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A recovery debt revealed by an ecosystem network-based approach.

Recovery debts can be revealed and quantified by ecosystem network-based approaches

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Author's Contribution: MD and JC planned and designed the research. MD and DG built the models. MD and JC analysed the results. MD, DG, MC and JC wrote the paper.

HIGHLIGHTS:

- Ecosystem that appear resilient to a disturbance can hide recovery debts.
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- Ecosystem network indicators can be used to identify and quantify recovery debts.
- Impacts of disturbance and recovery debts can propagate through trophic interactions into ecosystems and habitat that are not directly exposed to a disturbance.

Abstract

Ecosystems are increasingly disturbed by natural disturbances and human stressors. Understanding how a disturbance can propagate through an entire ecosystem and how induced changes can last after apparent recovery is key to guide management and ecosystem restoration strategies. Monitoring programs and impact assessment studies rely mostly on indicators based only on species relative abundance and biomass, potentially misinforming management efforts. Impacts on ecosystem structure and functioning, and subsequent delivery of ecosystem services, are too often overlooked.. Here we use an ecosystem network approach to assess the recovery pathway and potential recovery debts of a coral reef ecosystem, following a pulse disturbance. We show that, while species abundance and biomass indicators recovered in a decade after the perturbation, the ecosystem as a whole presented a recovery debt. The ecosystem structure lost complexity (became "food chain like") and lost about 29% of its overall cycling efficiency and 9% of

its transfer efficiency. While the ecosystem trophic network in the fore reef may have maintained its general functioning, the ecosystem network in the lagoon, not directly exposed to the disturbance, presented a stronger recovery debt. Our results give new insights on how ecosystem network approaches can help identify ecosystem impacts and recovery pathways.

KEYWORDS

ecological disturbance, coral reef, network analysis, trophic modelling, Ecopath

1 Introduction

Despite conservation efforts, ecosystems are increasingly being degraded worldwide (Maxwell et al. 2016). Chronic human stressors play an important role in altering ecosystems (Vanbergen et al. 2013, Crowther et al. 2015, Halpern et al. 2015), but pulse natural disturbance events can also lead to deep changes in composition of biological communities (Dulvy et al. 2003, Scheffer et al. 2009). Such changes can affect ecosystem functioning, thus altering the delivery of ecosystem services (Worm et al. 2006, Balvanera et al. 2013). Managing for sustainability not only requires an understanding of how an impact may propagate through a whole ecosystem but also the identification of recovery pathways at the ecosystem level (Lotze et al. 2011).

Estimating the recovery time of a specific population or a whole ecosystem following a disturbance is not straightforward (Lotze et al. 2011). Recovery is considered as "a return to the initial state" of a specific response variable (Lotze et al. 2011). It can be measured through changes in species abundance (Alter et al. 2007) or cover (Osborne et al. 2017), spawning stock size (Hutchings and Reynolds 2004), demographic metrics (Gerber and Heppell 2004) or more recently changes in trophic structure (Hempson et al. 2018). However, time-lags might exist at ecosystem scale and populations do not necessarily respond in the same pace (Tilman et al. 1994, Dullinger et al. 2013). Time-delayed response of species to disturbance, also called the "extinction debts"(Tilman et al. 1994),

might seriously underestimate the impact of the disturbance at the whole ecosystem scale while a system might exhibit a "recovery debt" (Moreno-Mateos et al. 2017).

The recovery debt was recently conceptualized as the resulting deficit in biodiversity and ecosystem functions during the process of recovery (Moreno-Mateos et al. 2017). Even if signs of recovery exist in many impacted ecosystems (Jones and Schmitz 2009, Graham et al. 2015, Cole et al. 2014), ecosystems might not have fully recovered and will potentially not in the future (Moreno-Mateos et al. 2017, Jones et al. 2018). As humans rely on fully functioning ecosystem, recovery debt is expected to affect ecosystem services supply (Isbell et al. 2015) and be of pivotal importance for sustainability of the social-ecological systems(Lafuite et al. 2017).

Evaluation of changes in ecosystem structure and functioning following a disturbance can be achieved through the use of a diversity of quantitative ecosystem indicators (Heymans et al. 2014, Coll and Steenbeek 2017). Indicators derived from the Ecosystem Network Analysis (ENA) (Ulanowicz and Abarca-Arenas 1997), which use network theory information, have the advantage of quantifying direct and indirect interactions and identifying emergent food-web properties, without reducing the model to only few dominant processes (Fath et al. 2007, Kones et al. 2009). These indicators have been widely used to analysed food-web changes over time (e.g. Heymans et al. 2004; 2007, Tomczak et al. 2013) to compare ecosystems functioning (Heymans et al. 2014) or to test the sensitivity of candidate indicators to a given pressure (Bourdaud et al. 2016, Chaalali

et al. 2016). Due to the complexity to consider uncertainty in complex food web models, most of older analyses using food web models relied on single indicator values. However, to identify significant changes over time and improve interpretation of model, derived indices uncertainty should be accounted for in model parametrization (Fulton 2010, Guesnet et al. 2015, Corrales et al. 2017, Piroddi et al. 2017).

Coral reefs are a good case studies to trial ecosystem network approaches and candidate indicators aimed at identifying recovery pathways following disturbances. They are biologically and functionally rich ecosystems (Bellwood et al. 2003) that provide vital and valuable services to coastal communities such as coastal protection, food production and recreational activities contributing to social and cultural identity (Moberg and Folke 1999). Coral reefs are also among the most vulnerable ecosystems (Halpern et al. 2007, Holbrook et al. 2015). They evolve under several natural disturbance regimes, such as extreme climatic events, outbreak of corallivorous crown-of-thorns sea stars (COTS), or mass bleaching events (Ban et al. 2014, Hughes et al. 2017). In their evolutionary history, coral communities have demonstrated the capacity to recover from these cycles of disturbances (Jackson 1992, Gilmour et al. 2013, Lamy et al. 2016). Today, global change and increasing demography are rapidly altering the dynamics of these ecosystems (Bozec and Mumby 2015, Williams et al. 2015): Coral reefs are increasingly shifting from a coral-dominated, biologically diverse, productive, states to macroalgae-dominated, poorer, less productive states (Gardner et al. 2003, Bruno and Selig 2007, Ainsworth et al.

2015, Hughes et al. 2017). Seen as major threat, overfishing is one of the most studied stressor on coral reef ecosystem components (Arias-González et al. 2004, Weijerman et al. 2013, Graham et al. 2017). However less is known about how natural disturbance regimes affect exploited reef structure and functioning (Ainsworth et al. 2015, Hempson et al. 2017). Furthermore, most coral reef studies have only addressed changes of small subsets of ecosystem interactions (Mumby 2009, Adam et al. 2014, Pratchett et al. 2011), neglecting wider off-stage changes on ecosystem structuring and functioning and the potential recovery debt.

Here, we investigate how a pulse disturbance affecting coral communities can cascade through a whole coral reef ecosystem and assess ecosystem transformations along its recovery pathways. We use as case study, the coral reef ecosystem of Moorea Island (French Polynesia) that undergone a serious decline in coral cover and shift in fish species composition following a crown-of-thorns sea stars outbreak and a cyclone (Lamy et al. 2015; 2016) but that currently shows large signs of recovery. Based on time series, we developed three food-web models *before*, *during* and *after* the disturbance, respectively and assessed trajectories of ecosystem structure and functioning using ecosystem network indicators. The variability of those indicators was accounted for by incorporating uncertainty distributions of model parameters in 1000 simulations for each model.

2 Methods

2.1 Studied ecosystem and environmental disturbances

Moorea is a volcanic high island located in the central south Pacific, 20 km north-west of Tahiti. This island is enclosed by an offshore barrier reef, the fore reef, that defines a shallow lagoon. In the past several decades, the offshore coral communities were severely impacted by repeated disturbances, including cyclones, bleaching events and crown-of-thorns sea stars (COTS) outbreaks (Adjeroud et al. 2009, Lamy et al. 2016). Each event have resulted in a drastic decline of living coral cover, as well as a turnover in fish communities (Adam et al. 2011, Lamy et al. 2015). However, until now, Moorea's offshore reef has displayed a high recovery potential by returning to a coral dominated ecosystems within a decade (Adjeroud et al. 2009, Adam et al. 2011, Lamy et al. 2016).

Here, we focus on the last COTS outbreak (2007-2010) and cyclone (2010) that occurred in Moorea. Immediately after those disturbances, coral cover in the fore reef was close to 0% but recovered after to levels around 40% similar to those before the environmental disturbances within about a decade (Fig. 1). Filamentous turf algae cover was inversely related to coral cover, and herbivorous fishes (such as parrot-fishes) doubled in biomass after the disturbance, thus controlling macro-algae development on the fore reef.

Coral communities inside the lagoon were not directly affected by the cyclone or COTS outbreak, so limited changes in coral cover and fish communities were observed in the lagoon (Fig. 1). Unlike the fore reef, the lagoon is subjected to land-based and marine anthropogenic drivers. However, over the time period considered here, no clear interactions were identified between these pressures and the ecosystem state (Leenhardt et al. 2017).

2.2 Ecosystem model

Three food web models were developed to represent ecosystem states *before* (2006), *during* (2010) and *after* (2016) the environmental disturbance (COTS outbreak and cyclone), respectively. In order to properly assess changes in ecosystem structure and network functioning, models were built with the same structure and area modelled using the Ecopath with Ecosim (EwE) modelling approach (Christensen and Pauly 1992, Christensen et al. 2005). Ecopath with Ecosim are powerful frameworks to capture complex ecological processes like those encountered in coral reefs. The Ecopath module of EwE enables to develop a static representation of the food-web in a given ecosystem for a specific period of time. The three Moorea Ecopath models developed in this study were structured using forty-six functional groups (Table. 1). Since the Ecopath model, the static module of the EwE approach, does not explicitly include any spatial dimension, we

accounted for the spatial structures in the ecosystem by assigning, where relevant, functional groups either to the fore reef or to the lagoon (see similar approaches in (Gu enette et al. 2014, Piroddi et al. 2015; 2017)). All benthic species and small territorial fishes were considered separately for the fore reef and lagoon, while larger and often mobile species were assumed to interact between the two habitats.

Each functional group i was represented by a production and consumption equation that ensure the mass balance within the system. The production for the group i was modelled as function of its total mortality so that:

$$P_i = Y_i + B_i.M2_i + E_i + BA_i + P_i.(1 - EE_i) \quad (1)$$

where P_i is the production ($t.km^{-2}.year^{-1}$) for the group i , Y_i the catch ($t.km^{-2}.year^{-1}$), B_i the biomass ($t.km^{-2}$), $M2_i$ the mortality predation rate ($year^{-1}$), E_i the net migration ($t.km^{-2}.year^{-1}$), BA_i the biomass accumulation ($t.km^{-2}.year^{-1}$) and $P_i.(1 - EE_i)$ is the flow to detritus related to the other mortality ($t.km^{-2}.year^{-1}$), with EE the ecotrophic efficiency of the group i.e. the proportion of the production that is used (consumed,harvested or accumulated) in the system. Consumption for the group i ($t.km^{-2}.year^{-1}$) was given by:

$$Q_i = P_i + R_i + GS_i \quad (2)$$

where R_i and GS_i are the respiration and egestion flows ($t.km^{-2}.year^{-1}$) respectively.

The parametrization of an Ecopath model requires at least five key inputs parameters: the biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), trophic interactions in a form of a diet matrix (DC_{ij}) linking functional groups, and fisheries catches. Most of biomass data were obtained from *insitu* observations (i.e. the CRIOBE annual transect surveys) and production and consumption over biomass ratios were calculated using empirical relationships or using values from the scientific literature on similar ecosystems (Supplementary Information Part I). Diet composition of sedentary fish groups was estimated from a database summarizing 282 dietary information of reef fishes available from the literature (Kulbicki, unpublished data) and adapted to biomass in the habitat of the study. Since mobile predators are using resource on both the fore reef and the lagoon habitats, their diet was divided according to the relative prey density, so that:

$$DC_{i,j,h} = DC_{i,j} * B_{i,h}/B_i \quad (3)$$

where $DC_{i,j,h}$ is the predation exerting by species j on species i in the habitat h and $B_{i,h}$ the biomass of the prey i on habitat h . Diet composition of benthic invertebrates was taken from Wabnitz et al. (2010). Annual catches were indirectly estimated from local consumption of food fishes assessed from social surveys (Fabre et al. 2018), and were assumed to increase from 2006 to 2016 as demography increased (Insee-ISPF 2007; 2012). Basic input and data sources used to parametrized the models are listed in Table.1 and detailed information is located in the Supplementary Material Part I.

2.3 Incorporating uncertainty into the ecosystem model

Model uncertainty was incorporated into initial parametrization options. For each input parameter (i.e. B, P/B, Q/B and DC), a log-normal probability distribution was applied following the pre-defined table of the Pedigree Index (Pauly et al. 2000, Funtowicz and Ravetz 1990, Christensen et al. 2005). The Pedigree module included in EwE allows for a score to be assigned to each individual input variable based on quality of data origin. According to Christensen et al. (2005), this score is then converted to a default value of a confidence interval expressed as $+ / - \%$. For instance, reef fish biomass data, which are locally collected by annual surveys, were assigned a Pedigree score of 5 conventionally assuming an uncertainty of 30% (Supplementary Information Table.6). We then generated, for each period, an ensemble of 1000 Ecopath models, meeting the ecotrophic efficiency balance ($EE < 1$), with input parameters varying within the uncertainty limits, using a Monte Carlo resampling routine. These Ecopath models were used to calculate the output result indicators and their respective confidence limits. This procedure used a suite of Matlab functions provided by Guesnet et al. (2015).

2.4 Analysing models outputs

2.4.1 Trophic spectra analysis

Once food web models are balanced and results are checked for consistency, changes in ecosystem structure and functioning were firstly assessed through trophic spectra i.e. the biomass distribution across trophic levels (Gascuel et al. 2005, Gascuel and Pauly 2009). This allowed us to analyse how the overall structure of the fore reef and lagoon sub-systems changed over time. The trophic spectra were calculated *before*, *during* and *after* disturbance models for both habitats (i.e. fore reef and lagoon) using the Ecotroph routine (Coll  ter et al. 2013) in R and the Ecopath results. For a given model and a given habitat, the trophic spectrum is built including each functional group of that habitat (i.e. sedentary and mobile groups) and represented as the sum of all groups' spectra. Since no data were available on the relative contribution of mobile groups on each habitat, we accounted for differential contribution according to the total surface area of each habitat. As fore reef accounts for 10% of the total area of the system, biomass of mobile species were assumed equal to 10% of their total biomass in the fore reef and 90% was assigned inside the lagoon which is inline with observed fish biomass Table.1.

2.4.2 Ecosystem network analysis

Changes in ecosystem structure and functioning between the *before*, *during* and *after* periods were also assessed by comparing trajectories of 12 ecosystem network analysis

indicators (Table.2). Here we considered three indicator categories: flow related indicators, path related indicators and structure related indicators.

Flow related indicators:

In this category we computed main flows of the ecosystem related to the *Total System Throughput*. The *Total System Throughput* (TST) is measured as the total flow magnitude of a network and has been defined as the size the system (Finn 1976). Related to TST we computed the sum of all flows coming to the *Detritus* (FD/TST), lost through the *Respiration* (R/TST) and coming from the *Consumption* (Q/TST). The *Ecotrophic Efficiency* is defined as the fraction of the production of group that is used in a system (Christensen et al. 2005). The mean *Ecotrophic Efficiency* ($Mean_{TL2}$) was thus computed as the average of the *ecotrophic efficiency* of all functional groups with a trophic level (TL) higher than 2.

Path related indicators:

These indicators have been computed to analyse all direct and indirect pathways of the system. The *Average Path Length* (APL) is the average number of groups through which each inflow passes weighted by the size of the inflows (Kones et al. 2009). FCI was proposed by Finn (1980) to quantify the cycling capacity of an ecosystem and is computed as the total throughflow that is recycled to the total system throughflow. The *Production*

to *Biomass* ratio of the communities with $TL > 2$ (P/B_{TL2}), averaged at the network scale, informs about the kinetic of trophic flows (Gascuel et al. 2008). The Efficiency Cumulated Indicator (*ECI*) was recently proposed by (Maureaud et al. 2017) to quantify the fraction of production passing from $TL = 2.0$ to $TL = 4.0$. *ECI* is computed as the product of all partial *Production to Consumption ratio* within each trophic class of the entire foodweb.

Structure related indicators:

This category refers to the whole network interactions. The *Average Mutual Information (AMI)* comes from the communication theory and is used to measure the amount of constraint in the network organization (Ulanowicz 2004). 'Constraint' of a system refers to any flow patterns that are well organized, non random. The stability of a network can be measured as the difference between the amount of its uncertainty (*Hc*, which can refer to any indirect flow patterns), and of its constraint (*AMI*) and is called the *Conditional Uncertainty (DR)* (Latham II 2006). The *Realized Uncertainty (RU)* is the *AMI* to *Hc* and refers to the proportion of the total uncertainty (Latham II 2006). The *System Omnivory Index (SOI)* measures the degree of feeding on several trophic levels and reflects the complexity of a system linkage (Ulanowicz and Abarca-Arenas 1997).

These indicators were computed on the basis of the Kones et al. (2009)'s Matlab function. They were calculated separately for the lagoon and the fore reef habitats by considering mobile species as common species in both habitat.

The state of indicators among the three periods were compared using permutational ANOVAs (Anderson 2001). Significant differences and confidence limits were further considered using the multiple comparison procedure of Tukey-Kramer method based on means comparisons (Tukey 1949).

2.4.3 Quantifying the recovery debt

The recovery debt, defined as the interim loss that accumulates during the recovery process was assessed, for each of our ecosystem indicators, at the whole ecosystem scale. Following Moreno-Mateos et al. (2017), we quantified the recovery debt as:

$$RD = X_r * T - AUC \quad (4)$$

with X_r the value of the variable before the disturbance (i.e. the reference value), T the recovery period (i.e. from 2010 to 2016) and AUC the Area Under the Curve. AUC were assessed using an exponential approximation. If the value in 2010 exceeded the pre-disturbance value we proceeded to an inverse-transformation as proposed by Moreno-Mateos et al. (2017). The recovery debt was then expressed as percentage:

$$RD_{\%} = 100 * \frac{RD}{X_r} \quad (5)$$

3 Results

3.1 Overall changes in trophic structure and functioning

Results of flow diagram allows for two sub-webs to be considered: the lagoon and the fore reef sub-webs, characterized by specific benthic-pelagic pathways, and connected through pelagic pathways (Fig. 2). The highest degree of connection are coming from the pools of detritus and turf which are the largest source of energy for the benthos and herbivorous fishes. Even if corals represent high biomass in the study area, they only marginally contribute to the transfer of energy in the foodweb as few connections stem from them. The benthic fauna biomass is substantially more represented in the lagoon than in the fore reef. The highest trophic levels are represented by mobile predators (such as Groupers, Jackfish, Large piscivores and Sharks) with trophic values up to 4. Changes between models representing different time periods are mainly observed in the fore reef, with a biomass decrease of coral communities and an increase of detritus and algae during the disturbance, resulting in a significantly higher bottom activity.

Biomass is unequally distributed across trophic levels (Fig. 3). Herbivore and detritivore species ($2 < TLs < 2.5$) always hold the largest biomasses in the fore reef and lagoon, while high trophic level communities ($TLs > 3.5$) are less represented. In both habitats the biomass of predators decreases during the disturbance period. In contrast intermediate trophic levels seems to benefit from the disturbance, with increasing biomass.

Nevertheless, this increase does not affect the same trophic levels in the two habitat sub-webs. In the fore reef it is significant between trophic levels 2.5 and 3.0 (mainly omnivores), while in the lagoon the increase during disturbance affects trophic levels ranging from 3.0 to 3.5 (mainly generalist carnivores). After the disturbance the biomass of intermediate TLs seems to have recovered in the fore reef, while biomass of trophic levels between 2.5 and 3 continues to decrease in the lagoon. In both habitats the decrease in biomass is also observed for predators (TLs > 3.5).

3.2 Changes in network flows

The disturbance of the coral reef ecosystem also affected the ecosystem flows differently in the fore reef and lagoon habitats (Fig. 4). In the lagoon the Flow to Detritus (FD/TST), total Dissipation (R/TST) and Consumption (Q/TST) were larger (+6%, +3% and +2.5% respectively) during the disturbance period compared to before and after the disturbance. Such changes were not observed in the fore reef, with a constant low flow to detritus and constant high rate for dissipation and consumption. The Mean Ecotrophic Efficiency ($meanEE_{TL>2}$) was oppositely affected in the lagoon (5.4% increasing) and the fore reef (2.9% decreasing) during the disturbance, with a return to its initial value in both systems.

3.3 Changes in network path

In the lagoon, the Average Path Length (APL) and the recycling capacity of the system (Finn's Cycling Index, FCI) decreased by 21% and 36%, respectively, during the disturbance, with no (or slight) return to previous values after the disturbance (Fig. 5). The total Production over Biomass ($P/B_{TL>2}$), remained unchanged in the fore reef but decreased by 20% in the lagoon during the disturbance before returning to its initial value after. The Efficiency Cumulating indice (ECI), increased by 10.8% in the fore reef while it decreased inside the lagoon along the disturbance pathway.

3.4 Changes in network structure

In the lagoon, the average Mutual Information (AMI), measuring the degree of a system organization, increased by 6.5% during and after the disturbance (Fig. 6) while no changes were observed in the fore reef. The pattern was opposite for the Conditional Uncertainty (H_c), measuring the diversity of the system, with a decrease in the fore reef (-9.7 %) and no change in the lagoon. The Realized Uncertainty (RU), that is the ratio of AMI over H_c , increased (+4.7%) in the lagoon during and after the disturbance while it increased (+4.4%) only after the disturbance in the fore reef. The System Omnivory Index (SOI)

responded in opposite ways in the fore reef and in the lagoon with a decrease (-26%) and an increase (+10.7%), respectively, during the disturbance.

3.5 Recovery debt

After 6 years of recovery, highest debt is found in the cycling processes (28.85% FCI). The Average Path Length (APL) is 17.43% shorter compared to the pre-disturbance value and the turnover ($P/B_{TL>2}$) is 10% slower. The whole ecosystem shows high transfer efficiency debt (9.17%) as well as constraint structure debt (8.61% *AMI*, 5.58% *SOI* and 5.54% *RU*).

4 Discussion

Fish biomass and coral cover indicators, as used in previous ecosystem assessment (e.g Adam et al. 2011; 2014, Lamy et al. 2015) suggest that the ecosystem has fully recovered from the last disturbances. However, using an ecosystem network approach, we show for the first time, that the studied ecosystem highlights an important recovery debt as evidenced by its changes in ecosystem structural and functional properties.

4.1 Combined top-down and bottom-up controls buffer the disturbance in the fore reef functioning

In many ecosystems, stress is expected to alter energy fluxes in food webs (Gascuel et al. 2008, Coll et al. 2009, Trebilco et al. 2013, Maureaud et al. 2017). In coral reefs, this has been evidenced for instance through a shift from long-lived species to high turnover species during a coral-algae transition state (Ainsworth et al. 2015). Here we show that, even if biomass and flow changed during the depletion of coral cover, relative flows (FD/TST , R/TST and Q/TST) and cycling indicators (APL , FCI and P/B_{TL2}) in the fore reef were not significantly changed over time suggesting that its functioning remained almost unaffected by the disturbance. Indeed, following the pulse natural disturbance, Moorea's fore reef experienced trophic cascading effects due to combined effects of top-down and bottom-up controls that buffered the effect of the disturbance on the fore reef general functioning. Hempson et al. (2017) recently highlighted that during an algae transition-state reefs displayed a concave trophic structure characterized by a decline in mid trophic levels (from 2.5 to 3), due to the loss of coral habitat making these mid trophic level organisms more vulnerable to the predation by upper trophic levels. Our trophic pyramid (Fig. 3) shows contrasting results. The decline in coral-dependent fishes were compensated at the same time by an increase in other small territorial fishes (such as planktivorous damselfishes and omnivores fishes) that benefited from the release of

predation from the mobile predators and consequently buffer the effect of the habitat loss on that trophic class. As a consequence of this biomass re-organization, fore reef turn over rate remains almost constant. The increase of mobile herbivores with high turn over was compensated at the same time by an increase in planktivores reef fishes with low turn over, and the cycling capacity was also unaffected since detritivorous species (such as macrobenthos and omnivorous fishes) were not reduced.

Trophic cascades following the declines of predators have been observed in many marine environments (Estes et al. 1998, Dulvy et al. 2004, Baum and Worm 2009) but a debate exists on the top-down control in coral reefs (Ruppert et al. 2013), that can be explained by the high diversity of trophic interactions in these systems (Thompson et al. 2007) weakening possible cascade effects (Casey et al. 2016). Here we add evidence that the removal of predators can lead to an increase in planktivorous damselfishes, but we also evidence that this top-down effect can also counterpart the bottom-up control due to coral decline.

4.2 The off-stage impacts on the lagoon functioning

While the lagoon has no direct impacts of the studied environmental disturbances, our network analysis reveals deep indirect changes in its functioning through time. During the disturbance, biomass of mobile species such as herbivores and invertebrate mobile feeders

was considerably increased disrupting its functioning. Contrary to the fore reef where there were changes in bottom composition, the lagoon sub-web did not experience a bottom up re-organization that likely buffered the increase of flows entering the system. Following the disturbances, the cycling and transfer of biomass in the lagoon were strongly affected. The loss of biomass of omnivores decreased the recycling processes and the food web chain was shortened compared to the before period (as indicated by the *Average Path Length*). This decrease is likely the result of the increase of the generalist carnivores that feed on both invertebrates and fishes. This generates a stress in the lagoon sub-system that is highly dependent on matter recycling for its overall functioning.

4.3 The overlooked impact on the entire ecosystem structure

Although "channelling" networks are increasingly observed in ecosystems enduring anthropogenic stressors (Tomczak et al. 2013, Ainsworth et al. 2015), we show that environmental disturbances can also lead to a simplification of food webs. Following the disturbance, mobile herbivorous species substantially increased in response to the food availability in the fore reef. As most energy are concentrated at low trophic levels, this high biomass production resulted in more organized flow pathways in the fore reef (as indicating by the *Conditional Uncertainty* and the *Realized Uncertainty*) and less

diversified (as indicated by the *System Omnivory Index*). The decrease in flow diversity is also likely the result of the loss of habitat structural complexity, with associated loss of coral-dependent species.

Beyond the structural change of the fore reef network, we show that the flows into the lagoon displayed a more constrained organisation during the disturbance (as indicated by *Average Mutual Information*). Contrary to the fore reef, this degree of organisation was not related to a decreased diversity of flows, since the *System Omnivory Index* tended to increase during the disturbance (and was reduced in the fore reef). This constrained organisation of flows in the lagoon reefs was likely the result of an increase in mobile fish biomass entering into the system that created new possible pathways especially through the increase of more generalist carnivores that take advantage during the fore reef disturbance.

While previous studies always showed a decrease of ecosystem diversity in regime shifted reefs (Ainsworth et al. 2015, Hempson et al. 2017), our results strongly suggest that even in case of recovered reefs, diversity of flows can be altered, leading to a more food chain-like system with evident changes at the structural and functioning levels.

4.4 The ecosystem recovery debt

We show that the system highlights a recovery debt. The structural and functional traits of the lagoon and fore reef sub-webs did not fully recover, although abundance did (Adam et al. 2011; 2014, Lamy et al. 2015).

We evidence here that disturbance of Moorea fore reef was propagated into the lagoon functioning, with overall recycling capacity reduced about 29% compared to levels prior the disturbance, after 6 years of recovery (Fig. 5 and 7). With a reduction in detritivorous species (like most of the benthos), the ecosystem is therefore switching from a productive state, mainly based on detrital pathways to a less productive state with slower nutrient cycling. Detrital pathways are an important source of organic matter entering the coral reef food web that greatly contribute to the transfer efficiency of primary production across the food web (Cebrian 1999; 2002). As cycling capacity is still low transfer efficiency was also reduced and remained 9% less efficient in the whole system than before disturbance (Fig. 5). As *Efficiency Cumulating Indice* only focus on transfers coming from growth and reproductive processes (Maureaud et al. 2017), our results suggest that communities still suffer higher metabolic losses than before the disturbance. Following the disturbance, higher predation mortality was exercised on communities (especially inside the lagoon), which were stressed and responded with higher respiration. As a result of this predation, small bodied size fishes were replaced during the disturbance by slow growing larger

species (like generalist carnivores), resulting in a high debt in ecosystem turnover (about 10% slower).

Structure related indicators revealed that both sub-webs changed from a web-like structure to a more chain-like system, with no apparent recovery. Eleven years after the disturbance, the whole ecosystem has lost [5-8]% of its internal structure flexibility, exhibiting more constrained flows than pre-disturbance state. These losses of ecosystem structural and functional traits may jeopardize future capacity of the system to recover from future natural or anthropogenic disturbance. The disturbance therefore created a disequilibrium between the organized (AMI) and non-organized (DR) part of the system, which can alter its capacity to outlast future disturbances (Saint-Béat et al. 2015).

5 Conclusion

Here we show that even when ecosystems appear resilient an ecosystem network approach can reveal a recovery debt. As such a debt can pertain to the intrinsic functioning of the ecosystem this can have serious implications for ecosystem services delivery. Those implications can be even stronger in coral reefs where societies highly depend on ecosystem services for their livelihoods. Monitoring programs, impact assessments and

resilience based management should not only account for species-based indicators but also track ecosystem network indicators that better reveal the functioning of ecosystems.

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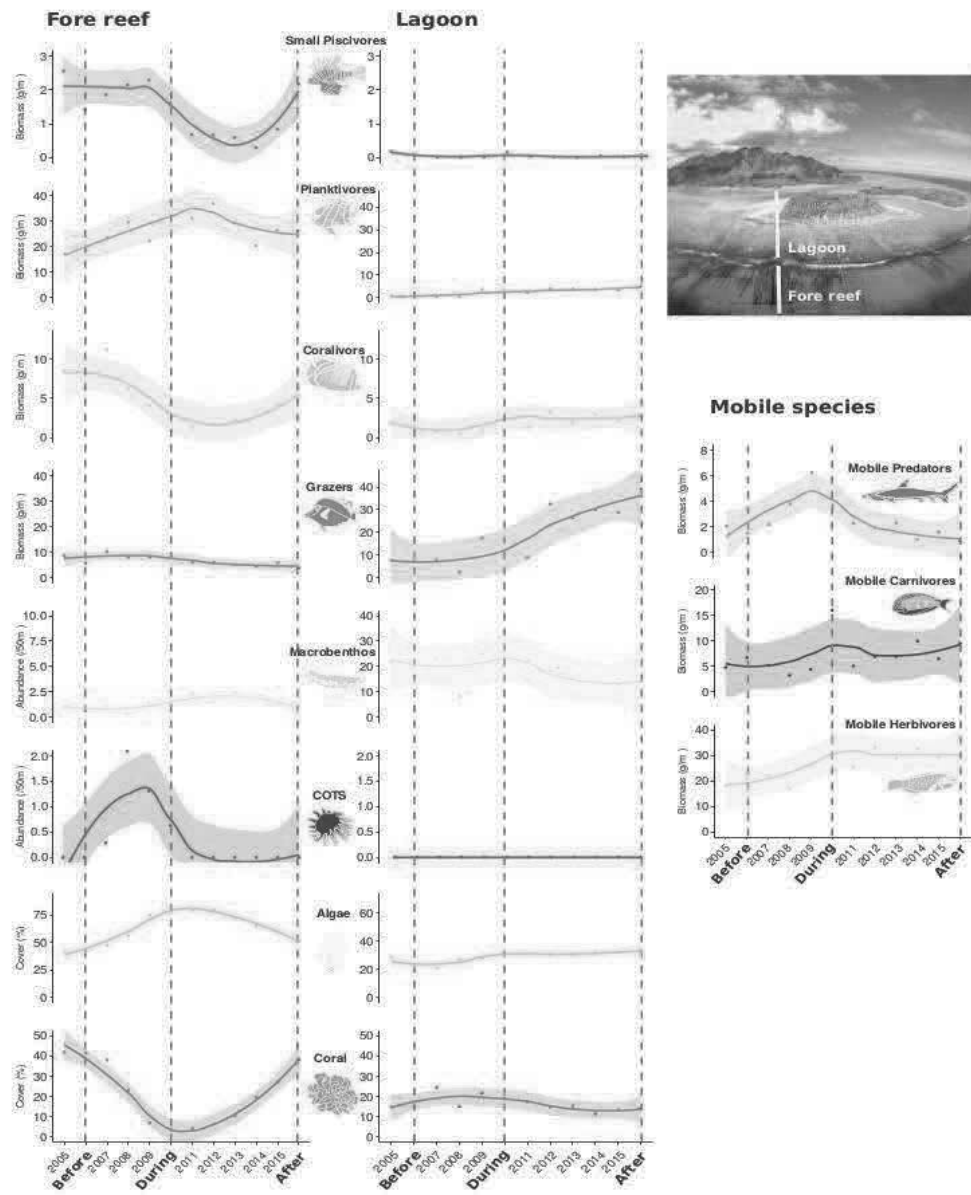


Figure 1: Biomass and cover of key reef species groups, inside and outside the lagoon for sedentary species and across those two subsystems for mobile species, along the disturbance (COTS outbreak that started in late 2006 and cyclone in 2010). Before, During and After disturbance periods used in subsequent analyses are highlighted. See Table.1 for more details on functional groups.

Table 1: Basic estimates of the three models (*before*, *during* and *after* the disturbance) for each functional group. Parameters in bold are parameters estimated by the model.

	Group names	Trophic level			Biomass (t/km ²)			Production / biomass (year)			Consumption / biomass (year)			Ecotrophic Efficiency			Production / Consumption		
		<i>Before</i>	<i>During</i>	<i>After</i>	<i>Before</i>	<i>During</i>	<i>After</i>	<i>Before</i>	<i>During</i>	<i>After</i>	<i>Before</i>	<i>During</i>	<i>After</i>	<i>Before</i>	<i>During</i>	<i>After</i>	<i>Before</i>	<i>During</i>	<i>After</i>
Predators																			
	Sharks	3.84	3.63	3.61	0.90	0.90	0.90	0.22	0.22	0.22	3.70	3.70	3.70	0.34	0.34	0.34	0.06	0.06	0.06
	Jackfish expl.	3.88	3.74	3.74	0.52	0.41	0.45	1.55	1.55	1.55	7.75	7.75	7.75	0.80	0.80	0.80	0.20	0.20	0.20
	Grouper expl.	3.91	3.92	3.71	0.36	0.37	0.30	1.56	1.56	1.56	7.80	7.80	7.80	0.80	0.80	0.80	0.20	0.20	0.20
	Piscivores large expl.	3.92	3.80	3.86	0.12	0.09	0.09	1.46	1.46	1.46	7.29	7.29	7.29	0.80	0.80	0.80	0.20	0.20	0.20
	Piscivores large	3.82	3.75	3.60	0.11	0.06	0.09	1.45	1.45	1.45	7.26	7.26	7.26	0.80	0.80	0.80	0.20	0.20	0.20
	Piscivores medium	3.77	3.80	3.60	0.43	0.66	0.20	0.64	0.64	0.64	8.15	8.15	8.15	0.77	0.49	0.81	0.10	0.10	0.10
Generalist carnivores																			
	Piscivores small Fo.	3.46	3.50	3.49	0.14	0.16	0.22	2.90	2.90	2.90	12.10	12.10	12.10	0.90	0.35	0.91	0.24	0.24	0.24
	Piscivores small Lag.	3.49	3.55	3.36	0.45	0.12	0.36	2.90	2.90	2.90	12.10	12.10	12.10	0.96	0.78	0.78	0.24	0.24	0.24
	Invertebrate Mobile Feeders expl.	3.48	3.41	3.29	2.27	5.54	4.06	1.91	1.91	2.14	10.30	10.30	10.30	0.88	0.92	0.75	0.19	0.19	0.21
	Invertebrate Mobile Feeders	3.33	3.28	3.31	4.46	9.10	5.14	1.16	1.16	1.16	10.80	10.80	10.80	0.98	0.93	0.80	0.11	0.11	0.11
	Myrristis expl.	3.24	3.33	3.36	0.12	0.47	0.22	2.20	2.20	2.20	11.01	11.01	11.01	0.80	0.80	0.80	0.20	0.20	0.20
Planktivores & Omnivores																			
	Planktivores Fo.	3.05	2.92	3.02	1.71	3.12	2.45	1.44	1.44	1.44	15.50	15.50	15.50	0.37	0.52	0.57	0.10	0.10	0.10
	Planktivores Lag.	3.05	2.97	3.00	0.29	1.05	3.10	1.44	1.44	1.44	15.50	15.50	15.50	0.71	0.81	0.74	0.10	0.10	0.10
	Omnivores Fo.	2.63	2.61	2.61	0.15	0.65	0.17	1.77	1.77	1.77	16.40	16.40	16.40	0.77	0.75	0.96	0.11	0.11	0.11
	Omnivores Lag.	2.71	2.63	2.68	0.09	0.29	0.44	1.77	1.77	1.77	16.40	16.40	16.40	0.92	0.91	0.73	0.11	0.11	0.11
	Coralivores Fo.	2.61	2.82	2.62	0.62	0.43	0.53	1.58	1.58	1.58	13.50	13.50	13.50	0.92	0.89	0.64	0.12	0.12	0.12
	Coralivores Lag.	2.61	2.58	2.57	1.05	2.84	1.94	1.58	1.58	1.58	13.50	13.50	13.50	0.96	0.82	0.88	0.12	0.12	0.12
Herbivores & Detritivores																			
	Scrapers expl.	2.08	2.06	2.06	17.00	28.64	28.37	4.06	4.06	3.82	9.60	9.60	9.60	0.19	0.10	0.13	0.32	0.32	0.33
	Grazers Fo.	2.22	2.18	2.20	0.57	0.84	0.38	2.95	2.95	2.95	38.00	38.00	38.00	0.93	0.97	0.72	0.10	0.10	0.10
	Grazers Lag.	2.22	2.13	2.14	4.89	6.97	26.78	2.95	2.95	2.95	38.00	38.00	38.00	0.50	0.86	0.48	0.10	0.10	0.10
	Grazers expl.	2.29	2.19	2.21	3.16	7.12	1.92	3.36	3.36	3.83	38.70	38.70	38.70	0.39	0.77	0.90	0.10	0.10	0.10
	Browsers expl.	2.27	2.25	2.18	0.17	0.19	0.09	3.86	3.86	3.86	19.30	19.30	19.30	0.80	0.80	0.80	0.20	0.20	0.20
Benthos																			
	COTS Fo.	2.49	2.20	2.49	0.00	0.88	0.00	0.53	0.53	0.53	9.42	9.42	9.42	0.89	0.96	0.89	0.06	0.06	0.06
	Urchins	2.22	2.16	2.20	14.60	12.35	0.33	0.70	0.70	0.70	3.58	3.58	3.58	0.07	0.47	0.00	0.20	0.20	0.20
	Giant Clam	1.72	1.74	1.73	2.80	17.00	18.30	0.54	0.54	0.54	1.08	1.08	1.08	0.00	0.25	0.00	0.50	0.50	0.50
	Large Benthos Fo.	2.86	2.82	2.87	0.17	0.23	0.12	1.50	1.50	1.50	7.90	7.90	7.90	0.91	0.90	0.79	0.19	0.19	0.19
	Large Benthos Lag.	2.86	2.92	2.88	32.67	28.84	14.11	1.50	1.50	1.50	7.90	7.90	7.90	0.54	0.98	0.71	0.19	0.19	0.19
	Small Benthos Fo.	2.27	2.25	2.29	2.14	4.01	2.59	5.40	5.40	5.40	21.35	21.35	21.35	0.96	0.95	0.98	0.25	0.25	0.25
	Small Benthos Lag.	2.27	2.31	2.31	6.80	10.92	11.43	5.40	5.40	5.40	21.35	21.35	21.35	0.96	0.98	0.96	0.25	0.25	0.25
	Meio Benthos Fo.	2.18	2.14	2.19	0.41	0.61	0.36	39.50	39.50	39.50	196.00	196.00	196.00	0.95	0.98	0.95	0.20	0.20	0.20
	Meio Benthos Lag.	2.18	2.22	2.20	16.02	10.83	13.05	39.50	39.50	39.50	196.00	196.00	196.00	0.36	0.45	0.39	0.20	0.20	0.20
Corals																			
	Coral Massive Fo.	1.43	1.41	1.44	2.60	0.34	1.91	1.10	1.10	1.10	2.20	2.20	2.20	0.79	0.93	0.36	0.50	0.50	0.50
	Coral Massive Lag.	1.43	1.46	1.45	15.48	29.51	15.15	1.10	1.10	1.10	2.20	2.20	2.20	0.96	0.81	0.72	0.50	0.50	0.50
	Coral Branching Fo.	1.43	1.41	1.44	6.55	0.51	6.32	1.10	1.10	1.10	2.20	2.20	2.20	0.84	0.94	0.52	0.50	0.50	0.50
	Coral Branching Lag.	1.43	1.46	1.45	11.97	9.58	10.30	1.10	1.10	1.10	2.20	2.20	2.20	0.96	0.88	0.83	0.50	0.50	0.50
Bacteria																			
	Benthic Bacteria Fo.	2.00	2.00	2.00	0.12	0.14	0.12	289.00	289.00	289.00	578.00	578.00	578.00	0.60	0.60	0.60	0.50	0.50	0.50
	Benthic Bacteria Lag.	2.00	2.00	2.00	3.29	2.98	3.08	289.00	289.00	289.00	578.00	578.00	578.00	0.60	0.60	0.60	0.50	0.50	0.50
Plankton																			
	Zooplankton	2.11	2.11	2.11	7.91	11.16	10.07	40.00	40.00	40.00	160.00	160.00	160.00	0.80	0.80	0.80	0.25	0.25	0.25
	Phytoplankton	1.00	1.00	1.00	2.45	3.58	3.30	10.30	10.30	10.30				0.25	0.36	0.15			
Algae																			
	Macroalgae Fo.	1.00	1.00	1.00	29.88	14.72	51.89	8.43	8.43	8.43				0.16	0.28	0.19			
	Macroalgae Lag.	1.00	1.00	1.00	11.20	21.17	13.30	37.07	37.07	37.07				0.14	0.22	0.14			
	Turf Fo.	1.00	1.00	1.00	29.88	54.13	49.90	37.07	37.07	37.07				0.26	0.27	0.53			
	Turf Lag.	1.00	1.00	1.00	22.08	27.60	25.62	70.00	70.00	70.00				0.98	0.98	0.98			
Detritus																			
	Detritus Fo.	1.00	1.00	1.00	7.60	116.00	6.80							0.29	0.27	0.23			
	Detritus Lag.	1.00	1.00	1.00	295.20	203.40	245.70							0.92	0.69	0.78			

Table 2: Ecosystem network indicators.

Indicator category	Indicator name	Code	Formula*	Unit	Definition
Flow related indicators	Flow to Detritus / Total System Throughput	FD/TST	$\frac{\sum_i \text{Flow to detritus}}{TST}$	%	Proportion of total trophic flows that flow into the detritus box.
	Respiration / Total System Throughput	R/TST	$\frac{\sum_i \text{Respiration}}{TST}$	%	Proportion of total trophic flows that is lost through dissipation.
	Consumption / Total System Throughput	Q/TST	$\frac{\sum_i T_j}{TST}$	%	Proportion of total trophic flows that is consumed.
	Mean ecotrophic efficiency of the communities with TL>2	meanEE _{TL>2}		%	Proportion of the production of communities with TL >2 that is utilized in the system.
Path related indicators	Average path Length	APL	$\frac{TST}{\sum_i \text{Exports} + \sum_i \text{Respiration}}$		Measures the average number of compartments through which each inflow passes, weighted by the sizes of the inflow.
	Finn's Cycling Index	FCI	$\frac{TST_c}{TST}$	%	Proportion of flow involved in microbial loops.
	Production / Biomass of communities with TL>2	P/B _{TL>2}	$\frac{\sum_i \text{Production}_{TL>2}}{\sum_i \text{Biomass}_{TL>2}}$		System turnover rate of the communities with TL>2.
Structure related indicators	Efficiency Cumulated Indicator	ECI	$\prod_{TL=2}^{TL=n} \left(\frac{P_i}{Q_i} \right)^{AMI}$	%	Proportion of production transferred from lower to higher trophic levels through consumption
	Average Mutual Information	AMI	$\sum_{i,j} \left(\frac{T_{ij}}{TST} \right) \log_2 \left(\frac{T_{ij} * TST}{T_j * T_i} \right)$	t/km ² /year/bit	Measures the organization of the exchanges among components.
	Conditional Uncertainty	DR	$-\sum_i \frac{T_i}{TST} \log_2 \left(\frac{T_i}{T_i + T_j} \right)$	t/km ² /year/bit	Measures the residual (conditional) diversity and/or freedom. Commonly known as the conditional entropy in information theory
	Realized Uncertainty	RU	$\frac{AMI}{H_c}$	%	Measures the proportion of total uncertainty accounted by the network structure as measured by the AMI. Measures the degree of constraint across systems
	System Omnivory Index	SOI	$\frac{\sum_i OI_i * \log(Q_i)}{\sum_i \log(Q_i)}$		Measure the degree of feeding on several trophic levels

*where :

T_i is the sum of all material leaving the ith componentT_j is the sum of all flows entering the jth componentTST is the Total System Throughput calculated as : $TST = \sum_{ij} T_{ij}$ T_{ci} is the total system cycled throughflowOI_i is the omnivory index of ith component calculated as : $OI_i = \sum_j (TL_j - (TL_i - 1))^2 * DC_{ij}$ C is the Developpement Capacity of the system calculated as : $C = \sum_{ij} T_{ij} \log_2 \left(\frac{T_{ij}}{TST} \right) = A + O$ H is the system Entropy calculated as : $H = -\sum_{ij} \frac{T_{ij}}{TST} \log_2 \left(\frac{T_{ij}}{TST} \right) = AMI + H_c$

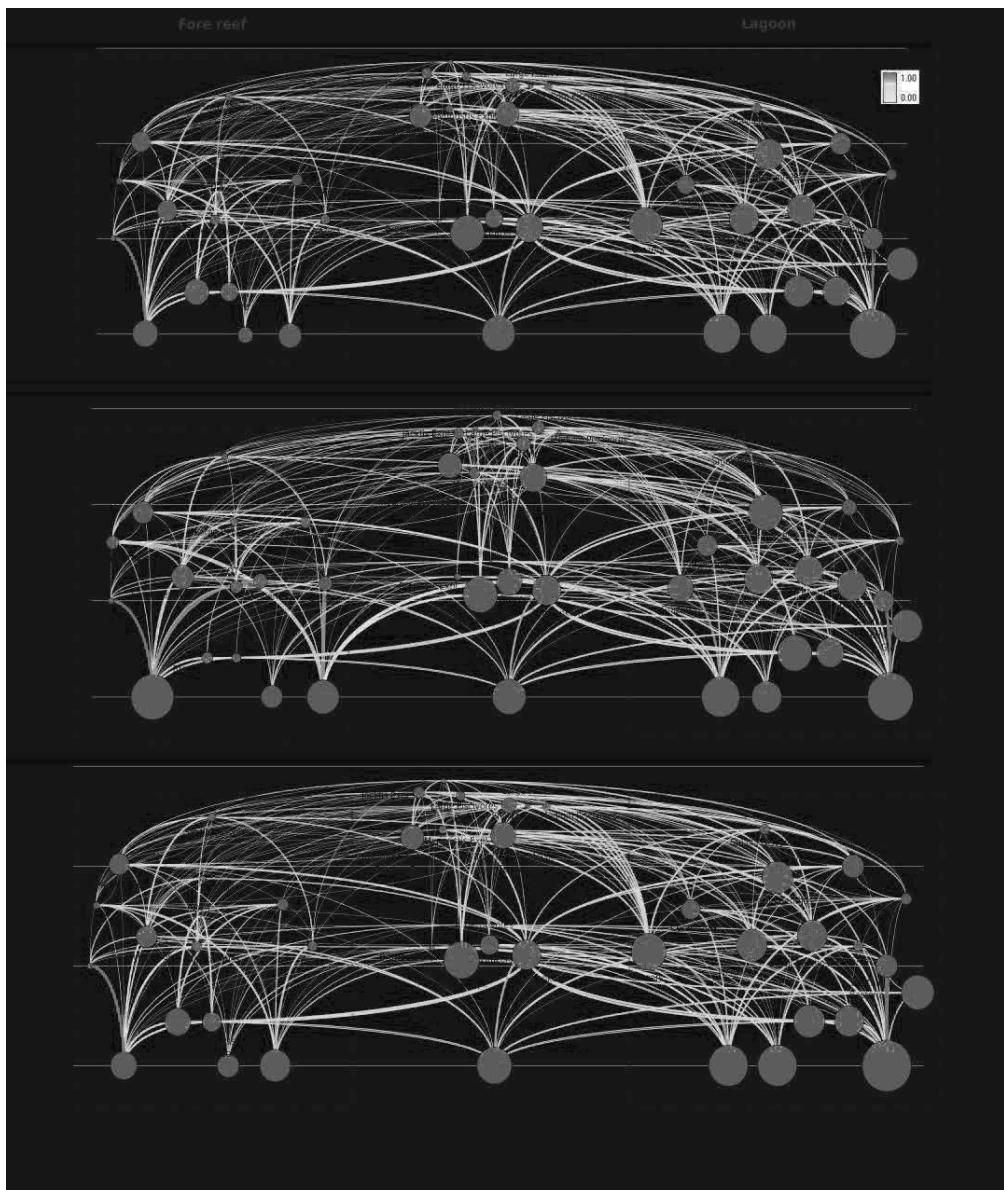


Figure 2: Flow diagram of the three Ecopath models (i.e. *before*, *during* and *after* the disturbance). Each node represent functional groups within the system and its size is logarithmically proportional to its biomass. Each line represents the trophic interaction among two given groups; the width of the line is scaled to flow proportion and colours are proportional to the magnitude of the flux. The light grey horizontal lines indicate trophic levels of the groups.

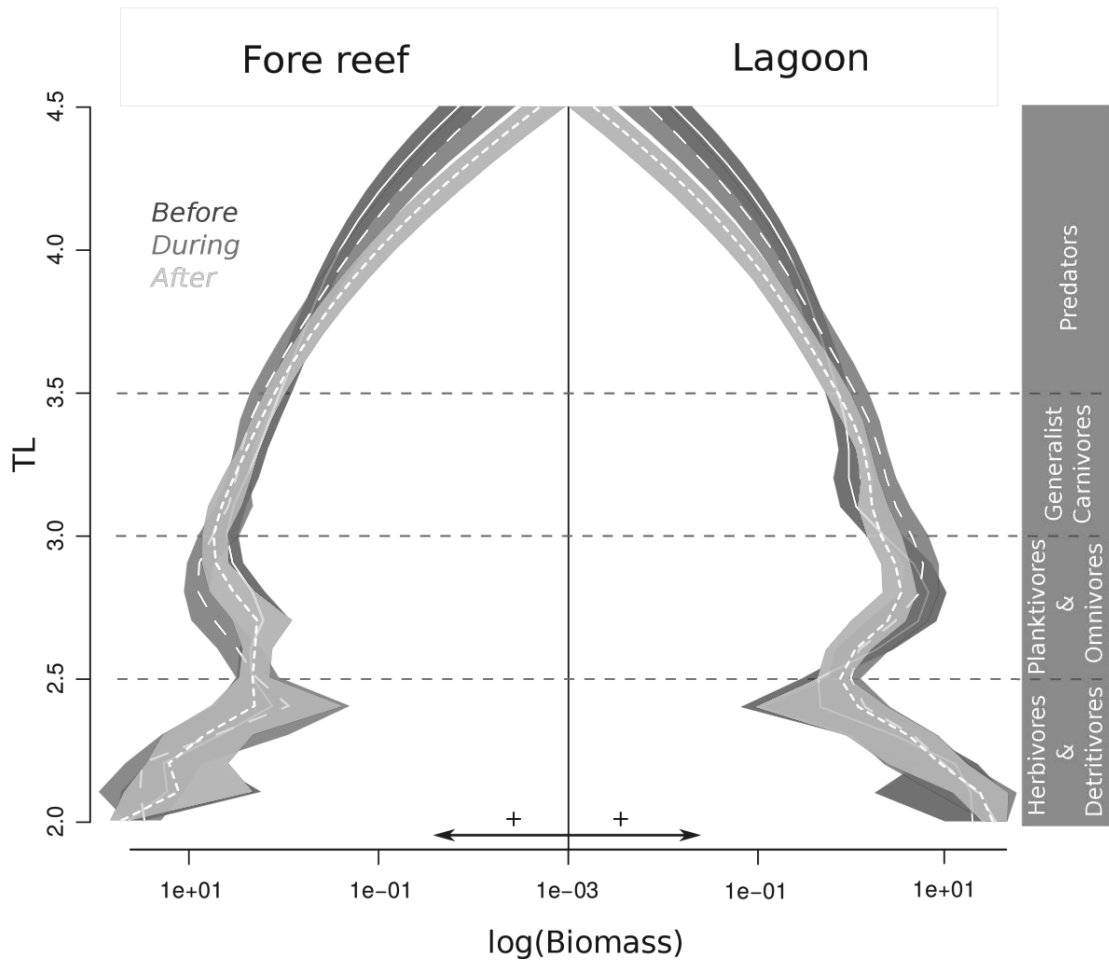


Figure 3: Trophic spectra of biomass (in g/m^2) for the fore reef and lagoon subsystems *before*, *during* and *after* disturbance.

Flow related indicators

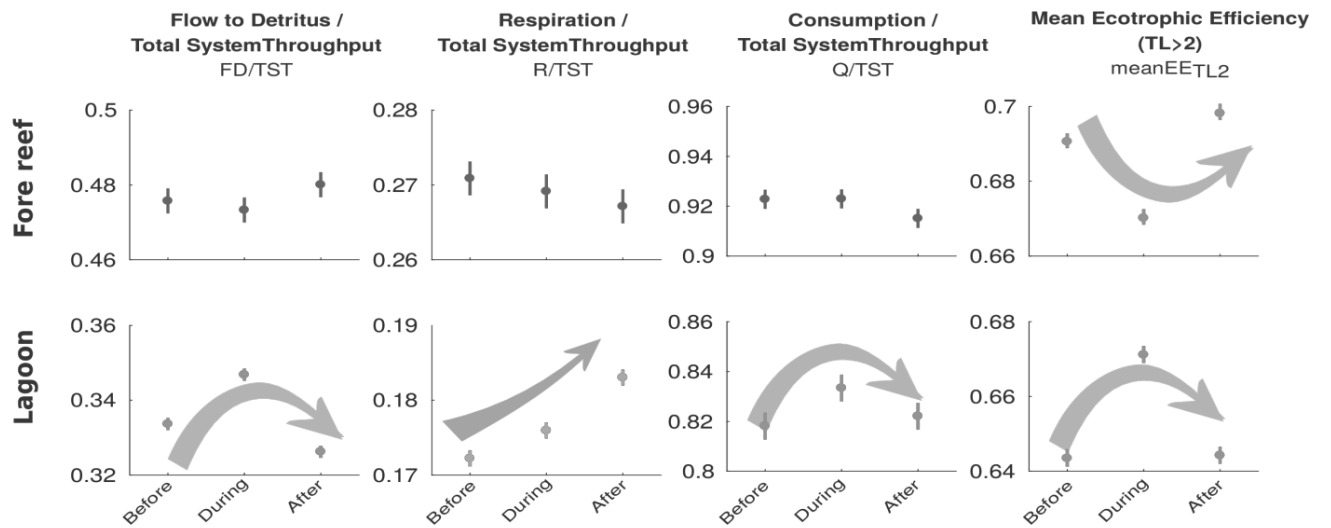


Figure 4: Flow related indicators trajectories along the disturbance. Coloured indicators show significant variations ($p < 0.05$) among the 3 periods. Blue arrows indicate indicators showing signs of recovery.

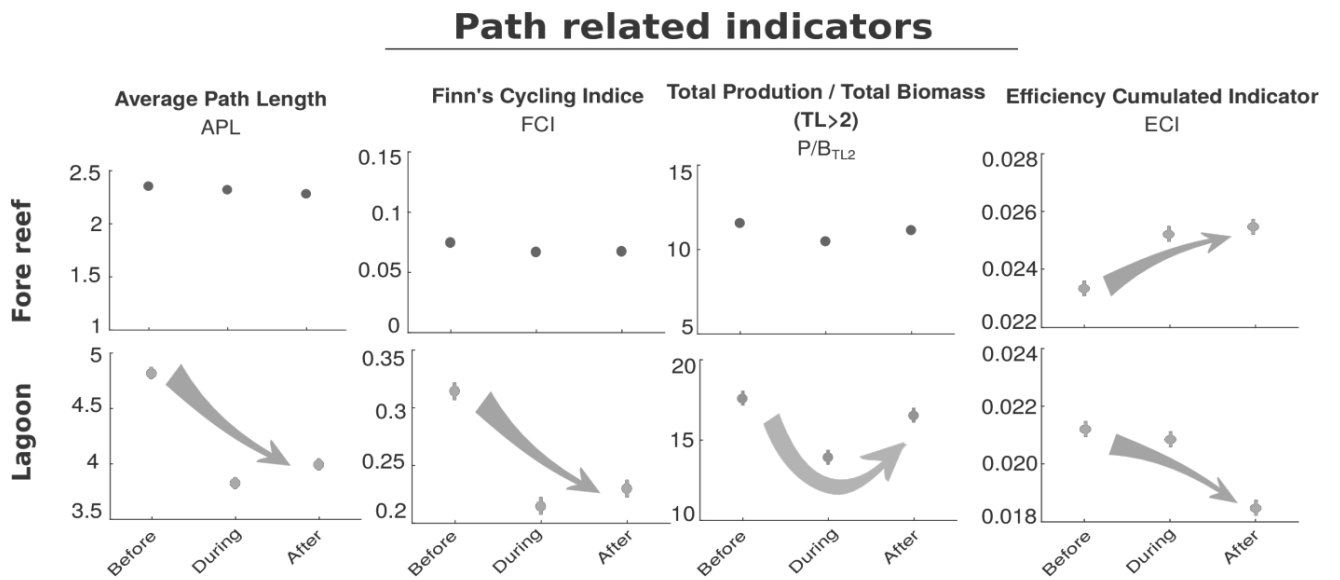


Figure 5: Path related indicators trajectories along the disturbance. Coloured indicators show significant variations (p value <0.05) among the 3 periods. Blue arrows indicate indicators showing signs of recovery.

Structure related indicators

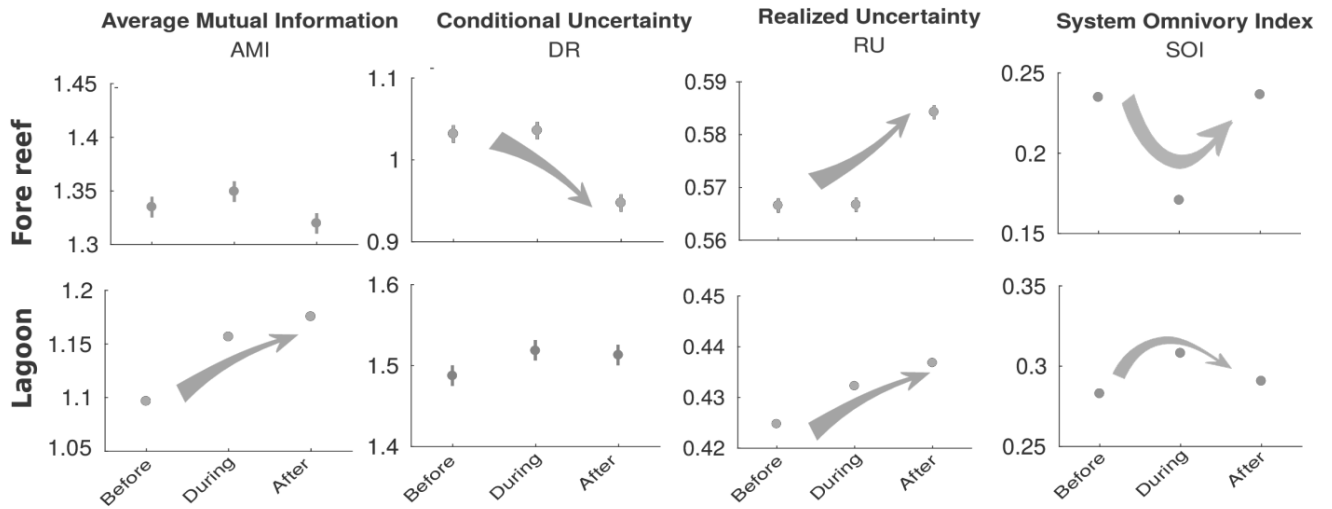


Figure 6: Structure related indicators trajectories along the disturbance. Coloured indicators show significant variations ($p < 0.05$) among the 3 periods. Blue arrows indicate indicators showing signs of recovery

Table 3: Recovery debt per annum estimated at the whole ecosystem scale.

Indicator	Recovery debt (%)	Standard error
FCI	28.85	0.07
APL	17.43	0.05
P/B_{TL2}	10.29	0.05
ECI	9.17	0.03
AMI	8.61	0.04
SOI	5.58	0.01
RU	5.54	0.01
R/TST	2.83	0.04
DR	2.24	0.03
FD/TST	1.47	0.04
Q/TST	0.58	0.04
$meanEE_{TL2}$	0.46	0.01

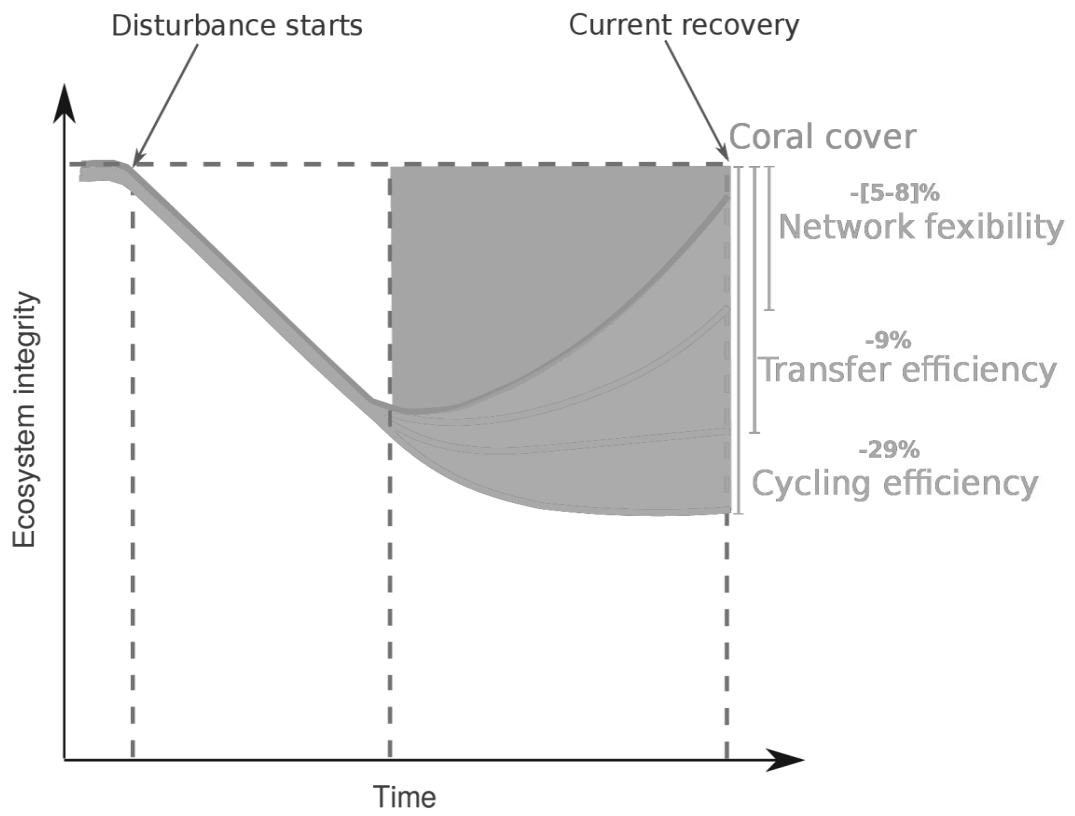


Figure 7: Schematic representation of the resulting losses of whole ecosystem structure and functioning of Moorea's coral reef after disturbance.