1,2,8</sup>, Gilles Siu<sup>1,2,5</sup>, Marguerite Taiarui<sup>1,2,8</sup>, Maggy M. Nugues<sup>1,2,5</sup>, Laetitia H edouin<sup>1,2,5</sup>

<sup>1</sup>PSL Universit  Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE, 98729 Papetoai, Mo'orea, French Polynesia

<sup>2</sup>Laboratoire d'Excellence 'CORAIL', Mo'orea, French Polynesia

<sup>3</sup>CMOANA Consulting, 98719 Taravao, French Polynesia

<sup>4</sup>CESAB - FRB, 5 Rue de l' cole de M decine, 34000, Montpellier, France

<sup>5</sup>PSL Research University: EPHE-CNRS-UPVD, USR 3278 CRIOBE, 66860 Perpignan CEDEX, France

<sup>6</sup>Coral Reef Ecology Consulting, 98703 Punaauia, French Polynesia

<sup>7</sup>Pacific community (SPC), Fisheries, Aquaculture and Marine Ecosystem division, 98848 Noumea, New Caledonia

<sup>8</sup>Direction des Ressources Marines, 98713 Papeete, French Polynesia

**ABSTRACT:** Coral reefs across the globe are facing threats from a variety of anthropogenic disturbances. Consequently, the proportional representation of live scleractinian corals in the benthic community has declined substantially in many regions. In contrast, parts of the reef ecosystem around Mo'orea (French Polynesia) have displayed remarkable rebound potential. Nevertheless, detailed studies of when, where, and to what extent reefs have been disturbed and subsequently recovered in the different reef habitats are lacking. Using long-term monitoring data (2004–2018), we reveal that the spatiotemporal dynamics of benthic communities differ markedly between the contiguous inner (fringing and barrier) and outer (fore) reefs. Coral communities on inner reefs vary spatially but were remarkably stable over 15 yr, exhibiting consistent levels of coral and algal cover, with no evidence for disturbance-driven regimes or community transitions. In contrast, the outer reefs showed marked declines in coral cover following consecutive acute disturbances, but coral recovered rapidly thereafter. Nevertheless, community composition changed significantly, with *Pocillopora* replacing *Acropora* as the dominant genus at several sites, indicating a more subtle but potentially critical transition into an alternative state defined by the prevalence of a single, fast-growing genus. Inner reef stability and outer reef recovery provide evidence that the effects of environmental disturbances and chronic anthropogenic stressors can manifest in fundamentally different ways, depending on prevailing conditions. Our results suggest important ecological and physical links between inner and outer reef systems that influence the observed dynamics, emphasizing that reef ecosystem management and conservation strategies need to consider all habitats.

**KEY WORDS:** Reef habitats · Spatial resilience · Natural perturbations · Pacific · *Pocillopora* · Regime shift

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## 1. INTRODUCTION

Disturbances are a natural component of ecosystems, shaping the composition of biological communities through time and space (Pickett et al. 1989).

The effects of disturbances depend on their severity, frequency, and environmental context. Due to the ever-increasing human footprint on our planet, many ecosystems are now experiencing altered disturbance regimes that can combine with characteristics

of the prevailing environment to shift communities into alternative states (Scheffer & Carpenter 2003, Hughes et al. 2013). As a consequence, several shifts between stable states induced by human-mediated disturbances have been reported in recent years, with some of them leading to undesirable ecological and economic outcomes (e.g. biodiversity loss, erosion of resilience, fishing and tourism industry loss of income; Pecl et al. 2017).

Despite being naturally prone to disturbance-driven changes in biotic structure (Madin & Connolly 2006), coral reefs are currently experiencing unprecedented declines due to a combination of natural and anthropogenic stressors at various scales (Bruno & Selig 2007, De'ath et al. 2012, Jackson et al. 2014, Smith et al. 2016, Hughes et al. 2017a,b). Disturbances on coral reefs range from tropical storms and cyclones (Foster et al. 2011, Perry et al. 2014, Gouezo et al. 2015) to outbreaks of predators such as the seastar *Acanthaster planci* (Moran 1986, Sano 2000, Adam et al. 2011, Kayal et al. 2011, 2012), or exposure to extreme environmental variations (e.g. seawater surface temperature anomalies or nutrient pollution; Adjeroud et al. 2009, Hughes et al. 2018a,b, Donovan et al. 2020). Responses of reefs to these disturbances can be measured in the spatial extent and composition of the benthic community. Change in the proportional occupation of the seafloor by corals, as the primary reef-building organisms, is the most common indicator of the status and trajectory of reefs (e.g. Bruno & Selig 2007, Gilmour et al. 2013). As such, examining benthic community composition and coral cover across space and time can inform us about the responses of reefs to disturbances, while providing a framework that allows for broad comparisons of reefs in different geographic regions or with varying prevailing conditions (Darling et al. 2019).

Naturally, there is great variability in how different disturbances affect coral reefs. Nevertheless, even the same disturbance can yield greatly differing responses on reefs, in both close spatial proximity (e.g. same island) or across large distances (e.g. biogeographic regions). For example, reefs on the Great Barrier Reef and in Micronesia that were affected by the same type of disturbances (*A. planci* outbreaks) varied substantially in their post-disturbance composition and recovery trajectories (i.e. the way and extent to which the reefs recovered; Graham et al. 2014, Houk et al. 2014). These divergent responses highlight the natural environmental variability at relatively small spatial scales such as neighboring islands (e.g. Wismer et al. 2009, Williams et al. 2013), which shapes coral reef communities and their inter-

actions with disturbances. On the scale of single islands or reef systems, environmental conditions can differ substantially, both based on the reef zone (e.g. inner and outer reefs) and the dominant wave exposure and direction (e.g. Done 1982, Alevizon et al. 1985). Exposed outer reefs are usually characterized by intense hydrodynamic pressure from wave action, often showing high susceptibility to cyclones and other severe weather events (Done 1992, Harmelin-Vivien 1994). In contrast, sheltered fore reefs or fringing and back reefs are usually dominated by calmer conditions but can be susceptible to disturbances created by nutrient run-off due to coastal development or temperature-induced coral bleaching (Donovan et al. 2020). Despite the important roles of fine-scale environmental conditions for mediating disturbance effects and recovery, there are few long-term assessments of fine-scale spatial differences in reef trajectories around single islands (Madin et al. 2018).

The capacity of each reef habitat to resist and/or respond to disturbances is reflected in the stability of their communities over time. While some reefs have demonstrated a strong capacity to absorb disturbances and remain in or return to a coral-dominant state (Jackson 1992, Pandolfi & Jackson 2006, Graham et al. 2015), others have changed to dominance by either small, weedy coral genera, or other benthic groups such as macroalgae, sponges, or soft corals (McManus & Polsenberg 2004, McClanahan et al. 2007, Bruno et al. 2009, Hughes et al. 2010, Darling & Côté 2018). The frequency and longevity of such phase shifts remains vigorously debated (Bruno et al. 2009, 2014, Graham et al. 2015, Mumby et al. 2016), not least because the recovery following natural and anthropogenic disturbances can exhibit marked variations in temporal and spatial scales (Connell 1997, Jackson et al. 2014). Long-term studies with sufficient resolution to document fine-scale changes in the coral community structure, leading to understanding the recovery dynamics at the island scale, are therefore indispensable (Roff & Mumby 2012).

With a contiguous reef system surrounding the entire island and a long history of research, the island of Mo'orea (French Polynesia) provides an excellent opportunity to evaluate the spatiotemporal dynamics and recovery potential of a coral reef ecosystem facing major disturbances across multiple sites and habitats (Table 1). The effects of major disturbances (e.g. a bleaching event in 1991, an *A. planci* outbreak in 2006–2009, and cyclone Oli in 2010) on the succession of benthic (Adjeroud et al. 2009, Kayal et al. 2012, Adjeroud et al. 2018)

Table 1. Disturbances that occurred in Mo'orea over the past 40 yr

Year	Type of disturbance			Source
	Bleaching	Cyclone	<i>Acanthaster planci</i> outbreak	
1978–1980			All around Mo'orea	Surveyed in Faure (1989) Reported in Bouchon (1985, 1996)
1983	Moderate			Reported in Glynn (1984, 1991), Williams & Bunckley-Williams (1990), Salvat (1992), Salvat & Aubanel (2002)
1987	Moderate			Authors' pers. comm.
1991	Strong			Surveyed by Salvat (1992), Gleason (1993)
1994	Strong			Surveyed by Fagerstrom & Rougerie (1994), Hoegh-Guldberg & Salvat (1995), Adjeroud et al. (2005)
2002	Strong			Surveyed by Carroll et al. (2017), Y. Chancerelle et al. unpubl. data, Penin et al. (2013), Adjeroud et al. (2005)
2006–2009			All around Mo'orea	Reported in Kayal et al. (2012), Lamy et al. (2015), Lamy et al. (2016)
2010		Oli in February		Reported in Lamy et al. (2015), Lamy et al. (2016), Adjeroud et al. (2018)

and fish communities (Lamy et al. 2015, Galzin et al. 2016, Lamy et al. 2016, Martin et al. 2017, Viviani et al. 2019) have been assessed at a few sites on the fore reefs. However, in-depth analyses of the long-term dynamics and transitory states of coral communities across habitats and locations are lacking (Holbrook et al. 2018). Here, we used long-term monitoring data on benthic cover and composition over 15 yr at 13 sites around the island to analyze the spatiotemporal dynamics of reefs from 3 habitats (fringing, barrier and fore reefs) under the consideration of various acute and chronic disturbances. Assessing changes in community composition over time and comparing pre-disturbance and post-disturbance coral reef characteristics, while quantifying the importance of local and broad scale factors on these changes, is key to a better understanding and management of the complex coral reef ecosystem surrounding Mo'orea.

## 2. MATERIALS AND METHODS

### 2.1. Study system

Mo'orea (17° 30' S, 149° 50' W) is a volcanic island in the Society Islands archipelago, French Polynesia (Fig. 1a), home to approximately 17 000 people, whose livelihoods are supported by the surrounding reef system through tourism, fishing, and other services. The reef around Mo'orea is structured from the shore to the open sea as follows: (1) the fringing reef, adjacent to the shore, (2) the barrier reef, separated

from the fringing reef by a deeper channel, and (3) the fore reef, from the barrier reef crest outwards.

### 2.2. Benthic monitoring data

We used data from the Mo'orea marine protected area (MPA) program from 2004 to 2018. This program uses the point intercept transect method (PIT, Hill & Wilkinson 2004) to estimate benthic community cover and composition (e.g. corals, identified to the genus level [Veron 1986, 2000, Bosserelle et al. 2014], algae, composed of macroalgae and turf, and abiotic substrate). For the PITs, points were placed every 0.25 m along 25 m length transects deployed at 10–12 m depth on the fore reef parallel to the reef slope, and at 0.5–2 m depth on the fringing and barrier reefs parallel to the coastline. The MPA program surveyed 13 sectors around Mo'orea, within all 3 habitats (fringing, barrier, and fore reefs; Fig. 1a) surveyed via 3 random transects (total  $N = 39 \text{ yr}^{-1}$ ). This dataset was used here to analyze the dynamics of the benthic community structure across space in the different habitats and time.

### 2.3. Statistical analyses

To characterize the dynamics of the disturbance–recovery cycle observed during the study period, we calculated the mean coral cover and the mean number of coral genera pre-disturbance (2004–2006) and post-disturbance (2016–2018) at each site across habitats, as well as the number of years when coral

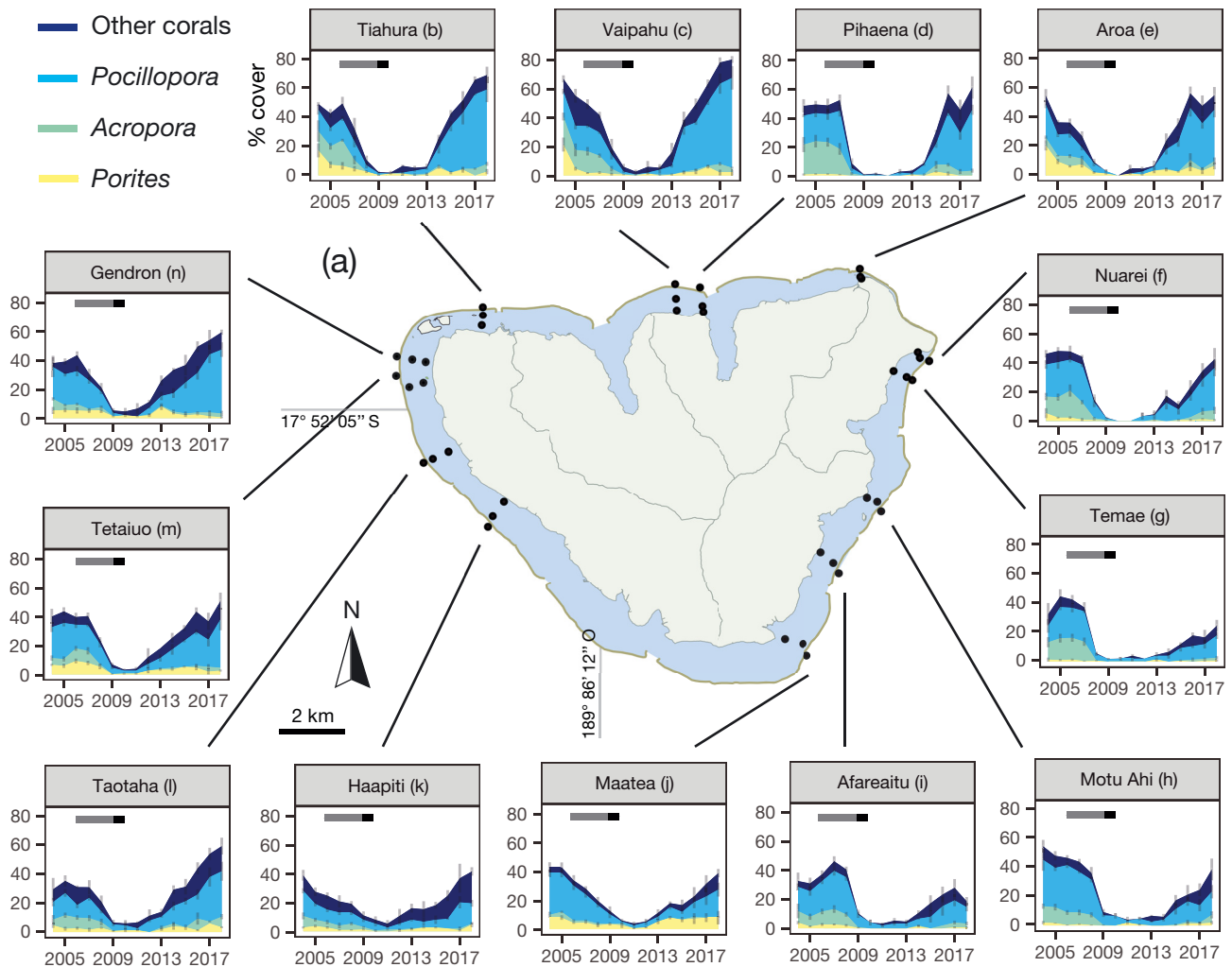


Fig. 1. (a) Map of Mo'orea showing the sampling locations on the continuum fringing, barrier, and fore reef (●). (b–n) Cumulated percent coral cover of the 3 main coral genera and other coral genera on the fore reef. Horizontal grey and black bars indicate, respectively, the 2006–2009 *Acanthaster planci* outbreak and the 2010 cyclone Oli. See Fig. S1 in the Supplement for fringing and barrier reef graphs

cover was <5% between these periods. For each habitat, we performed a hierarchical cluster analysis based on Euclidean distance between the sites (Gauch & Whittaker 1981) based on the scaled and centered matrix of these reef characteristics. We cut the resulting dendrogram at height = 3. For each habitat, we also used an ANOVA with the factor Period (2 levels: pre-disturbance and post-disturbance) and the factor Site (13 levels, one for each site) on coral cover and diversity to test the hypothesis that there are spatial differences of the surveyed reefs 'before' and 'after' disturbances. We used a Shapiro-Wilk test to assess the normality of the model residuals, which were normally distributed in all cases ( $p > 0.05$ ), and a Bartlett's test to assess homogeneity of variances, which were equal for all samples.

To assess the importance of the variables 'site', 'habitat' and 'year' on the fine-scale coral community composition, a permutational multivariate analysis of variance (PERMANOVA) was performed on a distance matrix generated with the coral genus data. Then, to assess the specific effects of the different habitats on community composition, a permutation test was performed using 'fringing reef', 'barrier reef' and 'fore reef'.

We computed a set of non-metric multidimensional scaling (nMDS) ordinations based on the Bray-Curtis measure of dissimilarity (Shepard 1962, Kruskal 1964) between each year, calculated on Hellinger-transformed coral genus data for the 3 habitats separately to visualize long-term trajectories in coral community composition (genus level) between 2004 and

2018 in each habitat. We ran an ANOSIM (analysis of similarities, in which  $R$  statistic  $> 0.2$  provides evidence for strong differences between 2 communities) to test the null hypothesis of no difference in relative genus composition between pre- (2004–2006) and post-disturbance (2016–2018) periods. All statistical analyses were performed in the statistical environment R version 3.1.2 with the *vegan* package (Oksanen et al. 2016, R Core Team 2017).

### 3. RESULTS

#### 3.1. Coral cover and genus diversity dynamics

Reef habitats within the lagoon displayed heterogeneous benthic communities across sites (Fig. 2a,e), especially on the fringing reef, but showed a high compositional stability of the major groups over time (Fig. 2; fringing: b–d and barrier: f–h). We detected

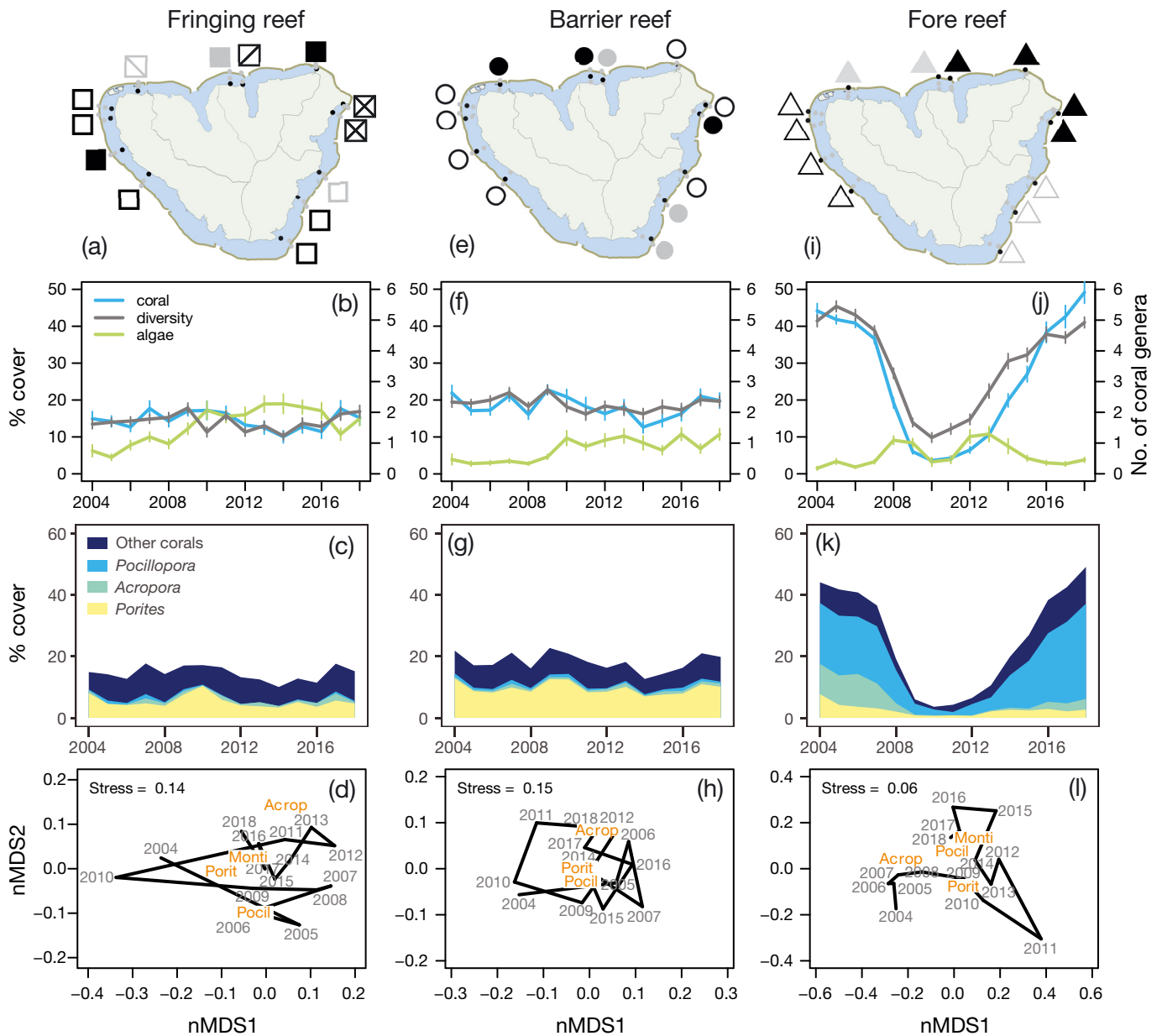


Fig. 2. (a,e,i) Maps of Mo'orea indicating site similarity: symbols filled similarly indicate site similarity (see Section 2 for details) for the 3 habitats (squares, circles and triangles for the fringing, barrier and fore reef, respectively) analyzed separately. (b,f,j) Percent coral cover, number of coral genera (diversity), and percent macroalgae-turf cover averaged across sites and replicates (vertical bars are SE; note the double y-axis scale). (c,g,k) Cumulated percent coral cover of the 3 main coral genera and other coral genera. (d,h,l) Non-metric multidimensional scaling (nMDS) of the coral assemblages showing the temporal trajectory of the coral community composition; the position of the main coral genera in the multidimensional space is indicated (Acrop: *Acropora*; Monti: *Montipora*; Pocil: *Pocillopora*; Porit: *Porites*)

no effects of disturbances on coral cover and coral diversity for these 2 habitats (ANOVA p-value > 0.05 for the Period factor), but sites varied significantly among them in terms of coral cover and diversity (ANOVA p-value for the Site factor < 0.05, and marginally different for coral cover on the barrier reef where p-value = 0.083). Despite a regular increase in algal cover over the study period on both habitats, it never exceeded coral cover on the barrier reef (Fig. 2b,f).

In contrast, the fore reef of Mo'orea displayed a much more dynamic community structure over time (Fig. 2j–l). The prevalence of algae (macroalgae and turf) was opposite to that of coral cover, but algae never permanently replaced coral as the dominant group around Mo'orea despite the acute disturbances (Fig. 2j). Coral cover pre- and post-disturbance showed no significant difference (Period factor p-value = 0.728, *F*-value = 0.127), and sites were not significantly different (Site factor p-value = 0.137, *F*-value = 1.915). Indeed, at all sites, the 2011–2018 period exhibited a remarkable recovery in coral cover, which reached  $49.2 \pm 18.4\%$  (mean  $\pm$  SD) in 2018 on average around the island (Fig. 2j), and up to  $80 \pm 4\%$  (mean  $\pm$  SD) at Vaipahu (north coast, Fig. 1c). More specifically, 8 yr after the lowest coral cover reported in Mo'orea in 2010, which decreased down to zero at all transects in Aroa and Nuarei, most outer reef sites (10 of the 13 sites investigated) reached similar (Pihaena, Aroa, Nuarei, Maatea, Haapiti, Tetaiuo: Fig. 1d–f,j,k,m) or higher (Tiahura, Vaipahu, Taotaha, Gendron: Fig. 1b,c,l,n) coral cover than recorded before the disturbances. Mean coral diversity, however, was significantly different pre- and post-disturbance (ANOVA p-value < 0.05 for the Period factor) but tended to go back to its original levels (Fig. 2j). Only Temae, Motu Ahi and Afareaitu showed disturbance-driven decreases in coral cover on the fore reef (Fig. 1g–i). Disturbance and recovery dynamics followed a gradient around the island, according to their geographic location (Fig. 2i), which were differently impacted by the disturbances: cyclone Oli mostly affected the northern coast, whereas the *Acanthaster planci* outbreak spread progressively around the entire island (see references in Table 1).

### 3.2. Coral community composition dynamics

Coral community composition differed significantly among habitats, sites, and years (PERMANOVA:  $p = 0.001$ ; Table 2). However, the stronger effects

Table 2. Results of the PERMANOVA performed on the distance matrix of coral community composition for habitat, site and year. SES: standardized effect sizes

	<i>F</i> -statistic	SES	Pr (perm)
Site	10.16	43.64	0.001
Habitat	208.91	441.91	0.001
Year	49.75	72.46	0.001

were found by far for habitat, followed by year, then site (standardized effect sizes, SES: Table 2). Within habitats, while the fore reef strongly differed from the fringing and barrier reefs (SES < -9), the difference between the fringing and barrier reefs was less pronounced (SES = 2.4, Table 3).

On the fore reef, *Pocillopora* was the dominant genus between 2004 and 2018 at almost all sites, followed by *Acropora*, *Montipora* and *Porites* in various orders (Fig. 3). However, coral community composition differed between 2004 and 2006 (pre-disturbance) and 2016 and 2018 (post-disturbance) at almost all sites (ANOSIM: *R* ranging from 0.218 to 0.988, p-value from 0.001 to 0.007), except Taotaha ( $R < 0.2$ ,  $p > 0.05$ ). Specifically, contributions of *Pocillopora* increased markedly at most sites, particularly on the northern coast, where *Acropora* corals drastically decreased after the disturbances (e.g. Fig. 3b: *Pocillopora* went from 21.66 to 63.03%, and *Acropora* went from 19.12 to 5.04%). In contrast, sites on the southeastern side of the island, in particular, showed slower recovery and a much less pronounced (or no) increase in *Pocillopora* cover.

On the inner reefs, coral community composition was stable pre- and post-disturbance at most sites (ANOSIM:  $R < 0.2$ ), with the exception of Nuarei on the fringing reef ( $R = 0.348$ ,  $p = 0.001$ ), and Aroa ( $R = 0.256$ ,  $p = 0.008$ ) and Vaipahu ( $R = 0.477$ ,  $p = 0.001$ ) on the barrier reef. *Porites* and *Montipora* characterized most of the inner reef sites around

Table 3. Results of the permutation test performed on the distance matrix of coral community composition in the reef habitats. SES: standardized effect sizes

	<i>F</i> -statistic	SES	Pr (perm)
Overall	86.17	80.80	0.001
Barrier reef – Fringing reef	2.37	2.40	0.015
Barrier reef – Fore reef	-9.70	-9.77	0.001
Fringing reef – Fore reef	-11.77	-11.96	0.001

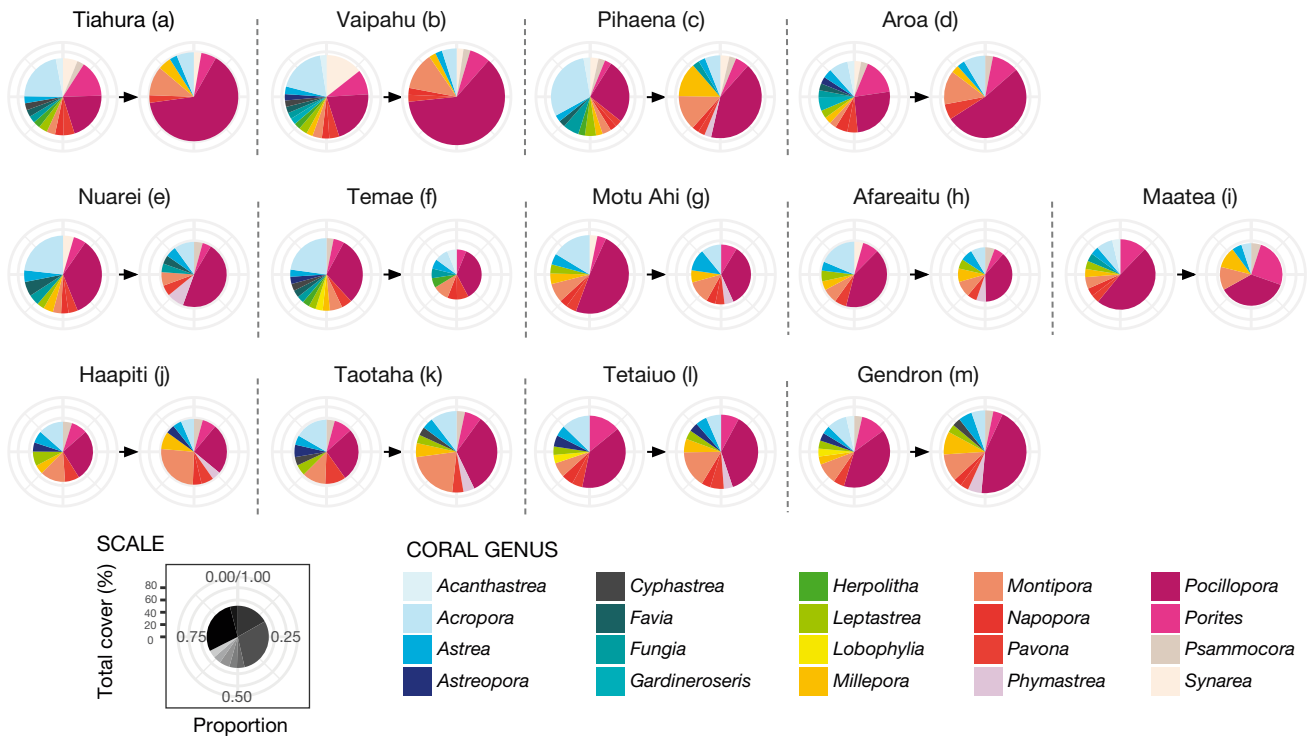


Fig. 3. Proportion of coral genera before (i.e. averaged over 2004–2006; left) and after (i.e. averaged over 2016–2018; right) the *Acanthaster planci* outbreak and cyclone Oli on the fore reef. Circle size is proportional to the coral percent cover. See Figs. S2 & S3 in the Supplement for fringing and barrier reef graphs

Mo'orea (Fig. 2c,g & Figs. S1, S2, S3 in the Supplement; [www.int-res.com/articles/suppl/m672p141\\_supp.pdf](http://www.int-res.com/articles/suppl/m672p141_supp.pdf)). Temae, Nuarei, Vaipahu, Pihaena and Motu Ahi were distinct from their neighbors in terms of coral composition (Fig. S2); *Acropora* dominated in Temae while other genera such as *Montipora* dominated in Motu Ahi (Figs. S1 & S2).

## 4. DISCUSSION

### 4.1. Habitat variation in reef dynamics

Although coral reefs are naturally prone to disturbances, increasing anthropogenic pressure has intensified interest in the response of reefs to natural and anthropogenic stressors. Our results show that, on the scale of a single island, disturbance and recovery dynamics depend greatly on the environmental settings of reefs. Specifically, we show fundamental differences between highly dynamic, rapidly recovering outer reefs subjected to acute natural disturbances and relatively stable inshore reefs with low but consistent coral cover (<20%) over 15 yr. Furthermore, we highlight that, despite a relatively consistent recovery on the exposed reefs, the extent and

nature of recovery hinges on contributions of a single genus (*Pocillopora*), for which population dynamics differ spatially. Our results suggest that, while the broad disturbance dynamics of reefs depend strongly on the prevailing ecological dynamics across habitats, more subtle characteristics of recovery trajectories can vary across sites in the same habitat at the scale of a small Pacific island.

Effects of various disturbances have been documented to differ according to the distance of reefs from shore, their depth, and habitats (Berkelmans & Oliver 1999, Fabricius et al. 2008, Baker et al. 2016), with near-shore reefs displaying greater vulnerability to land-based disturbances than offshore reefs (Smith et al. 2008a, Donovan et al. 2020). Reefs around Mo'orea are relatively sheltered from coastal anthropogenic developments compared to some other Pacific islands (e.g. Hawaii: Hunter & Evans 1995; Australia: Smith et al. 2008b), which may explain the stability of coral cover on the inner reefs in the present study. However, spatial differentiation of benthic communities was stronger on inner reefs compared to outer reefs. This suggests that long-standing differences in the geography of the island and the patterns of human development may have shaped these lagoonal reefs over the past few

decades, or even centuries. Recent results, which document interactive effects of nutrients and sea surface temperature on coral bleaching in Mo'orea's lagoon, support this line of evidence (Donovan et al. 2020). It is possible that the observed stability of inner reefs despite a suite of disturbances represents a hysteresis due to long-standing, chronic stressors that have shifted reefs into a stable state of disturbed benthic communities.

Conversely, outer reefs showed a highly dynamic response to disturbance, with dramatic losses but a rapid recovery. This observed recovery of outer reefs may, at least in part, be facilitated by the presence of the expansive lagoon around Mo'orea and its associated reefs. First, lagoonal reefs may absorb much of the human-derived local impacts (e.g. nitrogen pollution), which can facilitate the recovery of further reefs (i.e. closer to the reef crest) after disturbances (Donovan et al. 2020). Second, inner reefs with stable benthic communities may provide a nursery area for coral-dependent organisms that facilitate recovery (Rouzé et al. 2015, Morgan et al. 2016). For example, in Mo'orea, parrotfishes that recruit to stable nursery habitat within the lagoon can move offshore during the course of their ontogeny to reduce macroalgae on the outer reef, thus promoting coral settlement and growth after the reefs were completely denuded (Adam et al. 2011, Lamy et al. 2016, Martin et al. 2017, Viviani et al. 2019). In turn, outer reefs absorbed the brunt of the hydrodynamic damage imposed by the cyclone and suffered much higher damage from the *Acanthaster planci* outbreak, thus safeguarding inner reefs from these acute disturbances. This highlights the interdependence of inner and outer reefs and the importance of considering divergent responses of reef habitats to acute and chronic stressors in synergy (Done 1992).

#### 4.2. Processes underpinning recovery on outer reefs

The coral decline between 2006 and 2010 was the most dramatic reported on fore reefs in Mo'orea and was extremely consistent across sites. Nevertheless, 8 yr later, coral cover reached values similar to pre-disturbance levels at 10 of the 13 sites investigated, with an estimated recovery rate of 6.3% yr<sup>-1</sup>. Such fast recovery in Mo'orea is not without historical precedent, with comparable rates reported following an *A. planci* outbreak in 1979 and a cyclone in 1991 (Lamy et al. 2016). These recovery rates appear to be higher than many other reported cases (e.g. Colgan

1987, Connell et al. 1997, Sano 2000, Guzman & Cortés 2007, Gilmour et al. 2013, Morri et al. 2015, Gouezo et al. 2017) and strongly contrast with a complete lack of recovery on many Caribbean reefs (Jackson et al. 2014). There, several biotic and abiotic conditions combined with strong anthropogenic stressors appear to have interrupted recovery dynamics to shift reefs into low coral-cover states (Jackson et al. 2014). This long-term decline of *Acropora* in the Caribbean, where it was replaced by opportunistic, less structurally complex species (Green et al. 2008, Alvarez-Filip et al. 2011), provides a sobering example of stable shifts into alternative benthic compositional regimes, despite relatively consistent coral cover.

Contrasting with the Caribbean case, our results provide some insights into the potential processes that underpin recovery of the fore reefs in Mo'orea. Graham et al. (2015) suggested that high initial bottom complexity (3-dimensional structure) promotes reef recovery, but our results do not support this hypothesis as the recovery was preceded by a near-complete loss of structural complexity after the 2006–2010 disturbances. Instead, a combination of sufficient recruits (Adjeroud et al. 2018, Holbrook et al. 2018), sufficient herbivory (Martin et al. 2017, Viviani et al. 2019) and generally low algal prevalence due to high wave action may have permitted the essentially barren space to be colonized by competitive coral genera rather than algae. Indeed, bare substrate usually promotes the settlement of opportunistic genera, often attracting competitive and/or weedy corals (Darling et al. 2012), and reported peaks of *Pocillopora* recruitment (Adjeroud et al. 2018, Holbrook et al. 2018) support this assumption. In contrast to *Acropora* larvae (Tebben et al. 2015), *Pocillopora* larvae are more flexible and tend to colonize various microhabitats, from healthy reefs dominated by crustose coralline algae to ephemeral and exposed habitats (Riegl et al. 2013) and reefs altered by terrestrial runoff and dominated by macroalgae (Mwachireya et al. 2017). After settlement, a lack of competition on the mostly barren benthos may also have promoted a rapid growth and eventual dominance of young *Pocillopora* colonies, possibly because of the lack of competition with other corals and algae around. At sites where coral cover equaled or even exceeded pre-disturbance cover in 2018 (western and northern outer reef sites), the proportional contribution of *Pocillopora* invariably increased, predominantly at the expense of acroporid corals. Such dominance of *Pocillopora* over *Acropora* has been observed after previous disturbances on a



single reef in Mo'orea (Tiahura on the northern coast; Berumen & Pratchett 2006, Pratchett et al. 2011, Lamy et al. 2016). Our study confirms this dynamic around most (but not all) of the island (this study and Holbrook et al. 2018) and its importance for the recovery of coral cover. Indeed, on the eastern side of the island, the prevalence of *Pocillopora* did not show marked increases, and recovery was comparably poor.

While it is unclear whether dominance by *Pocillopora* after the disturbance is stable or merely a successional stage, the compositional changes have potential implications for the functioning of reefs around Mo'orea. While coral cover is a widely used metric to assess coral health worldwide, it may conceal important underlying ecological processes that are critical to our understanding of underlying ecological processes (Brandl et al. 2019). For instance, while reefs on the northern and western side of the island appeared to have been in excellent condition at the end of our monitoring (based on very good coral cover), the recovery may have been largely driven by the non-selective recruitment patterns of *Pocillopora* (Harriott 1983, Perez et al. 2014) associated with higher fecundity and population turnover than that of other genera (Darling et al. 2012). This may make these reefs functionally depauperate and vulnerable to future disturbance regimes. However, changes in coral community composition are likely to continue over the next decade around Mo'orea, with increasing contribution of the *Acropora* genus. But if the coral community remains monospecific on the mid-term, recovery from future disturbances (e.g. successive bleaching events, Hédouin et al. 2020) may be greatly compromised if conditions are less favorable for *Pocillopora*, as appears to be the case on the eastward side of the island. Monitoring and understanding the nuances of shifts in coral communities for the internal processes that govern coral reef ecosystem functioning and services present a critical objective for coral reef researchers and conservationists in the future.

While the present study is focused on how natural disturbances that occurred in Mo'orea more than 10 yr ago affected the reef, our findings can help mitigate anthropogenic stressors that are currently acting to shape coral reefs around the island. Specifically, by revealing the fundamentally different dynamics that act upon the different reef habitats around Mo'orea (mainly due here to natural disturbances caused by climate change and ocean warming and buffered beyond the barrier reef), our results make it clear that a single reef management plan for

the island is unlikely to succeed. Some levels of protection are already in place in Mo'orea, but there is little distinction between the 3 habitats. It is therefore important that the MPA program, which has been in place since 2004 (PGEM: 'Plan de Gestion de l'Espace Maritime'), considers the clear distinction among habitats in the future. Regular interactions between scientists, the population, consultants, practitioners in Moorea and the Government of French Polynesia regarding the PGEM and its benefits to the biological communities of the reef (e.g. Salvat & Aubanel 2002, Moreau et al. 2014, Moritz 2021) are encouraging to envision future improvement in the Government's management decisions to protect the reef in the long term. Indeed, protecting Mo'orea reefs from local anthropogenic stressors may better promote recovery after natural acute disturbance events, and, in return, understanding how these events shape the reef can allow managers to correctly implement appropriate measures at specific sites and habitats. Simultaneously, because local anthropogenic stressors are adding to the global-scale climate change and ocean warming effects on reef habitat and biological community dynamics, larger scale protection measures (such as reducing pollution at a global level) is now a necessity to increase the beneficial effects of protecting reefs locally by responsible governments.

*Data accessibility.* Data are available on the website SO CORAIL ([http://observatoire.criobe.pf/CRIOBEData/displayMPAMooreaBenthos\\_PIT.jsp](http://observatoire.criobe.pf/CRIOBEData/displayMPAMooreaBenthos_PIT.jsp)) and upon request to Serge Planes ([serge.planes@criobe.pf](mailto:serge.planes@criobe.pf)). R scripts are available upon request to Charlotte Moritz ([charlotte.moritz@gmail.com](mailto:charlotte.moritz@gmail.com)).

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