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Synchrony patterns reveal different degrees of trophic guild vulnerability after disturbances in a coral reef fish community

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Abstract

Aim: Chronic anthropogenic stressors are increasing in intensity, making ecosystems more vulnerable to acute disturbances. Recovery processes are not always well understood due to the complexity of ecosystems and the lack of appropriate indicators. Temporal synchrony is a valuable metric for assessing whether fluctuations in abundance of different species are homogeneous or heterogeneous over time. Theoretically, a great diversity of responses by species facing disturbances is associated with a stable ecosystem, with species turnover guaranteeing the persistence of key ecological processes. We analysed the fluctuations of synchrony of a fish community to assess its resilience in an ecosystem exposed to various disturbances.

Location: Moorea (French Polynesia).

Methods: Using one of the longest time series available for coral reefs (ca. 35 years), we examined the variations in substrate cover, and the abundance, synchrony and composition of different fish trophic guilds. Multivariate analyses involving synchrony were used to determine the stability of trophic guilds.

Results: Changes in fish community composition indicated incomplete taxonomic resilience. However, community synchrony was lower during periods of low coral cover, indicating greater response diversity, while total fish abundance remained fairly stable. Synchrony drop was due to relationships with coral cover that differed by trophic guild, or the differences in species responses within guilds. Some guilds such as sessile invertebrate feeders exhibited a strong homogeneity of response over time, indicating a greater vulnerability. We also highlighted that various types of disturbances had different effects on the synchrony of particular guilds.

Main conclusions: The fish community appeared functionally resilient, with stability of total abundance and most trophic guilds. This could be a factor explaining the rapid recovery of Moorea's coral reefs from disturbances. However, the homogeneous responses of some fish groups to disturbances may compromise the reef recovery potential on the long term if disturbances become more frequent.

KEYWORDS

coral reefs, disturbance, fish community, resilience, response diversity, synchrony, trophic guilds

1 | INTRODUCTION

The capacity of an ecosystem to recover its main ecological functions after disturbances is known as ecological resilience (Holling, 1973). The resilience of an ecosystem does not necessarily imply a return to the initial taxonomic composition observed before disturbance, but rather a return to the same functioning (Walker, 1981). Taxonomic richness is traditionally associated with improved ecosystem resilience (Mori, Furukawa, & Sasaki, 2013). However, higher species richness does not necessarily entail greater functional diversity (Cadotte, Cardinale, & Oakley, 2008; Hillebrand & Matthiessen, 2009; McGill, Enquist, Weiher, & Westoby, 2006; Mori et al., 2013) because similar functions can be shared by various species within an ecosystem (Walker, 1992). Therefore, investigating ecological resilience requires not only an understanding of species response to disturbance, but also an analysis of functional group responses and species redundancy within a function (Mori et al., 2013).

Temporal synchrony measures whether fluctuations of species' abundances are homogeneous (high synchrony) or heterogeneous (low synchrony) over a given time period (Loreau & Mazancourt, 2008). High synchrony indicates lower response diversity (Elmqvist et al., 2003; Mori et al., 2013) and is associated with a less resilient ecosystem (Loreau, 2001; Reich et al., 2012). Low synchrony indicates higher response diversity and is associated with a more resilient ecosystem. The response diversity is indeed associated with the concept of the "insurance hypothesis" (Yachi & Loreau, 1999), which states that a rich community is less likely to lose its functions during environmental fluctuations (Mori et al., 2013). For instance, if environmental fluctuations impact negatively most (or all) species inside a same functional group, it is likely that this function will be at risk (Elmqvist et al., 2003; Duffy, Richardson, & France, 2005). The loss of ecosystem functions can then affect the whole ecosystem through feedback loops such as bottom-up and top-down effects or trophic cascades (Eklof & Ebenman, 2006). Thus, response diversity is a key indicator of community stability for conservation studies.

Coral reefs are among the most productive and biologically diverse ecosystems on Earth (Moberg & Folke, 1999). The tremendous diversity of fish species they harbour makes coral reef ecosystems ideal models to test whether resilience is a function of species functional redundancy or response diversity. Increasing chronic anthropogenic pressures (Bennett et al., 2016; Hughes et al., 2017) such as overfishing (MacNeil et al., 2015), pollution (Szmant, 2002) or ocean acidification (Hoegh-Guldberg et al., 2007) are presently threatening coral reefs that are already exposed to acute natural and climatic disturbances exacerbated by anthropogenic activities such as cyclones (Bythell, Hillis-Starr, & Rogers, 2000), coral bleaching (Hoegh-Guldberg, 1999) and crown-of-thorns starfish (*Acanthaster planci*, Linnaeus 1758) outbreaks (Birkeland & Lucas, 1990). The responses of coral reefs to these disturbances are strongly dependent on the type and intensity of the disturbance as well as on the geographical location

(Graham, Cinner, Norström, & Nyström, 2014), as chronic anthropogenic stress compromises the capacity for resilience to acute environmental disturbances (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Graham, Nash, & Kool, 2011). Some fish species insure functions that are crucial for the capacity of resilience of coral reefs (Adam et al., 2011; Hughes et al., 2007) such as herbivory (Thibaut, Connolly, & Sweatman, 2012), recycling of nutrients or regulation of food web dynamics (Holmlund & Hammer, 1999). As these functions could be compromised by drastic changes in the composition of fish communities, more investigations are needed on how fish communities respond to acute disturbances.

Over the years following an acute disturbance, the fish community can either regain similar functioning, with or without regaining taxonomic composition, or fail in regaining both composition and functioning (Bellwood et al., 2012). Many studies have tackled the response of fish communities to environmental disturbances by focusing on abundance or biomass variations (McClanahan & Graham, 2015) coupled with analyses of global community composition (Adam et al., 2014; Boaden & Kingsford, 2015; Williamson, Ceccarelli, Evans, Jones, & Russ, 2014). These studies identified many relevant factors for the resilience of fish communities including coral reef rugosity (Emslie, Cheal, Sweatman, & Delean, 2008) or marine area protection level (Mellin, MacNeil, Cheal, Emslie, & Caley, 2016). The response diversity within functional groups has been increasingly studied in coral reef fish communities using spatial turnover (Lamy, Legendre, Chancerelle, Siu, & Claudet, 2015; Mellin, Bradshaw, Fordham, & Caley, 2014), cross-scale redundancy (Nash, Graham, Jennings, Wilson, & Bellwood, 2016) or proportional changes in species abundances with coral cover (Pratchett, Hoey, Wilson, Messmer, & Graham, 2011) as indicators. Some of these studies showed high response diversity following acute disturbances (Pratchett et al., 2011; Wilson et al., 2008). A decrease in temporal synchrony may be expected after acute disturbances because of the relationships between low temporal synchrony and high response diversity. However, a study carried out in a North Atlantic fish community (Pedersen et al., 2017) showed that the collapse of the fish community induced by both chronic anthropogenic stressors (overfishing) and physical perturbations (temperature) was associated with synchronous fluctuations of species biomass. Only few studies have investigated species spatial or temporal synchrony in coral reefs (Cheal, Delean, Sweatman, & Thompson, 2007; Thibaut et al., 2012) and never on a whole community and its trophic guilds in the context of acute disturbances over a long time-scale.

Here, we analysed the changes in the coral reef fish community of Moorea (French Polynesia) for a period of *circa* 35 years. Moorea's coral reefs historically exhibited high recovery of coral cover and fish abundance when exposed to various environmental disturbances (Galzin et al., 2016; Lamy, Galzin, Kulbicki, Lison de Loma, & Claudet, 2016; Martin, Moritz, Siu, & Galzin, 2016). Although the coral community has partially returned to its pre-disturbance composition (Adjeroud et al., 2018), disturbances induced long-term composition changes in the fish community (Berumen & Pratchett, 2006; Lamy et al., 2016). Such changes first indicate that fish species respond

differently to disturbances but also that the alteration of the fish community persists for at least a few years after coral cover recovery. As coral and fish communities are interdependent (McCook, Jompa, & Diaz-Pulido, 2001), the contrasts between the coral recovery and the changes in the fish community composition could be explained by a possible return to a pre-disturbance functioning of the fish community without a regain of taxonomic composition. Here, we investigated the functional resilience of the fish community by studying how disturbances affect the whole fish community and its major trophic guilds. After describing the changes in the fish community composition, we studied the variations of abundance and species synchrony for the whole community and its different trophic guilds. As investigating temporal synchrony requires long-term data, our 35-year-long dataset is not only adapted for such analyses but also rare among coral reef monitoring programs (Moritz et al., 2018; Wilkinson, Nowak, Miller, & Baker, 2013). As coral reef fish species are highly dependent on benthic composition, we hypothesized that the various trophic guilds were differently affected by varying substrate compositions (i.e., hard coral and other important benthic components). We also expected that species had different responses to varying substrate compositions due to their specific feeding or homing behaviours. Thus, we expected to find low values of the synchrony indicator for the whole fish community. We hypothesized that synchrony within trophic guilds would be higher, in particular in guilds that contain species with similar habitat requirements or that are strongly dependent on coral such as corallivores.

2 | METHODS

2.1 | Study system

Moorea Island is located in the Society Archipelago (French Polynesia), and its reefs have been intensively studied over the past decades (Adam et al., 2014; Adjeroud, 1997; Bertucci, Parmentier, Lecellier, Hawkins, & Lecchini, 2016; Gattuso, Pichon, Delesalle, & Frankignoulle, 1993; Han, Adam, Schmitt, Brooks, & Holbrook, 2016; Salvat et al., 1972). Tiahura lagoon and fore reef located on the north-west shelf of Moorea have been monitored for 35 years (Adjeroud, 1997; Galzin, 1987; Galzin et al., 2016), which is an exceptionally long time period for coral reef monitoring data globally (Moritz et al., 2018; Wilkinson et al., 2013). As we aimed at analysing the effect of acute disturbances on the fish community, we focused our analysis on the fore reef that has been strongly impacted during the last decades by acute environmental disturbances, especially cyclones and crown-of-thorns starfish (COTS) outbreaks (Adjeroud, 1997; Lamy et al., 2015, 2016). In contrast, the lagoon, protected by the barrier reef, showed less marked variations and was therefore not considered in the analysis.

2.2 | Data collection

The benthic composition and the fish community of Tiahura fore reef were monitored each year since 1987 (Galzin et al., 2016).

The benthic composition was monitored using four fixed 50-metre transects parallel to the barrier reef located at 6, 12, 20 and 25 m depth every year. Substrate per cent cover for eight categories (coral, macroalgae, pavement, crustose coralline algae, rubble, sand, turf and "others") was evaluated using the point intercept transect method by identifying substrate every metre along the transect (Hill & Wilkinson, 2004). We used the data of a previous study (Bouchon, 1985) to obtain the coral cover of Tiahura fore reef in 1983. The fish community was monitored by visual census using a 2 × 50 m benthic transect located at 12 m deep parallel to the barrier reef. One supplementary survey performed in 1983 (Bouchon, 1985) was included in our analysis. Fish were systematically counted and identified at the species level between September and November to avoid possible seasonal effects. We averaged fish abundance from the four temporal replicates sampled during the 2 days of counting.

2.3 | Statistical analyses

Several substrate components (turf, pavement, rubble and crustose coralline algae) were combined into a category called "cropped surface" because they represent the types of substrates used by grazing herbivores (Martin et al., 2016). Fish species were divided into six trophic guilds: herbivores, omnivores, mobile benthic invertebrate feeders (MBIF), sessile benthic invertebrate feeders (SBIF) that include corallivores and some rare sponge feeders, planktivores and piscivores (see Table S1). These trophic guilds were formed based on their general feeding preferences (Legendre, Galzin, & Harmelin-Vivien, 1997). To test if abundance and synchrony changes were related to feeding specializations, we performed analyses on the herbivore community both in its entirety and on its different subfunctions, that is, scrapers/excavators, grazers, browsers and detritivores. These subgroups indeed have different feeding preferences such as macroalgae for browsers or the epilithic algal matrix for the others (Green & Bellwood, 2009). These latter also select different compounds of the epilithic algal matrix (e.g., mainly algae for grazers, detritus for detritivores and microorganisms for scrapers and excavators). The differences in herbivore feeding behaviours are reflected by differences in their ecological functions (Green & Bellwood, 2009). Because large excavators, restricted to one species *Chlorurus microrhinos* (Bleeker, 1854), were very rare, we decided to investigate scrapers and excavators as a single subfunctional group. Some small unidentified juveniles (3 "species" among 210 species) were not included in the analysis.

The temporal variation in fish community composition was visualized using a non-metric multidimensional scaling (NMDS; McCune, Grace, & Urban, 2002) based on the Bray–Curtis dissimilarity index calculated on the log-transformed yearly abundance of all fish species.

The whole community synchrony as well as the synchrony of species within each trophic guilds (and herbivore subgroups) were calculated using the community synchrony index from Loreau and de Mazancourt (2008). This index is defined by the following equation:

$$\varphi = \frac{\sigma_{x_T}^2}{(\sum \sigma_{x_i})^2} \quad (1)$$

where $\sigma_{x_T}^2$ represents the temporal variance of the community times series and $(\sum \sigma_{x_i})^2$ represents the sum of the temporal standard deviation of the time series across all species. Total mean synchrony estimates were calculated between 1987 and 2016, and the evolution of synchrony was calculated using a running 5-year window ending in the year of interest as in Pedersen et al. (2017). An index of 0 reflects perfect asynchrony, while perfectly synchronous fluctuations of fish species abundance are represented by an index of 1. Statistical significance was determined with 1,000 replicates of Monte Carlo randomizations of each column of the data matrix (default parameter). Significant values ($\alpha = 0.05$) indicate synchronous fluctuations, while insignificant values indicate a lack of synchrony.

The relationships between fish community parameters (total abundance, total synchrony, abundance and synchrony of each trophic guild, abundance of some species) and the coral cover (and the cropped surface in some cases) were calculated using linear models. We applied a log-transformation to our abundance and substrate cover data when they were not normally distributed. We found rare temporal autocorrelations when applying the function “acf” (“stats”

version 3.4.1 package) for abundance. However, we found autocorrelations in most cases for synchrony. In these cases, we added time as a factor to the linear regression models ($Y \sim X + \text{year}$), which eliminated the temporal autocorrelations in some relationships. We did not include linear models for the remaining relationships: MBIF synchrony, browser synchrony, detritivore synchrony, omnivore synchrony, SBIF synchrony, scraper/excavator synchrony and MBIF abundance. The “acf” temporal correlation plots are available in Appendix S1.

All analyses were performed using R software version 3.4.1 (2017), and the “synchrony” version 0.2.3 (Gouhier & Guichard, 2014) and “vegan” version 2.4.3 (Oksanen et al., 2016) packages.

3 | RESULTS

The variations of coral cover of Tiahura fore reef (Figure 1) are characterized by periods of decline after disturbances followed by regain phases. Coral cover dropped to a minimum of 15.2% ($SE \pm 6.2$) after the 1991 cyclone and 10.4% ($SE \pm 5.7$) after the 2006 crown-of-thorns starfish (COTS) outbreak, and below 5% after the 2010 cyclone. Coral cover respectively took 4 and 10 years to recover

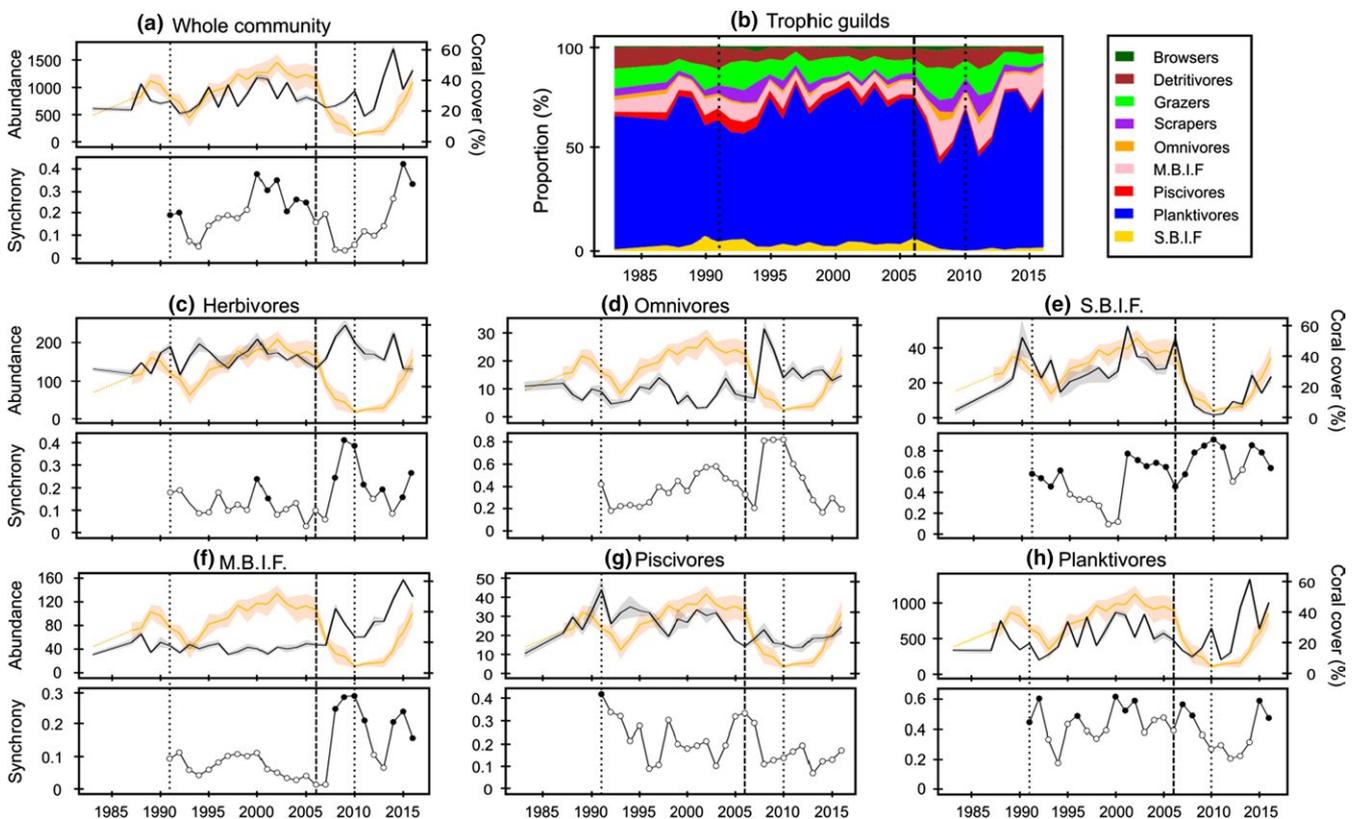


FIGURE 1 Temporal dynamics of the properties of the fish community (black lines) and coral cover (orange lines, $N = 124$; 31 years \times 4 transects). Variation in abundance ($N = 124$; 31 years \times 4 temporal replicates) and 5-year synchrony ($N = 26$ years) of (a) the whole fish community, (c) herbivores, (d) omnivores, (e) sessile benthic invertebrate feeders (S.B.I.F.), (f) mobile benthic invertebrate feeders (MBIF), (g) piscivores and (h) planktivores. The temporal variations in the proportions of trophic guilds are displayed in (b). Standard errors are displayed in shaded colours (when available) around the lines representing the mean values. Vertical dotted lines represent the 1991 and 2010 cyclones. The vertical dashed line indicates the start of the 2006 crown-of-thorns starfish outbreak. White circles indicate statistically non-significant synchrony, while black circles point out significant synchrony. All y-axes are not equivalent

TABLE 1 Linear models used in the study

| Model | Summary | | | | | Coefficients | | | |
|--------------------------------------|---------|-------|-------|------|-------------------|--------------|-------------------|-------|-------------------|
| | | | | | | Substrate | | Year | |
| | R^2 | $df1$ | $df2$ | F | p | T | p | T | p |
| log(cropped) ~ coral + year | 0.84 | 2 | 27 | 67.5 | <0.001*** | -8.47 | <0.001*** | 4.81 | <0.001*** |
| All ~ coral | 0.02 | 1 | 27 | 0.59 | 0.45 | | | | |
| Herbivores ~ coral | 0.12 | 1 | 27 | 3.79 | 0.06 | | | | |
| Omnivores ~ coral | 0.32 | 1 | 27 | 12.5 | 0.001*** | -3.54 | 0.001*** | | |
| SBIF ~ coral | 0.54 | 1 | 27 | 31.7 | <0.001*** | 5.63 | <0.001*** | | |
| Piscivores ~ coral | 0.14 | 1 | 27 | 4.3 | 0.05 [†] | 2.07 | 0.05 [†] | | |
| Planktivores ~ coral | 0.08 | 1 | 27 | 2.2 | 0.15 | | | | |
| log(scrapers) ~ coral | 0.64 | 1 | 27 | 48.6 | <0.001*** | -6.97 | <0.001*** | | |
| Grazer ~ coral | 0.04 | 1 | 27 | 1.2 | 0.27 | | | | |
| Browser ~ coral | 0.00 | 1 | 27 | 0.0 | 0.85 | | | | |
| Detritivore ~ coral | 0.00 | 1 | 27 | 0.1 | 0.74 | | | | |
| Herbivores ~ log(cropped) | 0.14 | 1 | 27 | 4.57 | 0.04 [†] | 2.14 | 0.04 [†] | | |
| Omnivores ~ log(cropped) | 0.41 | 1 | 27 | 18.8 | <0.001*** | 4.34 | <0.001*** | | |
| log(scrapers) ~ log(cropped) | 0.54 | 1 | 27 | 31.9 | <0.001*** | 5.64 | <0.001*** | | |
| Grazer ~ log(cropped) | 0.05 | 1 | 27 | 1.5 | 0.23 | | | | |
| Detritivore ~ cropped | 0.00 | 1 | 27 | 0.0 | 0.86 | | | | |
| Sync(all) ~ coral + year | 0.52 | 2 | 22 | 14.2 | <0.001*** | 5.16 | <0.001*** | 2.98 | 0.006** |
| log(sync(herbivores)) ~ coral + year | 0.19 | 2 | 22 | 2.7 | 0.09 | | | | |
| log(sync(piscivores)) ~ coral + year | 0.26 | 2 | 22 | 4.0 | 0.03 [†] | 0.80 | 0.43 | -2.27 | 0.03 [†] |
| Sync(planktivores) ~ coral + year | 0.25 | 2 | 22 | 3.7 | 0.04 [†] | 2.66 | 0.01 [†] | 0.46 | 0.65 |
| Sync(grazers) ~ coral + year | 0.49 | 2 | 22 | 10.4 | <0.001*** | -0.102 | 0.92 | 4.27 | <0.001*** |

Note. "Sync" indicates synchrony data, while unspecified parameters refer to abundances or substrate covers. "Substrate" coefficient refers to coral cover ("coral") or the cropped surface ("cropped") depending on the considered model. "All": whole fish community, log: log-transformation, SBIF: sessile benthic invertebrate feeders.

pre-disturbance levels after the 1991 cyclone and the 2006–2010 disturbances. The cropped surface increased with decreases in coral cover (Table 1, see Appendix S2).

The total fish abundance varied from 479 fish/100 m² in 2011 to 1707 fish/100 m² in 2014 (Figure 1a). No significant relationship was found between total fish abundance and coral cover (Table 1). The mean synchrony of the fish community was low indicating no significant synchronous fluctuations of species abundances when considering the whole investigated period (sync = 0.10, $p = 0.60$). However, the profile of community synchrony followed the variations in coral cover (Figure 1a, Table 1, Appendix S2). Years with high coral cover were associated with significant synchronous abundance fluctuations while the first 7–9 years after the 1991 cyclone and the 2006 COTS outbreak were associated with more heterogeneous fluctuations. Community composition varied greatly during and after the 2006 COTS outbreak (Figure 2). Changes in community composition were small and mostly occurred along axis 2 of the NMDS until 2006, while stronger variations were found later along axis 1 of the NMDS after 2006.

Changes in community composition first resulted from fluctuations in the proportions of the trophic guilds, which showed strong variations over time (Figure 1b). The fish community was dominated in terms of abundance by planktivores (41.9%–79.2% of all fish), and no other trophic guilds exceeded 20% of the total fish abundance. The variations in proportions are explained by different patterns among trophic guilds. The abundance of sessile benthic invertebrate feeders (SBIF), dominated by corallivorous butterflyfishes, closely followed the variations of live coral cover (Figure 1e, Table 1, Appendix S3a). On the contrary, the guilds that feed on the cropped surface (e.g., herbivores, omnivores and mobile benthic invertebrate feeders [MBIF]) increased after the 2006 COTS outbreak (Figure 1cdf). The abundances of omnivores (herbivores) were positively (weakly) related to the cropped surface (Table 1, Appendix S3bd). Herbivores and omnivores declined after the 2010 cyclone to their pre-2006 levels contrary to MBIF. Piscivores and planktivores were less impacted by coral cover fluctuations (Figure 1gh, Table 1) despite a significant relationship between piscivore abundance and coral cover (Table 1, Appendix S3e).

Synchrony patterns were heterogeneous across trophic guilds. SBIF presented homogeneous abundance fluctuations with a high mean synchrony over the sampled period ($\text{sync} = 0.54$, $p < 0.001$) despite a drop in the synchrony index between 1995 and 2000. Herbivores, omnivores and MBIF presented a lower mean synchrony (herbivores: $\text{sync} = 0.10$, $p = 0.01$; omnivores: $\text{sync} = 0.36$, $p = 0.36$; MBIF: $\text{sync} = 0.17$, $p = 0.05$) indicating more heterogeneous abundance fluctuations within these guilds. These three trophic guilds presented more homogeneous abundance fluctuations (peak of synchrony) after the 2006 COTS outbreak but synchrony quickly decreased after the 2010 cyclone. The mean synchrony values of piscivores ($\text{sync} = 0.20$, $p = 0.09$) and planktivores ($\text{sync} = 0.17$,

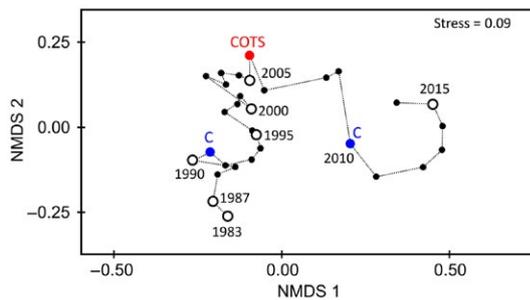


FIGURE 2 Temporal dynamics of the long-term trajectory of the total fish community resulting from a two-dimensional representation of the non-metric multidimensional scaling (NMDS) analysis ($N = 31$ years). “COTS” and the red circle represent the start of the 2006 crown-of-thorns starfish outbreak; “C” and the blue circles indicate the occurrence of the 2010 cyclone. White circles give information about the chronology by showing the start of the analysis and years ending by zero or five (except for 2010 due to cyclone)

$p = 0.69$) were also low. Piscivore synchrony significantly decreased with time (Table 1, Appendix S2) while planktivore synchrony significantly increased with coral cover (Table 1, Appendix S2).

The subdivision of herbivores also showed different responses to disturbances between but also within subgroups. Whereas the abundances of scraping/excavating species, grazers and detritivores increased after the 2006 COTS outbreak (Figure 3bcd), only the abundance of scraping/excavating species was positively and negatively related with the cropped surface and coral cover, respectively (Table 1, Appendix S4b). Browser abundance highly varied (Figure 3a) but was not related to coral cover (Table 1). The abundance fluctuations of most herbivore subgroups lacked synchrony over the studied period (grazers: $\text{sync} = 0.18$, $p = 0.04$; browsers: $\text{sync} = 0.77$, $p = 0.49$; detritivores: $\text{sync} = 0.27$, $p = 0.98$). However, scrapers/excavators showed significantly synchronous fluctuations ($\text{sync} = 0.28$, $p = 0.009$). The synchrony indexes of herbivore subfunctions varied over time but presented different patterns. Scrapper/excavator synchrony was high between 1991 and 1997 (Figure 3d). Their synchrony increased slightly after the 2006 COTS outbreak and declined after the 2010 cyclone. Grazer synchrony significantly increased with time (Table 1, Figure 3c, Appendix S2). Browser synchrony presented small variations over time. Detritivores displayed highly heterogeneous abundance fluctuations between 2000 and 2008.

The lack of synchrony in most herbivore subgroups is explained by differences in the abundance variations of their constituting species. In scraping/excavating species, *Chlorurus spilurus* (Valenciennes, 1840) and *Scarus psittacus* (Forsskål, 1775), which were responsible for most of the variation in abundance (see Appendix S4c), presented a strong and a weak negative relationships with coral cover (Figure 4ab), respectively. Grazers abundance showed widely varying relationships

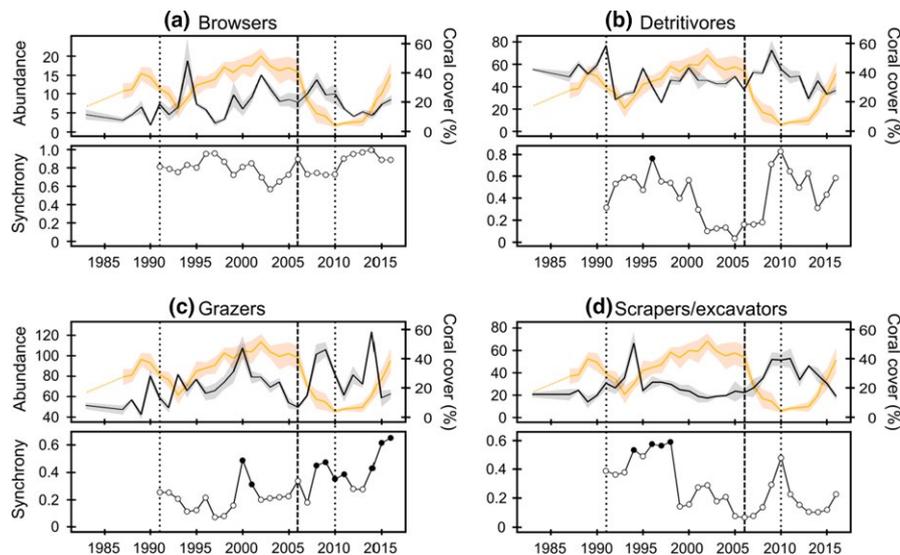


FIGURE 3 Temporal dynamics of herbivore subgroups (black lines): temporal variations of abundance ($N = 124$; 31 years \times 4 temporal replicates) and synchrony ($N = 26$ years) of (a) browsers, (b) detritivores, (c) grazers and (d) scrapers/excavators. The variations in coral cover are displayed in orange ($N = 124$; 31 years \times 4 transects). Standard errors are displayed in shaded colours (when available) around the lines representing the mean values. Vertical dotted lines represent the 1991 and 2010 cyclones. The vertical dashed line indicates the start of the 2006 crown-of-thorns starfish outbreak. White circles indicate statistically non-significant synchrony, while black circles point out significant synchrony

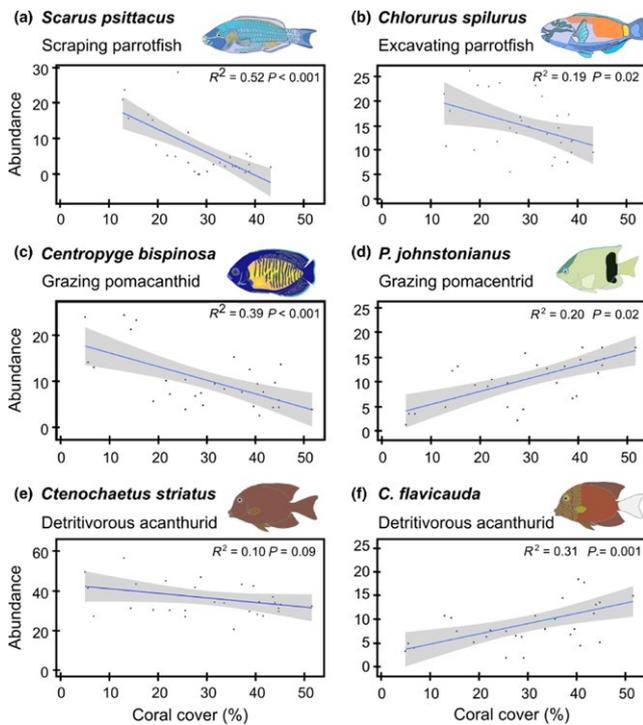


FIGURE 4 Relationships between the abundance of different herbivorous species and coral cover ($N = 31$ years). Linear regression models (blue lines) are represented with 95% confidence intervals (shaded grey). *P. johnstonianus* and *C. flavicauda* refer, respectively, to *Plectroglyphidodon johnstonianus* and *Ctenochaetus flavicauda*

with coral cover notably with negative and positive relationships for *Centropyge bispinosa* (Günther, 1860) and *Plectroglyphidodon johnstonianus*, respectively (Figure 4cd). Other grazers such as *Zebbrasoma scopas* (Cuvier, 1829) were positively impacted by the 2006 COTS outbreak but negatively by the 2010 cyclone (See Appendix S5). In detritivores, the two main species, *Ctenochaetus flavicauda* and *C. striatus*, had a weak positive relationship and an insignificant relationship with coral cover, respectively (Figure 4ef).

4 | DISCUSSION

The resilience of coral reefs depends on many factors such as coral community composition (Johns, Osborne, & Logan, 2014; Wilson et al., 2012), feedbacks between fish and benthic communities (McCook et al., 2001) or the functions fulfilled by the fish community (Graham et al., 2015). Moorea's coral reefs have been considered resilient (Adjeroud et al., 2009; Martin et al., 2016) due to the quick recovery of coral cover after recurrent disturbances. However, other studies have concluded that Moorea's reefs are not resilient due to the changes in the composition of fish communities (Berumen & Pratchett, 2006). Here, we also found a strong shift in the fish community composition after the 2006 COTS outbreak and the 2010 cyclone similarly to the study by Lamy et al. (2016) and showed that these taxonomic changes are maintained

during the subsequent recovery phase. Therefore, even if coral communities have partially returned to pre-disturbance composition (Adjeroud et al., 2018), there is no recovery of the taxonomical composition of the fish community. The contrasting results between coral and fish communities could be interpreted as lags in the fish community response to changes in the coral community (Graham et al., 2007). Moorea's fish community may need more time not only to respond to a decrease in coral cover, but also to fully recover in the years following a disturbance (Lamy et al., 2016). However, changes in taxonomical composition are not necessarily synonym of loss of functions (Bellwood et al., 2012) and the fish community of Tiahura could be functionally resilient (e.g., conservation of its ecological functions).

The stability of fish abundance despite strong coral cover fluctuations may be explained by compensatory dynamics. The absence of a positive relationship between total fish abundance and coral cover contradicts other studies in other parts of the world (Komyakova, Munday, & Jones, 2013), but agrees with studies previously carried out in Moorea (Holbrook, Schmitt, & Brooks, 2008; Lamy et al., 2016; see also Beldade, Mills, Claudet, & Côté, 2015). In Holbrook et al.'s study (2008), the fish community was mainly unaffected by changes in coral cover until the change reached a critical threshold (coral cover: 5%). Variations of fish community synchrony followed coral cover fluctuations. The abundance fluctuations of fish species within the fish community were first synchronous but disturbances induced a decrease in synchrony indicating a stronger response diversity after disturbances, as previously shown (Wilson et al., 2008). This increase in response diversity confirms that coral loss has variable effects on fish species (Bell & Galzin, 1984; Booth & Beretta, 2002; Lamy et al., 2015). Compensatory dynamics between fish species, highlighted by the loss of synchrony, may have contributed to the stability of total fish abundance because the decline of some species can be compensated by an increase of others (Gonzalez & Loreau, 2009). A previous study in a freshwater zooplankton community showed that compensatory dynamics differed among trophic guilds and could even lead to the extinction of the less heterogeneous guilds (Fischer, Frost, & Ives, 2001). Thus, the stability of the total fish abundance may hide a loss (or an alteration) of particular trophic guilds and is therefore not sufficient to conclude if the fish community is functionally resilient.

Trophic guilds presented various levels of vulnerability to disturbances (Figure 5). The routine approach to compare coral cover and fish abundance relationships (Adam et al., 2014; Friedlander & Parrish, 1998) notably showed positive relationships between SBIF abundance and coral cover or between herbivore abundance and cropped surface. These differences were attributed to high dependence on live coral (Irons, 1989) or their affinity for the cropped surface (Martin et al., 2016), respectively. SBIF are thus vulnerable to coral decrease. The investigation of synchrony by trophic guilds provides complementary information to the studies based on abundance patterns. The highly synchronous abundance fluctuations of SBIF were associated with reduced response diversity, while other guilds such as herbivores and planktivores presented higher response diversity (Pratchett et al., 2011; Thibaut et al., 2012; Wilson

et al., 2008). Therefore, SBIF are theoretically more vulnerable, while the communities of herbivores and planktivores are more stable due to high species turnover. An example of species turnover is the decrease of coral-associated damselfishes (Gajdzik, Parmentier, Sturaro, & Frédérich, 2016) after disturbances while other planktivores were less affected. However, some herbivore subgroups may be more vulnerable than others. The strong variations of abundance and high synchrony index of browsers may suggest greater vulnerability but may be explained by the reduced number of species in this subgroup. The increasing synchrony over the years associated with strong population fluctuations could also suggest increasing

vulnerability of grazers. However, the overall synchrony of scrapers and excavators can be explained by their common tendency to increase after each disturbance. Thus, scrapers and excavators appear less vulnerable. We acknowledge that trophic guilds containing many species will certainly have more different life-history traits than guilds containing fewer species when considering other traits than trophic preferences and that these differences may explain a part of the variation in response diversity.

Our study showed that compensatory dynamics, represented by the decrease in species synchrony, procured stability not only to total fish abundance but also to most of its trophic functions after the loss

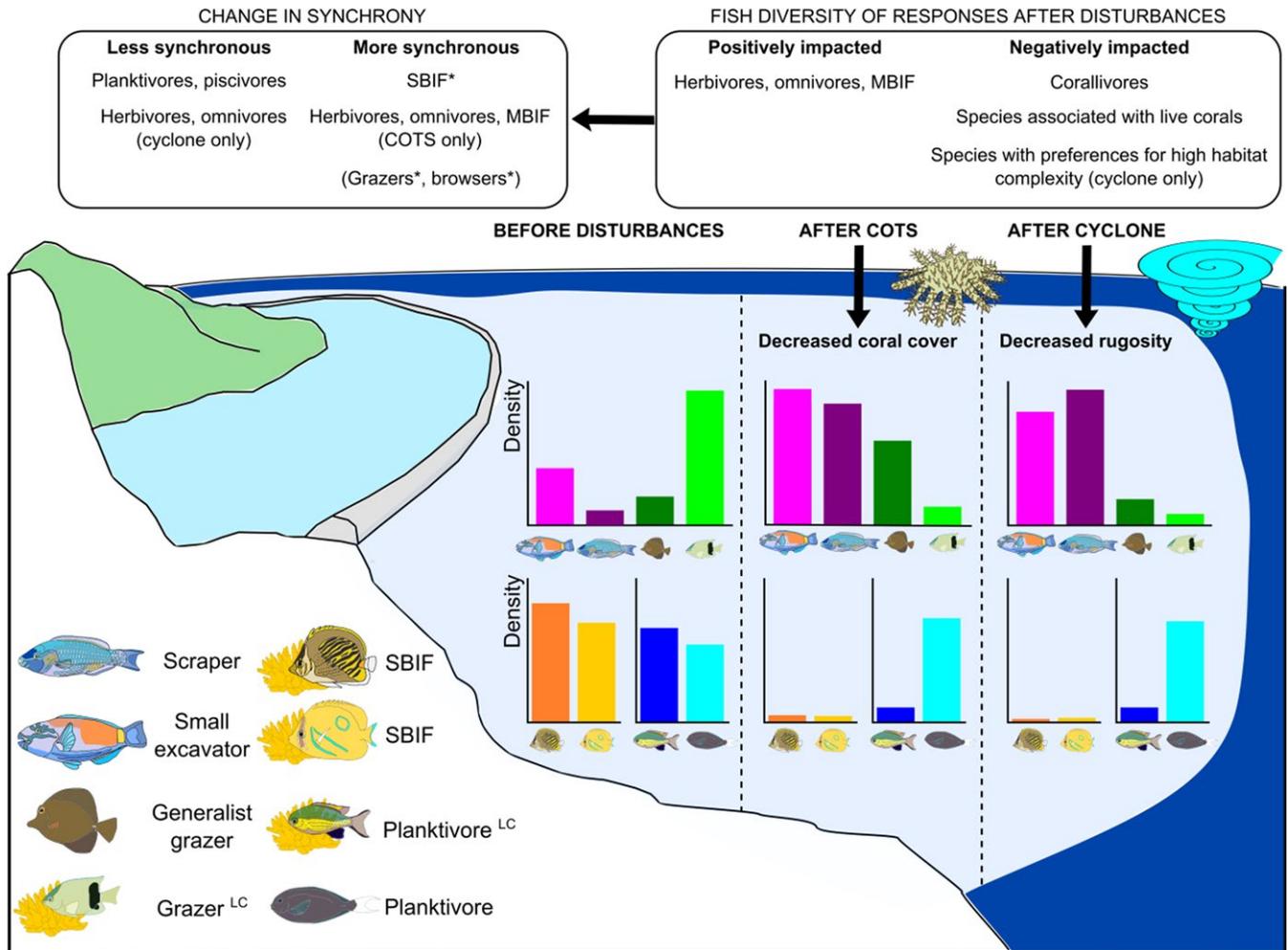


FIGURE 5 Schematic representation of some effects of crown-of-thorns starfish outbreaks and cyclones on fish communities. Before disturbances, total synchrony was high at the whole community level suggesting homogeneous abundance fluctuations of the different species. The succession of the 2006 crown-of-thorns starfish outbreak and the 2010 cyclone decreased the synchrony of the whole community through different effects on the species. For example, after the crown-of-thorns starfish outbreak, coral cover decreased, leading to a decrease in corallivore abundance and an increase in the abundances of herbivores, omnivores and mobile benthic invertebrate feeders. The increase in synchrony showed that these changes of abundance were shared by most species within these groups. In planktivores and piscivores, response diversity increased associated with a decrease in synchrony. Species associated with live coral decreased, while other species increased or remained stable. After the 2010 cyclone, rugosity decreased. Response diversity increased associated with a decrease in synchrony for herbivores and omnivores. Species with preferences for high structural complexity (homing or feeding behaviour) were more negatively impacted than others. The species shown on the figure were chosen for their importance for coral reef functioning or for being representative of a more general phenomenon. The barplots represent for each species its density in arbitrary units. Species are grouped in trophic guilds, for example, herbivores (which include browsers, grazers and scrapers/excavators), corallivores and planktivores. “COTS” indicates crown-of-thorns starfish outbreak. Asterisks indicate potentially more vulnerable guilds. MBIF: mobile benthic invertebrate feeders, SBIF: sessile benthic invertebrate feeders

of structural organisms. If the fish community does not regain its taxonomical composition, the stability of most of its functions suggests a functional resilience of the fish community. It is the first time that such results are highlighted in a whole coral reef fish community using synchrony. An equivalent example from a different ecosystem is the removal of the canopy-forming algae in a temperate rocky-shore environment, which decreased synchrony in an intertidal hard-bottom community, leading to a relative stability of the community properties and functions despite changes in its taxonomic composition (Valdivia, Golléty, Migné, Davoult, & Molis, 2012). On the contrary, another study showed that overfishing is associated with synchronous and drastic loss of fish abundance (Pedersen et al., 2017). The relative stability of total fish abundance and trophic functions such as herbivory may be one of the factors that favour the resilience of Moorea's reefs. The diversity of responses within herbivores is indeed fundamental for coral reefs because species turnover will insure the persistence of grazing pressure (Thibaut et al., 2012) and thus prevents the reefs from shifting towards a non-reversible macroalgae-dominant state. Among other herbivores, parrotfishes appeared as the most contributing fishes to grazing pressure after disturbances. The two most common species, *Chlorurus spilurus* and *Scarus psittacus*, strongly increased in abundance after disturbances and appeared essential for the resilience of Tiahura fore reef. Our study therefore confirms the results of the study conducted in Moorea by Adam et al. (2011), yet over an extended period, which included the 1991 hurricane. The highly antagonist relationship between *S. psittacus* abundance and coral cover may suggest a potential greater impact of this species on the resilience of Moorea's coral reefs.

Disturbance type induced different effect on species response diversity. The synchrony index of guilds associated with the cropped surface (herbivores, omnivores, MBIF) increased after the 2006 COTS outbreak in parallel with abundance increase. For herbivores, these more homogeneous responses contradicts Wilson et al.'s study (2008) that showed heterogeneity of responses in this community after coral loss. These opposite results may, however, be explained by the tridimensional structure of the reef, which varied in the two studies. The extreme loss of *Acropora* strongly reduced structural complexity in the case of Wilson et al. (2008). On the contrary, in Moorea, such branching corals were not dominant before the 2006 COTS outbreak (Lamy et al., 2016). The greater algal availability during the 2006 COTS outbreak may have contributed to an overall stimulation of herbivore, omnivore and MBIF population growths (Pratchett et al., 2011) and caused more synchronous abundance fluctuations in herbivores, omnivores and MBIF. The common tendency for grazers, detritivores and scraping/excavating species to increase in abundance after the 2006 COTS outbreak contributed to the increase in herbivore synchrony. Interestingly, we found a similar result as Wilson et al. (2008) after the cyclone of 2010 for herbivores (including in subgroups associated with the cropped surface), and also for MBIF and omnivores, for which the increase in response diversity after this disturbance could be linked with a decrease in reef rugosity. Cyclones decrease the structural complexity of coral reefs (Harmelin-Vivien, 1994) and have different effects on the fish

community than COTS outbreaks (Adam et al., 2014; Lamy et al., 2015; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Cyclones mostly impact species that depend on hard substrates or that feed on complex structures (Harmelin-Vivien, 1994). The response diversity after the 2010 cyclone may be explained by the presence of herbivores associated with high rugosity such as *Plectroglyphidodon* species (Gajdzik et al., 2016) or differences in the capacity of using different microhabitats for feeding (Brandl, Robbins, & Bellwood, 2015). Some grazers such as *Zebrasoma scopas* are indeed more adapted to feed in coral reefs with high structural complexity (Brandl et al., 2015; Robertson, Polunin, & Leighton, 1979).

The division of the fish community using feeding behaviours (or other traits) explains a part of species response diversity because the reliance of species on coral primarily depends on their feeding or homing behaviours (Jones, McCormick, Srinivasan, & Eagle, 2004). However, the synchrony index showed different patterns of response diversity among the different groups even when they were more finely divided (e.g., scrapers/excavators). Response diversity can depend on a complex combination of life-history traits or interspecific interactions (Ushio et al., 2018). If synchrony studies cannot uncover the factors themselves, they can still distinguish the combined effects of these factors on the fish community. The advantage of synchrony analysis is to estimate response diversity independently from coral cover contrary to other approaches (Pratchett et al., 2011). This allows assessing the levels of response diversity before and after disturbances and according to the type of disturbance.

We acknowledge that our study is based on correlation and cannot provide a definitive conclusion about the role of synchrony in coral reef resilience. However, synchrony analyses could be implemented in diverse monitoring programs to assess the stability of key functional groups to environmental fluctuations. Such studies only require repetitive estimations of fish specific abundances, which are commonly performed in most monitoring programs. Here, we showed a relative stability of most trophic guilds, which could promote reef resilience. We advocate that the potential vulnerability of some groups could compromise the potential of recovery of this reef in the future. We showed that COTS outbreaks and cyclones had different effects on species synchrony in some groups, due to their different impacts on coral cover and habitat rugosity. However, the COTS outbreak and cyclone impacted Moorea consecutively over a short period between 2006 and 2010. Thus, their impacts on the fish community are combined and must be interpreted with care. Further analyses are needed to disentangle the respective effects of these two disturbances on fish community synchrony and also compare with disturbances that occurred in other locations. We therefore advocate combining synchrony measures with disturbance history to grasp the complexity of ecosystem resilience processes.

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DATA ACCESSIBILITY

Data are available on the website SO CORAIL (<http://observatoire.criobe.pf/CRIOB/EData/displayLontermTiahuraFish.jsp>) and upon request to Serge Planes (serge.planes@criobe.pf).

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BIOSKETCH

This study was born from an extensive fieldwork aimed at investigating the diversity of parrotfish trophic affinities by focusing on their dentition, behavior and diet, which is the doctoral issue of J.V. The present collaborative work between the team "Evolution of vertebrate dentition" at the Institute of Functional Genomics of Lyon and the Center for Insular Researches and Observatory for the Environment of Moorea led to this more integrative study, which tackles the fields of coral reef ecology and conservation biology.

Author contributions: C.M. is a quantitative ecologist and ecological modeller interested in the spatio-temporal patterns of coral reef organisms. J.V., C.M., L.V., V.P., D.L. and R.G. designed the study. R.G. and G.S. collected the data. J.V. and C.M. conducted the analyses. J.V. and C.M. wrote the article. All authors contributed to manuscript editing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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