EXPLORING THE RELATIONSHIP BETWEEN FUNCTIONAL DIVERSITY AND RESILIENCE IN CORAL REEF COMMUNITIES WITH AN AGENT-BASED MODEL

by

Bruno S. Carturan

B.Sc., Université d’Avignon, 2005
M.Eng., Ecole National d’Ingénieurs de Limoges, 2008
M.Sc., Université des Sciences et Techniques de Limoges, 2008
M.Sc., Mediterranean Institute of Oceanography, 2011

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The following individuals certify that they have read, and recommend to the College of Graduate Studies for acceptance, a thesis/dissertation entitled:

**Exploring the relationship between functional diversity and resilience in coral reef communities with an agent-based model**

submitted by Bruno S. Carturan in partial fulfillment of the requirements of

the degree of Doctor of Philosophy.

Dr. Lael Parrott, Biology and EESC departments, Irving K. Barber Faculty of Science

Supervisor

Dr. Jason Pither, Biology department, Irving K. Barber Faculty of Science

Co-Supervisor

Dr. Robert Lalonde, Biology department, Irving K. Barber Faculty of Science

Supervisory Committee Member

Dr. Jacques-André Landry, École de technologie supérieure, University of Québec

Supervisory Committee Member

Dr. Corey Bradshaw, College of Science and Engineering, Flinders University, Australia

Supervisory Committee Member

Dr. Sylvie Desjardins, department of Computer Science, Mathematics, Physics and Statistics

University Examiner

Dr. Isabelle Côté, department of Biological Sciences, Simon Fraser University

External Examiner
Abstract

Corals are foundation species whose diversity regulates the functioning of coral reef ecosystems. Climate change and anthropogenic disturbances change the species composition of coral communities, and jeopardize reef persistence. Our capacity to mitigate these impacts is limited by key knowledge gaps about how coral diversity and specifically coral functional traits influence the resilience of reef ecosystems. In other ecosystems, experiments have shown support for the diversity-resilience hypothesis, whereby greater functional diversity enhances ecosystem resilience. Analogous evidence in reef ecosystems is lacking, in part because the high diversity and structural complexity of coral reefs render manipulative experiments infeasible at relevant temporal and spatial scales. Simulation models can overcome these limitations, but to date such models have been limited in their inclusion of relevant trait data and representation of key ecological processes.

My goal was to test the diversity-resilience hypothesis for reef ecosystems, focusing primarily on coral species. Building on previous efforts by plants ecologists, we first developed the effect, resistance and recovery trait framework, which accounts for processes of resistance and recovery—the two components of resilience. We illustrated via simulations how the framework can be used to predict the resilience of ecosystem functions.

Using the framework, we then developed an agent-based model combining trait-based and demographic approaches to simulate community dynamics from the scale of coral polyps to the entire community. Built from empirical data and expert knowledge, the model simulates processes with an unprecedented degree of detail, and can be configured to represent diverse coral communities. After calibration, the model captured the dynamics of three Caribbean coral communities that were affected by cyclones and bleaching, and produced realistic patterns of cover, recruitment and colony size distributions.

Lastly, we used the model to conduct a virtual experiment in which the initial functional trait diversity of coral communities was manipulated. These communities were subjected to cyclone and bleaching disturbances, and resilience was estimated by measuring their resistance, recovery rate and cover and rugosity 10 years after the disturbances. Using generalized linear models and model averaging, we found strong support for the diversity-resilience hypothesis: functional richness contributes significantly and positively to resilience.
Lay Summary

The goal of my PhD was to understand how the diversity of coral species influences the resilience of coral reef ecosystems, i.e., their capacity to resist and recover from disturbances such as cyclones and thermal stress. This issue is critical because disturbances change the diversity of coral species, which compromises the capacity of the reefs to persist and to provide their valuable benefits. We achieved our goal by first adapting an existing framework that allows to predict how coral populations increase and decrease due to disturbances and competition, and how these population fluctuations mediate key ecosystem properties, such as habitat complexity. Using the framework, we then established a computer model to simulate coral reef ecosystems under different environmental and management scenarios. Finally, we used the model to conduct a novel experiment which provided the first demonstration that reefs with more diverse coral species have a higher likelihood to be resilient.
Preface

Chapter 2 and Chapter 3 have been published as (i) Carturan BS, Parrott L, Pither J. 2018. A modified trait-based framework for assessing the resilience of ecosystem services provided by coral reef communities. Ecosphere 9:24 and (ii) Carturan BS, Pither J, Maréchal J-P, Bradshaw CJA, Parrott L. 2020. Combining agent-based, trait-based and demographic approaches to model coral-community dynamics. Elife 9:e55993, respectively. The agreed list of co-authors for the manuscript based on Chapter 4 includes: Bruno S. Carturan, Jason Pither and Lael Parrott.

For all three Chapters, I have been the principal investigator of the design and conduct of the research (i.e., model development and simulations), the analysis of the data and the writing of the manuscripts. Lael Parrott and Jason Pither provided strong support for the design of the research, the analysis of the data and the writing of the manuscripts. Corey J. A. Bradshaw contributed importantly to the design of the model global sensitivity analysis (Appendix G) and the writing of Carturan and colleagues’ (2020) manuscript. Jean-Philippe Maréchal supplied the empirical datasets used to calibrate the model (Appendix D) and provided valuable feedback for Carturan and colleagues’ (2020) manuscript.
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Figure A8. Expected resistance (left column) and recovery rate (middle and right columns) of the coral community defined in the model (expressed as population size in second and fourth rows) and the habitat provisioning function it provides (first and third rows) against bleaching disturbances, under different scenarios of disturbance intensity and reef connectivity. The initial
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Figure B1. Correlation analyses between the original aggressiveness rankings and the selected global computed ranking for each study (A: Sheppard, 1979; B: Abelson and Loya, 1999; C: Dai, 1990; D: Connell et al., 2004; E: Lang, 1973; F: Logan, 1984). Also displayed are the Spearman ρ (rₛ), the number of species (n) and the identity line (dashed lines) for visual aid. All P < 0.001 except for D, where P = 0.003.

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Chapter 1: Introduction

1.1. Coral reefs in the Anthropocene

1.1.1. The plight of the coral reefs

Coral reefs in the Anthropocene—the geological epoch following the Holocene that is characterized by the profound human impacts on the Earth’s geology and ecosystems (Steffen et al., 2011; Waters et al., 2016)—are going to change tremendously, and potentially disappear if we do not improve our science, management and governance (Hughes et al., 2017a). The total coral cover has declined worldwide over the last few decades (Bruno and Selig, 2007) (Bellwood et al., 2004; De’ath et al., 2012; Torda et al., 2018; Wilkinson, 2008). Certain coral reef communities have totally collapsed to assemblages dominated by macroalgae (Done, 1992; Graham et al., 2015) or, less frequently, by other organisms, such as bivalves, sponges, tunicates, zoanthids (Hughes et al., 2010). All the major tropical regions of the world are affected: the percentage of coral cover in the Caribbean decreased from 50 to 10% (which correspond to healthy and critical states, respectively) between 1975 and 2000 (Gardner et al., 2003), and from 43 to 22% between the early 1980s and 2003 in the Indo-Pacific region (Bruno and Selig, 2007). Even in the Australian’s Great Barrier Reef, which has been managed as a marine park since the 1980s, the coral cover decreased from 28% to 14% between 1985 and 2012 (De’ath et al., 2012). According to the last Global Coral Reef Monitoring Network (GCRMN) assessment, 19% of the original area of coral reefs (estimated before 2000) has been lost and is unlikely to recover, 15% is likely to be lost within the next 10 to 20 years, and 20% will be under threat or lost in the next 20-40 years (Wilkinson, 2008). However, these predictions have to be updated (the GCRMN will release a new global assessment at the end of 2020; gcrmn.ne) because the last global bleaching event that occurred between June 2014 and May 2017 was the most impactful event ever recorded, and affected more than 70% of the coral reefs worldwide (Heron et al., 2017). This event was superior in its intensity, spatial and temporal scales and impact on corals (Hughes et al., 2017b; Lough et al., 2018). For instance, the % cover of live coral in the Great Barrier Reef—the world’s largest reef system composed of 2900 reefs and stretching over 2300 kilometres—decreased by 30% after the bleaching event in 2016 (Hughes et al., 2018b).
Species differ in their sensitivity to climate change and other common disturbances (Hughes et al., 2003). Carpenter and colleagues (2008) estimated that one-third of tropical reef building coral species (i.e., 704 out of 845 zooxanthellate species with available data) are in the Threatened categories (i.e., Vulnerable, Endangered or Critically Endangered) of the International Union for Conservation of Nature (IUCN) Red List, and another quarter are in the Near Threatened category. Consequently, the reefs that will not transition toward a phase-shift will nevertheless experience a reassortment of coral reef taxa (Darling et al., 2013; Hughes et al., 2018b, 2012), and are referred as “novel coral systems” (Graham et al., 2014).

This thesis contributes to understanding the role of coral diversity for the functioning and resilience of coral reef ecosystems against several disturbances. We took a mechanistic modelling approach that embraces ecological complexity in order to answer fundamental research questions that cannot be addressed with non-virtual experiments.

1.1.2. The causes of the plight

Coral reef ecosystems are naturally embedded in different pulse disturbance regimes, such as bleaching events, coral diseases, *Acanthaster planci* (crown-of-thorn starfish) outbreaks, cyclones and floods. But human activities are modifying these regimes, making them more intense and frequent, and have introduced new types of press disturbances, such as fishing pressure, ocean acidification, sedimentation, pollution, nutrification (Connell, 1997; Mumby and Steneck, 2008; Nyström, 2006; Nyström et al., 2000; Salvat, 2015). Prior to the third global coral bleaching event in 2104 to 2016, cyclones, predation by *Acanthaster planci* and diseases were considered the major causes of coral mortality in the Great Barrier Reef (De’ath et al., 2012; Osborne et al., 2011). In the Caribbean, it was the combination of (i) decreasing herbivory, due to decades of overfishing and an epidemic that decimated the population of the grazer sea urchin *Diadema antillarum* (Hughes, 1994), and (ii) the decline of the architecturally complex and fast growing *Acropora palmata* and *A. cervicornis* due to white band disease outbreaks, hurricanes (Aronson and Precht, 2001), and decades of eutrophication and pollution (Cramer et al., 2020).

But since the last global bleaching event, it became apparent that global warming—which is caused by the increasing concentration of atmospheric carbon dioxide—is now the major threat to corals (Hughes et al., 2018b, 2017b). Bleaching events have increased in intensity—the 2015-16 thermal stress measured in 100 reefs distributed worldwide was 4.9 times higher compared to
pre-industrial global bleaching events (Lough et al., 2018)—and in frequency—from once every 27 years in the early 1980s to every 5.9 years in 2016 (Hughes et al., 2018a). This higher frequency compromises the capacity of many coral species to recover (Hughes et al., 2019).

In addition, reefs are affected by combinations of disturbances, which can result in synergetic effects (Brook et al., 2008; Harvey et al., 2018; Nyström et al., 2000; Sale, 2008). For instance, poor water quality increases bleaching and disease sensitivity of corals (Risk, 2014; S. a Wooldridge, 2009) and can decrease population density of herbivorous fish (Wolanski et al., 2004); cyclones can reduce grazing pressure by destroying the habitat of herbivorous fish (Connell, 1997); the scars left by Acanthaster planci can promote transmission of disease (Díaz and Madin, 2011); frequent warm temperature anomalies can increase disease sensitivity (Bruno et al., 2007); ocean acidification—also due to the increasing concentration of atmospheric carbon dioxide—reduces the rate of calcification of corals, which potentially affects their growth rates, fecundity and reduces their skeletal density (Hoegh-Guldberg et al., 2007), which affects their capacity to face other disturbances (Anthony et al., 2011).

### 1.1.3. Consequences, stakes and imperatives

Coral reefs are the world’s most diverse marine ecosystems and are critical for millions of people who depend on them because they supply valuable services: 

1. **Complex habitats**: they provide habitats that support a rich biodiversity.
2. **Regulation of coastal erosion**: they regulate coastal erosion, water quality, biogeochemical factors.
3. **Food and material resources**: they provide food and material resources.
4. **Cultural and spiritual values**: they represent cultural and spiritual values (Millennium Ecosystem Assessment, 2005; Moberg and Folke, 1999; Woodhead et al., 2019). In addition, they are often ecologically linked to other valuable ecosystems such as mangroves and seagrass habitats (Harborne et al., 2006). The overall value of the services that coral reefs provide is substantial. For instance, Costanza and colleagues (2014) estimated this value at (mean ± standard deviation) $352,000 ± 668,639$ USD ha$^{-1}$ yr$^{-1}$, which was the highest among the ten ecosystems they compared.

Securing the provisioning of these services necessitates preventing the collapse of coral reefs, which requires maintaining the drivers of changes (e.g., fishing intensity, atmospheric carbon dioxide concentration, nutrient concentration) within a “safe operating space”—the space defined by the range of values of the interacting drivers where coral reefs can persist (Norström et al., 2016)—and by supporting their resilience (Hughes et al., 2010). Keeping the atmospheric
carbon dioxide concentration to an acceptable level (i.e., 340-480 parts per million) is a \textit{sine qua non} for the maintenance of reefs, because above this level, the combined effects of global warming and ocean acidification will be too strong for the large majority of reefs to persist, and any other management actions will be ineffective (Frieler et al., 2013; Norström et al., 2016). Supporting coral reef resilience requires management approaches that are (i) adaptive (i.e., the capacity to readjust management approaches to a current location and time), (ii) ecosystem-based (i.e., consideration of the social, economic and ecological components of coral reef ecosystems), and (iii) resilience-based (i.e., support of the resilience of the ecosystem by acting on the appropriate mechanisms—such as larval dispersal, traditional fishing, processes—such as ecosystem functions, feedbacks, education, and related entities—such as coral and fish diversity, fisheries, customers) (Anthony et al., 2015; Harvey et al., 2018; Hughes et al., 2017a; McCook et al., 2010; Mcleod et al., 2019). But even controlling the atmospheric carbon dioxide emissions at an acceptable level and applying adequate management measures will not prevent the reefs from changing. The most pressing challenges now for coral reef ecologists are to predict the configuration (i.e., the species composition and interactions) of these novel ecosystems, how they will function (Graham et al., 2014; Hughes et al., 2017a), and to identify and support the ecosystem functions that are the most important for their resilience and the delivery of the ecosystem services we need (Bellwood et al., 2018). To address these challenges, it is imperative that we understand and quantify the mechanistic links between the drivers of change, species diversity, ecosystem functions and resilience (Bellwood et al., 2018).

1.2. \textbf{Biodiversity, ecosystem functioning and resilience}

To understand how drivers of change affect the functioning of ecosystems, it is necessary to consider (i) the factors responsible for the distribution of species in space and time, and (ii) how biodiversity influences the dynamics of ecosystems (i.e., their functioning and resilience). This dual role of biodiversity—as a dependent and an independent variable—involves different processes and effects.
1.2.1. Assembly rules in coral communities

Assembly rules are “any constraint on species coexistence”, and are crucial to understand in order to predict how communities will behave under future environmental conditions (Götzenberger et al., 2012). There are many different rules (or processes) that shape community structures in space and time; these rules can be classified into four main classes of processes: (i) speciation (i.e., the emergence of new species via random genetic mutations); (ii) selection (i.e., the exclusion or persistence of species resulting from deterministic local interactions among species (i.e., predation, competition and mutualism), and between species and their environment, (i.e., environmental filtering); (iii) dispersal (i.e., the movement of organisms across space); (iv) random drift (i.e., stochastic changes in species abundance, due to the intrinsic random nature of birth, death and offspring production rates) (Vellend, 2010). These processes are non-mutually exclusive; they contribute differently to shaping local community structures and occur at different scales. Selection and random drift are local scale processes; dispersal connects communities (which forms metacommunities), potentially over large regional scales if the species have such capacity. Conceptually, dispersal fills the regional species pool (i.e., the set of all species available that could potentially colonize and inhabit the focal habitat area) with species that can locally persist in at least one location (Cornell and Harrison, 2014). Comparatively, speciation fills the species pool with new species, and happens over regional and longer temporal scales. Trying to quantify the respective effects of each process in assembling species across several scales has been a fundamental objective in community ecology (Cornell and Lawton, 1992; Lamanna et al., 2014; Ricklefs, 2004, 1987), and in particular with coral communities.

Locally, coral communities are shaped by strong selection processes, such as interspecific competition and response to waves, storms, predation, tides, herbivory, light, temperature, and sedimentation (Connell et al., 2004; Huston, 1985). Interactions between competition and abiotic factors generate the “coral diversity gradient” (i.e., coral species richness increases with depth to a maximum around 20 m and then decreases), which is typical of coral communities worldwide (Huston, 1985). In shallow habitats, species richness is usually low, either because of strong competitive exclusion due to high levels of light, which favours competitive species (i.e., high autotrophy, fast growth rate and colony morphologies that allow to overtop competitors), or high extinction rates due to intense and frequent disturbance regimes (e.g., waves and cyclones).
Species richness is the highest at intermediate depths because of lower selection pressure due to weaker competition and disturbance regimes. Lower levels of light in deeper habitats filter species according to their heterotrophy (Cornell and Karlson, 2000). Note that these mechanistic explanations for the coral diversity gradient still need to be robustly tested with hypothesis-driven approaches (Roberts et al., 2019). Despite the ubiquity of the coral diversity gradient, coral community structure can vary greatly between reefs within and between regions due to the type, frequency intensity, and spatial scale of disturbances that occur (e.g., hurricanes, bleaching, outbreak of Acanthaster planci) (Connell et al., 1997; Hughes et al., 2012).

Local coral communities are also regionally enriched (i.e., their local richness is positively correlated with regional richness) (Cornell and Karlson, 2000, 1996; Karlson et al., 2004); also regional-local richness studies should be defined cautiously to avoid pseudoreplication (Srivastava, 1999). This general pattern is observed across diverse ecosystems and continents (Caley and Schluter, 1997) and implies that (i) coral communities are not saturated (i.e., local species richness is not limited by selection processes), and (ii) that their structure also depends on the migration of species from the regional pool, whose composition depends on dispersion and speciation (Cornell and Harrison, 2014).

Patterns of diversity at continental scales are shaped by the size of suitable habitats (larger habitats host more species), the presence of geological features (i.e., tectonic plates and mantle plume tracks) that act as steppingstones over long geological timescales, the distance from diversity hotspots, and the capacity of species to disperse and colonize diverse habitats (Bellwood and Hughes, 2001; Keith et al., 2013).

Finally, patterns of species richness across different spatial scales also differ between taxonomic or functional groups (i.e., set of species that share similar traits) (Hughes et al., 2012). Overall, these observations show that processes happening at different spatiotemporal scales, their interactions, and the capacity of species to compete, respond to disturbance and disperse need to be considered to understand patterns of biodiversity in coral communities. Experiments are needed to understand and predict how climate change and anthropogenic disturbances will affect the compositions of coral reef communities (Graham et al., 2014).
1.2.2. The effects of biodiversity on ecosystem functioning

Ecosystem functions are movements or storage of energy or material within an ecosystem that are mediated by the species present (Bellwood et al., 2018; Brandl et al., 2019). Biodiversity was first considered as a response variable and only abiotic factors, such as climate, disturbances, gradients of resources, could drive ecosystem functions. In the early 1990s, scientists started to investigate how changes in biodiversity affect ecosystem functioning. These investigations lead to a new sub-discipline, “biodiversity and ecosystem functioning”, which consists in quantifying the individual and collective contributions of species to ecosystem functions, such as biomass production, decomposition rates and nutrient cycling. Years of intense and highly debated research have led to the general conclusion that biodiversity plays a central role in ecosystem functioning, both as a response and as an explanatory variable (van der Plas, 2019). Additionally, several biodiversity effects have been identified. First, the presence of particular species in communities can affect ecosystem functioning independently of the number of species present via two possible effects: (1) the “dominance effect” or “mass ratio effect” (i.e., species contribute to ecosystem function proportionally to their abundance) (Grime, 1998), and (2) the “identity effect” (i.e., certain species contribute disproportionately more to ecosystem functions, regardless of their relative abundance) (Longo et al., 2013). Species can also contribute collectively to ecosystem functions, which results in a positive association between species richness and ecosystem functioning, i.e., the “diversity effect”. Three mechanisms can cause this positive association: (i) the “selection effect” (or “sampling effect”) suggests that communities with higher diversity have a higher probability to possess the most productive species by random draw from the species pool; under this effect, the productivity of communities cannot be greater than the productivity of a monoculture of the most productive species; (ii) the “complementarity effect” (or “niche complementarity”) suggests that a community of coexisting species uses resources more efficiently due to functional complementary, which leads to overyielding (i.e., the productivity of communities is greater than the productivity of a monoculture of the most productive species) (Loreau, 2000; Tilman et al., 2014); (iii) the “facilitative effect” suggests that co-occurring species can enhance functioning by facilitating the establishment and survival of other species, which also leads to overyielding (Cardinale et al., 2002; Jonsson and Malmqvist, 2003).
The ongoing high rate of species extinction on Earth affects the functioning of ecosystems globally and their capacity to provide essential services (Cardinale et al., 2012; Dirzo et al., 2014; Hooper et al., 2012; Naeem et al., 2012; Turvey and Cres, 2019). These effects are non-mutually exclusive and quantifying their respective influence is critical to anticipate how species extinction affects ecosystem functions. While it is generally agreed that higher diversity levels enhance functioning (Duffy et al., 2017; Tilman et al., 2014), there are no general rules about the respective contribution of these different effects, and the hundreds of experiments conducted on the biodiversity-ecosystem functioning relationship have yielded inconsistent results (Cardinale et al., 2011, 2007, 2006; Leš et al., 2001; Mokany et al., 2008; Sonkoly et al., 2019). The respective contribution of these different effects depends strongly on the type of ecosystem, the species present and the types of abiotic factors affecting the communities (van der Plas, 2019).

The majority of studies about the biodiversity-ecosystem functioning relationship have been conducted in species-poor temperate ecosystems, and rarely in tropical ecosystems, where biodiversity can be much higher. This constitutes an important gap because ecosystems in the tropics have a higher risk of species extinctions (Barlow et al., 2018; Finnegam et al., 2015) and there could be different “biodiversity-ecosystem functioning” relationships due to greater specialization (i.e., niche packing) (Clarke et al., 2017).

In coral reefs, evidence suggests that identity effects are prevalent over diversity effects (Brandl et al., 2019). For instance, the loss of structural complexity in Caribbean reefs was due principally to substantial loss of Acropora palmata and A. cervicornis, the two branching coral species that contributed the most to the calcification and habitat provisioning functions (Alvarez-Filip et al., 2013, 2009). Additionally, rates of reef growth in the western Atlantic reefs have been independent from coral species richness over the past 28 million years (Johnson et al., 2008). However, two recent experiments have shown that diversity effects also exist in coral communities. McWilliam and colleagues (2018) manipulated coral species richness and growth forms and found a significant diversity effect on primary productivity, which was due to a facilitation effect. Clements and Hay (2019) manipulated coral species richness in a field experiment and found a higher colony growth and survivorship (i.e., tissue mortality) in polycultures versus monocultures, which is consistent with a diversity effect. Further, they observed overyielding—indicating either complementarity or facilitation effects—earlier in their experiment, and a selection effect afterward, showing that the relative contribution of these
effects can vary in time. No other experiment testing the biodiversity-ecosystem functioning relationship have been conducted with corals.

1.2.3. The effects of biodiversity on resilience

The relationship between biodiversity and resilience has been a contentious topic in ecology (Cohen and Newman, 1985; Gardner and Ashby, 1970; Macarthur, 1955; May, 1972; McCann, 2000; Pimm, 1984) for several reasons. First, “resilience” and “stability” have had several different and confusing definitions (Desjardins et al., 2015; Ives and Carpenter, 2007; Quinlan et al., 2016). Holling (1973), who first introduced the concept of resilience in ecology, defined “stability” as the ability of a system to return to its equilibrium state after a disturbance, and “resilience” as “a measure of the persistence of a system and of its ability to absorb changes and disturbances and still maintain the same relationships between populations or state variables” (e.g., biomass, % cover). For Pimm (1984), “resilience” is a measure of “how fast state variables return toward their equilibrium after a perturbation”; for Carpenter and colleagues (2001), it is the “magnitude of disturbance that can be tolerated before a socioecological system moves to a different region of state space controlled by a different set of processes”; for Walker and colleagues (2004), “resilience” is the “capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks”. Resilience has also been decomposed into different attributes. For instance, Walker and colleagues (2004) defined (i) “latitude” (i.e., “the maximum amount a system can be changed before losing its ability to recover”), (ii) “resistance” (i.e., “the ease or difficulty of changing the system”), (iii) “precariousness” (i.e., “the current trajectory of the system, and how close it currently is to a limit or threshold”), and (iv) “panarchy” (i.e., how the three previous attributes are influenced by the states and dynamics of the system at scales above and below the focal scale). McClanahan and colleagues (2012) and Hodgson and colleagues (2015) suggested to represent “resilience” by two complementary aspects: (1) “resistance” (i.e., “the ability of a community to resist or survive a disturbance”), and (2) “recovery” (i.e., “the rate a community takes to return to its original condition”). We use this last definition in the rest of the thesis.

Confounding this debate are the multiple dimensions of disturbances, which Donohue and colleagues (2016) defined as “changes in the biotic or abiotic environment that alter the structure and dynamics of ecosystems”. Disturbances are characterised by their (i) magnitude (i.e., a
measure of change in the environment from its undisturbed state, such as the level of stress experienced by corals during a bleaching event, measured in degree heating weeks; Kayanne, 2017); (ii) duration, which is comprised between a short and shocking “pulse” (e.g., cyclones) and a long lasting “press” (e.g., ocean acidification); (iii) frequency; and (iv) directionality (i.e., how a disturbance changes in space and time; for instance, global bleaching events have increased in magnitude, frequency and spatial extent).

The definition of state variables has also confused the debate, because certain variables capture more information about resilience than other variables. Resilience and ecosystem functioning are not independent concepts because the capacity of a community to persist depends on its capacity to maintain essential ecosystem functions. Additionally, ecosystem functions can usually be supported by several different community structures. Consequently, metrics representing ecosystem functions rather than simply abundance and taxonomic community structure, such as species richness, are more informative (Oliver et al., 2015). In coral reefs, total coral cover has been used extensively to represent the general state of communities, and it was assumed that a reef with higher coral cover was “healthier” and more resilient. But total coral cover captures very little information about reef functioning and resilience compared to measures such as reef rugosity and functional diversity indices (Graham et al., 2015; Hughes et al., 2010; McWilliam et al., 2020).

To confuse the debate further, studies differed in their consideration of species interactions across trophic levels (“food webs”), which can have important implications for resilience. For instance, (i) weak interactions damp strong and destabilizing consumer-resource interactions; (ii) adaptive foraging stabilises consumer and producer populations and buffers environmental fluctuations; (iii) high modularity (i.e., weakly connected groups of highly connected species), nestedness (i.e., the degree to which specialists can only interact with subset of the species generalists interact with) and skewed degree distributions (i.e., the distribution of the number of links per species) limit extinction cascades; (iv) fast and slow “energy channels” generate asynchronous population dynamics between consumers (Kondoh, 2003; Landi et al., 2018; McCann, 2000; Rooney and McCann, 2012; Scheffer et al., 2012; Tilman et al., 2014).

Overall, results from theoretical and empirical experiments show that, in general, high biodiversity enhances the resilience of ecosystems (Hautier et al., 2015; Loreau et al., 2001; McCann, 2000), via different potential mechanisms and effects: (i) the “portfolio effect”, or
“statistical averaging”, predicts that in species rich communities, asynchronous fluctuations of independent populations generate stable community level aggregated variables such as biomass and productivity; (ii) the “insurance effect” or “compensatory fluctuations”, which results from the combination of “functional redundancy” (i.e., ecosystem functions are supported by multiple species) and “response diversity” (i.e., these species respond differently to disturbances) (Griffin et al., 2009; Mori et al., 2013). Importantly, ecosystem functioning and resilience are not independent concepts, so the effects described in the previous section (§1.2.2) can also contribute to resilience (Loreau and de Mazancourt, 2013). For instance, in a community where a dominance effect is strong, the resilience of the ecosystem will depend largely on the capacity of the dominant species to resist or recover.

There is considerable variability among the results from empirical and simulated experiments because of these many confounding factors (Griffin et al., 2009; Landi et al., 2018; Tilman et al., 2014). The majority of experiments manipulating species richness within a single trophic level have reported a positive effect of diversity on stability—defined as the inverse of the coefficient of variation of productivity or biomass—which is generally due to a combination of species asynchronous fluctuations and overyielding—caused by complementarity and/or facilitation effects. The lack of positive correlation is usually caused by species synchrony due to limited response diversity or low evenness (Griffin et al., 2009). Comparatively, measures of resistance and recovery have rarely been used, and results from experiments are highly dependent on the identity or dominance effects and the resilience of the associated species. For instance, Lepš and colleagues (1982) conducted a plant community experiment and found that diversity was positively associated to resistance and negatively to recovery because the species rich community was dominated by resistant species and the species poor community by species that recovered rapidly after disturbances. Contrastingly, DeClerck and colleagues (2006) and Steiner and colleagues (2006) found a positive relationship with recovery because of complementary effects after the disturbance due to increased resource availability, and a selection effect, where communities with higher richness were more likely to have a species with strong recovery and competitive capacities, respectively.

The majority of studies that have investigated the biodiversity-resilience relationship in coral reefs concern fish communities. For instance, Mellin and colleagues (2014) found a positive relationship between beta-diversity and stability (i.e., the spatial and temporal turnover of species
abundances, respectively) which was caused by asynchronous population fluctuations due to
differential response to disturbances; Nash and colleagues (2016) demonstrated that functional
redundancy and response diversity across functional groups and size classes of herbivores
promote coral communities recovery; Burkepile and Hay (2008) manipulated the number
of herbivorous fish species in a caging experiment and found that species richness enhanced
herbivory via a complementary feeding effect, which increased recruitment and reduced
mortality of corals. Contrastingly, Bellwood and colleagues (2006a) conducted a caging
experiment and found that the reversal of a coral-algae phase-shift was due to the presence of
one particular herbivorous fish species and was independent from its abundance and the presence
of 43 other species in the community. This example illustrates a strong identity effect and a lack
of functional redundancy, which might be prevalent in coral reefs (Hoey and Bellwood, 2009).
Further, Mouillot and colleagues (2014) found that more than one third of coral reef fish species
in tropical reefs are functionally unique, suggesting that the functions they support have no
insurance.

Functional redundancy in coral communities can also be limited, as illustrated by the
reduction of calcification and architectural complexity and in Caribbean reefs due to the
substantial loss of branching Acropora palmata and A. cervicornis (Bellwood et al., 2004; Mora
et al., 2016). This particular lack of redundancy is considered one of the main factors explaining
lower resilience of Caribbean reefs compared to reefs in the Indo-Pacific (Roff and Mumby,
2012). But the higher species diversity of coral communities in the Indo-Pacific reefs might not
provide resilience to the calcification and habitat provisioning functions because of low response
diversity. Indeed, branching and plating species contribute the most to these functions but have
similar sensitivities to disturbances such as hurricanes, global warming and diseases (Mora et al.,
2016).

Beside these clear relationships between diversity and resilience, there has been only one
test to quantify links between measures of coral community diversity and resilience. Zhang
and colleagues (2014) measured the associations between coral species richness and resistance
and recovery from 41 field studies conducted in 82 reefs across the tropics and found that
species-rich communities were less resistant and did not recover faster than reefs composed of
fewer species. The negative relationship between richness and resistance was likely due to the
dominance of branching or plating species in species rich communities—due to selection
effects—and to their high sensitivity to disturbances. The fact that species richness did not influence recovery remains unexplained. Importantly, no experiment has been conducted to test the biodiversity-resilience relationship with corals.

1.3. Functional diversity

Despite the identification of the effects involved in the relationships between biodiversity and ecosystem functioning and resilience, important knowledge gaps prevent the dissociation and quantification of the individual and collective contributions of species to the dynamics of ecosystems, which impedes our understanding and capacity to predict the effects of environmental changes on ecosystem functioning and services (Bellwood et al., 2018; Brandl et al., 2019; Bridle and Rensburg, 2014; Hughes et al., 2017a). These gaps originate from the prevalent use in early studies of diversity metrics, such as species richness, Shannon diversity index (Shannon, 1948), Simpson's index (Simpson, 1949) and their associated measure of evenness (Desrochers and Anand, 2004), that do not describe how individual species contribute to ecosystem functions, respond to their environment and interact with other species. For instance, this explains why species richness does not necessarily provide functional redundancy and response diversity (Mori et al., 2013; Mouillot et al., 2014).

Species traits (i.e., measurable properties of organisms, such as growth rate, body size and root depth that are used comparatively across species) and in particular “functional traits” (i.e., traits associated with performance processes such as growth, reproduction and survival, or to ecosystem functions) represent a possibility for mechanistically linking diversity, the abiotic environment, biotic interactions and ecosystem functioning (Bellwood et al., 2018; McGill et al., 2006; Violle et al., 2007). Functional diversity (i.e., the diversity of functional traits in a community) can be measured in different ways. The most basic approaches consist in defining functional groups based on broad physiological and morphological features and eventually taxonomy. For instance, Hughes and colleagues (2012) defined functional groups by separating Acropora species into morphological groups because growth forms are associated with certain performance processes. Using functional groups is particularly convenient to assess functional redundancy (e.g., Kang et al., 2015). But a coarse classification potentially neglects important
interspecific functional differences inside groups (Cadotte et al., 2009), or the traits used for the classification are loosely associated to functions (Bellwood et al., 2018, 2006b).

Functional diversity can also be represented continuously by considering each trait as a dimension in a functional space. This approach originates from Hutchinson (1957) who defined the “n-dimensional hypervolume” to quantify species fundamental niches, where each of the n dimensions represents a biotic or abiotic variable (e.g., temperature, food size) that describes ecological properties of species in the absence of competition. But the identification and quantification of species fundamental niches is challenging because species are only observed in their realised niches due to competition. Because functional traits directly link species to their environment, Violle and Jiang (2009) proposed to replace the original niche axes with functional traits, and defined “trait niches”, i.e., “functional spaces”.

The representation of species in their functional space has offered new avenues to quantify diversity, and several complementary indices have been defined, such as (i) functional richness (FRic), i.e., the volume occupied by a community in the functional space; (ii) functional evenness (FEve), i.e., how regularly species abundances are distributed in the functional space; (iii) functional divergence (FDiv), i.e., how far high species abundances are from the centre of the functional space; (iv) functional dispersion (FDis), i.e., the mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre, 2010; Mason et al., 2005; Mouchet et al., 2010; Villéger et al., 2008).

Because they represent mechanistic links between species and ecological processes, traits and their associated diversity metrics are superior to previous measures of diversity for explaining and predicting the effects of biodiversity on assembly rules (Kraft et al., 2015b; Kunstler et al., 2016; Lasky et al., 2014; Pavoine and Bonsall, 2011), ecosystem functioning (Cadotte, 2017; Gagic et al., 2015; Tilman et al., 1997; van der Plas, 2019), and resilience and stability (Kang et al., 2015; McLean et al., 2019; O’Brien et al., 2014; Pillar et al., 2013; Spasojevic et al., 2016). For instance, the theory predicts that species coexistence depends on the balance between interspecific differences in fitness—large differences lead to competitive exclusion—and resource use—large niche differences lead to resource partitioning and coexistence (Chesson, 2000; Vellend, 2010). Kraft and colleagues (2015) tested this theory by conducting a plant experiment and found that competitive exclusion between pairs of species was explained by single traits associated to fitness (e.g., late phenology, and larger maximum height, and leaf
area), while coexistence was explained by a combination of traits associated to resource acquisition (e.g., root length, canopy shape), suggesting either that mechanisms of resource partitioning were specific to species pairs, or stabilising niche differences involved multiple traits simultaneously. Gagic and colleagues (2015) analysed eight datasets of five animal groups (i.e., bees, carabid beetles, earthworms, soil nematodes and dung beetles) and found that ecosystem functions (i.e., pollination, biocontrol, bioturbation, nutrient cycling, dung removal) were best explained by either the community weighted mean of a single trait—revealing identity effects—or by FEve and FDiv, which were positively associated to functioning—revealing complementarity effects. McLean and colleagues (2019) analysed the evolution of fish community composition in the Seychelles Islands and English Channel and found that communities with stable trait structures had higher trait redundancy, while unstable communities had lower trait redundancy—i.e., insurance effect—and were dominated by pelagic species sensitive to disturbance; in the Seychelles, these species were small, gregarious corallivores and planktivores, which are particularly sensitive to coral bleaching.

Further, trait correlations and the involvement of traits in multiple processes can inform the resilience of ecosystem functions (Oliver et al., 2015). Lavorel and Garnier (2002), and subsequently Suding and colleagues (2008) defined the “trait-based response-effect” framework in order to predict how change in environmental factors can affect the functioning of terrestrial plant ecosystems. The framework requires identifying “effect traits” (i.e., those involved in ecosystem functions) and “response traits” (i.e., those implicated in response against disturbances). If a trait is both the response and effect, or if there is a correlation between an effect and a response trait, it is possible to predict the effect of a disturbance on an ecosystem function. The framework was further developed to consider multiple ecosystem functions simultaneously and their possible synergies or trade-offs (Lavorel and Grigulis, 2012), and multiple trophic levels (Lavorel et al., 2013). Such framework had yet to be applied to corals prior to this thesis project (Carturan et al., 2018).

Functional traits have been used to conceptually understand ecological processes in coral reefs for decades (e.g., Chappell 1980; Highsmith 1981; Porter 1976; Sheppard 1979). Recent efforts to quantify the link between individual coral traits to community composition have improved our understanding of community assembly processes (e.g., Keith et al., 2015, 2013). For instance, Sommer and colleagues (2014) compared the co-occurrence of coral species and their functional
dissimilarity—using six functional traits—along a latitudinal environmental gradient. They found that the environment filtered species principally via corallite size and colony morphology, suggesting that energy acquisition and resistance to hydrodynamic forces are determinant assembly processes for communities in high latitudes in the Great Barrier Reef. Efforts to quantify links between traits and ecological processes have improved our capacity to predict (i) species response to hydrodynamic disturbances (Edmunds et al., 2014; Madin et al., 2014; Madin and Connolly, 2006) and (ii) bleaching (Swain et al., 2016a), (iii) outcomes of competitive interactions (Precoda et al., 2017), (iv) reef structural complexity (Zawada et al., 2019b), (v) polyp fecundity (Álvarez-Noriega et al., 2016) and (vi) larval competency (Figueiredo et al., 2013).

The Coral Traits Database (Madin et al., 2016a) constitutes a significant advancement for adopting trait-based approaches in coral ecology (Madin et al., 2016b). The organisation of the coral trait database allows to identify functional trade-offs among species and to compare the functional structure of communities in space and time. For instance, Darling and colleagues (2012) used 14 functional traits and Grime’s (1977) C-S-R triangle to classify 143 coral species into competitive (C), stress-resistance (S), weedy (ruderal, R) and generalist life history strategies. This classification can help predict dynamics of coral communities in disturbed habitats because each group responds differently to single and combined disturbances (Darling et al., 2013). McWilliam and colleagues (2018b) used seven functional traits to compare FRic and functional redundancy across 12 biogeographically distinct provinces, and highlighted where ecosystem functions might be missing or have limited insurance. McWilliam and colleagues (2020) used seven effect traits to assess the recovery of coral communities after pulse disturbances and showed that communities failed to recover their functional structure despite recovering pre-disturbance cover, suggesting a lack of response diversity.

Traits and measures of functional diversity have often been used as proxies for ecosystem functioning and resilience, but quantitative causal links are lacking. Conducting experiments and field surveys in order to establish these links is a pressing objective for coral reef ecologists (Bellwood et al., 2018; Brandl et al., 2019; Graham et al., 2014).
1.4. Modelling coral reef resilience and complexity

1.4.1. Coral reefs as complex systems

Coral reefs, like other ecosystems, are adaptive complex systems because the dynamics of their populations, communities and meta-communities (i) are influenced by factors and processes operating at large (e.g., speciation, larval connectivity) and small (e.g., competition, environmental filtering, random drift) spatiotemporal scales, (ii) emerge from the additive contribution of individual polyps, colonies and individuals from other species via self-organisation, (iii) change as the system structure evolves and adapts to new conditions, (iv) are non-linear and chaotic (Anand et al., 2010; Dizon and Yap, 2006; Holling, 2001; Levin, 1998; Parrott, 2002; Solé et al., 1996; Solé and Bascompte, 2006). Coral reefs are notoriously known for having non-linear dynamics characterized by tipping points (i.e., threshold), phase shifts (i.e., significant changes in community structure and composition) that eventually become regime shifts if the changes are permanent, multiple (or alternative) stable states (or basins of attraction) and hysteresis (i.e., asymmetric response of a system to a symmetric reversal of an environmental variable) (Hughes et al., 2010; Knowlton, 1992; Nyström et al., 2008, 2000). These dynamics are caused by the structure of the food web and feedback processes (Scheffer et al., 2012), the latter being numerous and potentially interacting (van de Leemput et al., 2016).

For instance, the non-linearity of the classic coral to macroalgae phase shifts (Mumby et al., 2007), which in some reefs corresponds to a shift between two stable states (Schmitt et al., 2019), is due to a positive feedback where corals create a complex habitat that supports herbivorous fish populations, which in turn help corals to grow and recruit by consuming competing macroalgae. Alternatively, the decrease of structural complexity due to the loss of species with complex growth forms lead to a decrease in herbivory, an increase in macroalgae and finally a decrease of coral cover and associated complexity (Mumby, 2009). Additional feedback processes, such as the decreased palatability of mature algae, can reinforce the alternative state of the community (Mumby et al., 2007).
1.4.2. Models for coral reefs

A model is an abstract representation of a system or process. Ecosystems being infinitely complex, models in ecology always represent a simplified representation of reality. The level of ecological complexity that a model describes depends on its intended application. Minimal models represent a handful of variables (e.g., species populations) and processes (e.g., predation, growth, recruitment), and are consequently easy to parameterise, analyse and understand. Minimal models are useful for understanding general concepts, such as fluctuations in predator-prey population dynamics and hysteresis, but do not capture enough ecological details (e.g., species diversity, spatial interactions) to accurately predict the dynamics of real ecosystems. On the other side of the spectrum, complex models embrace complexity by representing multiple variables, processes and features (e.g., multiple dimensions and scales), and can be used as supporting tools for managing ecosystems. However, they require a substantial amount of empirical data for their parameterisation and calibration and are hard to analyse and understand.

Models of different types and complexity have been developed to understand and predict coral community dynamics (Kubicek and Borell, 2011; Weijerman et al., 2015). Differential equation modelling has been the most popular approach. These models represent populations at the population level (i.e., top-down approach), which prevents from implementing process that occur at the scale of individuals, and they usually do not represent space explicitly. These models have been useful to understand or predict feedbacks and multiple stable states in coral reefs (Fung et al., 2011; González-Rivero et al., 2011; van de Leemput et al., 2016), prey-predator dynamics (Antonelli and Kazarinoff, 1984), coexistence between different species (Connolly and Muko, 2003; Muko et al., 2001), resilience against multiple disturbances (Anthony et al., 2011; Blackwood et al., 2011) and future potential disturbance regimes (Fabina et al., 2015; Riegl et al., 2013). Most differential equation models are relatively simple, but complex implementations exist. For instance, McClanahan (1995) developed a multi-trophic energy-based model to predict how different fishing management scenarios affect primary production, herbivory and calcium carbonate production. Certain complex models, that notably implement larval dispersal at large scales, have been developed to support the management of real coral reefs (Melbourne-Thomas et al., 2011b, 2011a; Wolanski et al., 2004).

Population matrix models represent the discrete and non-spatial demographic structure (e.g., colony size class distributions) of populations. They are used to measure vital rates (i.e., survival,
growth and reproduction) of each demographic group and can help understand demographic dynamics and predict future population structures in local communities. They do not explicitly represent space and detailed mechanistic processes. Population matrix models have been used to understand processes influencing coral community dynamics (Riegl and Purkis, 2015; Tanner et al., 1994, 1996), assess the resilience of populations under different disturbance regimes (Andres et al., 1993; Done, 1988), inform active restoration practises by quantifying the minimum size and number of coral fragments needed to support a declining coral population (Mercado-Molina et al., 2015).

Integral projection models are an extension of population matrix models and describe population structures and related vital rates continuously. For instance, Kayal and colleagues (2018) used integral projection models to predict the population recovery of three coral species in different sites in Mo’orea (French Polynesia) after being affected by multiple disturbances. Integral projection models are also more flexible than matrix models and can implement mechanistic, eventually trait-related processes (Edmunds et al., 2014), such as the effect of water velocity on colony dislodgement and photosynthetic acquisition as a function of colony size and growth form (Madin et al., 2012b), and the effect of ocean acidification on calcification rate (Madin et al., 2012c). Combining trait-based and demographic approaches allows to represent more mechanistic and detailed representations of ecological processes and to predict population dynamics under novel environmental conditions (Salguero-Gómez et al., 2018; Smallegange and Ens, 2018).

Cellular automata are spatially explicit object-based (i.e., they represent a system by discrete entities whose states are described by a set of state variables and behaviour is determined by a set of rules) and computational (i.e., their variables, parameters and rules are encoded in an executable programming language) models. The objects are cells in a grid whose states are updated in discrete time steps according to rules that dependent on the states of neighbouring cells (Parrott and Kok, 2000). Cellular automata are appropriate to simulate the emergence of dynamics from lower scale processes (i.e., bottom-up approach). In coral reefs, they have been used to understand how spatially constrained and unconstrained grazing mediate competitive interactions between corals and algae (Sandin and McNamara, 2012) and recovery after pulse disturbances (Brito-Millán et al., 2019; Eynaud et al., 2016), to quantify the strength of feedback processes necessary to generate alternative stable states (Muthukrishnan et al., 2016), and to
predict community composition under different environmental scenarios (Langmead and Sheppard, 2004; van der Laan and Bradbury, 1990; Wakeford et al., 2008).

Agent-based (or individual-based) models are a more flexible object-based modeling approach compared to cellular automata because they can represent cells in a grid as well as other entities (or agents) that can move, interact in diverse ways and eventually learn and make informed decisions. They are also versatile and can implement diverse types of sub-models, such as statistical models, differential equations and networks. Like integral projection models, they can combine trait-based and demographic approaches (Smallegange and Ens, 2018) but have the advantage of being able to represent spatial interactions and distributions of individuals explicitly (Zakharova et al., 2019). Consequently, agent-based modeling is considered the most appropriate approach available to simulate the complex dynamics of ecosystems (DeAngelis and Grimm, 2014; Egli et al., 2019; Grimm and Railsback, 2005). For coral reefs, agent-based models have been used to inform restoration practices (Sleeman et al., 2005), understand the links between disease spread and colony spatial distribution (Brandt and McManus, 2009), predict under different disturbance regimes or management scenarios the composition of the coral community (Kubicek et al., 2012; Kubicek and Reuter, 2016; Mumby, 2006; Tam and Ang, 2012, 2009), eventually accounting for climate adaptation of the symbiont (Ortiz et al., 2014b) and corals (Kubicek et al., 2019), reef rugosity (Bozec et al., 2015), the existence of thresholds and multiple stable states (Bozec and Mumby, 2015; Mumby, 2009; Mumby et al., 2007). With proper calibration, agent-based models have been used to predict the composition or resilience of real coral communities under future climate and management scenarios (Edwards et al., 2011; Mumby et al., 2014; Ortiz et al., 2014a).

Agent-based models have been criticized for being complex, and difficult to parameterize, analyze and communicate. However, empirical, trait-based approaches and trait databases have become more prevalent, facilitating model parameterization. Additionally, standardized protocols—such as the Overview, Design concepts and Details (ODD) protocol and hierarchically structured validation—are now well-defined to help communicate and validate agent-based models (Grimm et al., 2020, 2010, 2006; Kubicek et al., 2015). A model to explore the effects of coral species and functional diversity on the dynamics of their community had yet to be created prior to this thesis research (Carturan et al., 2020).
1.5. Objectives

The functional diversity of coral communities in the Anthropocene is changing, which can compromise their capacity to provide complex habitats that support high biodiversity and resilience to disturbances. The adoption of trait-based approaches has significantly advanced our understanding of the processes involved in community assembly and ecosystem functioning and resilience. But predicting the outcomes of multiple interacting diversity-related processes is extremely challenging because ecosystems are complex. Experiments aiming at quantifying relationships between measures of biodiversity and measured of ecosystem states or dynamics help unraveling this complexity by testing the existence of these relationships and providing insight on the mechanisms generating them. Such experiments are lacking with coral species, which is an important research gap because these relationships, once established, can have significant applications for management. For instance, finding which aspect of coral diversity have to be enhanced for the resilience of a given reef can inform restoration practices. The goal of this PhD is to explore the biodiversity-resilience relationship with a virtual experiment, which we achieve by completing the three following objectives.

**Objective 1: To develop a framework that mechanistically and temporally links disturbances, coral diversity and ecosystem functioning (Chapter 2).** Building a model to explore the functional diversity-resilience relationship with coral communities require a framework to mechanistically link disturbances to species to ecosystem processes and functions. Suding and colleagues’ (2008) trait-based response and effect framework developed for plant ecosystems is appropriate but had not been applied to corals. Additionally, the framework does not distinguish between processes of resistance from processes of recovery, which is an important limitation considering that the model has to represent the temporal dynamics of communities. Our first objective is consequently to adapt the framework to corals species.

**Objective 2: To build, analysis and validate an agent-based model that can be used as a virtual experimental platform (Chapter 3).** Manipulating coral diversity experimentally is logistically extremely challenging, which greatly limits the number of species that can be manipulated and the spatial and temporal extents of experiments. Simulation models can
overcome these limitations, but there was no existing model that could be used for this purpose. Our second objective is to use the framework established in Chapter 2 and build a mechanistic model that is sufficiently detailed to consider coral functional diversity as an independent variable.

Objective 3: To conduct a virtual experiment to quantify the relationship between FRic and measures of resilience (Chapter 4). The diversity-resilience relationship has not been investigated experimentally with coral species. Our third objective is to address this gap using the model developed in Chapter 3 to conduct the experiment and the framework established in Chapter 2 to explain the results.
Chapter 2: A modified trait-based framework for assessing the resilience of ecosystem functions provided by coral reef communities

2.1. Synopsis

In this chapter, we define the conceptual framework that allows to mechanistically link disturbances to coral species to processes and functions. The framework represents the core concepts behind the model we developed (Chapter 3) to conduct the functional diversity-resilience experiment (Chapter 4).

We build on Suding and colleagues’ (2008) trait-based response and effect framework by distinguishing between “resistance traits” and “recovery traits”, so that coral traits associated to processes of resistance to disturbances and recovery can be identified and their mechanistic links with these processes can be assessed and eventually quantified. We start by presenting our “effect-resistance-recovery traits” framework. We then illustrate its applicability by focusing on habitat provisioning, which is a key ecosystem function that supports diverse services. We review the literature to identify relevant traits, and to ascertain their influence on (i) the habitat provisioning function, (ii) the resistance against cyclones or bleaching events, and / or (iii) in recovery processes. Based on our findings, we assemble an extensive database of trait data, drawing from the Coral Trait Database (Madin et al., 2016a) and from the primary literature. Using these data, we then quantify correlations and overlaps between the effect, resistance and recovery traits. We then demonstrate by way of a simple simulation model how these trait correlations and our proposed framework can be used to anticipate the resilience of the habitat provisioning function in a given coral community. Lastly, we discuss the different benefits the framework could provide to coral reef science.

This chapter has been published in Ecosphere (Carturan et al., 2018).
2.2. The effect-resistance-recovery traits framework

The effect-response traits framework defined by Suding and colleagues (2008) relies on the assumption that functional traits determine ecosystem functions and community response to disturbances (Figure 2.1 top row). In consequence, the order in which species are extirpated due to an environmental change is predicted with response traits. Predictions about the effects on the focal ecosystem function are informed by (i) effect traits and their correlations with response traits, and (ii) traits that are simultaneously implicated in effects and responses, a scenario we refer to as “trait functional overlap”. We propose to build on this framework by distinguishing between “resistance” and “recovery” traits (both being “response” traits) (Figure 2.1), a distinction we believe instructive for coral species as it allows for considering pulse disturbances (see discussion). In the following we consider how the existence and nature of correlations between effect and response traits could influence two key associations that are relevant to management strategies: (1) the association between disturbance intensity and the provisioning of an ecosystem function (i.e., the degree to which the function is maintained); and (2) the association between time since disturbance and the provisioning of the same ecosystem function.

For reference, we include in our framework a series of null expectations, derived from a scenario in which the response capacities of individual colonies are drawn at random from those of species present in the community. This removes any correlation between effect and response within the community (dashed lines in Figure 2.1). With no correlation between effect and resistance traits (Figure 2.1A1), the provisioning of function will decline (Figure 2.1A2) or recover as expected with the null model (Figure 2.1A3). When effect and resistance traits are positively correlated (Figure 2.1B1) (i.e., the most resistant species contribute most to the function), we can expect a smaller change of the ecosystem function (Figure 2.1B2) compared to the former scenario. The function is more resistant to disturbance. We also expect a faster recovery of the function under the scenario of positive trait correlation (i.e., the species contributing most to the function recover faster) (Figure 2.1B3). In these cases, the level of function will surpass null model expectations. When effect and resistance traits are negatively correlated (Figure 2.1C1) (i.e., the species contributing the most to the service are the most vulnerable), functioning is expected to decline more rapidly in response to increasing disturbance intensity (Figure 2.1C2). The function is considered non-resistant. We also expect a slower
recovery of function in this scenario (Figure 2.1C3), and the level of the function will be below null model expectations.

With this framework in place, our objective is to apply it to a coral reef example by (i) synthesizing knowledge and assumptions about traits and their respective roles in effect, resistance and recovery, (ii) quantifying associations among traits, and (iii) demonstrating our capacity to predict the resilience of an ecosystem function using the framework and the available data. Lastly, (iv) we discuss the benefits of applying this framework and how it helps prioritizes future research efforts.
Figure 2.1. The effect-resistance-recovery traits framework: assumptions about traits’ roles in an ecosystem process (top row) and correlations between effect and resistance or recovery traits (A1, B1, C1) allow for predicting the resistance and the recovery of the function against a disturbance. Solid lines represent the level of the ecosystem function just after a disturbance (A2, B2, C2) or its post-disturbance recovery (A3, B3, C3); the dashed black lines indicate null expectations (i.e., the capacity of individual colonies to respond is randomly drawn from the different species-specific capacities of the species present in the community).

2.3. Materials and methods

All data processing and analysis as well as simulations were conducted using R (version 3.4.0, R-Core Team 2016). The functional traits data frame we compiled as well as the R scripts for
statistical analyses, figures and model simulations are available on the Open Science Framework platform (https://osf.io/b76dt).

2.3.1. **Knowledge synthesis and evaluation of assumptions**

We first reviewed the literature about the traits and assumptions of their involvement in the habitat provisioning function, resistance against cyclones and bleaching events and post disturbance recovery. We also documented existing evidence of trait correlations in the literature. We used the online academic search tool Google Scholar to search for published peer-reviewed sources using coral traits and processes’ names as search terms. We then collected trait values from the coraltraits.org database (https://coraltraits.org, Madin et al. 2016a), and other sources from the primary literature (Table A1). We limited our analysis to zooxanthellate coral species, as our main focus is on species forming typical tropical reef habitats (Stanley and Cairns, 1988). We considered a total of 828 coral species after correcting for nomenclature using the World Register of Marine Species (WoRMS, http://www.marinespecies.org/) as a reference. If after correcting for names, duplicate species had highly contrasting trait values, we discarded the values of species whose names had been updated. Trait values were averaged at the species level. Data were typically reported as single values, means, or medians. If sample sizes were reported alongside means or medians, we calculated weighted averages, treating medians as means for consistency. Additional trait information is summarized in Table A1.

We used the Bleaching Response Index (taxon-BRI) to further assess the assumptions about resistance traits in relation to bleaching response. The taxon-BRI represents the species-specific average percentage cover that bleached or died during an event. It was obtained from 2036 records concerning 316 sites, 374 taxa (304 when considering species level values and after correcting for taxonomic errors), between 1982 and 2006 by Swain et al. (2016c).

2.3.2. **Trait associations analyses**

We quantified associations between pairs of traits. Substantial gaps in the trait data precluded creation of a single, multivariate trait model. Correlations between pairs of numeric or ordinal traits were quantified using Spearman rank correlation as most bivariate relationships did not conform to assumptions of Pearson correlation analysis. When evaluating maximum colony
diameter in relation to “mode of larval development”, which has only two possible values (brooder and spawner), we used a permutation test (10000 permutations) to test the null hypothesis of no difference in the average maximum colony diameter among brooders and spawners. We used a $\chi^2$ contingency test to test for an association between growth form (an ordinal variable) and mode of larval development, and P-values were calculated via resampling methods to cope with the sparseness of the data in certain categories (Long et al., 2010). In order to facilitate interpretations of graphs, traits were log-transformed, or logit-transformed in case the trait is expressed as a proportion (Warton and Hui, 2011).

2.3.3. Virtual case study (prediction)

We illustrate our framework using simulations, because key data and knowledge gaps (see Discussion) presently limit the applicability of our framework to real world coral communities. Our simulation model, implemented in R, illustrates how the assumptions we documented from the literature (Table A1) and the trait functional overlaps and correlations we quantified (Figure 2.2; Figure A2; Figure A3; Figure A4) can be used to predict the resilience of an ecosystem function (Figure 2.1). Details of the model are presented in Appendix A. In brief, the model represents a virtual coral community composed of a few functionally distinct species whose characteristics collectively reflect the diverse associations we found between effect, resistance and recovery. The focal community is subjected to a pulse-disturbance, to which the constituent species respond according to their capacity to resist. The different populations then recover at their respective rates. Each species contributes differently to the habitat provisioning function. The total amount of habitat provided by the community at any given time emerges from the cumulative contribution of the populations. In order to consider the effect of disturbance intensity and larval connectivity, we simulated eight different scenarios: two levels of larval connectivity (i.e., high and low) $\times$ two different disturbances (i.e., cyclone and bleaching) $\times$ two disturbance intensities (i.e., moderate and intense). For simplicity we assume that (i) the disturbances only affect the focal community; (ii) the ecosystem is far from a tipping point so the disturbances cannot push the ecosystem into an alternative stable state and the community always recovers; (iii) the regional pool comprises the same species as the ones present in the focal community.
For reference, we also simulated communities in which the capacity to resist the disturbance and to recover were assigned at random among species, and thus any inherent covariation between effect and response was removed. This provides an appropriate null model against which to compare the patterns emerging from the main simulations. For example, if the species contributing the most to the function are the ones having the highest capacity to recover (Figure 2.1B1), the recovery of the function is expected to be faster, on average, than under the null model outcomes (Figure 2.1B3).

2.4. Results

2.4.1. Coral traits

From the literature we identified 25 relevant functional traits in total: two effect traits for the habitat provisioning function, two for the resistance against cyclones, 15 for the resistance against bleaching events and 11 recovery traits (certain traits fall in several categories due to trait functional overlap) (Table 2.1). Fourteen of the 25 traits were excluded from our correlation analyses for one or more of the following reasons: (i) data were available for too few species (e.g., age and size at maturity, colony fecundity, HSP concentration, MAAs), (ii) the values of the trait depended strongly on other factors (e.g., colony fecundity with size of the colony, egg size and heterotrophic rate with stress level), (iii) the measurements were too imprecise (e.g., generation length: out of the 695 species for which information is available, 673 have a 10 year generation length) (iv) no consistent methods for measuring the trait have been established (e.g., capacity to generate viable fragments, mucus production, physiological integration) or, (v) the trait is assumed to be associated with another trait but the information is rarely available at the species level (e.g., reproduction frequency and symbiont acquisition with mode of larval reproduction).
Table 2.1. Coral functional traits involved in the “habitat provisioning” function, resistance and recovery against disturbances (cyclone and coral bleaching). The table shows the type of process(es) (effect, Eff.; resistance, Res.; recovery, Rec.), function (habitat provisioning, Hab), and disturbance(s) (cyclone, Cyc; bleaching, Blea) in which each trait is implicated. A summary of the corresponding mechanisms at play and associated references are provided, as well as the number of species for which the trait value is available. Energy reserves and fluorescent pigment concentration were assessed using lipid and chlorophyll “a” concentration, respectively.

<table>
<thead>
<tr>
<th>Functional traits</th>
<th>Type</th>
<th>Explanation</th>
<th># sp Used here</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age and size at maturity</td>
<td>Both</td>
<td>Later maturity causes lower post disturbance recruitment rates but there is a trade-off between starting reproduction early, while being still very vulnerable</td>
<td>3 for age; 7 for size</td>
<td>(Hall and Hughes, 1996; Hughes, 1984)</td>
</tr>
<tr>
<td>Capacity of fragment regeneration</td>
<td>Cyc</td>
<td>Reduced mortality rate, increased recovery rate</td>
<td>Proxy? -</td>
<td>(Highsmith, 1982)</td>
</tr>
<tr>
<td>Colony fecundity</td>
<td>Both</td>
<td>Higher fecundity implies higher potential offspring. Proxy for energy reserves (?)</td>
<td>12 -</td>
<td>(Álvarez-Noriega et al., 2016)</td>
</tr>
<tr>
<td>Coralith area</td>
<td>Blea</td>
<td>Enhance heterotrophy by determining the range size of prey</td>
<td>713 ✓</td>
<td>(Darling et al., 2012; van Woesik et al., 2012a; Houlbrèque et al., 2009)</td>
</tr>
<tr>
<td>Colony maximum diameter</td>
<td>Hab</td>
<td>Colonies with more complex morphologies contribute more to the architectural complexity</td>
<td>307 ✓</td>
<td>(Darling et al., 2017)</td>
</tr>
<tr>
<td></td>
<td>Cyc</td>
<td>Colonies with more complex morphologies tend to be more fragile as they grow bigger; opposite for simpler ones</td>
<td></td>
<td>(Madin et al., 2014; Madin and Connolly, 2006)</td>
</tr>
<tr>
<td></td>
<td>Blea</td>
<td>Higher S/V ratio facilitates intake of DIC but creates a boundary layer that reduces mass transfer and reduces feeding rate because of “shading effect”</td>
<td></td>
<td>(Houlbrèque et al., 2009; Kim and Lasker, 1998; Porter, 1976; van Woesik et al., 2012b; Wooldridge, 2014)</td>
</tr>
<tr>
<td>Egg size</td>
<td>Both</td>
<td>Smaller eggs have a shorter time to motility which favors local recruitment</td>
<td>25 -</td>
<td>(Figueiredo et al., 2013)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bigger egg implies more lipid reserves and so higher probability of recruitment (not proven for coral)</td>
<td></td>
<td>(Álvarez-Noriega et al. 2016 and references therein)</td>
</tr>
<tr>
<td>Energy reserves</td>
<td>Blea</td>
<td>Reduces coral susceptibility, increases recovery rates and facilitates acclimation.</td>
<td>8 ✓</td>
<td>(Anthony et al., 2009; Grottoli et al., 2014)</td>
</tr>
<tr>
<td>Fluorescent pigment concentration</td>
<td>Blea</td>
<td>Provides photoprotection, but not under higher temperature (?)</td>
<td>22 ✓</td>
<td>(Baird et al., 2009a; Hidaka, 2016; Salih et al., 1998)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Dove, 2004)</td>
</tr>
<tr>
<td>Functional traits</td>
<td>Type</td>
<td>Explanation</td>
<td># sp</td>
<td>Used here</td>
</tr>
<tr>
<td>-------------------</td>
<td>------</td>
<td>-------------</td>
<td>------</td>
<td>-----------</td>
</tr>
<tr>
<td>Generation length</td>
<td>Both</td>
<td>Older colonies are more fertile</td>
<td>845</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Both</td>
<td>Shorter generation length increases recovery rate (weedy species)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth form</td>
<td>Hab</td>
<td>More complex morphologies contribute more to the architectural complexity</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cyc</td>
<td>More complex morphologies are more fragile</td>
<td>816</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>Blea</td>
<td>Modulates thickness of boundary layer and so mass transfer; Modulates DIC diffusion from water to symbiont. Mediates predation rate (heterotrophy) depending on S/V ration and “shading effect</td>
<td>20</td>
<td>✓</td>
</tr>
<tr>
<td>Growth rate</td>
<td>Blea</td>
<td>Rapid recovery of free space</td>
<td>125</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>Be</td>
<td>Allows to meet the required DME despite the loss of the symbiont</td>
<td>Proxy?</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Blea</td>
<td>Corals with low growth rates and high metabolic rates acclimatize more effectively</td>
<td>20</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>Both</td>
<td>Brooded larvae have a lower post-settlement mortality rate (why?), and can settle on more diverse substrates Brooded larvae can settle more rapidly, which favors local recruitment</td>
<td>313</td>
<td>✓</td>
</tr>
<tr>
<td>Mucus production</td>
<td>Blea</td>
<td>Mucus (polysaccharide) has a solar screening protection role and reduces photoinhibition.</td>
<td>?</td>
<td>-</td>
</tr>
<tr>
<td>MAAs</td>
<td>Blea</td>
<td>Absorb UV and functions as an antioxidant</td>
<td>?</td>
<td>-</td>
</tr>
<tr>
<td>Physiological integration</td>
<td>Blea</td>
<td>Influences the patchiness of bleaching and induced tissue mortality on the colony</td>
<td>Proxy?</td>
<td>-</td>
</tr>
<tr>
<td>Microscopic reduced scattering coefficient ($\mu_{s,m}$)</td>
<td>Blea</td>
<td>Influences light-scattering and so the endosymbiont light environment</td>
<td>93</td>
<td>✓</td>
</tr>
<tr>
<td>Reproduction frequency</td>
<td>Both</td>
<td>Reproducing during one or two short periods per year increases fertilization rate, saturates predators but is more risky against environmental stochasticity</td>
<td>?</td>
<td>-</td>
</tr>
<tr>
<td>Functional traits</td>
<td>Type</td>
<td>Explanation</td>
<td># sp</td>
<td>Used here</td>
</tr>
<tr>
<td>---------------------------</td>
<td>------</td>
<td>-----------------------------------------------------------------------------</td>
<td>------</td>
<td>-----------</td>
</tr>
<tr>
<td>Reproductive investment</td>
<td>Both</td>
<td>Eggs with more energy reserve are more likely to be recruited (?)</td>
<td>?</td>
<td>-</td>
</tr>
<tr>
<td>Symbiont acquisition</td>
<td>Both</td>
<td>Larvae obtaining the symbiont vertically can have more energy and so can survive disperse further</td>
<td>?</td>
<td>-</td>
</tr>
<tr>
<td>Symbiont density</td>
<td>Blea</td>
<td>Higher amount of ROS produced in case of the disruption of photosystem II</td>
<td>35</td>
<td>✓</td>
</tr>
<tr>
<td>Tissue thickness</td>
<td>Blea</td>
<td>Mediates shading protection to endosymbiont</td>
<td>20</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mediates DIC diffusion</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
2.4.2. Review of functional traits and associations assumptions

2.4.2.1 Effect traits involved in the habitat provisioning function

Structural complexity is a key reef attribute, and is estimated either visually (Wilson et al., 2007), with the rugosity index (Risk, 1972) or by measuring the number and size of holes (Friedlander and Parrish, 1998). Greater structural complexity provides a greater combination of microhabitats (Holbrook et al., 2002), which in turn reduce competition and predation rate, protect against currents, increase the amount of prey for predators (Graham and Nash, 2013) and provide more recruitment sites for plankton (Graham et al., 2006). Consequently, reefs with greater structural complexity support greater richness and abundance of fish species (e.g., Holbrook et al. 2002, Plass-Johnson et al. 2016) and macroinvertebrates (Fabricius et al., 2014; Nelson et al., 2016). We focus on “growth form” and “colony maximum diameter” (i.e., the maximum colony diameter observed for a given species) as two effect traits directly involved in the habitat provisioning function (Table 2.1). Complex growth forms are particularly important for juvenile and small size fish species (Emslie et al., 2008; Wilson et al., 2006) because reef fish occupy refuges corresponding to their body-size (Hixon and Beets, 1993). The size of the colony, on the other hand, contributes to the reef rugosity (Alvarez-Filip et al. 2011a; Newman et al. 2015). We assumed that complex colonies contribute more than simpler ones to the structure of the habitat, and considered growth form as an ordinal trait, ranking values from the most to least complex as follows: “branching” (open, closed and hispido), “table or plate”, “corymbose”, “digitate”, “laminar”, “columnar “, “massive” (massive and submassive), “encrusting long upright” and “encrusting”. Similarly, we assumed that species with greater maximum colony diameter contribute more to the function habitat provisioning.

2.4.2.2 Resistance traits

Cyclones

Cyclones (storms and hurricanes are included in the term) generate immediate colony breakage and dislodgement, increase sedimentation, turbidity, lower salinity, and change the sea level (Harmelin-Vivien, 1994). For simplicity, we only consider breakage and dislodgement. Cyclones
affect coral colonies differently depending on the strength of attachment to the substrate (Massel and Done, 1993) and on the colony’s growth form and size (Madin and Connolly, 2006). We selected “growth form” and “colony maximum diameter” as the two major resistance traits involved in the response against a cyclone (Table 2.1) based on the colony shape factor (CSF) established by Madin and Connolly (2006). The CSF is a dimensionless measure of mechanical vulnerability to hydrodynamic disturbance specific to coral colony’s morphology and size. The CSF shows that branching morphology is the most vulnerable, followed by plate/tabular, then digitate, corymbose and finally massive. In addition, it shows that more complex colonies (i.e., branching, plate/tabular and digitate) become more vulnerable as they grow bigger, in contrast with simpler morphologies (i.e., corymbose and massive), which become more resistant.

**Coral bleaching**

Coral bleaching is a more complex process than mechanical breakage and is most commonly triggered by a combination of high temperature and radiation, and low water current (Brown, 1997; Hidaka, 2016). The latter conditions simultaneously increase the demand in CO$_2$ of the zooxanthellae and reduce the external supply of dissolved inorganic carbon (i.e., CO$_2$ and HCO$_3^-$) (Wooldridge, 2014). An insufficient provisioning of CO$_2$ to the symbiont disrupts its photosystem, which generates reactive oxygen species (ROS) that are harmful for the host’s cells and lead to cellular metabolism dysfunction, arrest of proliferation and eventually apoptosis (Baird et al., 2009a). To protect itself, the host expels its symbiont, but risks dying from nutrient deficiency when bleaching lasts too long (Hidaka, 2016). The bleaching response varies considerably among species (McClanahan, 2004; Swain et al., 2016b) due to the different strategies corals have to exploit and manage their symbiotic relationship (Wooldridge, 2014), including: (i) increasing the heterotrophic carbon supply to the symbiont, (ii) protecting the symbiont against radiation in order to reduce its demand in CO$_2$, (iii) reducing symbiont density, (iv) increasing heterotrophy to compensate for the loss of the symbiont and/or (v) actively repairing the damage caused by ROS. Correspondingly, numerous functional traits are potentially involved (Table 2.1) and estimating their respective importance in the bleaching response is challenging.

The relationship with the symbiodinium is another important bleaching resistance trait. For instance, different lineages show contrasting types of symbiotic interactions (i.e., mutualistic
versus parasitic) (Stat et al., 2008) and thermotolerance (Swain et al., 2017), both of which can influence short-term responses and acclimation (Berkelmans and van Oppen, 2006; Grottoli et al., 2014). We were unable to explore these issues in more detail first because of inconsistency in the nomenclature associated with a high diversity of thermotolerance capability among closely related phylotypes (Howells et al., 2012; Swain et al., 2017), which precludes the merging of different datasets. Second, coral species show different degrees of symbiotic fidelity and we have limited understanding of the functional consequences of these unique associations (Hidaka, 2016). Third, a single colony can show a high rate of symbiotic turnover because of seasonality (Hume et al., 2015) and post disturbance reshuffling (Silverstein et al., 2015), which precludes the definition of a symbiotic functional diversity trait aggregated at the coral species level.

The analysis reveals four weak but significant correlations with the taxon-BRI: (i) a positive correlation with maximum colony diameter (Figure A1B; Spearman $r_s = 0.34$; n = 155; $P < 0.001$), which could be explained by a decrease of the surface to volume ratio as a colony grows bigger (except for branching species), which reduces mass transfer and consequently increases the propensity for bleaching (van Woesik et al., 2012b); (ii) a negative correlation with corallite area (Figure A1C; Spearman $r_s = -0.23$; n = 294; $P < 0.001$), which represents polyp size and could be positively associated with energy reserves (van Woesik et al., 2012a) and diversity of prey (Table 2.1); (iii) a positive association with growth rate (Figure A1D; Spearman $r_s = 0.38$; n = 104; $P < 0.001$), which is in accordance with the commonly observed higher bleaching susceptibility of fast growing species (Graham et al., 2006; Marshall and Baird, 2000). Gates and Edmunds (1999) suggested that a potential trade-off between growth rate and metabolic rate would be involved in the species-specific bleaching susceptibility: species with faster growth rates and low metabolic rates have a lower capacity to adapt to stressful conditions because of a poorer investment in protein metabolism involved in repairing and/or stabilizing impacted physiological processes. Although we did not find a significant association between metabolic rate (using dark respiration rate as a proxy) and growth rate (Figure A5; Spearman $r_s = -0.22$; n = 17; $P = 0.399$) or with the taxon-BRI (Figure A1E; Spearman $r_s = 0.06$; n = 19; $P = 0.792$), which would also support this hypothesis, we lacked statistical power due to limited sample size (Table A1). Lastly (iv), and in contrast with expectations, we observed only a weak association between growth form and the taxon-BRI (Figure A1A; Spearman $r_s = 0.12$; n = 304; $P = 0.042$). Branching and plating species are often reported as more bleaching sensitive compared to
massive and encrusting species (Baker et al., 2008). Explanations supporting these observations are: (1) more complex colonies have lower predation rate due to “self-shading” (i.e., certain parts of the colony cannot access prey because of the obstruction of other parts) (Kim and Lasker, 1998; Porter, 1976), though some field observations conflict with this (Houlbrèque et al., 2009); (2) more complex colonies have thicker boundary layers, which limit the access to both prey and dissolved CO$_2$ (van Woesik et al., 2012b). The weak association documented here potentially results from the influence of other resistance traits confounding the association between growth form and taxon-BRI (see section “Quantifying trait associations”). In any case, we caution that growth form may not constitute a reliable single predictor of bleaching susceptibility.

The microscopic reduced scattering-coefficient ($\mu'_s,m$) was not correlated to the taxon-BRI (Figure A1H; Spearman $r_s = -0.08$; $n = 78$; $P = 0.492$). This is surprising considering this trait characterizes the capacity of the superficial layer of the coral skeleton to reduce the scattering of light within the skeleton, allowing species with a higher coefficient to be less sensitive to bleaching (Marcelino et al., 2013; Swain et al., 2016a).

The other resistance traits did not yield significant correlations, though sample sizes were limited ($\leq 30$) (Figure A1).

2.4.2.3 Recovery traits

Recovery involves a combination of sexual and asexual reproduction of the remaining, eventually fragmented, coral colonies and surviving fragments, as well as external larval supply from undisturbed connected reefs. Species differ in the way they invest in the process of recovery and several traits are involved (Table 2.1).

Recovery via asexual reproduction

Coral regrowth can allow for faster recovery than sexual reproduction (Guest et al., 2016; Highsmith, 1982). Indeed, surviving corals might not be able to reproduce sexually during the months or years after a disturbance because the polyps must repair and maintain their own integrity, and smaller colonies (including those that have been reduced in size) are usually less fecund (Hughes, 1984; Ritson-Williams et al., 2009). Whether a colony is partially or fully damaged can depend on the species and the disturbance type. Those that are partially damaged
can sometimes regenerate more rapidly from remaining structures. Growth of damaged colonies and fragments is the primary means of post-cyclone recovery for many species (Harrison and Wallace, 1990; Hughes et al., 1992), allowing them to recover freed space relatively fast (e.g., five to 10 years). This mode of reproduction is observed in species belonging to different morphological groups (Highsmith 1982), but predominates among large and complex species. Indeed, small colonies are more vulnerable to partial mortality (Meesters et al., 1996) and morphological characteristics of certain branching species allow them to reduce their mortality rate (Madin et al., 2014). Similarly, the colony of certain coral species only partially bleaches and(or) dies, as opposed to sharing the stress over the entire colony. Polyp physiological integration is the functional trait potentially involved in the patchiness of the response (Baird and Marshall, 2002). This allows the surviving colony to regrow tissue on the dead portion of its colony, a phenomenon named the “phoenix effect” (Roff et al., 2014). We could not include this trait in our analysis because no measure has been defined for it.

**Recovery via sexual reproduction**

Sexual recruitment can be decomposed into three successive phases: (i) larval production, (ii) settlement success and (iii) post-settlement survival and growth (Ritson-Williams et al., 2009). Recruitment success varies greatly between species (Hughes and Connell, 1999) due to the different strategies corals have to complete these three stages.

Species differ in the number of oocytes they produce by colony (i.e., colony fecundity) (e.g., Hall and Hughes 1996) and the amount of energy invested in each egg (Harrison and Wallace, 1990). Recently, Álvarez-Noriega et al. (2016) have found trade-offs among species belonging to four functional groups (two species per group): massive species have a higher colony fecundity but a smaller colony reproductive investment (i.e., total amount of carbon invested in all the eggs produced by one colony) than plating or digitate species. The implication of this trade-off for larval settlement and recruitment is unknown, but potentially of importance because many species produce ecithotrophic larvae (i.e., they rely solely on maternal energy reserves).

Mode of larval development is associated with other recovery traits and is consequently involved directly or indirectly in larval production, settlement success and post-settlement survival. There are two main modes of larval development: the “broadcast spawners” and the “brooders”, depending if fertilization happens externally or internally (Baird et al., 2009b). The
extent to which each mode facilitates recovery is difficult to determine as it results from the combination of life-history strategies, suitable substrate availability (Vermeij, 2005), habitat type (Doropoulos et al., 2015), species-specific larval preference for substratum (Golbuu and Richmond, 2007), larval connectivity and scale of disturbances (Underwood et al. 2007), and composition of the species pool (Glynn and Colley, 2009). Under unfavorable conditions (i.e., stressful environment, isolation), brooders are considered better suited for local sexual recruitment (Edinger and Risk, 1995; Keith et al., 2015; Szmant, 1986). First, brooder populations are “facultatively closed”: brooder larvae reach competency a few hours after release and often recruit close to parental colonies (Underwood et al. 2007) but also have the capacity to disperse over longer distances (Figueiredo et al., 2013; Jones et al., 2009; Torda et al., 2013; Vermeij, 2005) whereas broadcast spawner populations are considered open (Doropoulos et al., 2015). Second, most of the brooded larvae become autotrophic via vertical inheritance of the symbiont (Baird et al., 2009b), which provides them with an early source of energy and potentially enhances survival. Third, they tend to have more reproductive cycles throughout the year (Ritson-Williams et al., 2009), which stabilizes recruitment rate (Vermeij, 2005) and reduces the risk of recruitment failure in case of synchrony between the timing of reproduction and a disturbance (Harrison and Wallace, 1990). Fourth, brooders have a shorter life cycle and reproduce earlier (Darling et al., 2012), which favors recovery. Finally, Ritson-Williams et al. (2016) have shown that brooder larvae are potentially less dependent on the presence of certain crustose coralline algae species to settle compared to spawners. Their observation, however, cannot be generalized due to the small number of species considered (three brooding and four spawning species) and contrasting results (Golbuu and Richmond, 2007).

2.4.3. Quantifying trait associations

2.4.3.1 Effect and resistance traits

Growth form and colony maximum diameter are two key traits implicated in both the habitat provisioning function and the resistance against cyclones and coral bleaching (Table 2.1, Table 2.2, Figure 2.2A, D). For cyclones, simpler morphologies tend to become more resistant as they grow bigger, as opposed to more complex growth forms, which tend to become more vulnerable (Figure 2.2A, C, D). Consequently, the part of the habitat provisioning function supported by
large complex colonies is not resistant, as opposed to the part of the function supported by large massive colonies. Growth form is also significantly associated with four resistance traits: (i) maximum colony diameter (Figure 2.2B, C; Spearman $r_s = 0.29$; $n = 306$; $P < 0.001$): more complex morphologies tend to reach bigger diameters; (ii) corallite area (Figure 2.2E; Spearman $r_s = -0.50$; $n = 713$; $P < 0.001$): more complex morphologies have smaller corallites; (iii) tissue thickness (Figure A2B; Spearman $r_s = -0.60$; $n = 20$; $P = 0.005$): more complex morphologies have thinner tissue; (iv) growth rate (Figure 2.2G; Spearman $r_s = 0.75$; $n = 125$; $P < 0.001$): more complex morphologies grow on average faster than simpler ones. Microscopic reduced scattering coefficient (Figure A2E; Spearman $r_s = -0.11$; $n = 93$; $P = 0.298$) and symbiont density (Figure A2C; Spearman $r_s = -0.23$; $n = 35$; $P = 0.183$) do not show a correlation with growth form complexity. The small sample sizes (usually > 10 species per morphological group) associated with the remaining three resistance traits—respiration rate, chlorophyll a concentration, and lipid content—precludes meaningful analysis (Figure A2A, D, F).

Maximum colony diameter is significantly negatively correlated with corallite area (Figure 2.2F, Spearman $r_s = -0.294$; $n = 295$; $P < 0.001$) and growth rate (Figure 2.2H; Spearman $r_s = 0.33$; $n = 72$; $P < 0.001$). The rest of the traits are either not significantly correlated: microscopic reduced-scattering coefficient (Figure A2K; Spearman $r_s = 0.22$; $n = 51$; $P = 0.115$), symbiont density (Figure A2I, Spearman $r_s = 0.10$; $n = 23$; $P = 0.634$); or not enough data were available for the analysis to be informative (Figure A2G, H, J, L).

2.4.3.2 Effect and recovery traits

Growth rate and mode of larval development are the only two recovery traits for which sample sizes permitted correlation analysis. Mode of larval development is significantly associated with maximum colony diameter: brooding species are on average smaller than spawning species (Figure 2.2J; permutation test; 10000 permutations; $P < 0.001$). We found no differences between spawners and brooders for growth form (Figure 2.2I; $\chi^2$ contingency test; Monte Carlo resampling: $\chi^2 = 12.20$; $n = 313$; $P = 0.142$). As seen in the previous section, growth rate is significantly associated with growth form and colony maximum diameter (Figure 2.2G, H).
Figure 2.2. Associations between effect, resistance, and recovery traits. The colored circles with a blue positive or an orange negative sign respectively refer to a positive or a negative relationship between effect and resistance or recovery and correspond to the color system in Figure 2.1. For example, the positive correlation between maximum colony diameter and growth rate.
rate implies a negative correlation between effect and bleaching resistance (H): species reaching bigger sizes contribute more to the habitat complexity and species with faster growth rates are more bleaching sensitive (Table 2.1, Figure A1D). The grey circled “X” refers to multidirectional relationship between effect and resistance (C, D). Growth forms are ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Each grey circle represents the trait value averaged by species, the black point is the averaged trait value over all the species by category, the error bars extend to +/- one standard error (SE). Statistical tests used: Spearman’s rank correlation ($r_s$); contingency test ($\chi^2$) (I); permutation test (J). Asterisks indicate the test statistics’ significance: *P<0.05; **P<0.01; ***P<0.001.

Table 2.2. Summary of the associations of effect traits with resistance and recovery traits related to the “habitat provisioning” function, cyclone and coral bleaching disturbances. The sign of the correlation corresponds to the relationship between the species’ contribution to the function and their response (e.g., if species contributing the most to the function are the most resistant, the relationship is positive; see Figure 2.1 and Figure 2.2).

<table>
<thead>
<tr>
<th>Functional traits</th>
<th>Resistance</th>
<th>Recovery</th>
<th>Effect traits</th>
<th>Growth form</th>
<th>Maximum colony diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth form</td>
<td>✔</td>
<td></td>
<td></td>
<td>Negative (C2, cyclone)</td>
<td>Negative (C2, cyclone)</td>
</tr>
<tr>
<td>Colony</td>
<td></td>
<td></td>
<td></td>
<td>Negative (C2, Bleaching)</td>
<td>Negative (C2, Bleaching)</td>
</tr>
<tr>
<td>Maximum diameter</td>
<td>✔</td>
<td></td>
<td></td>
<td>Dual (B2, C2, cyclone) †</td>
<td>Dual (B2, C2, cyclone) †</td>
</tr>
<tr>
<td>Corallite area</td>
<td>✔</td>
<td></td>
<td></td>
<td>Negative (C2, Bleaching)</td>
<td>Negative (C2, Bleaching)</td>
</tr>
<tr>
<td>Chlorophyll a concentration</td>
<td>✔</td>
<td></td>
<td></td>
<td>Not enough data (Bleaching)</td>
<td>Not enough data (Bleaching)</td>
</tr>
<tr>
<td>Dark respiration</td>
<td>✔</td>
<td></td>
<td></td>
<td>Not enough data (Bleaching)</td>
<td>Not enough data (Bleaching)</td>
</tr>
<tr>
<td>Lipid content</td>
<td>✔</td>
<td></td>
<td></td>
<td>Not enough data (Bleaching)</td>
<td>Not enough data (Bleaching)</td>
</tr>
<tr>
<td>Microscopic reduced scattering coefficient ($\mu_s\text{m}$)</td>
<td>✔</td>
<td></td>
<td>None (A2, Bleaching)</td>
<td>None (A2, Bleaching)</td>
<td></td>
</tr>
<tr>
<td>Symbiont density</td>
<td>✔</td>
<td></td>
<td></td>
<td>Not enough data (Bleaching)</td>
<td>Not enough data (Bleaching)</td>
</tr>
<tr>
<td>Tissue thickness</td>
<td>✔</td>
<td></td>
<td></td>
<td>Not enough data (Bleaching)</td>
<td>Not enough data (Bleaching)</td>
</tr>
<tr>
<td>Growth rate</td>
<td>✔</td>
<td>✔</td>
<td></td>
<td>Negative (C2, Bleaching)</td>
<td>Negative (C2, Bleaching)</td>
</tr>
<tr>
<td>Growth rate</td>
<td>✔</td>
<td>✔</td>
<td></td>
<td>Positive (B3)</td>
<td>Positive (B3)</td>
</tr>
<tr>
<td>Mode of larval development</td>
<td>✔</td>
<td></td>
<td>None (A3)</td>
<td>Negative (C3)</td>
<td></td>
</tr>
</tbody>
</table>

† combination of a positive and a negative correlation: larger massive colonies are more resistant to cyclone, as opposed to colonies with complex growth forms.
2.4.4. Predictions for the resilience of the habitat provisioning function

We now illustrate how the combination of certain assumptions and trait associations (documented above) can be used to assess the resilience of the habitat provisioning function.

2.4.4.1 Description of the simulated coral community

The information described above informed the parameterization of our simulation model (see Appendix A), including the trait characteristics of the three virtual coral species, which are visualized in Figure 2.3. Species 1 (left panel) has a complex morphology (i.e., branching or plating colonies). Its population contributes the most to the complexity of the habitat, but is the most vulnerable against cyclones and the most bleaching sensitive because of the larger size of the colonies (Figure 2.2C; Figure A3B), smaller polyps (Figure 2.2E, F; Figure A3A, C), and faster growth rates (Figure 2.2G, H; Figure A1D). As a consequence of the latter, it is the fastest of the three species to recover free space through vegetative growth. It is a broadcast spawner (Figure 2.2J; Figure A4A) and consequently contributes less to local recruitment but benefits more from regional input of larvae compared to brooding species. Species 2 contributes moderately to the habitat because it provides rugosity but no small-scale complexity. It is very resistant to cyclones, but bleaching sensitive because of its larger size (Figure 2.2B; Figure A3B) and its smaller polyps (Figure A3A, C). Compared to Species 1, Species 2 recovers much more slowly via vegetative growth (Figure 2.2G; Figure A3D) but equally via larval recruitment because it too is a spawner (Figure A4B). Species 3 is small in size and intermediately complex in shape. Its small size contributes little to the complexity of the habitat compared to the two other species, but it provides resistance against cyclones. It is the most bleaching resistant species due to its small size (Figure 2.2C, Figure A1B) and larger corallites (Figure 2.2F, Figure A1C). It has a faster growth rate than Species 2 but slower than Species 1 (Figure 2.2G). Finally, it is a brooding species (Figure 2.2J), and is consequently better at recruiting larvae locally than the two other species.

Coincidentally, the virtual species we describe align well with the three life-history strategies identified by (Darling et al., 2012). Importantly, our framework can be used to explore any combination of ecosystem functions and / or disturbances, and does not require the adoption of any pre-defined functional groups.
Figure 2.3. Functional characteristics of the three species defined in the model. Each vertex of the web corresponds to a process: contribution to the habitat provisioning function, capacity to recover via recruitment of larvae regionally and locally produced and via vegetative growth, resistance to bleaching events and cyclones. The coloured polygons represent the abilities of the species to perform in each process, with highest capacity at the extremities and no capacity at the center of the web. The positions reached on each axis correspond to the normalized parameter values used in the simulation model (Table A4), and reflect our qualitative assessment based on our review of assumptions and trait associations. Values for the three recovery processes are comparable with one another and between species.

2.4.4.2 Predictions

The part of the habitat created by the large complex species is not resistant to cyclones, contrary to the part supported by the large massive species (Figure 2.4A, G). The habitat provisioning function decreases faster in relation to disturbance intensity than expected based on the null model outcomes (Figure 2.4A, G). This is because the colonies contributing the most to the function have a higher probability of being extirpated (case corresponding to Figure 2.1C2). In the case of a medium sized perturbation, we can expect the habitat to recover rapidly due to the high growth rate of the surviving species 1 colonies (Figure 2.4E, F). Larval connectivity has only a small influence on the recovery rate (Figure 2.4B, C). In the case of a more intense perturbation, most of the remaining habitat is supported by Species 2 (Figure 2.4G, J). The recovery of the function starts more slowly because the population recovery of Species 1 is first happening mostly via regional larval input (Figure 2.4H, K). In consequence, the rate of recovery of the function is strongly influenced by connectivity (Figure 2.4H, L). In contrast, Species 3 is less affected by isolation (Figure 2.4K, L) because its surviving population is large enough to
recover both via vegetative growth and local larval recruitment—two processes of similar efficiency for this species (Figure 2.3, Table A3). In these four different scenarios, the recovery rate of the function increases more rapidly than observed in the null model when the Species 1 population becomes large enough to rapidly recover empty space predominantly via vegetative growth (Figure 2.1B3).

The major difference of the bleaching response compared to a cyclone scenario (Figure A8) is the low resistance of Species 2, which results in a higher vulnerability of the habitat (only Species 3 colonies are resistant; Figure A8A, D). Species 2 has the lowest capacity to recover vegetatively due to its slow growth rate, and is less efficient than Species 3 at self-recruiting larvae (Figure 2.3, Table A3). Consequently, Species 2 almost fails to recover in the case of high disturbance intensity and low larval connectivity (Figure A8L).
Figure 2.4. Expected resistance (left column) and recovery rate (middle and right columns) of the coral community defined in the model (expressed as population size in second and fourth rows) and the habitat provisioning function it provides (first and third rows) against cyclone disturbances, under different scenarios of disturbance intensity and reef connectivity. The initial (disturbance intensity = 0) habitat provisioning values of each species in the left-hand panels (A, G) reflect the values assigned to species and depicted in Figure 2.3. The vertical red lines (left column) represent the disturbance intensity used to evaluate community recovery (middle and right column) for a moderate (two first rows) and intense (two last rows) perturbation. Thicker lines are the averaged response over 40 replicates (thinner lines) of the three species (see text for details). The magenta line represents the cumulative habitat provisioning provided by the whole community; the black dashed line represents the cumulative and averaged habitat provisioning provided by the null model communities. In our focal virtual communities, the habitat
provisioning function is less resistant (panels A and G) and recovers faster (panels B, C, H, I) than in the null model communities (dashed black lines), in which an individual’s capacity to respond is randomly drawn from the three species-specific capacities.

2.5. Discussion

Suding and colleagues’s (2008) framework has proven to be successful in quantitatively predicting the effect of an environmental change on ecosystem functions, and in yielding a better mechanistic understanding of the processes at play (e.g., Klumpp and Soussana 2009, Solé-Senan et al. 2017). Their framework also enabled prediction of the functional composition of a community in response to a long-lasting change in environmental conditions (i.e., long enough for the community to reach functional equilibrium). While developed and applied principally in terrestrial plant ecosystems, similar trait-based frameworks have been used for other organisms or systems, including ectomycorrhizal fungi (Koide et al., 2014), beetles (Fountain-Jones et al., 2015), bees (Forrest et al., 2015), soil invertebrates (Pey et al., 2014), and birds (Davies et al., 2010; Luck et al., 2013). It is time to apply an analogous framework for corals. Here we built on the work of Suding and colleagues (2008) by distinguishing between “resistance” and “recovery” traits. This enabled us to consider the temporal aspect of a response after a pulse-disturbance. This distinction is especially important for coral reef ecosystems because they are naturally embedded within intense pulse and press disturbance regimes (Connell et al., 1997), which leads species to develop very distinct response strategies (Darling et al., 2012) and communities to show high species turnover (Connell et al., 2004) and succession (Tanner et al., 1994). By considering recovery as an aspect of response, one can better anticipate the expected time to recovery for a function.

We illustrated the application of the framework with a virtual community. For real coral communities, trait information is missing for numerous species and/or traits (Table 2.1, Table 2.2) and the relationships between many traits and processes have not been quantified. The veracity of the trait associations we quantified depends on the number of species sampled and consistency in measurement protocols. Adopting a framework such as the one proposed here helps clarify the key knowledge and data gaps, and advance coral research in general. In particular, such an approach could inform the following four research objectives: (i) to gain a better understanding of relationships between traits and processes, (ii) to make accurate,
quantitative predictions about ecosystem functioning, \((iii)\) to identify key traits for gap-filling the coral trait database, and \((iv)\) to improve management of coral communities.

2.5.1. Linking traits to processes

Comprehensively linking traits to processes requires understanding the mechanisms at play and identifying the associated traits. Qualifying traits as effect, resistance or recovery necessitates careful consideration of the mechanisms and associated traits involved in the processes. Once reviewed, traits and processes can be linked in a conceptual, correlative or mechanistic model. For instance, Figueiredo and colleagues (2013) modeled species-specific coral larval retention implementing egg size; Madin and Connolly (2006) and Hoogenboom and Connolly (2009) established mechanistic models respectively determining the hydrodynamic vulnerability and the daily photosynthetic energy acquisition of colonies depending on their size and growth form. Processes such as bleaching or recruitment are more complex and involve numerous aspects of coral physiology. Efforts to combine mechanisms and associated traits to disentangle the complexity of these processes (e.g., Baird et al. 2009a, Wooldridge 2014) and to quantify relationships between traits and processes (e.g., Swain et al., 2016a) would benefit from a systematic and more rigorous trait classification scheme. For instance, we identified 15 bleaching resistance traits and 11 recovery traits (Table 2.1), and yet rarely do models implement more than one coral trait to predict species bleaching response (e.g., Swain et al., 2016a) or recruitment (e.g., Kubicek et al. 2012, Magris et al. 2015), if they consider traits at all. The framework highlights the traits and mechanisms that require investigating (Table 2.1, Table 2.2) such that multi-trait models can be developed to better predict species-specific performance.

2.5.2. Integrating quantitative modeling of ecosystem functioning

The framework is especially suitable for predicting the effects of disturbances on ecosystem functioning (e.g., the delivery of a service), as trait correlations and functional overlaps link together processes related to ecosystem functioning and resilience (i.e., resistance and recovery). We have illustrated this with a simple simulation model, but other approaches are possible. Minden and Kleyer (2011) implemented Suding and colleagues’ (2008) framework in structural equation models (SEM) to quantify the indirect effects of abiotic factors (e.g., salinity, nutrient
availability) on productivity in salt marshes through the causal relationships with response and effect traits (e.g., stem biomass, specific leaf area). Subsequently, SEMs have been used to expand on the framework by considering multiple ecosystem functions and their trade-offs (Lavorel and Grigulis 2012) and additional trophic levels (Lavorel et al. 2013). Agent-based models (ABMs) are another appropriate modeling approach as they can simulate the dynamics of a community from the individual’s response, growth and reproduction (Grimm and Railsback, 2005) and can incorporate any number of mechanisms and agent-specific features (DeAngelis and Grimm, 2014). Bozec and colleagues (2015) and Kubicek and Reuter (2016) have, for instance, developed ABMs to quantify the effect of disturbances (i.e., cyclone, bleaching, fishing) on the rugosity of the reef through the effect on coral cover and diversity using coral functional traits. Finally, Edmunds and colleagues (2014) advocated for the use of integral projection models (IPMs) to quantitatively predict the structure of a coral population (e.g., size class distribution) under different environmental scenarios. We suggest using IPMs’ outputs to further quantify an ecosystem function provided by a population by using the appropriate effect traits.

### 2.5.3. Identifying key traits and gap-filling the trait database

Filling gaps in the trait database is a pressing challenge if we wish to adopt a trait-based approach to advance coral science (Madin et al. 2016b). Measuring all functional traits on all coral species is not feasible so we must define a strategy for (i) selecting a set of relevant and easy to measure functional traits, and (ii) extrapolating trait values to the rest of the coral phylogeny. Qualifying traits as effect, resistance or recovery would provide a strategy for selecting suitable, representative and measurable traits. For instance, among the 15 bleaching resistance traits we highlighted (Table 2.1), five are difficult to measure (e.g., heterotrophy, physiological integration), and another five have been measured on an insufficient number of species (Table 2.2). Before investing in measuring these traits on a larger number of species, we should first determine if the trait data we have in hand (i.e., growth form, colony maximum diameter, corallite area, $\mu^{s,m}$, growth rate) can be used as reliable proxies for other traits according to the type(s) of process(es) they influence. For instance, (1) corallite area is potentially related to processes involved in the use of heterotrophic energy, and could consequently be correlated to lipid content, heterotrophy and tissue thickness; (2) the
microscopic reduced scattering coefficient is implicated in autotrophic energy regulation, and is therefore a good proxy candidate for symbiont density, tissue thickness and pigment concentration; (3) growth rate and dark respiration represent potential trade-offs in energy investment and could consequently directly influence metabolic cellular processes such as Heat-shock proteins (HSPs) and myco-sporine-like amino acids (MAAs) production. Defining these key proxy traits might require conducting experiments on a subset of coral species in order to ascertain their correlation with traits that have been insufficiently surveyed or are challenging to measure, and to confirm their influence on the process of interest (if not already demonstrated experimentally). Once a key proxy trait is defined, its value can be extrapolated to the rest of the unmeasured coral phylogeny. For instance, Madin et al. (2016b) used multiple regression to predict growth rate using colony morphology and molecular families as predictors. Growth rate has been measured on 125 species (Table 2.1) distributed among most of the coral families. Many of the potential key proxy traits have been measured on an insufficient number of species (Table 2.1), preventing the possibility of predicting trait values to unmeasured parts of the phylogeny. We believe that agreeing on a set of coral species on which to measure the selected key traits is necessary, considering the important gaps present in the database (Madin et al., 2016a). We further propose to strategically select these species in reference to their position in the coral phylogeny (i.e., the set of coral species should cover the whole phylogeny) in order to better quantify phylogenetic conservatism in traits and achieve better prediction. In addition, we highlight alternative phylogenetically-informed imputation methods such as phylogenetic generalized linear models, phylogenetic eigenvectors (Swenson, 2014a), multivariate imputation by chained equations (MICE), missForest (Penone et al., 2014) and the hierarchical Bayesian approach BHPMF (Schrodt et al. 2015).

2.5.4. Informing active restoration strategies

Maintaining reefs in their pristine state is an unrealistic goal regarding current trends in human development and associated disturbances (Graham et al., 2014). Managing for the functions reefs provide and their resilience requires combining adaptive ecosystem-based (e.g., McCook et al. 2010) and resilience-based (Anthony et al., 2015) approaches so we can intervene on the appropriate drivers and processes at the suitable scales to maintain or place individual reef systems within a safe operating space (Hughes et al., 2017a). A better theoretical understanding
of ecosystem dynamics (Scheffer et al., 2001) has brought new management options: in addition to act on the drivers themselves, measures aiming at manipulating thresholds and feedback processes are now considered (Hughes et al., 2017a). One promising approach consists of combining the “gardening concept” (i.e., importing farmed colonies into local reefs) (Rinkevich, 2014) with assisted evolution methods (e.g., preconditioning, epigenetic programming, selective breeding of colonies) (van Oppen et al., 2017, 2015) so that the imported colonies are more resilient and eventually increase the genetic diversity of local populations. This approach requires identifying the traits that provide resilience to coral populations and their heritability (van Oppen et al., 2015). Meanwhile, this approach should also satisfy the need to preserve ecosystem functions and structure (van Oppen et al., 2017), an objective impeded by important knowledge gaps concerning the effect of community change on ecosystem functions (Hughes et al., 2017a). The framework we propose here can help reach these two objectives by identifying appropriate resistance and recovery traits, and by yielding qualitative predictions about how the enhancement of certain trait configurations in local communities can affect ecosystem functions. In other words, it would help with selecting the best candidate species for farming and for assisted evolution depending on their contribution to ecosystem functions, their resilience (i.e., resistance and recovery), and their complementarity with the other species already present locally.
Chapter 3: Combining agent-based, trait-based and demographic approaches to model coral-community dynamics

3.1. Synopsis

In this chapter we present the model we developed from the “effect-resistance-recovery traits” framework (Chapter 2) to conduct the functional diversity-resilience experiment (Chapter 4).

The model is a new spatially explicit, agent-based model representing benthic communities in tropical reefs composed of coral species and six functional groups of algae. Individual colonies grow, reproduce, compete for space, and respond to disturbances as a function of their size and trait-process relationships, which we defined using eleven functional traits informed by published empirical data (Figure 3.1; Figure 3.2; Table 3.1). The number of coral species present in the community can be varied without impacting model complexity and processing time. Functional diversity can be varied by sampling species from a set of 798 functionally realistic species, which we obtained by imputing missing trait data based on values measured for real species (Madin et al., 2016a). Importantly, we used empirical data and previously established models to implement most of the processes represented in the model (Table 3.2). We provide in this chapter the full description of our model’s design, concepts, and capabilities. In the main text we present a streamlined description, and use the Appendices for details regarding: (i) traits and imputation of missing data (Appendix B), (ii) the Overview, Design concepts and Details protocol (Appendix C and Appendix E), (iii) calibration with empirical data (Appendix D), (iv) hierarchically structured validation (Appendix F), and (v) global sensitivity analysis (Appendix G).

The model implements a number of ecological details and processes that surpass previous models, and produces community dynamics that are ecologically sound. The model can be used as a simulation platform for virtual experiments aimed at testing hypotheses about the effects of coral diversity on ecosystem functioning and resilience.

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3.2. Materials and methods

3.2.1. Sources and software

We collected coral-trait data from coraltraits.org (Madin et al., 2016a) and other resources from the peer-reviewed literature (Appendix B). We systematically verified and corrected coral-species nomenclature using the World Register of Marine Species as a reference. We used R (version 3.5.0, R-Core Team, 2017) to manipulate datasets, for statistical analyses, and to manage model simulations. We developed the model with the open-source, Java object-oriented programming language *Repast Simphony* 2.5.0 (North et al., 2013). We launched simulations using the R package *rrepast* 0.7.0 (García and Rodríguez-Patón, 2016) and *rJava* 0.9-10 (Urbanek, 2018). We used the R package *missForest* 1.4 (Stekhoven and Bühlmann, 2012) to impute missing trait data. We included phylogenetic information as a predictor using Huang and Roy's (2015) phylogenetic supertrees to improve predictions; we manipulated the supertrees using the R packages *ape* 5.0 (Paradis and Schliep, 2018) and *phytools* 0.5-38 (Revell, 2012) (Appendix B). We defined coral bleaching probabilities using the R packages *MuMIn* 1.40.0 (Bartón, 2017), *betareg* 3.1-0 (Cribari-Neto and Zeileis, 2010), *lme4* 1.1-15 (Bates et al., 2015), *lmtest* 0.9-35 and (Zeileis and Hothorn, 2002) (Appendix E). For the global sensitivity analysis, we drew a Latin hypercube sample from the parameter space using the *randomLHS* function from the R package *lhs* 0.16 (Carnell, 2018), and we measured the influence of parameters on different response variables by fitting boosted regression trees using the *gbm.step* function from the R package *dismo* 1.1-4 (Hijmans et al., 2017).

3.2.2. Model description

We provide here a brief description of the model following the Overview, Design concepts, and Details protocol (Grimm et al., 2020, 2010, 2006). A complete protocol that contains all the details about parameterization and process implementation along with a review of the supporting literature is available in Appendix C and 0.
3.2.2.1 Purpose and patterns

The purpose of the model is to predict coral population dynamics as a function of hydrodynamic (i.e., waves and cyclones) and thermal disturbances, grazing pressure, larval connectivity, sedimentation (i.e., sand import and export), interspecific competitive interactions, and benthic community diversity (species richness and functional diversity). Time series defining disturbance regimes, sand cover and the diversity and number of external coral larvae are imposed and need to be defined before launching simulations. The grazing regime is imposed but can also be determined by activating the feedback process linking reef rugosity (created by colonies) to herbivore fish density to grazing pressure. Patterns in species cover, colony size distributions, recruitment rates and rugosity are used to understand the model’s dynamics and its accuracy.

3.2.2.2 Entities, state variables, and scales

The model consists of grid-cell agents each representing 1 cm\(^2\), so that the benthic community is represented at a scale of organization smaller than the colony (equivalent to that of a polyp, although polyp size varies among species by several orders of magnitude) (Figure 3.1). During a simulation, an agent can be temporally part of a coral colony (798 species), a patch of algae (i.e., macroalgae, allopathic macroalgae, Halimeda spp., turf, articulated coralline algae or crustose coralline algae), sand, or bare substratum. Each agent is characterized by 33 variables that describe where the agent is in space (its position is fixed), its species identity (i.e., one of the 798 coral species or six functional groups of algae) and related functional characteristics, its age, the colony’s planar area and identification number, if it is bleached or was grazed recently, et cetera (Table C1). Coral colonies and patches of algae are entities composed of multiple agents sharing the same variable values (except for their spatial coordinates) and changing their state simultaneously during certain processes. For instance, dislodgement is simulated by converting all the agents forming the dislodged colony into barren ground; a turf algae overgrowing a colony is simulated by converting the coral agents constituting the overgrown part into turf, but conserving the information about the colony (i.e., identification number, size, species, growth form).

The size of the reef and the length of a time step are changeable. We defined a 25 m\(^2\) reef for our simulations (i.e., 250,000 agents) which is usually the scale at which benthic communities
are assessed in detail (e.g., Holbrook et al. 2018, Torda et al. 2018). We defined a 6-month time step because the empirical data we used to calibrate the model were collected biannually. We acknowledge that six months is a coarse time step, potentially preventing the simulation of subtle dynamics, for instance changes triggered by mild disturbances. We opted for this timestep considering that (i) corals grow slowly (< 180 mm yr\(^{-1}\)), and (ii) their reproductive cycles, and (iii) thermal and hydrodynamic disturbance regimes are seasonal. It is, however, possible to define shorter periods (i.e., three and 4-month time steps) as time steps in the model.

The model estimates 3-dimensional colony surface areas using geometric formulae (Table C5) to determine the number of larvae produced in each colony (see §C.7.2.1.1), and (optionally) the rugosity of the reef (see §C.7.1.2.2). The model also accounts for colony and algae heights in overtopping processes (see §C.7.5.2.2 and §C.7.5.3.2). Algae have constant heights and colony heights equal the radius of the colony planar area, assuming the latter is circular (Table C18).

3.2.2.3 Process overview and scheduling

Each time step includes following consecutive processes: (i) grazing—patches of agents are randomly selected and grazed until a certain proportion of the reef is reached, (ii) coral reproduction—locally and regionally produced larvae attempt to settle, (iii) thermal disturbance, which, if triggered, eventually causes colonies to bleach and/or die; (iv) dislodgement and fragmentation—the effect of waves and cyclones on certain colonies, (v) growth—each living agent, selected in a random order, attempts to convert its neighbouring agents within a certain radius to its own state, (vi) sedimentation—barren ground agents are converted to sand and vice versa until the desired sand cover is reached, (vii) algae invasion—the remaining ungrazed, barren-ground agents are converted into algae agents (Figure 3.2). (Note that the process differs from species invasion.) The order at which processes iii, iv, and v happen must be defined beforehand.

During each time step, the model exports response variables: the cover of each benthic group (coral, algae, and sand), the planar area of each colony present per species, the number of recruited coral larvae m\(^{-2}\) species\(^{-1}\), and the reef rugosity (in cases when rugosity-grazing feedback is activated). The first two variables are collected after processes iii, iv, and vii, and the third and fourth variable after process vii. There are six variables imported each time step; their values respectively determine the cover to be grazed, the intensity of waves or cyclone, and of
thermal stress, the number of external larvae m$^2$ entering the reef, the order that reproduction, bleaching, and wave or cyclone events happen, and the cover of sand to be achieved. We present a complete schedule that includes additional model-related processes in §C.3.

3.2.2.4 Design concepts

**Basic principles:** the model combines agent-based, trait-based, and demographic approaches to simulate coral reef community dynamics in imposed environmental scenarios. The model captures fundamental principles in ecology: (i) biodiversity influences ecosystem resilience and (ii) functioning, (iii) disturbance regimes filter species and mediate interspecific competition, (iv) interspecific functional differences (or strategies) mediate competitive exclusion and coexistence, and (v) source-sink dynamics regulate species coexistence in metacommunities.

**Emergence:** The dynamics of the benthic community emerge from species traits and the imposed disturbance regime (waves, cyclone, thermal stress), larval connectivity, sedimentation and grazing pressure intensity (which can also emerge from reef rugosity). Cell agents do not make decisions and their behaviour results from imposed deterministic or probabilistic rules.

**Interactions:** Agents on the edge of coral colonies and patches of algae interact with one another when competing for space. The outcome of a coral-coral interaction is determined by its specific pairwise outcome probabilities—the probability of coral-algae interactions are the same for all coral species, and algae-algae interactions result in a stand-off except when competing against crustose coralline algae. Branching and plating species also have the capacity to overtop other colonies and algae depending on their size (see §C.7.5).

**Stochasticity:** The model draws success or failure outcomes each time a patch of algae is grazed, a larva attempts to settle and survive the first six months, an agent tries to convert another living agent (see §C.7.1, §C.7.2 and §C.7.5), and a colony is thermally stressed (i.e., bleaching and bleaching-induced mortality; see §E.2 and §E.3). Each of these random events is based on a probability of success specific to the process and the species involved. During initialization, colonies are created and placed randomly in space; their sizes are drawn from right-skewed
frequency distributions (see §C.5.1). Finally, grazing and larval settlement happen randomly in space.

**Collectives**: Collective behaviour of agents happens when a colony is (i) dislodged—agents sharing the same colony (i.e., coral and algae agents growing on a colony) are converted to barren ground (see §C.7.3), (ii) bleaches or dies—the coral agents of the colony are converted to a bleached or dead state, respectively (see §C.7.4), or (iii) reproduces—the number of larvae or gametes produces by a colony depends on certain coral traits and the size and age of the colony (see §C.7.2).

**Observation**: Four types of data are collected during a simulation: (i) percentage cover of each taxon, (ii) number of recruits for each coral species m$^2$, (iii) planar area of each colony species$^{-1}$, and (iv) optionally, the rugosity created by the coral colonies (Figure 3.2).

### 3.2.2.5 Initialization

The initial composition of the benthic community (i.e., the cover of coral species, algae, barren ground, and sand) is defined by the user and is imported from a comma-delimited text file. The space is filled first by creating circular coral colonies randomly in space. The colony diameters are drawn from skewed distributions that we defined using empirical data (E. H. Meesters and R. P. M. Bak, personal communication, May 2017) and as a function of the trait *colony maximum diameter*. Circular patches of algae (314 cm$^2$) are then created and the remaining agents are converted into barren ground and sand (see §C.5).

### 3.2.2.6 Input data

Predefined time series (recorded in the text files) of input data are used to define the environmental context of the reef (Figure 3.2). At each time step, the model imports values for the corresponding period of the (i) surface grazed (%), (ii) number of external larvae settling, (iii) intensity of waves of cyclones (in dislodgement mechanical threshold, a dimensionless measure of the mechanical threshold imposed by waves and cyclones), (vi) thermal stress intensity (in degree-heating weeks), and (v) sand cover (%).
3.2.2.7 Submodels

**Grazing:** The reef is grazed by randomly selecting circular patches of agents (29 cm$^2$) until a certain percentage cover is reached. The cover to reach can be either exclusively imposed (imported from a file) or it can result from the rugosity that coral colonies create if the rugosity-grazing feedback process is activated. We used Bozec and colleagues’ (2013) empirically established model to determine herbivorous fish density from reef rugosity and Williams and Polunin's (2001) data to estimate grazing pressure from herbivorous fish density (see §C.7.1).

**Reproduction and recruitment:** Coral larvae locally produced and arriving from the regional pool attempt to settle in the reef, at a random location. The number of larvae produced locally for each species depends on species traits (i.e., polyp fecundity, corallite area, growth form, sexual system)—we used McWilliam and colleagues’ (2018b) geometric formulae to calculate colony surface area from planar area—and the distribution of colony planar areas in their population—we used Álvarez-Noriega and colleagues’ (2016) models to determine the proportion of fecund polyps in colonies as a function of planar area. We used Figueiredo and colleagues’ (2013) models to determine the proportion of spawned eggs remaining in the reef from water retention time and egg diameter—species producing larger eggs also produce larvae having a greater time to motility and a higher chance of being exported outside the reef. Species with a brooding mode of larval development release larvae ready to settle and are not affected by water retention time (see §C.7.2.1.1). The number of external larvae arriving at the reef can either be defined beforehand and imported from a file, or is calculated as a function of the connectivity imposed—we used Connolly and Baird’s (2010) models to determine the proportion of alive and competent larvae as a function of distance travelled (see §C.7.2.1.2). Larvae have a chance of settling successfully on barren ground, crustose coralline algae, and dead coral agents. We used Ritson-Williams and colleagues’ (2016) data to define the proportion of settled larvae surviving the duration represented by a time step (see §C.7.2.1.3). Algae recruit at the end of a time step, by filling up the remaining available space (i.e., ungrazed barren ground and dead coral agents) (see §C.7.2.2).
**Wave and cyclone damage:** We modelled colony dislodgment using Madin and Connolly's 2006 colony shape factor, which is compared for each colony to the intensity of the disturbance (expressed as dislodgement mechanical threshold). We implemented branching-colony fragmentation by modifying the relationship between fragment size and survival established by Highsmith et al. (1980). We defined our own models to simulate the effect on the algae community because no relationships have been established empirically (see §C.7.3).

**Bleaching:** We first defined a species-specific index of bleaching susceptibility using bleaching-resistance traits and Swain and colleagues’ (2016) bleaching response index. We then used this index to establish species-specific logistic bleaching responses as a function of the intensity of the thermal stress (in degree heating-week) using Eakin and colleagues’ (2010) data. Finally, we defined a bleaching-induced mortality logistic-response model (see §C.7.4 and 0).

**Growth and spatial competition:** Coral and algae agents on the edge of their colony or patch attempt to convert neighbouring agents within a certain radius. The size of the radius depends on the species growth rate and the state of the neighbouring agents—we simulated the effect of direct competition with a living agent on growth rate by reducing the length of the radius. We used Precoda and colleagues’ (2017) competitive outcome probabilities to simulate between coral interactions (see §C.7.5.2); we used the trait aggressiveness if the species were not present in their list (see Appendix B). Branching and plating colonies can also overtop other colonies and algae. We used empirical estimates of competitive outcome probability to simulate competition between coral and algae (Brown and colleagues (2017); K. T. Brown, personal communication, October 2017; see §C.7.5.3). We considered algal functional groups as equal competitors and therefore they cannot overgrow each other, except for crustose coralline algae, which is a weaker competitor (see §C.7.5.4).
**Table 3.1.** The eleven functional traits we used to implement ecological processes in the model.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Related processes and details</th>
</tr>
</thead>
<tbody>
<tr>
<td>age at maturity (yr)</td>
<td>The minimum age required for a coral colony to reproduce (see §C.7.2.1.1.a)</td>
</tr>
<tr>
<td>aggressiveness (0 to 100)</td>
<td>Spatial direct competition for space between coral species; the trait is only used for species not considered in Precoda and colleagues’s (2017) study on probability of species-pair interactions (see §B.1.2)</td>
</tr>
<tr>
<td>colony max diameter (cm)</td>
<td>Initial colony size distributions (see §C.5.2); colony fecundity (for the species with small colonies; see §C.7.2.1.1.b); bleaching (see §C.7.4.2.1 and 0); colony vegetative growth (to define maximum planar area; see §C.7.5.1)</td>
</tr>
<tr>
<td>corallite area (cm²)</td>
<td>Colony fecundity (see §C.7.2.1.1.b); bleaching (see §C.7.4.2.1 and 0)</td>
</tr>
<tr>
<td>egg diameter (mm)</td>
<td>Time to motility of coral larvae (see §C.7.2.1.1.d)</td>
</tr>
<tr>
<td>polyp fecundity</td>
<td>Colony fecundity (see §C.7.2.1.1.b)</td>
</tr>
<tr>
<td>growth form</td>
<td>Formation of reef rugosity (see §C.7.1.2.2); colony fecundity (see §C.7.2.1.1.b); dislodgement (see §C.7.3.1.2); spatial competition (overtopping; see §C.7.5)</td>
</tr>
<tr>
<td>growth rate (mm.yr⁻¹)</td>
<td>Bleaching (see §C.7.4.2.1 and 0); vegetative growth (see §C.7.5.1)</td>
</tr>
<tr>
<td>mode of larval development</td>
<td>Coral reproduction (see §C.7.2.1.1)</td>
</tr>
<tr>
<td>microscopic reduced scattering coefficient (μs,m, mm⁻¹)</td>
<td>Bleaching (see §C.7.4.2.1 and 0)</td>
</tr>
<tr>
<td>sexual system</td>
<td>Colony fecundity (see §C.7.2.1.1.b)</td>
</tr>
</tbody>
</table>
Table 3.2. Empirical data and models we used to implement ecological processes in the model.

<table>
<thead>
<tr>
<th>Processes / variables</th>
<th>Comments</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>colony size (initialization)</td>
<td>We used colony size distributions measured for eleven species and <em>maximum colony diameter</em> to define colony size distributions for each species (see §C.5.2.2)</td>
<td>E. H. Meesters and R. P. M. Bak, personal communication, May 2017</td>
</tr>
<tr>
<td>herbivorous fish density supported by the reef rugosity</td>
<td>We used an empirical model to determine the density of herbivore fish present in the reef as a function of reef rugosity (see §C.7.1.2.2)</td>
<td>(Bozec et al., 2013)</td>
</tr>
<tr>
<td>grazing intensity due to herbivorous fish density</td>
<td>We defined a model using empirical data to determine the surface of the reef grazed as a function of herbivorous fish density (see §C.7.1.2.2)</td>
<td>(Williams and Polunin, 2001)</td>
</tr>
<tr>
<td>polyp maturity in colonies</td>
<td>We defined a model from models established empirically to determine the proportion of mature polyps in a colony as a function of colony planar area using data for eight species (see §C.7.2.1.1.b)</td>
<td>(Álvarez-Noriega et al., 2016)</td>
</tr>
<tr>
<td>larval competency</td>
<td>We used a model established empirically to determine time to motility of coral larvae as a function of <em>egg diameter</em> (see §C.7.2.1.1.d)</td>
<td>(Figueiredo et al., 2013)</td>
</tr>
<tr>
<td>larval retention</td>
<td>We used models established empirically to determine the proportion of competent larvae remaining in the reef as a function of time to motility and water retention time (see §C.7.2.1.1.d)</td>
<td>(Figueiredo et al., 2013)</td>
</tr>
<tr>
<td>larval competency loss</td>
<td>We defined a model from models established empirically to determine the proportion of external competent larvae settling on the focal reef as a function of the distance travelled (see §C.7.2.1.2.b)</td>
<td>(Connolly and Baird, 2010)</td>
</tr>
<tr>
<td>larval post-settlement survival</td>
<td>We defined a model using empirical data to determine the proportion of surviving settled larvae as a function of time (see §C.7.2.1.3.b)</td>
<td>(Ritson-Williams et al., 2016)</td>
</tr>
<tr>
<td>Processes / variables</td>
<td>Comments</td>
<td>References</td>
</tr>
<tr>
<td>-----------------------</td>
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</tr>
<tr>
<td>colony dislodgement</td>
<td>We used models established empirically to determine if a colony is dislodged as a function of colony growth form, planar area and the intensity of the hydrodynamic disturbance (see §C.7.3.1.2.a)</td>
<td>(Madin and Connolly, 2006)</td>
</tr>
<tr>
<td>survival of dislodged branching colonies</td>
<td>We defined a model using a model established empirically to determine the proportion of a dislodged branching colony that survives dislodgement (see §C.7.3.1.2.b)</td>
<td>(Highsmith et al., 1980)</td>
</tr>
<tr>
<td>coral bleaching</td>
<td>We used the empirically established bleaching response index to determine species bleaching susceptibility from functional traits (see §C.7.4.2 and 0)</td>
<td>(Swain et al., 2016b)</td>
</tr>
<tr>
<td>coral competition</td>
<td>We used species-pair probabilities of interaction outcomes established from mix-effect models and a review of empirical data (see §C.7.5.2.2.a)</td>
<td>(Precoda et al., 2017)</td>
</tr>
<tr>
<td>coral-algae competition</td>
<td>We defined probabilities of interaction outcomes using proportions of interaction won and lost between coral species and the different functional group of algae implemented measured experimentally (see §C.7.5.3)</td>
<td>(Brown et al., 2017) and K. T. Brown, personal communication, October 2017</td>
</tr>
</tbody>
</table>
Figure 3.1. Description of the agent-based model. Six different variables as model inputs determine (i) initial community composition, (ii) number of larvae coming from the regional pool (total number divided among different species, with annual supply for spawning species, and biannual supply for brooding species), (iii) thermal stress in degree-heating weeks, (iv) hydrodynamic regime intensity expressed as dislodgment mechanical threshold (unitless), (v) sedimentation, and (vi) the percentage of reef grazed. All variables are inputs at every time period except for the initial community composition that is determined during initialization. The model represents a 25-m² coral reef community and is composed of 1-cm² cell agents. Once every time step, living agents (algae and corals) grow by converting their neighbouring agents within a certain radius (white arrows in middle panel). Different processes affect the community at different spatial scales. For instance, the grazing process lasts until the imposed percentage cover grazed over the entire reef is reached. In contrast, coral colonies are individually considered for dislodgment during hydrodynamic disturbance and a single agent is potentially converted into a new coral recruit when larvae settle successfully. Radar charts represent the functional characteristics of coral species (defined by a specific colour): each vertex corresponds to a functional trait and the coloured polygon indicates the trait values of the species (higher values are farther away from the centre of the web). At the end of each time step, the model provides the percentage cover, the number of coral recruits, and the size of each colony for every taxon, and optionally, the reef rugosity created by coral colonies (bottom panel). The benthic community at the largest scale is a screenshot of the model output.
Figure 3.2. Ordering of processes in the coral agent-based model: white rectangles represent processes, dark grey rectangles with white text are input data, and light grey rectangles with black text are outputs. Large white arrows define the ordering of processes and black arrows show the direction of data transfer; dashed black arrows are optional processes (not activated for the analyses we present here). The order of occurrence of coral reproduction, bleaching, and colony dislodgement and fragmentation is imposed to simulate recruitment failure due to the occurrence of a disturbance prior to reproduction. The intensity of waves and cyclones is expressed as a dimensionless dislodgement mechanical threshold; thermal stress is expressed in degree-heating weeks.
3.2.3. Model calibration

We provide here a short description of the calibration. All details are presented in Appendix D.

3.2.3.1 Study sites and related data

We used data collected between November 2001 and July 2011 in three sites located in Martinique in the Caribbean: Fond Boucher (14° 39’ 21.07” N, 61° 09’ 38.98” W), Pointe Borgnesse (14° 26’ 48.74” N, 60° 54’ 12.72” W), and Ilet à Rats (14° 40’ 58.04” N, 60° 54’ 1.18” W). The data were collected biannually (once per dry and wet seasons) by the Observatoire du Milieu Marin Martiniquais (OMMM) for the program Initiative Française pour les REcifs CORalliens (IFRECOR). These data describe the benthic, macroinvertebrate, and fish communities at the species or genus levels, as well as sand cover for each site and at each sampling time (Figure D1; Figure D2). We downloaded values of degree-heating weeks for the corresponding location from the US National Oceanic and Atmospheric Administration data server ERDDAP (Environmental Research Division's Data Access Program; coastwatch.pfeg.noaa.gov/erddap) (Figure D3). We identified cyclone tracks using the National Oceanic and Atmospheric Administration Historical Hurricane Tracks website (coast.noaa.gov/hurricanes).

3.2.3.2 Definition of the environmental context

We modelled thermal stress by inputting at each time step the maximum degree-heating week value found for the corresponding period. We represented the intensity of hydrodynamic regimes by inputting values of the dislodgement mechanical threshold (Madin and Connolly 2006). We imposed a constant value in the absence of cyclone and a lower value when Hurricane Dean affected the reefs in August 2007 (its intensity changed from Category 1 to 2 while passing over Martinique). We chose threshold values arbitrarily considering wave exposure and cyclone intensity. Because of this uncertainty, we defined three different hydrodynamic regimes that we included in the calibration procedure for each site (Figure D5).

To estimate the percentage of the reef grazed at each time step, we first defined models predicting grazing intensity (i.e., percentage cover maintained in a cropped state) as a function of
herbivorous fish and urchin density (we did not activate the rugosity-grazing feedback process). We defined these models using the empirical data from Williams and Polunin (2001) and Sammarco (1980) for fish and urchins, respectively (Figure D6). We then used these models and the population densities of Acanthuridae spp., Scaridae spp., and sea urchins measured in the three sites to predict their respective grazing regimes. Finally, we defined three additional similar regimes of different intensities, which we included in the calibration procedure (Figure D8).

The model adjusts the amount of sand cover (i.e., by removing or adding sand patches) at each time step according to the observed cover measured in each site (Figure D4). Having no information about larval connectivity at the three sites, we set the number of larvae m\(^{-2}\) at 700 during each reproductive time period (i.e., once a year). This number corresponds to our estimate of competent larvae arriving on a hypothetical reef 20 km from an upstream reef having a 50% coral cover (see §C.7.2.1.2). The number is realistic considering that the distance separating the three sites from other coral communities is lower, but the average coral cover in the French West Indies is on average < 40% (Wilkinson, 2008).

3.2.3.3 General procedure

We calibrated the model for each site independently. We selected twelve parameters, for which we defined between two to five potential values (Table D1). We defined an algorithm to explore the parameter space optimally. The algorithm first selects the centroid, the most extreme values, and the values situated at mid-distance between the centroid and the extremes. A simulation with each parameter value is launched and replicated five times. We measured the fit between the empirical and simulated cover time series using an objective function. The objective function measures the performance of a given run by calculating the Euclidian distance between the empirical and simulated cover time series (averaged over five replicates), averaged over all the taxa (see §D.3.2). Performance is thus a positive value, with smaller values indicating higher performance (lower difference between simulated and empirical values). The algorithm then selects the ten runs providing the best performance and generates for each of them the five closest (using the Gower’s distance metric; Gower 1971) and untested parameter combinations. The algorithm then launches these new simulations and repeats the procedure once more.
To compare the performance of model runs to a null expectation, we generated a null distribution of performance values for each empirical dataset by randomizing cover values within each row and calculating the distance from the original datasets.

3.2.4. Hierarchically structured validation

Models are often validated by comparing outputs of a single level of organization (i.e., individual, population, community) to equivalent empirical datasets (individual species covers in our case), but this approach only examines lower dimensionality for more complex models. Following the recommendation of Kubicek et al. (2015), and aligned with the approach of pattern-oriented modelling (Grimm et al., 2005), we used a hierarchical approach to assess whether the different processes implemented in our model—starting from the those occurring at the lowest scales, to those affecting the entire system—produce ecologically realistic patterns by comparing them to expectations formulated a priori. We based several of the expectations using Grime’s (1977) classification of life-history strategies into competitive, stress-tolerant and ruderal (CSR) (or weedy) functional groups; a classification which was adapted to corals (Darling et al., 2012). This ‘CSR’ classification is independent from the effect, resistance and recovery trait classification that we adapted to corals (see Chapter 2 and Carturan et al. 2018), and which we used to select the traits to implement in the model.

We assessed the following processes of our model: (i) we expected colony lateral growth to equal the species growth rate in absence of spatial interaction and to decrease as space becomes saturated by colonies; (ii) recruitment rate should increase as a population grows from low initial cover, and then decreases as space saturates; for competition under different (iii) disturbance-regime intensities—we expected the competitive species to dominate the community under low-disturbance regimes, and ruderal or stress-tolerant species otherwise; (iv) larval connectivity—we expected species with higher colony fecundity or brooding mode of larval development to dominate the community under low connectivity, and the competitive ones otherwise; (v) grazing—under low grazing pressure, the benthic community should be dominated by algae, and by corals otherwise. In procedures iii, iv, and v, we varied the intensity of one factor at time while maintaining the other factors at intermediate values. This design generated factor combinations that are not realistic (e.g., grazing pressure and larval connectivity usually decrease after a strong disturbance), but is more rigorous because it prevented us from subjectively
defining time series of grazing and larval connectivity that would yield more realistic population
dynamics. We did not activate the rugosity-grazing feedback process in the analysis.

Because we expected the community dynamics to depend on species-specific trait differences,
we did procedures iii, iv, and v with two different communities, each composed of a competitive,
a ruderal, and a stress-tolerant species, originating from the Eastern Pacific and Western Atlantic,
respectively. Note that our goal was not to use suites of species that accurately reflect the
taxonomic composition of particular reefs or species pools, but rather to select species based on
their functional trait attributes. Although we refer to species by name, the names themselves
therefore matter less than their functionality. It is well known that reefs with different
biogeographic or evolutionary histories host species that are functionally similar (McWilliam et
al., 2018b). All details are in Appendix F.

3.2.5. Global sensitivity analysis

Our goal was to estimate the sensitivity of the predicted dynamics of the model to parameter
variation during a process of recovery after a strong pulse-disturbance. We constructed a global
sensitivity analysis for 10 of the calibrated parameters and six additional parameters with high
uncertainty (Table G1). For each parameter, we defined a range around the value(s) calibrated
(for the 10 parameters considered in the calibration) or the value used in the simulations (for the
six additional parameters). These parameters are all continuous but vary in their type (i.e.,
probabilities, ratio, heights, sub-model coefficients). We defined their respective ranges
considering parameter uncertainty, realistic boundaries, and what values might improve the
model performance based on model calibration and hierarchically structured validation. We did
the procedure for each site independently because certain parameters were calibrated on different
values between sites and because the coral communities differ.

We simulated our model for 10 years with a bleaching event of an intensity of 12 degree-
heating weeks occurring after four years. We consequently assessed model sensitivity six years
after the disturbance, a time when the communities in most runs were still recovering. We kept
the following processes constant: grazing (50%; we did not activate the rugosity-grazing
feedback process), wave hydrodynamic regime (dislodgement mechanical threshold = 120,
which is equivalent to strong wave regimes that colonies experience at the reef crest), and larval
input from the regional pool (700 larvae m$^{-2}$). We defined the same initial benthic composition as the one observed in the Caribbean sites.

We defined five response variables that represent the ecological state of the community at the end of the simulation: (i) total coral cover, (ii) difference of total coral cover at year 10 and just after the bleaching event, (iii) Pielou’s evenness, (iv) coral species richness (only the species having ≥ 1% cover), and (v) number of recruits m$^{-2}$.

We estimated the relative importance of the parameters selected on each response variable following the efficient protocol of Prowse et al. (2016). For each site, we sampled 1000 combinations of parameter values from a continuous parameter space using Latin hypercube sampling and continuous distributions. We launched each combination once (no replicates). We then fitted boosted regression trees on the input parameter values for each response variable—the procedure provides the respective influence of each predictor (i.e., model parameter) on the variation of the response variable in question. We ensured the sampling was sufficient by comparing the influence of the parameters obtained with $n = 1000$ samples with values obtained with subsamples ($n = 100, 250, 500$ and $750$); sampling is estimated sufficient when the influence of the parameters converge to similar values as sample size increases. All the details of the procedure are in Appendix G.

3.3. Results

3.3.1. Model calibration

Model performance (the Euclidian distance between the empirical and simulated cover time series averaged over all taxa) varies between 28 and 10 (lower values = better performance), and were all lower than the lower 95% confidence bound of the random distribution (Figure D9). This shows that, despite the model’s complexity and parameter uncertainty, the model outputs population dynamics closer to the empirical data compared to random. The best performance values converged toward 10 among the three sites (i.e., minimum ± standard error: 10.93 ± 3.677, 10.89 ± 2.872, 10.39 ± 3.119 for Fond Boucher, Pointe Borgnesse and Ilet à Rats, respectively).

With the combination of parameter estimates yielding the best fit, the model produces time series of total coral cover similar to the empirical ones for each site (Figure 3.3; Figure D14;
The difference between the simulated and real total coral cover does not exceed 15, 20, and 11% for Fond Boucher, Pointe Borgnesse and Ilet à Rats, respectively. Results at the species level are more variable, but the cover difference of individual coral populations never exceeds 8%. For some species, the simulated cover closely predicts the empirical data—for instance, *O. faveolata* and *O. annularis* at Ilet à Rats (Figure 3.3) and *A. agaricites* and *S. siderea* at Fond Boucher (Figure D14). The model failed to predict the population dynamics of some other species accurately; for instance, in the simulated reefs, *M. mirabilis*, *M. decactis* and *P. furcata* became the dominant species, while the cover of *P. atreoides* and *M. meandrites* approached zero at Fond Boucher; *M. mirabilis* outcompeted *O. annularis*, *O. faveolata*, *O. franksi* and *P. astreoides* at Pointe Borgnesse (Figure D14, Figure D15), while the *P. astreoides*’s population decreased at Ilet à Rats (Figure 3.3).

The simulated cover of algae also closely mimics the empirical data for most algal groups (Figure 3.3, Figure D14, Figure D15). The difference of percentage cover is the highest for turf and reaches a maximum of 29, 22 and 24% for Fond Boucher, Pointe Borgnesse and Ilet à Rats, respectively. These percentages are high compared to other groups or taxa, but this can be explained partially by the high variance in algal turf cover observed at the reefs. Turf cover generally fluctuates by > 20%, a pattern that our model was able to reproduce at all three sites (Figure 3.3; Appendix 3: Figure D14, Figure D15). Notably, crustose coralline algae are systematically less abundant in the simulated reefs compared to the observed data, a phenomenon we attempted to correct in the calibration procedure (see §D.3.3). Finally, the model could not reproduce the high cover of *Halimeda* spp. observed at Ilet à Rats (Figure 3.3) compared to the other sites. See Appendix D for more detailed results and discussion regarding the between-site comparison.
Figure 3.3. Comparison of empirical and simulated taxa cover for the combination of parameter values providing the best fit for site Ilet à Rats. Solid lines in the simulated time series are the percentage cover means (averaged over five replicates) and the shaded areas show the standard error. The right panels display the cover difference between simulated and empirical time series.
3.3.2. Hierarchically structured validation

The hierarchically structured validation shows that the model produces ecologically realistic population dynamics under different environmental conditions. Here we provide a summary of the results, but a more-complete description and explanation are available in Appendix G.

*Growth:* Coral colonies grew *ipso facto* at their species-specific growth rate at low population density. However, as space filled up, colonies began constraining each other spatially and their growth rates decreased until eventual stasis (Figure F4).

*Recruitment:* For a single coral population, the different patterns of recruitment observed among three functionally distinct species (Figure F6) results from the interaction of several factors: 

1. individual colony fecundity determined by its planar area, species-specific polyp fecundity, corallite area (polyp size), growth form, sexual system, and mode of larval development;
2. the distribution of colony size in the population, which depends on maximum colony diameter; and
3. the amount of surface available for larval settlement. Weedy (*Agaricia tenuifolia*) and stress-tolerant species (*Echinophyllia orpheensis*) produced bell-shape recruitment patterns (Figure F8). Recruitment rate was initially low because populations were composed of small, low-fecundity colonies, but the rate increased as colonies grew and became more fertile (Figure F8). Recruitment subsequently decreased as space became saturated. In contrast, recruitment rate for competitive species (*Acropora gemmifera*) was initially high and only decreased as cover occupancy increased. This pattern is essentially due to a higher vegetative growth rate associated with a population initially composed of fewer but larger, more fecund colonies (Figure F8).

*Disturbance intensity:* In both the Western Atlantic and Eastern Pacific communities (we compared the two functionally distinct coral communities in the rest of the analysis), the competitive species dominated the coral community under low wave exposure (Figure F10; Figure F11; Figure F14). The success of the competitive species was due mainly to two interacting processes—with a higher vegetative growth rate, competitive species (*i*) overcame free space before other species, and (*ii*) enhanced recruitment by achieving large colony size rapidly. Higher wave exposure reduced the cover of competitive species because colonies were dislodged at a certain colony size, which reduced recruitment rate and provided other species with more available space to grow and recruit.
In the Western Atlantic community, increased availability of space favoured the weedy species (*Madracis pharencis*) over the stress-tolerant species (*Orbicella annularis*), principally because of the former’s brooding mode of larval development (twice a year), faster growth rate, and high wave-resistance of its growth form (digitate). In contrast, species coexisted in the Eastern Pacific community under the highest-intensity disturbances (Figure F14). Both the competitive (*Pocillopora elegans*) and stress-tolerant species (*Porites lutea*) recruited more than weedy species (*P. damicornis*) due to their spawning mode of reproduction; spawning species received three times more larvae from the regional pool (see §C.7.2.1.2). However, the weedy species recruited twice as frequently and is slightly more aggressive than the other two species. The stress-tolerant species has a massive growth form, which conferred higher resistance to waves compared to the other two branching species. Nonetheless, this advantage barely compensated for its slower growth rate and lower colony fecundity.

Population(s) recovered to pre-disturbance cover after only one year, regardless of the intensity of the event. This recovery is faster than most dynamics observed in real reef systems and arises because we imposed a constant and high number of larvae (7000 m$^{-2}$) coming from the regional pool. In reality, larval supplies are reduced because a strong bleaching disturbance would also affect the surrounding reefs (Hughes et al., 2019). Another reason for this outcome was that recruitment preceded growth in the model (Figure 3.2), which inflated the former process because more space was available for settlement.

*Larval connectivity*: Low larval connectivity influenced the two coral communities differently (see §F.5). In the Western Atlantic, the weedy species thrived under zero to moderate larval input (0, 66, 700 larvae m$^{-2}$) while the other two species went locally extinct (Figure F17). The weedy species produced ready-to-settle larvae twice a year, while the other two species reproduced annually and only a portion of their larvae were able to settle because of their time to motility (see §C.7.2.1.1.d). In contrast, the stress-tolerant species dominated in the Eastern Pacific community (Figure F18), due to its higher wave-resistance compared to the other two branching species.

Under the highest larval connectivity (7000 and 35,000 larvae m$^{-2}$), the competitive species dominated in both communities, principally because of their higher growth rates, spawning mode of reproduction, and their capacity to overtop smaller colonies.
**Grazing:** Population dynamics were similar between the two communities (Figure F20; Figure F25). The total coral cover corresponded approximately to the imposed percentage of reef grazed, and the remaining ungrazed part of the reef was occupied by algae (also, ungrazed coral agents potentially exist). We observed no hysteresis because we did not implement feedback processes. Turf dominated the algae community in all simulated grazing regimes, despite having the highest palatability among algae (Table C3). The success of turf was due to its much higher growth rate compared to other algae (Table C19).

Coral recruitment rates at the steady state were the highest under medium grazing pressure (50%) because under lower and higher grazing intensities, space was saturated by turf and coral colonies, respectively. Under the lowest grazing pressure, most of the colonies were ≤ 100 cm² in surface area (Figure F22) and coral populations were rescued by external larval input. At intermediate pressures (30 and 50%), the competitive species dominated the coral community mainly because of their higher external larval input compared to the brooding (weedy) species, and their higher growth rate than the stress-tolerant species. Having a high growth rate was particularly important under low grazing pressure because this trait compensated better for the cover lost in competition with turf, which wins all its interactions with corals in the model (Table C19).

Under higher grazing pressures (70 and 90%), there were more coral-coral and fewer coral-algae interactions, which changed coral species dominance. The Western Atlantic community was dominated by the weedy species, followed by the stress-tolerant species and the competitive species was competitively excluded, mainly because of its lower aggressiveness and highest vulnerability to waves (Figure F10). In the Eastern Pacific community, the stress-tolerant species dominated the coral community and slowly outcompeted the other two species mainly because of its much higher wave resistance (Figure F27).

### 3.3.3. Global sensitivity analysis

The parameters that had the most important effects on the response variables (i.e., total coral cover, Pielou’s evenness, difference cover, coral species richness and the number of coral recruits m⁻², all measured 10.5 years after the disturbance) were *growth rate reduction interaction* (the reduction of lateral growth rate of an organism overgrowing another one) and
otherProportions (coefficient controlling the number of larvae produced locally), followed by probabilities for larvae to settle on different substrata, and the probabilities of algal grazing. The remaining ten parameters did not have an important influence on any of the five response variables (Figure G1).

Globally, all the influential parameters affected the response variables according to expectations. For instance, increasing growth-rate reduction when organisms interact (mostly turf over corals) reduced the competitive advantage of the dominant taxa, which increased coral richness, total coral cover (due to reduced competitiveness of algae), and consequently enhanced the difference in coral cover and the number of coral recruits (Figure G1). Increasing otherProportions increased the number of larvae produced by each coral population, which positively affected coral cover, cover difference and the number of coral recruits. The parameter was negatively correlated with richness and evenness because higher values disproportionately benefitted species capable of higher recruitment (e.g., brooder; Figure G3).

In general, the parameters influenced the response variables in consistent ways among sites (Figure G1). Differences were mainly due to different ranges of values tested for particular parameters. For instance, probability of grazing allopathic macroalgae had a stronger effect at Pointe Borgnesse compared to the other two sites because its range included smaller values, implying lower palatability, higher abundance (Table G1; Figure G4), and a larger effect.

Ten of the parameters had a negligible effect on the response variables, because the processes they contributed to did not occur in these simulations. For instance, probability of algae to cover crustose coralline algae did not have an effect because crustose coralline algae was not present in high enough abundance (Figure G4), and height of big algae and height of turf did not have an effect because most of the branching colonies did not reach sizes large enough to overtop these algae (Figure G5).

3.4. Discussion

Our primary goal was to develop a model that captured the spatiotemporal dynamics of community composition in coral reefs as component coral and algal species responded to interspecies competitive interactions and external disturbances. Our trait-based and demographic approaches provided a combination that yielded better predictions and a better understanding of
coral ecosystem dynamics relative to single-component models (Edmunds et al., 2014; Salguero-Gómez et al., 2018; Violle et al., 2007). The spatial structure we imposed—a grid of 1-cm² agents that collectively comprise a sizeable reef (tens of m²) as inspired by previous models (e.g., Langmead and Sheppard 2004, Sleeman et al. 2005, Tam and Ang 2009, Sandin and McNamara 2012)—yielded emergence, scaling, self-organization, and unpredictability, each of which is a property of complex systems (Parrott, 2002) including coral reefs (Dizon and Yap, 2006; Hatcher, 1997). Operating at such a small spatial grain, processes can be modelled at the appropriate scale (e.g., dislodgement removes entire colonies while spatial competition affects colony edges) (Figure 3.1) to generate distributions of colony size, and in turn, colony fitness and performance. Overall, the population dynamics resulted from the collective performance of each colony, which implies that at the scale of the community, a given species’ fitness depended on its capacity to persist under a certain environmental context and compete with functionally dissimilar species. As in the real world, macro-scale community dynamics emerged from finer-scale processes and interactions, a phenomenon clearly demonstrated by the hierarchically structured validation (Appendix F). The model structure can also accommodate the initialization of a specific spatial colony arrangement based on empirical data. This feature is absent in previous models (but see Wakeford et al. 2008), despite the importance of spatial patterns for herbivory (Eynaud et al., 2016) and coral population dynamics (Brito-Millán et al., 2019).

Our model is unique in being designed to simulate the effects of coral species richness and functional diversity on ecosystem dynamics. Most coral models have been developed to describe the effect of external drivers (mainly disturbances) on the state of the coral community (usually total cover) (e.g., Bozec and Mumby, 2015; Kubicek et al., 2019; Kubicek and Reuter, 2016; Madin et al., 2012b; Melbourne-Thomas et al., 2011a). In contrast, few models exist that assess the influences of aspects of diversity on community or ecosystem dynamics (e.g., Tam and Ang 2012, Ortiz et al. 2014, Fabina et al. 2015), but these have represented diversity with limited detail, and consequently have limited capacity to evaluate the effects of identity and diversity on ecosystem functioning (Brandl et al., 2019), or the effects of functional redundancy and response diversity on ecosystem resilience (Mcleod et al., 2019). In contrast, our model represents diversity in detail; we considered eleven functional traits and included their influence over eight ecological processes applied to 798 functionally realistic species. In addition, we ensured that species richness can be varied without affecting computation time. Our model therefore enables
exploration of many realistic assemblage scenarios within an easily modified experimental setting.

Our calibrated model was able to reproduce similar total coral-cover dynamics in the three sites (Figure 3.3; Figure D14; Figure D15). At the population level, results were more varied, with several populations well predicted, others less so. Overall, these results are remarkable considering model complexity, the large number of parameters, and the limited data describing the environmental context and diversity at the three sites. Note that we validated the population dynamics of the species within an imposed environmental context. Specifically, we determined the external larval supply, hydrodynamic, thermal, grazing and sand input regimes before the simulations. In reality, feedback processes emerge and contribute in shaping community dynamics (van de Leemput et al., 2016). Implementing additional feedback processes would have increased model complexity, and we estimated that the empirical data we had were insufficient to validate these. For instance, the model offers the option to activate the feedback process between structural complexity and grazing pressure (see §C.7.1.2), but validating this model with this process requires better population density estimates of the major herbivorous fishes.

A useful model should ideally be calibrated and validated with empirical data at each level of organization (e.g., colony, population, community) (Kubicek et al., 2015). However, empirical data are usually lacking for some or even all of these levels. Coral models have therefore been validated against one or a few community-aggregated variables, and rarely at the species level. Sampling additional data specifically for the model and at the sites used for calibration and benefiting from the opinion of local experts can improve the capacity of the model considerably to reproduce realistic dynamics. For instance Mumby (2006) developed a spatially explicit, mechanistic model to reproduce the total coral and macroalgae cover observed in Jamaican reefs. In two subsequent developments of the model, Ortiz and colleagues (2014) reproduced accurate recovery rates and final community composition of six coral taxa at fourteen reefs in the Great Barrier Reef, and Bozec and colleagues (2015) reproduced the cover of seven coral species and the rugosity in reefs in Cozumel (Mexico). With a similar model, Kubicek and colleagues (2012) generated time series of major coral taxa cover at Chumbe Island (Tanzania) similar to real data. Further, Kayal and colleagues (2018) accurately reproduced colony density distributions of three
coral species in four different sites in Moorea, French Polynesia, using integral-projection models.

In contrast with conventional approaches, we developed our model independently of the empirical data upon which calibration was based. Instead, our model included the ecological details required for achieving our primary objective. Below we discuss the primary sources of uncertainty in our model calibration and suggest realistic ways for improvement.

**Grazing:** We estimated average grazing pressure over six months (% of reef grazed) based on a biannual assessment of sea urchin and herbivorous fish (Scaridae spp. and Acanthuridae spp.) populations. Acanthuridae spp. are mobile herbivores (Thibaut et al., 2012), so frequent assessments are necessary to obtain accurate estimates of mean population size. More data collection could improve the accuracy of the modelled processes, has others have done for several fish species (e.g., Bozec et al., 2016; Mumby, 2006).

**Hydrodynamic regime:** We defined time series of dislodgement mechanical threshold as a function of site exposure and cyclone intensity. Measuring the real dislodgement mechanical threshold over time in each site would improve the precision of the simulations. This would require measuring horizontal water velocity and tensile strength of the substratum (Madin et al., 2012a; Madin and Connolly, 2006).

**Recruitment:** There is high uncertainty in our implementation of recruitment because we did not have estimates of recruitment rates and of the proportion of recruits originating from the local reef versus the regional pool. We therefore fixed the number of external larvae coming into the reef and controlled recruitment rate with one parameter (otherProportions). The sensitivity analysis revealed that the parameter has a strong influence on the model’s predictions. Reducing this uncertainty requires better estimates of recruitment rates, which can be achieved with tile experiments (e.g., Ritson-Williams et al., 2016) or visual assessment of new recruits along transects (e.g., Gilmour et al., 2013; Holbrook et al., 2018). The proportion of locally versus regionally recruited larvae can be estimated with population genetics (e.g., Almany et al., 2017; Johnson et al., 2018) or by modelling larvae plumes (e.g., Golbuu et al., 2012; Wolanski and Kingsford, 2014).

**Trait data:** The hierarchically structured validation showed that between-species trait differences influenced community dynamics. Considerable gaps in the coral-trait database (Madin et al., 2016a) limited our capacity to estimate traits accurately for many coral species.
Collecting reliable trait data is critical to predict coral-community dynamics and ecosystem functioning (Madin et al., 2016b). Further precision in the prediction would be gained by measuring traits locally, because traits can vary substantially among populations in different locations (e.g., Diaz-Pulido et al., 2009), and factors such as nutrient concentration affect both algae and corals growth (Wear and Thurber, 2015; Zaneveld et al., 2016).

*The third dimension:* The model represents flat benthic communities and estimates the height and surface area of colonies using simple geometric formulae. These approximations potentially misrepresent certain processes such as larval production, formation of reef rugosity, overtopping, and their interspecific differences. Recent efforts to quantify physical attributes of the colony from planar areas and growth forms (Zawada et al., 2019a) provide potential opportunities to improve our model’s accuracy.

Our model is flexible and can be tailored to represent coral communities around the world, and to explore many different questions pertaining to the links between diversity and ecosystem dynamics. This version of the model focusses primarily on coral diversity and the effect of two disturbance types, but other disturbance types, and additional processes and aspects of reef diversity, could be easily implemented provided sufficient data are available. Examples include functions related to herbivory, algal diversity, disturbance types, and feedback processes, which we elaborate below.

Herbivores differ in their foraging behaviour (reviewed in §C.7.1.1), which affects benthic diversity, coral reef recovery, and functioning (Burkepile and Hay, 2010; Cheal et al., 2013, 2010; Nash et al., 2016; Pratchett et al., 2014). A few models have described aspects of herbivore diversity; for instance, Sandin and McNamara (2012) modelled the effect of spatially differentiated foraging behaviour between fish and urchins on the dynamics of a coral community, and Bozec and colleagues (2016) modelled the population dynamics of several parrot fish species and their respective species and size-specific contribution to grazing. However, herbivore diversity has generally been neglected in coral-reef models. Accommodating herbivore diversity and its effect on the benthic community in our model is feasible, provided associations between population densities and processes (e.g., grazing, bioerosion) are empirically established for different taxonomic or functional groups (e.g., see §D.2.3).

Algal diversity is potentially as important as coral and herbivore diversity for reef functioning and recovery (e.g., Roff et al. 2015). Yet, most coral-reef models describe the algal community
with no more than three functional groups (macroalgae, crustose coralline algae, turf). Our model is the first to implement six functional groups, which accommodated additional ecological details such as grazing preferences and coral-algae interactions (see §C.7.1.2 and §C.7.5.3, respectively). To date, trait-based research on tropical reef algae is modest compared to fishes and corals (Brandl et al., 2019) and an algal-trait database has not yet been created.

We implemented the effects of hydrodynamic variation, thermal disturbances, and changes in grazing pressure, but reefs are also affected by other disturbances, and some of these have been implemented in previous models—including ocean acidification (e.g., Anthony et al., 2011; Madin et al., 2012b), predation by Acanthaster planci (e.g., Hogeweg and Hesper, 1990; Van der Laanm and Bradbury, 1990), disease (e.g., Brandt and McManus, 2009), destructive fishing (e.g., Kubicek et al., 2012), and pollution (e.g., Wolanski et al. 2004, Melbourne-Thomas et al. 2011, Kennedy et al. 2013). We are currently not able to model the species-specific effects of these disturbances on coral assemblages because it is not clear what traits are relevant, nor how these relate to ecological processes and responses. Such information is necessary to parameterize mechanistic models such as ours, as exemplified by our trait-based model of the response of corals to bleaching (Appendix E). Nevertheless, our model would benefit from further validation, and is missing important variables (e.g., symbiont diversity) for which data are lacking (Chapter 2; Carturan et al., 2018).

Feedback processes affect population dynamics by generating thresholds, hysteresis, and by shaping basins of attraction (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Coral reefs are notorious for feedback processes (Hughes et al., 2010; Mumby and Steneck, 2008), some of which have been implemented in models (e.g., Mumby et al. 2007, Muthukrishnan et al. 2016, Kubicek and Reuter 2016). Van de Leemput and colleagues (2016) reviewed over 20 different feedback processes observed in reefs and demonstrated with a simple model that the combination of several feedback processes, although weak individually, can have important effects on system dynamics. However, the empirical quantification of these processes remains to be established (van de Leemput et al., 2016).

The model we present here is suitable for simulating the local response of benthic coral reef communities to disturbances over short time periods (< 2 decades). Predicting community dynamics over longer periods (e.g., under different climate-change scenarios) requires calibrating the model with longer empirical time series because we cannot guarantee that the
actual calibration will yield realistic community dynamics beyond the periods we considered. For testing and demonstration purposes, we implemented the model for small spatial extents. Consequently, the size-class distributions of certain coral species comprising large colonies might not be realistic, and certain influential processes happening at larger scales (e.g., connectivity along environmental gradients and from refuges) are not implemented in our simulations. However, the model can be run for larger spatial extents, but such simulations require substantial computational power due to the high ecological detail and 1-cm² spatial resolution of the model. Ongoing model development includes improving computational efficiency to accommodate the simulation of larger spatial scales and related processes.

Minimal models of coral reef systems (e.g., differential equation systems) have generally been developed to simulate the response of state variables to different processes (i.e., pulse and press-disturbances, feedback processes) (Weijerman et al., 2015). Our model, while developed for the same objectives, provides the possibility to represent realistic benthic diversity and its effect on community dynamics. Comparing the results of our model to those obtained from minimal models would help establish the degree to which ecological details are necessary.
Chapter 4: Functional richness promotes resilience in coral reef communities

4.1. Synopsis

In this chapter, we present and discuss the results of the experiment we conducted using the model we present in Chapter 3 to quantify the relationship between functional richness (FRic) and resilience in coral reef communities.

In this experiment, we assemble 245 coral communities of nine species by sampling species in a functional space defined by eight functional traits associated with the species contribution to the habitat provisioning function (i.e., effect traits), processes of resistance to cyclones and bleaching events (i.e., resistance traits) and recovery (i.e., recovery traits), and competition (§4.2.2.1). Each community is characterized by its FRic and its location in the functional space (i.e., centroids). We simulate scenarios where the communities are affected by a strong cyclone or bleaching event. The independent variables are initial FRic and the initial communities’ centroid, which is represented by PC.1 and PC.2—the first two components of a principal component analysis (PCA) we did to reduce the number of dimensions of the centroid variable. The dependent variables are different measure of resilience: resistance, recovery and “general resilience”, which represent the state of the communities 10 years after the pulse disturbance. We use total coral cover and reef rugosity to assess the state of the communities during the simulations. We averaged the values of the dependent variables between the cyclone and the bleaching scenarios in order to estimate the overall resilience of communities to multiple disturbances.

Our results show that FRic is positively associated to general resilience and recovery and weakly and negatively to resistance. We use the “effect-resistance-recovery traits” framework we define in Chapter 2 to explain the potential effects responsible for these results and discuss the relevance of our simulated experiment for real-life coral reef ecosystems.

This is the first experiment conducted on the diversity-resilience relationship and the first demonstration of a positive effect of FRic on resilience with coral communities.
4.2. Methods

4.2.1. Software

We used the Java object-oriented programming language Repast Simphony 2.5.0 (North et al., 2013) to run simulations and R (version 3.5.0, R Core Team, 2017) to manage the simulations. We launched simulations using the R package `rrepast 0.7.0` (García and Rodríguez-Patón, 2016) and `rJava 0.9-10` (Urbanek, 2018). We used R (version 3.6.1, R Core Team, 2019) to manipulate datasets and conduct statistical analyses.

4.2.2. Experiment

4.2.2.1 Community assembly

We initiated communities of nine coral species by sampling species from a functional space we defined using the traits that have a direct and clear implication in certain processes: (1) colony maximum diameter; (2) colony complexity; (3) dislodgement susceptibility; (4) bleaching susceptibility; (5) colony fecundity; (6) mode of larval development; (7) growth rate; (8) overtop capacity. Traits (1), (6) and (7) are originally present in the trait database we assembled and constrain colony size, define reproduction and dispersal and determine vegetative growth, respectively (Table B1). We derived the remaining five traits from traits originally present in the database: colony complexity (2) is the rugosity of a colony, which we determined by calculating the colony surface area for each growth form using geometric formulas (Figure H1); (3) dislodgement susceptibility is a measure of colony vulnerability to cyclones and waves and corresponds to the slope of the relationship between the colony shape factor and colony planar area for each growth form; (4) bleaching susceptibility is the species-specific coefficient of bleaching susceptibility defined from growth rate, colony maximum diameter, corallite area and microscopic reduced scattering coefficient (Appendix E); (5) colony fecundity is the number of eggs.cm\(^{-2}\) of colony planar area and is defined using the traits polyp fecundity, sexual system, corallite area and growth form; (8) overtop capacity is a binary trait indicating if a species has a colony growth forms that can overtop other organisms (see §H.1.1 for details). In the model these traits are mechanistically implicated in the effect that a colony has on the habitat provisioning function (i.e., colony complexity), its capacity to resist a disturbance (i.e.,
dislodgement susceptibility, bleaching susceptibility), or to recover from it (i.e., colony fecundity, mode of larval development, growth rate), and its competitiveness (colony maximum diameter, growth rate) (Table 4.1). We reduced the number of dimensions of the functional space by conducting a principal component analysis (PCA), retaining the four first of eight principal components (§H.1.2). We then developed an algorithm to assemble 245 different communities, each initially comprising nine species, and each exhibiting unique functional trait characteristics; specifically, the communities’ centroids span the entire functional space and the range of functional volume they occupy span over four orders of magnitude (§H.1.3).

4.2.2.2 Model configuration and scenarios

We defined a 25 m² benthic surface and a six-month time step. We activated the feedback process between architectural complexity created by the coral community and grazing pressure data (see §C.7.1.2.2 for details). We set at 7.5% the initial cover of each coral species, macroalgae, turf and crustose coralline algae. We maintained a mild and constant wave hydrodynamic regime (dislodgement mechanical threshold = 200), and triggered an intense pulse disturbance at year four, either a cyclone (dislodgement mechanical threshold = 30) or a bleaching even (degree heating = 14 °C-weeks) depending on the scenario. We simulated the effect of the disturbance on larval connectivity (Connell, 1997; Gilmour et al., 2013) by initially setting the number of external larvae entering the reef at 700 m², then suppressing it in the six months following the disturbance and letting it increase to 700 m² during the subsequent 10 years using the following model:

\[
\text{larvae}_{\text{external}} = 2.9 \times \text{time}^2 + 17.5 \times \text{time} - 116.7
\]

where \(\text{larvae}_{\text{external}}\) = number of external larvae m², \(\text{time}\) is in yr. We ran the simulations for 20 years. Finally, we imposed a minimum of 30% of cover grazed to represent the presence of other grazers, such as sea urchins, which are not dependent on the rugosity created by coral colonies.
4.2.2.3 Variables

We defined four dependent variables that represent some of the numerous different definitions of resilience (Carpenter et al., 2001; Desjardins et al., 2015). Resilience cover and resilience rugosity are the 10 years post-disturbance total coral cover and reef rugosity, respectively; they capture the capacity of the ecosystem to absorb disturbance and to reorganise while undergoing changes so as to still retain essentially the same function, structure, identity and feedbacks (Walker et al., 2004). Resistance cover—one minus the proportional reduction of total coral cover caused by the pulse disturbance and recovery cover—the rate of recovery during the first three years after the disturbance (% cover yr\(^{-1}\)) represent two complementary aspects of resilience (Hodgson et al., 2015). We averaged these variables between the bleaching and cyclone scenarios, so they represent resilience against multiple disturbances (Figure H6). Note that we did not define resistance rugosity and recovery rugosity because the bleaching disturbance does not directly reduce the rugosity of the reef as the skeleton of dead coral colonies remain after the event.

We defined three independent variables that represent two aspects of the communities’ functional trait characteristics. We used functional richness (FRic)—the volume occupied in the functional space by a community (Laliberté and Legendre, 2010; Villéger et al., 2008)—to quantify the effect of functional diversity on resilience. We calculated FRic from the first four principal components of a PCA we did on the species trait dataset (by considering species as observations and the eight traits as variables) using the prcomp function from the R package stats 3.6.1. (R Core Team, 2019). We log-transformed FRic to reduce the skewness of its distribution (Figure H4). We calculated FRic using the R code provided by Mouillot and colleagues (2013) and using the convhulln function from the R package geometry 0.4.5. (Habel et al., 2019). We defined PC.1 and PC.2—the first two principal components of a PCA we conducted using communities as observations and their weighted trait averages as variables—to represent the location of the communities’ centroids in the functional space (PC.1 and PC.2 represented 53.2 and 26.7% of variance, respectively). We centered and scaled FRic, PC.1 and PC.2 to a mean of zero and unit variance in order to compare their effect sizes; we used the scale function from the R package base 3.6.1. (R Core Team, 2019).
4.2.3. Statistical analyses

4.2.3.1 Test of the biodiversity-resilience hypothesis

For each measure of resilience (resilience cover, resilience rugosity, resistance cover, recovery cover), we first fitted full (i.e., with all three explanatory variables and their interactions) linear model candidates (i.e., with different link functions or variance structures). We selected the best full model using the corrected Akaike information criterion (AICc)—we used the AICc because sample size divided by number of parameters < 40 (Burnham and Anderson, 2002)—and residual diagnostic plots (i.e., to check normality and homoscedasticity of the residuals). From each full model selected, we generated models with all possible combinations of predictors, selected the 95% confidence set using AICc, and calculated model-averaged coefficients and 95% confidence intervals using the “full average” method (Bartoń, 2019). We conducted model averaging using the R package MuMIn 1.43.6. (Bartoń, 2019).

For resilience cover and resistance cover we fitted beta regressions using the R package betareg 3.1.3. (Cribari-Neto and Zeileis, 2010); we used this approach because beta regressions are appropriate with response variables that represent proportions and two categories (e.g., coral and non-coral cover) (Douma and Weedon, 2019). We fitted and compared all possible full model candidates considering each link function for the mean model (i.e., logit, probit, cauchit, log, cloglog, loglog), and each possible combination of predictors (and their interactions) and each link function for the precision model (i.e., identity, log, sqrt). Following Espinheira and colleagues’ (2008) recommendation, we used the “standardised weighted residuals 2” for the diagnostic plots. We removed one outlier to meet the assumptions of the full model for resistance cover (Figure H11; Figure H12). We verified that the maximum likelihood estimator did not overestimate the parameters of the selected full beta regression models by comparing the parameter estimates of the same models but using bias-corrected and bias-reduced estimators (Grün et al., 2012). The selected full and averaged models for resilience cover and resistance cover are presented in Table H3, Table H4, Table H5 and Table H6, respectively. We computed the confidence interval of the fitted values using bootstrap using the percentile method and 1000 replications.

We fitted gamma generalised linear models for resilience rugosity—after subtracting one to the response variable so it belonged to $[0, +\infty[$—and compared full model candidates with different
link functions (i.e., inverse, identity, log). We fitted the models using the \texttt{glm} function from the R package \texttt{stats} 3.6.1. (R Core Team, 2019). We removed four outliers to meet the models’ assumptions using the \texttt{outlierTest} function from the R package \texttt{car} 3.0.3. (Fox and Weisberg, 2019) (Figure H7; Figure H8). We used the deviance residuals to check the full models’ assumptions (Zuur et al., 2009 and references therein). We present the selected full and averaged models in Table H1 and Table H2, respectively.

We fitted full linear models for \textit{recovery cover} and applied residual variance structure to account for identifiable structure in the error residuals (Zuur et al., 2009). First, we used AICc to determine the best variance structure function to apply to each variable (dependent and independent) by comparing a full linear model and full models with a variance structure applied to one variable, for each variance structure available (i.e., fixed, exponential, constant plus power of the variance covariate functions). We then fitted full model candidates for all the possible variables - variance structure function associations. We present the full linear model, the model with variance structure and the averaged model with variance structure in Table H7, Table H8 and Table H9, respectively.

We calculated for each model the McFadden’s (1977) pseudo $R^2 = 1 - \frac{\text{likelihood value of fitted model}}{\text{likelihood value of null model}}$. Its value is comprised between 0 and 1 for logistic regression models and tend to be considerably lower than other pseudo $R^2$; for instance, values between 0.2 and 0.4 are considered “an excellent fit”. Note that McFadden’s pseudo $R^2$ is negative if the models’ log likelihood values are positive. For instance, values $< -1$ correspond cases where the goodness of fit of the model is more than twice larger than the goodness of fit of the null model. We obtained the McFadden’s pseudo $R^2$ of the averaged models by calculating the weighted average of the McFadden’s pseudo $R^2$ of the models in the 95% confidence set using their AICc weights (rescaled to the model set). For comparison, we calculated another pseudo $R^2$, defined as the square of the sample correlation coefficient between the original and predicted values of the response variable on the scale of the link function (Ferrari and Cribari-Neto, 2004).
4.2.3.2 Trait correlations

We performed Spearman rank correlations to quantify associations between two continuous or ordinal traits using the `cor.test` function from the R package `Stats`. We calculated the Glass rank biserial correlation to quantify the association between a continuous or ordinal trait and a dichotomous trait (Glass, 1965); we determined 95% confidence limits by bootstrap using the percentile method and 1000 randomisations; we used the `wilcoxonRG` function from the R package `rcompanion` (Mangiafico, 2020).
**Table 4.1.** The eight functional traits we used to define the functional space.

| Trait                        | Process(es) involved                                                                 | Details                                                                 
|------------------------------|--------------------------------------------------------------------------------------|-------------------------------------------------------------------------|
| colony maximum diameter      | Initial colony size distributions (§C.5.2.2); vegetative growth (defines maximum colony planar area; §C.7.5.1) | Transformed with logarithm base 10 (original scale is cm)               
| colony complexity             | Provision of reef rugosity (§C.7.1.2.2)                                              | The square root of the ratio between the area and planar area of a colony, measured when colony planar area = 1000 cm² (Figure H1); transformed with logarithm base 10 |
| dislodgement susceptibility   | Dislodgement due to waves and cyclones (§C.7.3.1.2)                                   | The slope of the colony shape factor and colony planar area (on the logarithm scale) for each growth form (Figure C12) |
| bleaching susceptibility      | Bleaching due to thermal stress (§C.7.4.2)                                            | The species-specific coefficient of bleaching susceptibility defined from the growth rate, colony maximum diameter, corallite area and microscopic reduced scattering coefficient (Appendix E) |
| colony fecundity             | Coral reproduction (§C.7.2.1.1.b)                                                      | Transformed with logarithm base 10 (original scale is no. eggs cm⁻² of colony planar area) |
| mode of larval development    | Coral reproduction (brooders reproduce twice a year, spawners only once; brooders receive three times fewer external larvae) | We attributed one to spawner and negative one to brooder                 |
| growth rate                  | Vegetative lateral growth of colonies                                                | Transformed with logarithm base 10 (original scale is mm.yr⁻¹)            |
| overtop capacity             | Branching and plating colonies can overtop small colonies and algae (§C.7.5)        | We attributed one to branching and plating growth forms and zero otherwise |
4.3. Results

4.3.1. Test of the biodiversity-resilience hypothesis

We found strong support for the diversity-resilience hypothesis for all measures of resilience except resistance cover (Figure 4.1). FRic had significant positive effect on resilience rugosity (0.43, 95% CI: 0.370 to 0.498; Table H2), resilience cover (1.82, 95% CI: 1.420 to 2.228; Table H4) and recovery cover (2.47, 95% CI: 1.927 to 3.010; Table H9). Its effect was strongest for resilience rugosity, and was similar in magnitude to that of PC.1 (-0.41, 95% CI: -0.487 to -0.339), and was four times greater than that of PC.2 (-0.11, 95% CI: -0.175 to -0.036). The interaction between FRic and PC.1 was the only significant interaction term and was positive (0.15, 95% CI: 0.086 to 0.204; Table H2): the positive effect of FRic was stronger for higher values of PC.1 (Figure 4.1; Figure 4.2).

The effect of FRic on resilience cover was approximately one third smaller than the effect of PC.1 (-2.87, 95% CI: -3.443 to -2.315) and twice larger than the effect of PC.2 (-0.97, 95% CI: -1.306 to -0.668). Interaction terms between FRic and PC.1 and PC.2 were significant and relatively strong (1.67, 95% CI: 0.988 to 2.353 and -1.06, 95% CI: -1.391 to -0.733, respectively; Table H4): the positive effect of FRic was stronger for higher and lower values of PC.1 and PC.2, respectively (Figure 4.1; Figure H10).

The effect of FRic on recovery cover was three times smaller than that of PC.1 (-7.27, 95% CI: -7.852 to -6.682). PC.2 did not have an effect (0.03, 95% CI: -0.721 to 0.784), but its interaction with FRic and PC.1 was significant (-1.24, 95% CI: -1.865 to -0.623 and 0.55, 95% CI: 0.053 to 1.048, respectively; Table H9): the positive effect of FRic and negative effect of PC.1 increased for lower values of PC.2 (Figure 4.1; Figure H16).

FRic had a weak but significant negative effect on resistance cover (-0.04, 95% CI: 0.081 to 0.001), which was approximately seven and two times smaller than those of PC.1 and PC.2 (0.30, 95% CI: 0.251 to 0.349 and 0.08, 95% CI: 0.032 to 0.120, respectively; Table H6) (Figure 4.1; Figure H13).

Overall, the averaged models explained sizeable fractions of the variation in the response variables: for resilience rugosity (GLM with gamma distribution), pseudo $R^2 = 0.71$ and McFadden’s pseudo $R^2 = 0.38 \pm 0.001$ (Table H2); for resistance cover (beta regression), pseudo $R^2 = 0.69$ and McFadden’s pseudo $R^2 = -1.95 \pm 0.009$ (Table H6); for recovery cover (linear model
with exponential variance structure), pseudo $R^2 = 0.74$ and McFadden’s pseudo $R^2 = 0.20 \pm 0.000$ (Table H9); for resilience cover (beta regression), pseudo $R^2 = 0.10$ and McFadden’s pseudo $R^2 = -1.15 \pm 0.001$ (Table H4). The low pseudo $R^2$ of the model fitted for resilience cover was smaller than the ones obtained with other link functions ($> 0.7$). This was surprising considering that the selected model had a much smaller AICc (delta AICc > 60). We discuss this outcome in the Discussion.

### 4.3.2. Trait correlations

*Colony complexity* was strongly and positively correlated with *dislodgement susceptibility* (Spearman $r_s = 0.71$; $P < 0.001$), *growth rate* (Spearman $r_s = 0.68$; $P < 0.001$) and *colony fecundity* (Spearman $r_s = 0.64$; $P < 0.001$); it was weakly correlated with bleaching susceptibility (Spearman $r_s = 0.14$; $P < 0.001$) and *mode of larval development* (brooders were on average more complex than spawners; Glass $r_g = 0.12$; 95% CI: 0.004 to 0.239; Figure 4.3).

*Dislodgement susceptibility* was strongly and positively correlated with *growth rate* (Spearman $r_s = 0.76$; $P < 0.001$) and *colony fecundity* (Spearman $r_s = 0.56$; $P < 0.001$), and weakly with *mode of larval development* (brooders were on average more susceptible than spawners; Glass $r_g = 0.16$; 95% CI: 0.045 to 0.268; Figure 4.4). *Bleaching susceptibility* was strongly correlated with *mode of larval development* (spawners were on average more susceptible than brooders; Glass $r_g = -0.62$; 95% CI: -0.696 to -0.543), moderately and positively correlated with *growth rate* (Spearman $r_s = 0.28$; $P < 0.001$), and not correlated with *colony fecundity* (Spearman $r_s = 0.06$; $P = 0.10$).

*Bleaching and dislodgement susceptibilities* are weakly and positively correlated (Spearman $r_s = 0.21$; $P < 0.001$; Figure H19).

*Overtop capacity* is strongly associated with *colony complexity* (colony that can overtop are complex; Glass $r_g = -0.78$; 95% CI: -0.825 to -0.241; Figure H20), *dislodgement susceptibility* (colony that can overtop are the most susceptible; Glass $r_g = -1$; 95% CI: -1 to -1); *growth rate* (colony that can overtop are grow fast; Glass $r_g = -0.88$; 95% CI: -0.911 to -0.840) and *colony fecundity* (colony that can overtop have high fecundity; Glass $r_g = -0.58$; 95% CI: -0.645 to -0.526); it is not associated with *bleaching susceptibility* (colony that can overtop are complex; Glass $r_g = -0.15$; 95% CI: -0.241 to -0.066).
Figure 4.1. Multi-model-averaged parameter coefficient and 95% confidence intervals (right panels) and illustration of the corresponding relationship between $FRic$ (functional richness, log-transformed and scaled) and the four measures of resilience for different values of $PC.1$ and $PC.2$ (the community centroids along the first two principal components of the PCA; left and middle panels) (see §4.2.2.3 for details). Coloured lines are model fits with 95% confidence intervals (we determined the confidence intervals for resilience cover and resistance cover by bootstrap, using the percentile method and 1000 replications); in the left panels, green, blue and purple lines represent model fits with $PC.1 = 1^{st}$, median, and $3^{rd}$ quartile of its distribution in the sample ($n = 245$), respectively, and $PC.2 = \text{median}$. Middle panels show model fits with $PC.2 = 1^{st}$, median, and $3^{rd}$ quartile and $PC.1 = \text{median}$. 
Figure 4.2. Results and predictions of the “full” gamma generalised linear model fitted for Resilience _rugosity_ (= the rugosity created by the coral community 10 years after the pulse disturbance, averaged between the bleaching and cyclone scenarios). Grey (a, c) and black arrows (f) represent the loadings of the first and second principal components of the initial weighted community centroids (PC.1 and PC.2, respectively); OC = overtop capacity; MLD = mode of larval development; GR = growth rate; CF = colony fecundity; DS = dislodgement susceptibility; CMD = colony maximum diameter; CC = colony complexity; BS = bleaching susceptibility. Black circles (b, d, e) show the communities’ initial functional richness (FRic, log-transformed and scaled) and position along PC.1 and PC.2; we
used these communities (n = 245) to predict resilience (red to blue colour ramp) in the entire parameter space (we set \( FRic \), \( PC.1 \) and \( PC.2 \) to their median value in e, d and b, respectively). The yellow symbols designate the communities presented in Figure 4.5.
**Figure 4.3.** Correlations among species (n = 798) between the effect trait *colony complexity* and resistance traits: *dislodgement* and *bleaching susceptibilities*; and recovery traits: *model of larval development*, *growth rate* (mm.yr⁻¹; log₁₀-transformed) and *colony fecundity* (no. eggs cm⁻² of colony planar area; log₁₀-transformed) (see text for a complete definition of these traits). Each gray circle represents the trait value averaged by species; the horizontal dashed line indicates the mean of the trait displayed on the vertical axis; boxes delimit 1ˢᵗ and 3ʳᵈ quartiles, whiskers extend to 1.5 × IQR, thick vertical lines represent group medians, black circles represent group means. Also shown is the Spearman’s rank correlation statistic ($r_s$) and associated significance level (**three stars** corresponds to $P < 0.001$), the Glass’ rank biserial correlation statistic ($r_g$) and associated 95% confidence intervals and loess lines for visual aid.
Figure 4.4. Correlations among species (n = 798) between the resistance traits *dislodgement* and *bleaching susceptibilities* and the recovery traits *model of larval development*, *growth rate* (mm.yr⁻¹; log₁₀-transformed) and *colony fecundity* (no. eggs cm⁻² of colony planar area; log₁₀-transformed) (see text for a complete definition of these traits). Each gray circle represents the trait value averaged by species; the horizontal dashed line indicates the mean of the trait displayed on the vertical axis; boxes delimit 1st and 3rd quartiles, whiskers extend to 1.5 × IQR, thick vertical lines represent group medians, black circles represent group means. Also shown is the Spearman’s rank correlation statistic (rₛ) and associated significance level (*** corresponds to P < 0.001), the Glass’ rank biserial correlation statistic (rᵣ) and associated 95% confidence intervals and loess lines for visual aid.
**Figure 4.5.** Examples communities being resilient (i.e., they have > 80 % coral cover 10 years after the disturbance) through different processes: from left to right, communities recovered via (i) the presence of a brooding species (red) which recruited soon after the disturbance; (ii) high vegetative growth rate of the most competitive species (purple); (iii) high recruitment rate due to high colony fecundity; or (iv) by resisting the disturbance. Top row represents the rugosity created by the colonies; the middle row displays individual species cover in colour and total coral cover in black; the bottom row shows recruit density for each species (solid lines and shaded area represent mean ± standard error over five replicates; each dot is the number of recruits .m⁻² at a given time for a given replicate). Symbols on the top left corner of the plots in the first row are used to indicate where these communities are in the variable space in Figure 4.2, Figure H10, Figure H13 and Figure H16.
4.4. Discussion

Biodiversity is essential to the functioning of ecosystems (Cardinale et al., 2012; Hooper et al., 2012), and to their capacity to persist in a changing environment (Oliver et al., 2015; Walker et al., 2004). The ongoing changes in the species composition of coral communities are affecting the functioning of coral reef ecosystems, and compromise their capacity to persist in the Anthropocene (Graham et al., 2014; Hughes et al., 2018b; Perry and Alvarez-Filip, 2019; Williams and Graham, 2019). Our lack of understanding of the mechanistic links between disturbances, diversity, ecosystem functioning and resilience impedes our capacity to predict the future composition of coral assemblages and their functioning (Bellwood et al., 2018; Hughes et al., 2017a). Adopting trait-based approaches facilitates the evaluation of these links (Cadotte et al., 2011; Madin et al., 2016b; McGill et al., 2006; Violle et al., 2007), comparison of biodiversity in space and time (e.g., McWilliam et al., 2020, 2018b) and understanding the processes responsible for community assembly (e.g., Kraft et al., 2015), ecosystem functioning (van der Plas, 2019) and resilience (e.g., McLean et al., 2019). However, attempts to quantify the effects of functional diversity on rates of ecological processes in coral communities are lacking (Brandl et al., 2019), notably because of the daunting challenges associated with manipulating coral diversity experimentally (e.g., Clements and Hay, 2019; McWilliam et al., 2018a). The diversity-resilience hypothesis has been investigated experimentally in terrestrial plant and aquatic systems for decades (Griffin et al., 2009) but never with coral communities. It is now generally admitted that biodiversity contributes positively to ecosystem functioning and resilience, but the generalisation of these results to other ecosystems is inappropriate because the dynamics of ecosystems depend importantly on the abiotic environment, the identity of the species present in communities and the structure of the food web (Griffin et al., 2009; Tilman et al., 2014; van der Plas, 2019). The model we developed (Chapter 3) provided an alternative approach to overcome the challenges of experimenting with corals and to test the biodiversity-resilience hypothesis by enabling the manipulation of functional diversity and examination of key responses to disturbance over extensive scales of time and space. Thanks to its unparalleled leveraging of trait and demographic data, our experiment yielded insights that, despite being in silico, promise to be highly informative in practice.
Our results support the diversity-resilience hypothesis, as we found significant and positive effects of functional richness (FRic) on resilience rugosity, resilience cover and recovery cover (Figure 4.1). In terms of magnitude, the effects of FRic were between the effects of PC.1 and PC.2 for all three measures of resilience. Remarkably, it was equivalent to the effect of PC.1 on resilience rugosity. PC.1 and PC.2 were strong predictors of resilience, as attested by their large effects (Figure 4.1) and the high pseudo R² values of the models. This is consistent with expectations because pre-disturbance community trait structures—which PC.1 and PC.2 represented at 53.2% and 26.7%, respectively—are strong predictors of community resilience (McLean et al., 2019; Mokany et al., 2008; Williams et al., 2010), especially since the traits we used were “functional” (Violle et al., 2007), as we implemented the mechanistic links between them and the processes that collectively generated the community dynamics. This is an advantage compared to many trait-based studies where causal links between traits and processes are assumed and not quantified (Bellwood et al., 2018). Thus, the fact that the effects of FRic were comparable in magnitude to that of PC.1 and PC.2 demonstrates the importance of FRic for community resilience in our experiment. Notably, the effects of the interaction terms between FRic and PC.1 were positive and relatively strong for both resilience rugosity and resilience cover, suggesting that the positive effect of FRic was stronger in the locations of the functional space that were not suitable for resilience (i.e., at higher PC.1 values, which corresponds to communities dominated by species with slow growth rate, low colony complexity, low colony fecundity; Figure 4.2a, b; Figure H10a, b).

The small pseudo R² of the model fitted with resilience cover (= 0.10) was due to the high number of values close to zero and one. The Cauchit link function accommodated this distribution better compared to the other link functions, according to the AICc. However, several observations on the link scale were much more extreme with the Cauchit function than with other link functions. Consequently, the pseudo R²—which is based on the correlations of observed and fitted values on the link scale—was strongly affected. This measure of pseudo R² was consequently not a good measure of fit in this case (A. Zeileis, personal communication, July 18 2020). Comparatively, the McFadden’s pseudo R² < -1, which suggests that the model fitted the data much better than the null model.

To better understand these results, it is instructive to consider the effect of the rugosity-grazing feedback process and correlations between effect (colony complexity), resistance
(bleaching and dislodgement susceptibilities), recovery traits (mode of larval development, colony fecundity, growth rate), and competitive traits (overtop capacity, growth rate). The feedback process generated a strong relationship between rugosity, grazing intensity and resilience (Figure H17; Figure H18). Communities able to maintain or recover sufficient rugosity benefited from grazing levels that allowed their colonies to grow and recruit, and, therefore, to maintain or recover high percentage cover. Resilience rugosity and resilience cover were consequently strongly correlated (Spearman $r_s = 0.98$; $n = 245; P < 0.001$), which explains the similar relative effects of $FRic$, $PC.1$ and $PC.2$ for these two response variables (Figure 4.1).

$PC.1$ had by far the strongest effect size on recovery cover (Figure 4.1; Table H9) for four reasons. First, $PC.1$ represents most of the variation of the communities’ centroids along growth rate and colony fecundity, which are two important recovery traits (Figure H16a). Our results show that communities dominated by species having high growth rates and/or high colony fecundity recovered faster (Figure H16a, b). Second, species with high growth rate and high colony fecundity tend to have high colony complexity (Figure 4.3), which enhanced recovery via its positive effect on grazing. Third, these species also tend to have high dislodgement susceptibility (Figure 4.3) and, to a lesser extent, high bleaching susceptibilities (Figure 4.4). Consequently, communities with high recovery cover were more affected by the disturbances and could recover more surface area compared to communities that were less affected. Finally, these strong correlations between traits allowed $PC.1$ to capture most of the communities’ functional attributes that were important for recovery cover (Figure H16a).

$PC.1$ had the strongest effect size on resistance cover (Figure 4.1) because it captured most of the variation of the community centroids along dislodgement susceptibility, as well as some of the variation along bleaching susceptibility (Figure H13a). $PC.2$ had the second strongest effect size because it captured most of the variation along bleaching susceptibility (Figure H13c). Note that $PC.1$ and $PC.2$ had positive effects, which contrasts with the other measures of resilience. Hence, the communities with high resistance cover had the opposite functional characteristics compared to the communities with high recovery cover (i.e., slow growth rate, low colony fecundity and complexity). This is due to strong trade-offs between effect, resistance and recovery traits: species having lower bleaching and dislodgement susceptibilities tend to have slower growth rate, lower colony fecundity (for dislodgement susceptibility only; Figure 4.4) and lower colony complexity (Figure 4.3). Note that these communities had a lower recovery cover not
only because of their functional traits, but also because they had less cover to recover in three years due to their higher resistance. The negative effect of FRic on resistance cover, which also contrasts with other measures of resilience (Figure 4.1), is due to the increased chance of communities with higher FRic to have competitive species (see after for details).

The similar effects of PC.1 on resilience rugosity, resilience cover and recovery cover (Figure 4.1) suggests that the communities that had the higher recovery rates also reached higher rugosity and cover 10 years after the disturbances. This does not imply that the resistant communities did not end up being resilient afterward (e.g., Figure 4.5). Because of the strong rugosity-grazing feedback process and the trade-offs between colony complexity and cyclone and bleaching susceptibilities (Figure 4.3), resistant communities had lower rugosity and total coral cover 10 years after the disturbances compared to communities that recovered quickly, but could nevertheless maintain coral dominance. PC.1 had such a strong negative effect also because several communities with very low averaged colony complexity (i.e., high PC.1) were unable to maintain sufficient grazing and were collapsing before the disturbance (Figure H17; Figure H18).

In Chapter 1 (§1.2.2 and §1.2.3), we describe the different effects potentially involved in the relationships between biodiversity and ecosystem functioning (i.e., dominance, identity, selection, complementarity, facilitation) and resilience (i.e., portfolio and insurance). The dynamics differed between communities (Figure 4.5), suggesting that different effect(s) occurred depending on species composition. Here we examine the effect(s) that were prevalent in the experiment, using the effect sizes, the trait correlations, and our knowledge about the model implementation and experimental design. Note that selection and complementarity effects were first defined considering species richness; we assume the definition holds with functional richness.

A combination of selection effect (i.e., communities with higher diversity are more likely to have a species that contributes more to reef rugosity) and dominance effect (i.e., species contribute to reef rugosity proportionally to their abundance) presumably prevailed in our experiment. As shown by the results, the scenarios we imposed advantaged species with traits conferring both a strong capacity for recovery (via high growth rate and / or colony fecundity) and to provide rugosity (via high colony complexity). Additionally, most species with the capacity to overtop—which confers a competitive advantage—also have the functional attributes
suitable for recovery (Figure H20). Consequently, communities with higher FRic were more likely to have species with these traits—which we now refer to as “competitive”—and these species would likely occupy a large surface cover, which provides the community with a strong capacity to rapidly reach high levels of rugosity after the disturbances. The significant positive effects of the interaction between FRic and PC.1 for resilience rugosity and resilience cover (Figure 4.1) show that the selection effect was particularly strong for communities with centroids located far from these competitive traits (i.e., along the upper end of PC.1). Competitive species were also more susceptible to disturbances due to functional trait trade-offs (Figure 4.3; Figure 4.4; Figure H20), which explains the negative effect of FRic on resistance cover (Figure 4.1). This demonstration aligns with observations reporting that more diverse coral communities—usually situated in protected habitats—are often less resistant to bleaching and cyclones because they are dominated by susceptible species (Côté and Darling, 2010; Zhang et al., 2014).

   The necessity for corals to have sufficient cover to contribute to reef rugosity disqualifies the identity effect (i.e., species contributing disproportionately more to ecosystem functions regardless of their relative abundance). Brandl and colleagues (2019) argued that identity effects are prevalent in coral reefs; we suggest that, while this might be true for communities like fish (e.g., Bellwood et al., 2006), corals contribute to ecosystem functions via the dominance effect (Alvarez-Filip et al., 2011).

   Diversity effects (i.e., complementary and facilitation) did not occur. Complementary effects suggest that a community of coexisting species use resources more efficiently than a monoculture of the most efficient species. Plant experiments have shown that complementarity effects result from complex combinations of multiple traits related to the acquisition of several resources (Cadotte, 2017; Kraft et al., 2015b). These effects could not occur in our simulations because coral species competed only for space, as the model assumes that other resources such as light, nutrients and dissolved inorganic carbon—necessary for photosynthesis—were unlimited. Like plant species, coral species have different strategies to acquire diverse resources (Darling et al., 2012), which suggests that complementarity effects are possible in real communities. However, attempts to measure these effects are lacking, which prevents from assessing how critical this model limitation might be.

   Facilitation effects did not occur in our simulations because we did not implement the associated processes. This is a limitation because experiments have shown that facilitation
effects increase photosynthesis and growth rates in coral polycultures versus monocultures, due to diverse potential mechanisms such as modification of water flow (which affects photosynthesis), reduction of corallivory and disease transmissions (Aeby et al., 2011; Clements and Hay, 2019; Kayal et al., 2011; McWilliam et al., 2018a).

The portfolio effect (i.e., asynchronous fluctuations of independent populations generate stable community level aggregated values) probably did not occur in our simulations because coral populations interact with one another by competing for space. In real reefs, the portfolio effect can be responsible for the stability of communities of mobile species, such as fish (e.g., Mellin et al., 2014); but it seems reasonable to assume that coral populations are not independent in their communities because of space constraints.

The insurance effect (i.e., the combination of functional redundancy and response diversity provide resilience to ecosystem functions) was not prevalent but likely happened in multiple communities and could have contributed to the positive effect of FRic on resilience. While we did not design our experiment to specifically test and measure this effect, there is evidence suggesting that the insurance effect contributed to the positive effect of FRic on resilience. First, the model allowed for response diversity and functional redundancy. Indeed, the correlations between effect and response traits show that despite being potentially strong, there are substantial variations of resistance and recovery traits among species with high colony complexity (Figure 4.3). While the most common dynamics among resilient communities was the domination of competitive species (i.e., selection and dominance effects), these variations in response traits allowed certain communities to recover or maintain rugosity via other mechanisms, such as recovery due to the presence of (i) a brooding species (brooders could reproduce sooner after the disturbance compared to spawners), (ii) multiple species with high colony fecundity, or (iii) high resistance due to the species with low disturbance susceptibility (Figure 4.5). These observations show that the model allowed species with different responses to contribute to reef rugosity and resilience. Second, FRic could increase the chance of communities to benefit from the insurance effect. Indeed, communities with higher FRic were more likely to have species with higher colony complexity, and when more than one species with high colony complexity was present, they likely responded differently to disturbances because of the variability of response traits among species with high colony complexity. Further, the insurance effect was most likely to
occur in communities with intermediate FRic and high average colony complexity—there would have been less redundancy with higher FRic, and less response diversity with lower FRic.

Interestingly, the magnitude of FRic’s effects relative to that of PC.1 and PC.2 seem to depend on the number of possible trait-related mechanisms that the measure of resilience depended upon, which could reveal that, indeed, FRic did contribute in generating insurance effects in our experiment. The effect of FRic was the weakest with resistance cover, which only depends on one resistance trait in each scenario (either bleaching or dislodgement susceptibility). The effect could have been superior if there was a trade-off between the two resistance traits (i.e., a strong negative correlation)—as this would have created more response diversity—but we found a moderate and positive correlation (Figure H19). In comparison, FRic had a stronger effect on recovery cover, which was influenced by several processes associated to the recovery traits growth rate, colony fecundity and mode of larval development (Figure 4.5). Finally, FRic had the strongest effect on resilience rugosity and resilience cover, which accounted for both resistance and recovery processes. This could suggest that FRic provided more opportunities for resilience when multiple responses were available (i.e., the insurance effect).

In summary, we found that our results were mostly due to (i) the critical role of colony complexity and of the rugosity-grazing feedback process, and (ii) the prevalence of combined selection and dominance effects due to the presence of competitive species. We now evaluate the relevance of these causes.

Despite using empirical data for its implementation, the rugosity-grazing feedback process was probably stronger than in real coral reef ecosystems, as suggested by the collapse before the disturbance of the communities that could not provide enough rugosity (Figure H17; Figure H18), and the fast recovery rate we observed in several communities (< 3 years) (Figure 4.5). The strength of the rugosity-grazing feedback process was due to several potential model limitations. First, only coral colonies provided rugosity, while in reality, other organisms and features contribute to structural complexity, such as the reef framework (Emslie et al., 2008; Halford and Caley, 2009). Second, our quantification of rugosity from colonies was approximate because we used geometric formulas (McWilliam et al., 2018b) (Table C5) that do not account for the vertical dimension and that yielded a ranking of colony complexity between growth forms that is arguable (Figure H1). Several measures to quantify colony morphology have now been developed (Zawada et al., 2019a), but have yet to be associated with density of the population of
herbivores and so cannot be implemented in the model. Finally, we did not implement other potential feedback processes that could slow down the recovery of the community, such as the decreased palatability of mature algae stands (van de Leemput et al., 2016). However, considering the abundance of evidence about the importance of (i) colony complexity in shaping reef rugosity (Alvarez-Filip et al., 2011; Bozec et al., 2015; Darling et al., 2017), (ii) rugosity in supporting herbivory (Bozec et al., 2013; Heenan et al., 2016; Vergès et al., 2011), and (iii) herbivory for the resilience of the coral community (Mumby, 2006; Mumby et al., 2007, 2006; Suchley and Alvarez-Filip, 2017), we argue that the strong rugosity-grazing feedback process we implemented remains a valid approximation.

The selection and dominance effects that prevailed in our experiment could have been exacerbated by the strong rugosity-feedback processes, as well as the lack of mechanisms facilitating coexistence. As previously explained, the model does not implement processes related to the acquisition of multiple resources—which limits niche partitioning—and to facilitation, as well as other mechanisms that can facilitate coexistence, such as spatial heterogeneity and frequency dependence predation (Chesson, 2000). Additionally, we assembled fictional communities based on the location and distances of species in the functional space, without considering the realism of their functional structure. Hence, fitness differences among species were potentially too strong to allow for coexistence in several communities. However, these limitations do not curtail the relevance of our results for real coral communities because the strength of the selection and dominance effects in our simulations are realistic. Indeed, our experiment simulated conditions found in shallow habitats (i.e., where light is not limited) relatively protected from waves (mechanical dislodgment threshold = 200; Madin and Connolly, 2006), which usually leads to communities dominated by one or a few competitive species (Cornell and Karlson, 2000; Huston, 1985). In addition, these competitive species are notorious for contributing the most to the complexity of the habitat (Alvarez-Filip et al., 2009; Darling et al., 2012).

Our results contrast with current observations showing that species with competitive traits are the “losers” against climate change (Hughes et al., 2018b; Loya et al., 2001; McCowan et al., 2012; van Woesik et al., 2011). The increased frequency and intensity of major bleaching events (Eakin et al., 2010; Hughes et al., 2017b)—now too frequent for the recovery of these species (Hughes et al., 2018a)—and the cumulative effects of other disturbances, such as ocean
acidification, overfishing and pollution (Pendleton et al., 2016; Tkachenko, 2015) are responsible for the change in species composition that we observe. However, our goal was not to test the resilience of real communities under these contemporary conditions, but to test the diversity-resilience hypothesis with coral communities across a large functional diversity gradient and to identify the prevalent effects that generated community dynamics. We defined simple scenarios with only one pulse disturbance to facilitate the analysis of the results. These scenarios are nonetheless similar to conditions found in preserved and protected reefs or before reefs were strongly affected by climate change and anthropogenic disturbances. Under these conditions, there have been multiple observations of rapid recovery of species with these traits after pulse disturbances such as bleaching and cyclones (Diaz-Pulido et al., 2009; Gilmour et al., 2013; Halford et al., 2004; Highsmith, 1982).

Considering the above discussion and the fact that the model implementation and trait values were informed from empirical data and expert knowledge, we are confident that similar results would have been obtained with a non-virtual but similar experiment. It could be argue that our process of forming communities limits the applicability of our results to real coral reefs because real coral communities are not neutral (Bode et al., 2012; Connolly et al., 2014) and result mostly from species traits and local and regional factors (Keith et al., 2013). This is a legitimate argument that has been previously formulated for plant experiments (Schmid and Hector, 2004), and to which we answer with the three following assertions.

First, experiments contribute in establishing general rules, which has been a fundamental objective in ecology (Lawton, 1999). Finding generalities in the relationships between diversity and ecosystem functioning and resilience can only be obtained from exploring the dynamics of communities across a large diversity of trait structure and environmental conditions. Each experiment contributes its own way in providing support (or opposition) to a hypothesis; it is only through the accumulation of proofs across a large diversity of communities and environmental conditions that a hypothesis can be accepted as a general rule. Evidence of the beneficial effects of coral diversity on ecosystem functioning and resilience is scarce, partly because of the difficulty to conduct experiments with corals (Clements and Hay, 2019; Duffy, 2019; McWilliam et al., 2018a). Consequently, our experiment is a rare and valuable contribution to the diversity-resilience relationship debate with corals.
Second, there is considerable uncertainty concerning the future composition of coral communities and their functioning (Graham et al., 2014; Hughes et al., 2017a; Williams and Graham, 2019). Conducting experiments that only represent existing community trait structures would prevent from anticipating potential futures. Additionally, active reef restoration (Rinkevich, 2014, 2005), eventually combined with assisted evolution (van Oppen et al., 2017, 2015), increases the diversity of coral communities that could be realized.

Third, besides conducting an experiment to test the diversity-resilience relationship, we also demonstrated how the effect, resistance and recovery trait framework could be used to identify the prevalent mechanisms generating dynamics across multiple communities. We argue that using the framework similarly could shed light upon unexplained results from previous studies that measured the relationship between diversity and resilience across multiple coral communities (e.g., Zhang et al., 2014).

For this experiment we averaged the four different measures of resilience between the cyclone and bleaching scenarios because our goal was to capture the effect of FRic on the overall resilience of communities to multiple disturbances. The approach has some limitations from a management perspective because the averaged resilience does not inform us about the resilience to a single, specific disturbance. For instance, our approach does not distinguish a community being moderately resilient to both disturbances from a community being highly resilient to one disturbance and highly vulnerable to another. From a management perspective, it might be most important to identify the minimum value of resilience to any set of disturbances, because that might ultimately define the fate of the reef.

Finally, our results suggest that the loss of competitive species in the regional pools will decrease the capacity of coral communities to provide and recover high levels of structural complexity, which will affect grazing and reduce coral cover. These trends have been amply documented worldwide (Alvarez-Filip et al., 2013, 2009; Bozec et al., 2015; Graham et al., 2015; Hughes et al., 2018b). Excluding competitive species from the functional space would certainly decrease the positive effect of FRic on resilience, because the selection and dominance effects will not prevail anymore. However, our results also revealed that there was sufficient trait variability among species with complex morphologies to allow for other biodiversity effects, in particular the insurance and complementarity effects. Future experiments consisting in finding which coral community assemblies maximise insurance and / or complementarity effects would
considerably improve our understanding and capacity to intervene on coral reef functioning and resilience. We suggest that an optimal strategy to achieve these goals and to address the numerous gaps in trait-based approaches is to combine real-life experiments—to quantify links between traits and processes—and virtual experiments—to quantify links between diversity indices and ecosystem function and resilience.
Chapter 5: Conclusion

Preserving coral reefs in their pristine states is an impossible goal because we cannot prevent the exclusion of susceptible species from the species pools due to climate change and anthropogenic disturbance (Graham et al., 2014; Hughes et al., 2017a). Instead, a more realistic goal is to manage the traits supporting the resilience of the ecosystem functions that are related to the ecosystem services we want to protect (Bellwood et al., 2018; Woodhead et al., 2019). For instance, fisheries, recreation and tourism activities are important services that rely on the provision of calcium carbonate and complex habitats, two key ecosystem functions supported by coral communities (Brandl et al., 2019). The resilience of these functions depends on the trait structures that provide coral communities with the capacity to maintain sufficient growth and structural complexity in a changing environment. Thanks to their traits, competitive species (which have complex growth forms, fast growth rates and can overtop other organisms) have contributed importantly to the capacity of communities to provide resilient and complex habitats. Unfortunately, these species are overly affected by cumulative disturbances and are becoming rare in many coral communities in the world. Consequently, the capacity of these reefs to provide resilient habitats is affected (Alvarez-Filip et al., 2011, 2009; Hughes et al., 2018b). To manage fisheries, recreational and tourism activities, it is critical to investigate if and to which extent other assemblages can support these essential ecosystem functions in new environmental conditions. By quantifying links between species and processes, trait-based approaches offer the opportunity to address this pressing challenge. However, important gaps in the Coral Trait Database have to be filled (Madin et al., 2016a) and many trait-process associations have to be identified and quantified (e.g., for bleaching) (Bellwood et al., 2018). Additionally, even with a complete trait database and well-defined association between traits and processes, predicting the outcomes of multiple interacting processes remain extremely challenging.

The research we conducted contributed to answering the following fundamental questions. How can the data available in the Coral Trait Database be used to understand the dynamics of coral communities and predict the resilience of their ecosystem function? What are the main mechanisms driving the resilience of ecosystem functions in coral communities? What are the most important functional characteristic of communities for their resilience? How can we address these last two questions?
In Chapter 2, we built on previous efforts of plant ecologists and proposed a framework to use functional traits to predict the resistance and recovery of ecosystem functions provided by coral communities. Suding and colleagues’ (2008) trait-based response-effect framework could not account for processes of recovery, which is critical because coral reef ecosystems are imbedded in disturbance regimes that are more frequent than most plant ecosystems. Additionally, natural pulse disturbances, such as cyclones and bleaching events, are becoming more frequent so most reefs are in constant transition and maintained away from their stable states. Quantifying traits with recovery processes allows to predict the dynamics of ecosystem functions over short temporal scales, which is critical for managing the reefs.

Establishing the framework was a preliminary step for the development of the model presented in Chapter 3, but adopting the framework can provide several benefits. In Chapter 2, we explained how it can provide a strategy for organising the collection of trait data and the efforts to link these traits to processes. We also illustrated with a simple simulation example how the framework can be used to predict the resilience of an ecosystem function in a focal coral community. In Chapter 4, we used the framework to identify the prevalent mechanisms responsible for the strength and direction of associations between indices of community diversity and resilience measured across multiple communities. We believe this approach could help understand the mechanisms responsible for the diversity-resilience relationships measured in real communities (e.g., Zhang et al., 2014).

The framework however lacks the capacity to account for competitive interactions between species. Considering including “competitive traits”, such as the capacity to overtop, would complete the framework and link together all the trait-related processes responsible for community dynamics (i.e., environmental filtering, competitive exclusion, ecosystem functioning).

In Chapter 3, we presented a new agent-based model that combines trait-based and demographics approaches and implement ecological details and processes to an unprecedented level. The results from our extensive analyses show that the model produced dynamics under different abiotic constraints and species diversity that were ecologically sound. It can consequently be used as a virtual platform to conduct experiments to simulate community dynamics as a function of initial coral diversity, grazing, larval connectivity, thermal and hydrodynamics disturbances. As demonstrated with the hierarchically structured validation
(Appendix F) and in Chapter 4, experiments conducted with the model can help unravel the complex process interactions that lead to the observed community dynamics.

Experiments consisting of manipulating coral diversity are extremely challenging with live corals, which limits considerably the diversity, factors and processes that can be considered. Our model constitutes an alternative approach that can overcome many of these challenges and assesses the dynamics over gradient of diversity, time scales and spatial extents that would be otherwise unmanageable. While it does not replace in situ experiments, we suggest using our model in complement to live coral experiments. Our model has several limitations; for instance, it does not implement many ecological processes that can potentially affect community dynamics (see §3.4 for details about limitation and potential solutions to address them). Consequently, certain mechanisms related to coral diversity cannot be simulated, such as the complementarity and facilitation effects (see §4.4). Implementing the processes associated to these effects requires to empirically establish the links with their associated traits. Live coral experiments could be conducted to establish these links. One could then implement these relationships in the model and conduct experiments to determine, for instance, which community trait structures maximised these effects.

As discussed in Chapter 3 (§3.4), using the model to predict the dynamics of real communities requires substantial amounts of empirical data to calibrate the model properly as well as the potential implementation of additional processes that are particularly influent in the focal reefs. However, because the implementation of processes is trait-based, mechanistic and built from empirically informed data and expert knowledge, we are confident that the actual model can be calibrated to capture accurately the dynamics of real communities across different geographic regions. While not all processes are implemented in the model, there are sufficient parameters that can be calibrated to indirectly account for these processes. For instance, nutrient inputs can affect corals by reducing their recruitments rates and enhancing the growth rate of certain algae. The effects of nutrification—the level of which would have to be described with an input variable—could be accounted for via the parameters otherProportions (which controls the total number of larvae produced locally), the probabilities of larval settlement on barren ground, dead coral and crustose coralline algae and the probabilities of the different algae to be grazed.

The long-term objective is to develop the model so it becomes a powerful, user-friendly simulation tool that managers can use to predict the dynamics of real reefs in different
environmental and management scenarios. This will require substantial development and the involvement of ecologists, model developers and managers.

In Chapter 4, we conducted the first experiments to quantify a measure of diversity (functional richness, FRic) with measures of resilience in coral communities. The study of the diversity-resilience hypothesis is a major field of research in ecology. Understanding under which circumstances ecosystems are resilient is crucial for their management and necessitates to identify the mechanisms responsible for their dynamics. Here we found that communities with higher FRic were in general more resilient (i.e., they recovered or maintained a higher level of rugosity and surface cover after the pulse disturbances). Further, by using the results and the effect, resistance, recovery trait framework, we could determine that this positive relationship between FRic and resilience was due to a combination of selection and dominance effects: communities with higher FRic were more likely to have competitive species that provided resilience by recovering rapidly after the disturbances, over-competing other species and contributing importantly to the reef rugosity—the latter contribution being critical for maintaining sufficient grazing. These results suggest that the loss of competitive species from regional pools will affect their capacity to provide resilient complex habitats. Determining if other species can provide resilience to the habitat provisioning functions is consequently critical. Our experiment revealed that there was sufficient functional redundancy and response diversity among coral species in our dataset to allow for alternative resilient dynamics.

This experiment has to be considered as a first step in a long walk leading to understanding the diversity-resilience relationship in coral communities. The results we found were mostly due to the presence of competitive species in the trait dataset. Considering that these species will become rare in the reefs, an appropriate follow-up study would be to conduct an identical experiment but excluding competitive species from the trait dataset. This would allow to test if the positive relationship between FRic and resilience holds, and what are the prevalent effects driving the relationship. We suspect that the exclusion of competitive species can leave room for more insurance effects.

FRic only describes one aspect of functional diversity (see §1.3). Quantifying the relationship of other indices with resilience would provide a more complete understanding of the diversity-resilience hypothesis and using several complementary measures of diversity would probably yield stronger predictive power. Establishing clear relationships between different diversity
indices and measure of resilience could considerably inform management by providing the necessary levels of diversity that a community should have in order to maintain resilient ecosystem functions.

However, strong identity and dominance effects present in the reefs might limit the predictive power of these diversity indices because the presence or absence of a single species could eventually affect the whole community dynamics. We therefore suggest conducting similar experiments where the diversity of a focal community would be completed by adding species at different locations in the functional space and at diverse distances from the community centroid, and where scenarios representing realistic environmental contexts would be simulated. Such experiments would help identify a set of species that would enhance the resilience and functioning of the focal reef.

Coral reefs are heading to a dark future and sustaining their resilience in the Anthropocene promises to be a path marked with difficulties. However, solutions are hiding in the gloom and this work has contributed in making a few steps towards some of them.
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Appendices

Appendix A. Chapter 2: Supporting information

The functional traits data frame we compiled as well as the R scripts for statistical analyses, figures and model simulations are available on the Open Science Framework platform (https://osf.io/b76dt).

A.1. Data sources and correlations
Table A1. Summary of the sources and the methods of compilation of the functional trait data. (the numbers in brackets include the 30 species not in the phylogeny and without numerical trait information). All the trait information from the coraltrait.org dataset was downloaded between March 30\textsuperscript{th} and April 10\textsuperscript{th} 2017.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Sources</th>
<th>No. sp.</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll a concentration (µg.cm\textsuperscript{2})</td>
<td>CoralTrait database</td>
<td>22</td>
<td>-</td>
</tr>
<tr>
<td>Colony max diameter (cm)</td>
<td>CoralTrait database</td>
<td>307</td>
<td>The maximum value was retained in case of duplicated species</td>
</tr>
<tr>
<td>Corallite area (cm\textsuperscript{2})</td>
<td>CoralTrait database</td>
<td>713</td>
<td>It was obtained from “corallite width maximum” and “corallite width minimum” traits; the average values was given when both were available.</td>
</tr>
<tr>
<td>Dark respiration rate (µmol O\textsubscript{2}.cm\textsuperscript{2}.h\textsuperscript{-1})</td>
<td>CoralTrait database (Cooper et al., 2011; Hennige et al., 2010; Reynaud-Vaganay et al., 2001; Ulstrup et al., 2011)</td>
<td>20</td>
<td>-</td>
</tr>
<tr>
<td>Growth form</td>
<td>CoralTrait database</td>
<td>816</td>
<td>The “growth form typical” was used. We grouped under “branching” the “open and closed branching” and “hispidose”; “massive” also comprises “submassive:”</td>
</tr>
<tr>
<td>Growth rate (mm.y\textsuperscript{-1})</td>
<td>CoralTrait database</td>
<td>125</td>
<td>We converted radial to linear/diametral measurements</td>
</tr>
<tr>
<td>Lipid content (mg.cm\textsuperscript{-2})</td>
<td>CoralTrait database (Leuzinger et al., 2003; Middlebrook et al., 2010; Rodrigues and Grottoli, 2007)</td>
<td>8</td>
<td>-</td>
</tr>
<tr>
<td>Mode of larval development</td>
<td>CoralTrait database</td>
<td>313</td>
<td>-</td>
</tr>
<tr>
<td>Traits</td>
<td>Sources</td>
<td>No. sp.</td>
<td>Comments</td>
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<td>--------------------------------------------</td>
<td>----------------------------------------------</td>
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<td>----------------------------------------------------------------</td>
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<tr>
<td>Reduced scattering coefficient</td>
<td>(Marcelino et al., 2013; Swain et al., 2016a)</td>
<td>93</td>
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<td>(µ’s,m, mm⁻¹)</td>
<td></td>
<td></td>
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<tr>
<td>Response bleaching index</td>
<td>(Marcelino et al., 2013; Swain et al., 2016b, 2016a)</td>
<td>304</td>
<td>We removed observations for which only the genera was known</td>
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<td>(taxon-BRI, 0-100)</td>
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<td></td>
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<td>Symbiont density</td>
<td>CoralTrait database</td>
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<td>Values measured during or after a bleaching event were not considered</td>
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<td>(units.cm⁻²)</td>
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<td>Tissue thickness</td>
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<td>-</td>
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<tr>
<td>(mm)</td>
<td>(Loya et al., 2001)</td>
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<tr>
<td>Zooxanthellate</td>
<td>CoralTrait database</td>
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<td>-</td>
</tr>
<tr>
<td>Total number of species</td>
<td>828</td>
<td></td>
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</table>
Correlation analyses between the taxon-BRI (logit transformed) and bleaching resistance traits. Growth forms ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Each grey circle represents the trait value averaged by species, the error bars extend to +/- one standard error (SE). Statistical tests used: Spearman’s rank correlation ($r_s$). Asterisks indicate the test statistics’ significance: *P<0.05; **P<0.01; ***P<0.001.
Figure A2. Correlation analyses between effect traits and resistance traits. Growth forms ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Each grey circle represents the trait value averaged by species, the black point is the averaged trait value over all the species by
category, the horizontal error bars extend to +/- one standard error (SE). Statistical tests used: Spearman’s rank correlation ($r_s$). Asterisks indicate the test statistics’ significance: *$P<0.05$; **$P<0.01$; ***$P<0.001$.

Figure A3. Correlations between corallite area, maximum colony diameter and the taxon-BRI for species with complex (i.e., branching and plating, blue diamonds) and massive morphologies (red circles). Each red circle or blue diamond represents the trait value averaged by species. Statistical tests used: Spearman’s rank correlation ($r_s$). Asterisks indicate the test statistics’ significance: *$P<0.05$; **$P<0.01$; ***$P<0.001$. 
**Figure A4.** Comparison of maximum colony diameter with mode of larval development for complex (i.e., branching plating) and massive species. Each grey circle represents the trait value averaged by species, the black point is the averaged trait value over all the species by category, the horizontal error bars extend to +/- one standard error (SE). Statistical tests used: permutation test.

**Figure A5.** Correlation between growth rate and dark respiration. Each grey circle represents the trait value averaged by species, the black line is the linear least squares regression. Statistical tests used: Spearman’s rank correlation ($r_s$). Asterisks indicate the test statistics’ significance: *P<0.05; **P<0.01; ***P<0.001.
A.2. Qualitative mechanistic model

A.2.1. Goal

The goal of the model is to illustrate the application of the framework. We implement one simple computational approach, though many others are possible (e.g., mathematical models) and additional ecological processes could be considered (e.g., competition, feedbacks, synergies).

A.2.2. General structure

The model represents a virtual coral community composed of functionally different species. Each population is represented by 100 cells. A cell can be “occupied” by a colony or “empty” and is specific to a unique species throughout the simulations. This implies that the populations have a constant and identical maximum size and species do not compete with one another for space. Occupied cells contribute to the complexity of the habitat, resist against disturbances and recover differently accordingly to their species-specific functional characteristic. We conducted “resistance” and “recovery” simulations. In the former, all the cells are occupied and consecutively resist a disturbance of a given intensity according to a certain probability. The procedure is repeated for each intensity tested and replicated 40 times. In the “recovery” simulations, the initial population size of each species corresponds to the number of cells that “survived” the disturbance (averaged over the 40 replicates). During a time step, the empty cells have the possibility to recover depending on a probability defined by (i) vegetative growth and (ii) local larval input from the occupied cells and (iii) regional larval input (see below). The amount of habitat provided by the community at any given time corresponds to the sum of the individual contributions of the occupied cells.

A.2.3. Null model simulations

For reference, we constructed null model simulations in which a cell’s capacity to resist and recover is determined by a random draw of probability values from the three species. In this way, any inherent covariation among traits is broken, and this provides an appropriate baseline for comparison (dashed lines in Figure 2.1 and Figure 2.4). The function is considered resistant
(Figure 2.1B2) or to recover fast (Figure 2.1B3) if the level of the function in the first model is above the level of the function obtained from the null model. Vice versa, the function is considered not resistant (Figure 2.1C2) or to recover slowly (Figure 2.1C3) if its level is underneath the null model’s line.

A.2.4. Parameterization

We defined the values of the different parameters of the model to qualitatively describe the functionality of the three species. The values were chosen based on the results of our literature review and correlation analysis, and aim to reproduce the respective importance that similar mechanisms (e.g., recovery via vegetative growth, local and regional larval recruitment) have on the same process (e.g., recovery) and to compare the functionality between species (e.g., Species 1 contributes three times more than Species 2 to the habitat provisioning function). We did not attempt to approximate real parameter values because the goal of the model is simply to illustrate how correlations between effect and resistance and recovery traits moderate the resilience of an ecosystem function. We present the justification for the definition of the three species in §2.3.3.

Contribution to the habitat provisioning function

Species 1 (large and complex) contributes 2.6 and 6.7 times more to the habitat provisioning function than Species 2 (large and massive) and Species 3 (small), respectively (Figure 2.3, Table A4).

Probability to resist a disturbance

The probability of an empty cell to resist a disturbance decreases linearly with disturbance intensity (Figure A6, Table A2). For a cyclone, the decrease is respectively 5.0 and 2.3 times faster for Species 1 and Species 3 compared to Species 2. For a bleaching event, the decrease is respectively 3.6 and 2.3 faster for Species 1 and Species 2 compared to Species 3 (Figure 2.3, Table A4).
Probability of an empty cell to recover

The probability of an empty cell recovering ($P_{\text{recover}}$) depends on (i) the capacity of the “occupied” cell to recover empty cells via vegetative growth ($P_{\text{growth}}$), (ii) and local larval recruitment ($P_{\text{recruit_local}}$) and (iii) on larval recruitment from the regional pool ($P_{\text{recruit_regional}}$).

$P_{\text{growth}}$ and $P_{\text{recruit_local}}$ depend on the size of the population ($S_{\text{population}}$) whereas $P_{\text{recruit_regional}}$ depends on the level of connectivity.

The general formula is:

$$P_{\text{recover}} = P_{\text{growth}} + P_{\text{recruit_local}} + P_{\text{recruit_regional}}$$

$$= (\alpha_{\text{growth}} + \alpha_{\text{recruit_local}}) \times S_{\text{population}} + P_{\text{recruit_regional}}$$

The probabilities $P_{\text{growth}}$ and $P_{\text{recruit_local}}$ increase linearly with population size $S_{\text{population}}$ (Figure A7). The coefficient $\alpha_{\text{growth}}$ and $\alpha_{\text{recruit_local}}$ correspond to their respective slopes (Table A3).

Species 1 recovers free space via vegetative growth respectively 5.9 and 3.0 times faster than Species 2 and Species 3. The process of recovery via local larval recruitment is respectively 7.7 and 1.3 times slower for Species 1 and Species 2 compared to recovery via growth. It is identical for Species 3 (Table A4). Brooding species (Species 3) recruit locally 2.5 faster than spawning species (Species 1 and Species 2) and 2.4 slower regionally in case of high connectivity (Table A4). Regional larval recruitment is identical between spawners and brooders in case of low connectivity and is 100 and 40 times slower compared to high connectivity, respectively for spawners and brooders (Table A3).

Table A2. Parameter values of the functions determining the probability of an occupied cell to resist as a function of disturbance intensity for the three species defined in the model.

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1 (large and complex)</td>
<td>-0.020</td>
<td>1</td>
</tr>
<tr>
<td>Species 2 (large and massive)</td>
<td>-0.004</td>
<td>1</td>
</tr>
<tr>
<td>Species 3 (small)</td>
<td>-0.009</td>
<td>1</td>
</tr>
</tbody>
</table>
Table A3. Parameter values of the functions determining the probability of an empty cell to recover as a function of population size for the three species defined in the model.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vegetative growth slope ($\alpha_{\text{growth}}$)</th>
<th>Local larval recruitment slope ($\alpha_{\text{recrui_local}}$)</th>
<th>Regional larval recruitment intercept ($P_{\text{recrui_regional}}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>0.0060</td>
<td>0.0008</td>
<td>0.100</td>
</tr>
<tr>
<td>Species 2</td>
<td>0.0010</td>
<td>0.0008</td>
<td>0.100</td>
</tr>
<tr>
<td>Species 3</td>
<td>0.0020</td>
<td>0.0020</td>
<td>0.040</td>
</tr>
</tbody>
</table>

Table A4. Normalized trait values of the three species defined in the model. The values are dimensionless and qualitatively distinguish the species from one another. Values within a same process (i.e., delivery of the function, resistance to disturbance and recovery) can be compared with one another. These values were used to construct the spider diagrams (Figure 2.3).

<table>
<thead>
<tr>
<th>Species</th>
<th>Effect on habitat</th>
<th>Resistance</th>
<th>Recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cyclone</td>
<td>Bleaching</td>
<td>Cyclone</td>
</tr>
<tr>
<td>Species 1</td>
<td>1.00</td>
<td>0.20</td>
<td>0.20</td>
</tr>
<tr>
<td>Species 2</td>
<td>0.38</td>
<td>1.00</td>
<td>0.32</td>
</tr>
<tr>
<td>Species 3</td>
<td>0.15</td>
<td>0.44</td>
<td>0.72</td>
</tr>
</tbody>
</table>
Figure A6. The relationship between the probability that a cell resists a disturbance and disturbance intensity, shown for the three species (Species 1: large and complex; Species 2: large and massive; Species 3: small). The dashed black line is a visual aid for comparison between the two disturbances.

Figure A7. The relationship between the probability that an empty cell recovers after a disturbance and population size, shown for the three virtual species (Species 1: large and complex; Species 2: large and massive; Species 3: small). The left panel represent the probability to recover via vegetative growth of the “occupied” cells. The right panel displays the probability for spawners (sp; Species 1 and 2) and brooders (br; Species 3) to recover via recruitment of larvae locally produced (solid lines) and coming from connected reefs (dashed coloured lines). The dashed black line represents the probability of recovery if the reef is isolated and is the same for spawners and brooders.
Figure A8. Expected resistance (left column) and recovery rate (middle and right columns) of the coral community defined in the model (expressed as population size in second and fourth rows) and the habitat provisioning function it provides (first and third rows) against bleaching disturbances, under different scenarios of disturbance intensity and reef connectivity. The initial (disturbance intensity = 0) habitat provisioning values of each species in the left-hand panels (A, G) reflect the values assigned to species and depicted in Figure 2.3. The vertical red lines (left column) represent the disturbance intensity used to evaluate community recovery (middle and right column) for a moderate (two first rows) and intense (two last rows) perturbation. Thicker lines are the averaged response over 40 replicates (thinner lines) of the three species (see text for details). The magenta line represents the cumulative habitat provisioning provided by the whole community; the black dashed line represents the cumulative and averaged habitat provisioning provided by the null model communities. In our focal virtual communities, the habitat
provisioning function is less resistant (panels A and G) and recovers faster (panels B, C, H, I) than in the null model communities (dashed black lines), in which an individual’s capacity to respond is randomly drawn from the three species-specific capacities.
Appendix B. Chapter 3: Functional traits, phylogeny, and trait imputation

Assembling diverse virtual coral communities composed of species occupying different locations in functional space requires a complete dataset of the traits implemented in the model. The Coral Trait Database (Madin et al., 2016a), from which we downloaded most of the trait values has many data gaps (Madin et al., 2016b). We consequently applied a data-imputation method to fill in these gaps, including phylogenetic information to improve prediction. We present here the traits we used, the phylogenetic information and finally, the trait in-filling procedure.

B.1. Functional trait data

B.1.1. Trait summary

We collected trait values from coraltraits.org (Madin et al. 2016a), and other sources from the primary literature (Table B1). We limited our analysis to zooxanthellate scleractinian coral species, because our main focus is on species forming typical tropical-reef habitats. We first assembled a total of 828 coral species after correcting for nomenclature using the World Register of Marine Species (marinespecies.org) as a reference. We then removed 30 species that had only categorical trait values available (e.g., growth form, model of larval development, sexual system) and for which we did not have phylogenetic information. We included the categorical traits ‘coloniality’ and ‘sexual system’ to increase the number of predictors in the random-forest imputation procedure, because these traits have been defined for many species and have different degrees of phylogenetic conservation (i.e., sexual system is conserved, whereas coloniality has evolved several times within different lineages; Baird et al., 2009; Kitahara et al., 2010).

Related code:
Manuscript / Rscripts / Appendix S1 - Functional traits.R
All the R scripts related to a functional trait and trait_data_compilation.R are inside Traits_and_imputation / Rscripts.
**Table B1.** Summary of the sources and the methods of compilation of the functional-trait data. We downloaded all trait information from coraltrait.org between 30 March 2017 and 19 April 2018 (taxon-BRI: Bleaching Response Index).

<table>
<thead>
<tr>
<th>Traits</th>
<th>Sources</th>
<th>No. sp.</th>
<th>Used in model</th>
<th>Used for imputation</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>age at maturity (yr)</td>
<td>Coral Trait Database</td>
<td>3</td>
<td>yes</td>
<td>no</td>
<td>This trait is not used in the trait in-filling process because it is defined for too few species</td>
</tr>
<tr>
<td>aggressiveness (0 to 100)</td>
<td>Abelson and Loya, 1999</td>
<td></td>
<td></td>
<td></td>
<td>Values 0 and 100 correspond to the lowest and highest possible aggressiveness, respectively (see §B.1.2)</td>
</tr>
<tr>
<td></td>
<td>Connell et al., 2004</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dai, 1990</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lang, 1973</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Logan, 1984</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sheppard, 1979</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>116</td>
<td>yes</td>
<td>yes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>coloniality</td>
<td>Coral Trait Database</td>
<td>743</td>
<td>no</td>
<td>yes</td>
<td>Used to increase the number of predictors in the imputation random forest procedure</td>
</tr>
<tr>
<td>colony max diameter (cm)</td>
<td>Coral Trait Database</td>
<td>307</td>
<td>yes</td>
<td>yes</td>
<td>We considered the maximum value in case of duplicated species</td>
</tr>
<tr>
<td>corallite area (cm²)</td>
<td>Coral Trait Database</td>
<td>712</td>
<td>yes</td>
<td>yes</td>
<td>Obtained from “corallite width maximum” and “corallite width minimum”; we calculated the average when both values were available</td>
</tr>
<tr>
<td>egg diameter (mm)</td>
<td>(Figueiredo et al., 2013)</td>
<td>25</td>
<td>yes</td>
<td>yes</td>
<td>We obtained values from the coral trait database from “egg size” (two species) and “mature egg diameter” (four species); values were averages when possible</td>
</tr>
<tr>
<td></td>
<td>Coral Trait Database</td>
<td></td>
<td></td>
<td></td>
<td>Values obtained from “polyp fecundity” (10 species) and “mesentery fecundity” (three species); we averaged values when possible</td>
</tr>
<tr>
<td>polyp fecundity</td>
<td>Coral Trait Database</td>
<td>13</td>
<td>yes</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Traits</td>
<td>Sources</td>
<td>No. sp.</td>
<td>Used in model</td>
<td>Used for imputation</td>
<td>Comments</td>
</tr>
<tr>
<td>---------------------------------------</td>
<td>--------------------------------</td>
<td>---------</td>
<td>---------------</td>
<td>---------------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>growth form</td>
<td>Coral Trait Database</td>
<td>791</td>
<td>yes</td>
<td>yes</td>
<td>We used “growth form typical”. We grouped under “branching” the “open” and “closed branching” and “hispidose”; “massive” also comprises “submassive”</td>
</tr>
<tr>
<td>growth rate (mm.yr(^{-1}))</td>
<td>Coral Trait Database</td>
<td>125</td>
<td>yes</td>
<td>yes</td>
<td>We converted radial to linear/diametral measurements</td>
</tr>
<tr>
<td>mode of larval development</td>
<td>Coral Trait Database</td>
<td>312</td>
<td>yes</td>
<td>yes</td>
<td><em>Pocillopora ankeri</em> and <em>P. damicornis</em> can be both brooder and spawner, but are considered brooder in the model</td>
</tr>
<tr>
<td>microscopic reduced scattering</td>
<td>(Marcelino et al., 2013; Swain et al., 2016a)</td>
<td>93</td>
<td>yes</td>
<td>yes</td>
<td>-                                                                 ■</td>
</tr>
<tr>
<td>coefficient ((\mu_s, m, mm^{-1}))</td>
<td>(Marcelino et al., 2013; Swain et al., 2016b, 2016a)</td>
<td>304</td>
<td>no</td>
<td>no</td>
<td>We removed observations for which only the genera was known and for non-scleractinian coral</td>
</tr>
<tr>
<td>taxon-BRI (0-100)</td>
<td>(Marcelino et al., 2013; Swain et al., 2016b, 2016a)</td>
<td>304</td>
<td>no</td>
<td>yes</td>
<td>To increase the number of predictors in the imputation random-forest procedure. This trait is particularly well-conserved (Baird et al., 2009b)</td>
</tr>
<tr>
<td>sexual system</td>
<td>Coral Trait Database</td>
<td>306</td>
<td>no</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td><strong>Total number of species</strong></td>
<td></td>
<td><strong>798</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
B.1.2. Aggressiveness ranking

For most species, the outcome of direct interactions between coral colonies is determined using the probability of species-pair interactions from Precoda and colleagues (2017) (see §C.7.5.2). We also defined for each species an aggressiveness ranking value, which is used to determine if a colony can overgrow another species’ colony. Aggressiveness values are only used for the species not considered by Precoda and colleagues (2017).

We defined aggressiveness ranking values combining six lists of coral species whose interspecific dominance relationships were assessed (Table B2). We first ranked the species in each study based on the metrics the authors used. Because each list had at least one species in common with another list, we could combine the six lists and rank all species considered from the least to the most competitive. We used the iterative partial rank-aggregation pivoting algorithm (IPRAPA) developed and explained in detail by Swain and colleagues (2017) (the authors used the method to rank 110 symbiodinium phylotypes aggregated from 35 reports based on their thermotolerance). The IPRAPA implements the ranking method based on consensus-based, Borda-rank aggregation (developed in voting systems) and updates ranks by a pivot element (i.e., a species shared between input lists). When more than one species is present in both lists, the species with the least uncertainty is designated as pivot element. In case of equal uncertainty, we selected the first species of the first list. We repeated the process 10 times. Each iteration provides an updated ranking score from the previous iteration. Ranking scores are decimal values comprised between 0 and 100, which represent the lowest and highest aggressiveness, respectively.

We selected the final ranking scores of a particular iteration based on two metrics: (i) the percentage of species-pair associations that were reversed after the aggregation compared to the original ranking in each list (i.e., $Ppa$, a change in dominance to equality or vice versa was not counted as reversed), and (ii) the Kendall’s $\tau$, which is a measure of ordinal association between two quantities ($\tau = 0$ if all the species-pair associations are discordant, and $\tau = 1$ if they are preserved). Finally, we measured the match between the final global ranking and the individual ranking of each study with the Spearman rank $\rho$. By ranking species in each list separately using the ranking score, we can see that the procedure conserves most of the initial ranking in each list (Figure B1).
**Related code:**

*Traits_and_imputation / Rscripts / aggressiveness.R*

**Table B2.** References used to define the aggressiveness ranking index per species (CI: Coral Index).

<table>
<thead>
<tr>
<th>References</th>
<th>Metrics</th>
<th>Original no. of taxa</th>
<th>Final no. of species</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Lang, 1973)</td>
<td>ranking number based on number of subordinates</td>
<td>27</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>(Sheppard, 1979)</td>
<td>CI</td>
<td>26</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>(Logan, 1984)</td>
<td>number of subordinates</td>
<td>17</td>
<td>15</td>
<td>Paired-interactions showing opposite result between field and lab experiment were not considered</td>
</tr>
<tr>
<td>(Dai, 1990)</td>
<td>classification in five categories based on CI</td>
<td>76</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td>(Abelson and Loya, 1999)</td>
<td>ranking number based on frequency of wins and losses and composition of losing and winning species</td>
<td>33</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>(Connell et al., 2004)</td>
<td>% of winning interactions</td>
<td>13</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td><strong>Total number of species:</strong></td>
<td></td>
<td><strong>147</strong></td>
<td><strong>116</strong></td>
<td></td>
</tr>
</tbody>
</table>
Figure B1. Correlation analyses between the original aggressiveness rankings and the selected global computed ranking for each study (A: Sheppard, 1979; B: Abelson and Loya, 1999; C: Dai, 1990; D: Connell et al., 2004; E: Lang, 1973; F: Logan, 1984). Also displayed are the Spearman ρ (r_s), the number of species (n) and the identity line (dashed lines) for visual aid. All P < 0.001 except for D, where P = 0.003.

B.2. Phylogeny

We used the phylogenetic supertrees of Huang and Roy (2015) to include phylogenetic information as a predictor for the imputation of missing trait data. They reconstructed phylogenetic supertrees of the scleractinian clade from different trees (i.e., a molecular phylogeny, 13 morphological trees and one taxonomic tree). Their methodology resulted in 1000 fully resolved supertrees, comprising 1547 coral species We updated the name of 113 species and removed 47 species whose corrected name was already present in the tree. We used the drop.tip function from the R package ape 5.0 (Paradis and Schliep, 2018). We then removed 712 azooxanthellae species (based on the trait “zooxanthellate” from the Coral Trait Database). Finally, we added 10 species at the genus level using the add.species.to.genus function from the R package phytools 0.5-38 (Revell, 2012). We added these species randomly along the edges
to maintain binary nodes in the trees and avoid polytomies. The resulting supertrees are composed of 798 species.

Related code:

*Traits_and_imputation / Rscripts / phylogeny_coral.R* and
*phylogeny_coral_and_functional_traits.R*

### B.3. Imputation of missing trait data

#### B.3.1. Including phylogenetic information in the functional-trait table

We combined phylogenetic information with species functional traits to improve the prediction of missing trait data. The reasoning is based on the following assumptions: 

(i) closely related species are generally more functionally similar because of phylogenetic conservation of traits, and 

(ii) species having similar values for certain traits might have similar values for other traits because of functional trade-offs (Darling et al., 2012).

The phylogenetic information is included in the form of eigenvectors obtained from doing a principal component analysis on the distance matrix representing the phylogenetic branch length separating each species in the phylogeny (Swenson, 2014a). We first calculated the distance matrix of each of the 1000 trees using the function *cophenet* from the R package *stats* (R Core Team, 2017). We averaged the 1000 matrices to obtain a final distance matrix. We then did a principal components analysis using the function *prcomp* from the R package *stats*. We selected the first nine eigenvectors using the broken stick method and used them as predictors (Figure B2). We retained the nine principal components because each describe different levels of the phylogeny (Swenson, 2014b).
Figure B2. Percentage of variance explained by the nine first eigenvectors produced by the PCA on the averaged phylogenetic distance matrix.

B.3.2. Imputation of missing data

Among the different statistical methods available to perform imputation of missing data in functional-trait datasets (Penone et al., 2014; Schrodt et al., 2015), we chose the random-forest algorithm (Breiman, 2001) because it can handle highly dimensional datasets, does not rely on distributional assumptions, and is particularly appropriate for modelling complex interactions and non-linear relationships among variables. It is one of the best-performing techniques and allows the inclusion of phylogenetic information (Penone et al., 2014). We used the R package missForest 1.4 (Stekhoven and Bühlmann, 2012) to do the imputation. We set the maximum number of iterations to 10 and the number of trees generated by iteration to 100 (default values). Performance is evaluated with the normalized root mean squared error for numerical traits and proportion of falsely classified entries for categorical traits (good performance leads to a value close to 0, and bad performance to a value close to one). The method stopped after five iterations. It produced little error (normalized root mean squared error = 0.0985; proportion of falsely classified = 0.0735), and conserved the shape of the trait distributions (Figure B3; Figure B4; Figure B5).

Related code:

Traits_and_imputation / Rscripts / imputation_traits_missForest.R
Figure B3. Comparisons of frequency distributions of trait values between the original dataset (left column) and the imputed dataset (right column) for aggressiveness (A, B); coloniality (C, D); colony maximum diameter (E, F); corallite area (G, H) (total \( n = 798 \)).
Figure B4. Comparisons of frequency distributions of trait values between the original dataset (left column) and the imputed dataset (right column) for egg diameter (A, B); polyp fecundity (C, D); growth forms: branching (bra), plate (pla), corymbose (cor), digitate (dig), laminar (lam), columnar (col), massive (mas), encrusting long upright (elu), encrusting (enc) (E, F); growth rate (G, H) (total $n = 798$).
**Figure B5.** Comparisons of frequency distributions of trait values between the original dataset (left column) and the imputed dataset (right column) for model of larval development (A, B); microscopic reduced scattering coefficient (mRSC; C, D); sexual system (E, F) (total $n = 798$).
Appendix C. Chapter 3: Overview, Design concepts and Details protocol

C.1. Purpose and patterns

The purpose of the model is to predict coral population dynamics as a function of cyclone and bleaching intensity and frequency, grazing pressure, larval connectivity, interspecific competitive interactions, and benthic community diversity (species richness and functional diversity). The higher-level purpose is to understand what aspects of diversity contribute to the coral ecosystem functioning and resilience, which is achievable by analysing patterns of population percentage cover, larval recruitment rates, colony class distributions, reef rugosity and grazing pressure, and by comparing these patterns between functionally distinct benthic communities and across different environmental scenarios. These patterns are essential in understanding the emerging community dynamics because they reflect the different biodiversity-related processes at play (see Appendix F for detailed expected versus observed patterns as a function of both functional diversity and the environmental context). Additionally, the model accuracy can be evaluated by comparing these patterns to real data (see Appendix D for the model calibration with empirical data).

C.2. Entities, state variables, and scale

The model consists of an ensemble of grid-cell agents, which are both spatial units and agents. Each grid-cell agent represents 1 cm$^2$, so that the benthic community is represented at a scale of organization smaller than the colony (equivalent to that of a polyp, although polyp size varies among species by several orders of magnitude) (Figure 3.1; Figure C1). We chose such a small grain to represent certain processes at the appropriate scale (e.g., settlement, growth and spatial interactions), which permits to simulate higher level dynamics as the emergent outcome of agent level processes (e.g., colony size distribution). Each agent is characterized by 33 variables that describe where the agent is in space (its position is fixed), its species identity and related functional characteristics, its age, the colony’s planar area and identification number, if it is bleached or was grazed recently (Table C1). Coral colonies and patches of algae are entities
composed of multiple agents sharing several variable values (except for their spatial coordinates) and changing their state simultaneously during certain processes. For instance, dislodgement is simulated by converting all the agents forming the dislodged colony into barren ground; a turf algae overgrowing a colony is simulated by converting the coral agents constituting the overgrown part into turf, but conserving the information about the colony (i.e., identification number, size, species, growth form).

We decided to use grid-cell agents for two reasons. First for simplicity, because grid-cell agents constitute the spatial unit (i.e., the grid) and can represent both non-living elements that can interact with living entities (i.e., barren ground is suitable for vegetative growth and settlement while sand is not), and living sessile organisms. Second, because grid-cell agents allow to accurately present the dual level of organization at which a coral colony can be described: a set of smaller interacting entities (i.e., polyps) or a single individual in a population. In the latter, grid-cell agents forming a colony form a collective of grid-cell agents that share state variables that are unique to their colony, such as: IDNumber, planar_area_colony and the timeRecoveryBleaching (Table C1).

The size of the reef and the length of a time step are changeable. We defined a 25 m² reef (i.e., 250,000 agents) for the model calibration and analysis (Figure C1), which is usually the scale at which benthic communities are assessed in detail (e.g., Holbrook et al. 2018, Torda et al. 2018). Representing larger areas is possible but more computationally intensive. We used a six-month time step for our model calibration and analysis because the empirical data we used to calibrate the model were collected biannually. Alternatively, it is possible to define three, four, six or 12-month time steps (using the parameter yearDivision).

**Related code:**

*coralreef2/src/coralreef2/Agent.java*
*coralreef2/src/coralreef2/InputData/FunctionalTraitData.java*
Table C1. Grid-cell agent attributes, state variables (*) and other variables.

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>context</td>
<td>The “context” (a Java object that encapsulates the agents and projections; it is static, and all the agents belong to the same context).</td>
</tr>
<tr>
<td>grid</td>
<td>The “grid”, a spatial Projection associated to the Context and allowing to place and locate the agents spatially (it is static, and all the agents are part of the same Grid).</td>
</tr>
<tr>
<td>x *</td>
<td>The x coordinate of the agent in the grid (static).</td>
</tr>
<tr>
<td>y *</td>
<td>The y coordinate of the agent in the grid (static).</td>
</tr>
<tr>
<td>substrateCategory *</td>
<td>First categorisation of the agents: BarrenGround for barren ground and sand; Algae for algae; Coral for corals.</td>
</tr>
<tr>
<td></td>
<td>Value are imported from data/functionalTraitDF_model.csv</td>
</tr>
<tr>
<td>substrateSubCategory *</td>
<td>Second categorisation of the agents: BarrenGround for barren ground and sand; Macroalgae, AMA, Halimeda, Turf, ACA and CCA for macroalgae, allopathic macroalgae, Halimeda spp., turf, articulated coralline algae and crustose coralline algae, respectively; BleachedCoral, DeadCoral, LiveCoral for bleached, dead and living corals, respectively.</td>
</tr>
<tr>
<td></td>
<td>Value imported from data/functionalTraitDF_model.csv</td>
</tr>
<tr>
<td>species *</td>
<td>Third categorisation of the agents: BarrenGround for barren ground; sand for sand; Macroalgae, AMA, Halimeda, Turf, ACA and CCA for macroalgae, allopathic macroalgae, Halimeda spp., turf, articulated coralline algae and crustose coralline algae, respectively; coral species names for corals (e.g., Acanthastrea brevis).</td>
</tr>
<tr>
<td></td>
<td>Value imported from data/functionalTraitDF_model.csv</td>
</tr>
<tr>
<td>age *</td>
<td>Age (yr) of living agents.</td>
</tr>
<tr>
<td>Variable name</td>
<td>Description</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>age_maturity</td>
<td></td>
</tr>
<tr>
<td>aggressiveness</td>
<td></td>
</tr>
<tr>
<td>bleaching_probability</td>
<td></td>
</tr>
<tr>
<td>coloniality</td>
<td></td>
</tr>
<tr>
<td>colony_maximum_diameter</td>
<td>Species traits (see Table B1)</td>
</tr>
<tr>
<td>corallite_area</td>
<td>Value imported from data/functionalTraitDF_model.csv</td>
</tr>
<tr>
<td>egg_diameter</td>
<td></td>
</tr>
<tr>
<td>fecundity_polyp</td>
<td></td>
</tr>
<tr>
<td>growth_form</td>
<td></td>
</tr>
<tr>
<td>mode_larval_development</td>
<td></td>
</tr>
<tr>
<td>reduced_scattering_coefficient</td>
<td></td>
</tr>
<tr>
<td>sexual_system</td>
<td></td>
</tr>
<tr>
<td>size_maturity</td>
<td></td>
</tr>
<tr>
<td>growth_rate</td>
<td>The maximum radius ( r_{\text{max}} ) within which an agent can convert</td>
</tr>
<tr>
<td></td>
<td>neighboring agents (see §C.7.5.1).</td>
</tr>
<tr>
<td>correction_coeff_polypFecundity</td>
<td>A coefficient to apply to small species (( \text{colony}<em>\text{maximum}</em>\text{diameter} &lt; 16.7 \text{ cm} )) when</td>
</tr>
<tr>
<td></td>
<td>determining the proportion of mature polyps in the colony (see §C.7.2.1.1.b).</td>
</tr>
<tr>
<td>timeRecoveryBleaching</td>
<td>Time (yr) remaining before the agent totally recovers from bleaching (see</td>
</tr>
<tr>
<td></td>
<td>§C.7.4).</td>
</tr>
<tr>
<td>IDNumber</td>
<td>The identification number; unique to each colony and shared by the agents</td>
</tr>
<tr>
<td></td>
<td>forming a same colony.</td>
</tr>
<tr>
<td>red</td>
<td>The Red Green Blue (RGB) colour code to represent each benthic entity.</td>
</tr>
<tr>
<td>green</td>
<td>Value imported from data/functionalTraitDF_model.csv</td>
</tr>
<tr>
<td>blue</td>
<td></td>
</tr>
<tr>
<td>canIGrow</td>
<td>Boolean variable used to allow or forbid an agent to grow.</td>
</tr>
<tr>
<td>Variable name</td>
<td>Description</td>
</tr>
<tr>
<td>----------------------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>haveIbeenConverted*</td>
<td>Boolean variable used to forbid an agent to grow during the <em>Growth</em> procedure (Figure 3.2) if it has already been converted (i.e., overgrown) by another agent during the same <em>Growth</em> procedure.</td>
</tr>
<tr>
<td>haveIbeenGrazed*</td>
<td>Boolean variable used to forbid an algae agent to overgrow another non-algae agent if the latter has been grazed during the <em>Grazing</em> procedure of the same time step (Figure 3.2).</td>
</tr>
<tr>
<td>planar_area_colony</td>
<td>The planar area (cm²) of the colony formed by the agent (the value equals the number of agents forming the colony).</td>
</tr>
<tr>
<td>newRecruit*</td>
<td>Boolean variable used to indicate if the agent is a new recruit (i.e., if it settled during the <em>Coral reproduction</em> procedure of the present time step; Figure 3.2).</td>
</tr>
<tr>
<td>size_UpDated*</td>
<td>Boolean variable used to indicate if the agent’s planar_area_colony has been updated during a procedure of colony size update (i.e., after each disturbance and at the end of a time step; Figure 3.2).</td>
</tr>
</tbody>
</table>
Figure C1. Screenshots displaying a 25-m² of the benthic community at Ilet à Rats taken after the execution of the bleaching process (left) and at the end of the same six-month time step (right). We used parameter values calibrated with the empirical data describing this specific site (see Appendix D). Coral colonies (pink, orange, blue, dark blue, white and light grey shapes) and algae (macroalgae, turf, allopathic macroalgae, and crustose coralline algae are in green, light green, dark green and beige shapes, respectively) compete spatially. Colourful coral colonies were not affected by the thermal disturbance, light grey colonies bleached and survived, and white colonies died. Grey and yellow agents represent barren ground and sand, respectively.
C.3. Process overview and scheduling

Each time step is constituted of different consecutive processes (Figure 3.2), which we detail here with the corresponding name of the method and eventually the related files:

1) Initialization
   a. *CoralReef2Builder()*:
      i. All the lists the model uses are erased, then all the necessary data related to the simulation are imported: the values of the parameters defined in the general user interface (GUI); time series of the number and diversity of larvae coming from the regional pool (either a constant or a time series imported from data/ Disturbance_larvalConnectivity.csv), the cover of sand (imported from data/ Disturbance_sand.csv), of the thermal (in degree heating week; imported from data/ Disturbance_bleaching.csv) and hydrodynamic disturbance regimes (in dislodgement mechanical threshold, imported from data/ Disturbance_cyclone.csv), of the grazing pressure (in % cover; imported from data/ Disturbance_grazing.csv); the order of occurrence for coral reproduction, hydrodynamic and thermal disturbances (imported from data/ Disturbance_priority.csv); the functional traits table (imported from data/ functionalTraitDF_model.csv); the coral species and algae functional groups present and their associated initial % cover (imported from data/ Initial_benthic_composition.csv); the length (yr) of the simulation.
      ii. All the parameter values used for this specific simulation are exported in output/ Parameters_values/ Parameters_values_simulations.csv.
      iii. Creation of the context and the *grid*, then of the agents, according to the initial % cover of each living and non-living benthic groups previously imported. When an agent is created, its x and y variables are set relatively to its the position in the *grid*, its functional traits and colour variables are set accordingly to its benthic group (Table C1), whose characteristics were imported previously (see §C.5.2 on how the space is filled up).

2) Sub-initialization (i.e., the initialization executed each time step)
   a. Display is updated.
   b. *RunTimer()*: year is checked to see if it corresponds to the end of the simulation.
c. *checkDisturbance()*: the environment imports for the corresponding year *(i)* the intensity of the thermal disturbance (in degree-heating weeks) from data/ Disturbance_bleaching.csv and update the variable bleaching_DHW; *(ii)* the intensity of the hydrodynamic disturbance (in dislodgement mechanical threshold) from data/ Disturbance_cyclone.csv and update the variable cyclone_DMT; *(iii)* the intensity of the grazing pressure (in % cover) from data/ Disturbance_grazing.csv and update the variable percentage_reef_grazed; *(iv)* the order at which coral reproduction, thermal and hydrodynamic disturbances are executed, from data/ Disturbance_priority.csv and update the variables priority_1, priority_2, priority_3, and season (either “dry” or “wet”).

d. *calculatePercentateCover_and_NumberRecruits()*: calculate the % cover of each living and non-living benthic group and the mean number of recruits m² for each coral species. The data is exported in the simulation-related file output/ PercentageCover/PercentageCover_...csv and NumberRecruits/NumberRecruits_...csv, respectively. This method is executed here (at the beginning of the time step) only at year = 0.0; it is executed systematically after a disturbance and at the end of the time step.

e. *setDefaultParameters()*: each agent updates certain of its variables:
   i. The Boolean variables canIGrow, haveIBeenConverted, sizeUpDated, haveIbeenGrazed, and newRecruit are set to false.
   ii. If the agent is recovering from bleaching (i.e., timeRecoveryBleaching > 0.0), then timeRecoveryBleaching is updated. If once updated 0.0 < timeRecoveryBleaching ≤ 0.5, the agent recovers its normal growth rate and colour (i.e., growthRate, red, blue and green are set to their original values); else, if timeRecoveryBleaching = 0.0, the agent recovers its capacity to produce gametes (i.e., polyp_fecundity is set to its initial value).

f. *updateAgentColonySize()*: each agent associated to a colony (alive and dead coral and algae growing on a dead colony) have their planar_area_colony updated, and then their sizeUpDated set to true. If year = 0.0, the planar area of each colony, associated with its IDnumber, species, and year_event and the name of the event (i.e., “cyclone”) are exported in the simulation-related file output/ ColonyPlanarArea/ ColonyPlanarArea_... csv.

3) *grazing()*:
   a. Display is updated.
b. \textit{rugosityToGrazing}(): the methods is only activated if the model parameter \\
\textit{Rugosity\_Grazing} = \text{true}. The rugosity created by coral colonies is calculated and used to \\
determine the grazing pressure (% cover) generated by the herbivorous fish supported by \\
the coral community (see §C.7.1.2.2). The value of cover grazed is added to \\
\textit{percentage\_reef\_grazed}. The rugosity, % cover grazed due to the fish community, \\
\textit{percentage\_reef\_grazed} and year are exported in the simulation-related file output/ \\
RugosityCoverGrazed/RugosityCoverGrazed\_...csv.

c. Circular clusters of 29 agents are selected randomly and grazed (only the agents having \\
\textit{have\_been\_grazed} = \text{false} can be grazed) until the percentage of the reef grazed = \\
\textit{percentage\_reef\_grazed}. All agents grazed have their \textit{have\_been\_grazed} variable set to \\
true. Algae agent successfully grazed are converted into the substrate on which they were \\
growing (i.e., barren ground or dead coral colony) (see §C.7.1.2.1).

4) \textit{Disturbance\_and\_reproduction}(): first the variable \textit{year\_event} = \text{year}, then the following \\
methods are executed in an order defined by \textit{priority\_1}, \textit{priority\_2} and \textit{priority\_3}:

a. Display is updated.

b. \textit{coralReproduction}(): the following methods are executed:

i. \textit{coralLarvaeTotalProduction}(): the number of larvae produced locally and coming from \\
the regional pool is calculated for each species (see §C.7.2.1).

ii. \textit{coralSettlement}(): agents are randomly selected and eventually converted into a new \\
coral recruit; new recruits take variables related to their coral species and \\
planar\_area\_colony = 1 \text{ cm}^2, \textit{newRecruits} = \text{true}. Agent potentially converted are barren \\
ground, dead coral and crustose coralline algae. Twenty agents are selected at a time for \\
each species; the procedure is repeated until all the number of larvae calculated in \\
\textit{coralLarvaeTotalProduction}() is reached.

c. \textit{bleaching}():

i. All the coral colonies are selected one after another and eventually bleach, according to \\
a probability defined as a function of the species bleaching susceptibility (i.e., \\
\textit{bleaching\_probability}) and the intensity of the thermal stress (i.e., \textit{bleaching\_DHW}). A \\
bleached colony eventually dies, according to a probability that depends uniquely on the \\
intensity of the thermal stress (see §C.7.4). Agents of a dying colony have their \\
substrateSubCategory = \text{“DeadCoral”}, growth\_rate = 0.0, aggressiveness = 0, age = 0.0,
become white (i.e., red = 255, green = 255, blue = 255), canIGrow = false, timeRecoveryBleaching = 0.0, newRecruit = false. Agents of a surviving bleached colony have their substrateSubCategory = “BleachedCoral”, growth_rate reduced by half during at least six months (depending on the temporal representation of a time step), fecundity_polyp = 0.0 during the next year, become light grey (i.e., red = 245, green = 245, blue = 245), timeRecoveryBleaching = 1.0.

ii. year_event = year_event + 0.1.

iii. calculatePercentageCover_and_NumberRecruits(): see 2) c. for details.

iv. updateAgentColonySize(): see 2) e. for details. In addition, the planar area of each colony, associated with its IDnumber, species, and year_event and the name of the event (i.e., “bleaching”) are exported in the simulation-related file output/ColonyPlanarArea/ColonyPlanarArea...csv.

d. cyclone():

i. cyclone_DMT(): all the coral colonies are selected one after another, their colony shape factor (i.e., fragility) is calculated as a function of their growth_form and planar_area_colony. If the colony shape factor > cyclone_DMT (i.e., intensity of the disturbance), the colony is dislodged. In that case, all the coral agents forming the colony are converted into barren ground (only context, grid, x and y remain unchanged). Branching colonies can potentially fragment and survive. A proportion of algae are removed by patches of agents (i.e., the algae agents are converted to the substrate supporting them) as a function of the algae susceptibility and the intensity of the disturbance (see §C.7.3).

ii. year_event = year_event + 0.1.

iii. calculatePercentageCover_and_NumberRecruits(): see 2) c. for details.

iv. updateAgentColonySize(): see 2) e. for details. The data is exported in the simulation-related file.

5) grow():

a. Display is updated.

b. agents are selected in a random order and have to opportunity to grow—to convert neighbouring agents within a certain radius into their own state: for the majority of interactions, all the agent own variables are updated except context, grid, x and y; in the
case algae agents convert coral agents, the newly converted algae agents keep several of
their previous state variables (i.e., species, age_maturity, coloniality,
colony_max_diameter, corallite_area, egg_diameter, fecundity_polyp, growth_form,
mode_of_larval_development, reduced_scattering_coefficient, sexual_system,
size_maturity, correction_coeff_polypFecundity, IDNumber, planar_area_colony) so as to
simulate the growth of algae on coral colonies. Only living agents have the opportunity to
grow and the rules of interactions are complex (see §C.7.5).

6) smoothingCoralColonie(): coral colonies are smoothed by converting into barren ground
coral agents that have three or four Von Neumann neighbour agents not from the same
colony.

7) sandImport(): sand is added or removed by converting random patches of barren ground
agents into sand (i.e., species = “sand”; red = 255, green = 255, blue = 51) or patches of sand
agents into barren ground (i.e., species = “BarrenGround”; red = 160, green = 160, blue =
160), respectively. The desired sand cover of a given time step (sand_cover) is imported
from data/Disturbance_sand.csv.

8) AlgaeInvasion(): barren ground and dead coral agents that have not been grazed (i.e.,
haveIbeenGrazed = false) during the previously executed grazing() method are converted
into algae agents. Interactively, patches of these agents are selected randomly in space and
converted successively into one of the algae functional groups initially present.

9) substrateCompositionCSV():
   a. year is incremented.
   b. calculatePercentageCover_and_NumberRecruits(): see 2) c. for details. Data is exported
      in the simulation-related files.
   c. updateAgentColonySize(): see 2) e. for details. Data is exported in the simulation-related
      file.
   d. If this is the last time step: rugosityToGrazing() (see 3) a. for details) and data is exported
      in the simulation-related file.

Discussion:
We decided to implement coral growth, spatial competition, recruitment, their response to
thermal and hydrodynamic disturbances and grazing pressure because they are fundamental
ecological processes that shape coral communities and their dynamics. Additionally, these processes have been well studied, and associated functional traits have been collected on numerous species.

Executing these processes simultaneously, like in reality, is not possible because grid-cell agents can only be activated one after another. We consequently had to decide upon the order at which these processes were executed. We placed grazing, thermal and hydrodynamic disturbances before growth so they would affect the growth and interactions between coral colonies and algae. We implemented the possibility to decide on the order of occurrence between disturbances and coral reproduction because the timing of incidence of these events can be critical for coral population dynamics. Once all the organisms grow and compete, sand is imported or exported to a desired % cover. We did not implement a process of sedimentation (associated to hydrodynamic disturbances, for instance) due to insufficient empirical data. We thought it necessary to potentially represent sand cover because sand can occupy a large proportion of the reef and is an unstable substrate that prevents organisms from growing and settling. We placed this sedimentation process between growth and algae invasion to secure a sand cover close to the desired value and to constrain the remaining available space for the last process. Finally, we implemented algae invasion because we assumed that available non-grazed surface would be occupied by an algae within a several-month period in a real reef.

Related code:
coralreef2 / src / coralreef2 / CoralReef2Builder.java and ContextCoralReef2.java

C.4. Design concepts

Basic principles: The model combines three fundamental approaches: (i) a complex agent-based approach (Breckling et al., 2006; Grimm, 2019; Grimm and Railsback, 2005)—the dynamics observed at higher levels of organization (e.g., population percentage cover, recruitment rates, colony size distributions, rugosity) emerge from agent-related processes happening at the lower scales (e.g., conversion of a barren ground agent to a new coral recruit agent, dislodgement of a single colony); (ii) a functional trait-based approach (Madin et al., 2016b; McGill et al., 2006)—species diversity and dynamics are determined by mechanistically linked trait-process
associations; (iii) a demographic approach (Edmunds et al., 2014; Tuljapurkar and Caswell, 1997)—the dynamics of a population depends on its demographic structure (e.g., colony size distribution) because the size of a colony influences its capacity to reproduce, compete and resist disturbances. We combined these three approaches by implementing evidence-based trait-process mechanistic associations at an appropriate spatial scale (e.g., single agent for a larvae recruiting, all the agents forming a colony during a bleaching event) and accounting for size-process interactions (e.g., proportion of fecund polyps in a colony, colony shape factor for dislodgement).

The model captures several fundamental principles: (i) species diversity influences ecosystem resilience (i.e., the diversity-stability relationship; Ives and Carpenter, 2007; McCann, 2000; Nyström, 2006) and (ii) functioning (i.e., the diversity-ecosystem functioning relationship; Brandl et al., 2019; Loreau, 2000), (iii) disturbance regimes shape communities by filtering species and mediating interspecific competition (Kraft et al., 2015a; Sommer et al., 2014), (iv) interspecific functional differences (or strategies) mediate competitive exclusion and coexistence (Kraft et al., 2015b; Vellend, 2010), (v) source-sink dynamics regulate species coexistence in metacommunities (Amarasekare and Nisbet, 2001; Loreau and Mouquet, 1999). Note that there are many mechanisms leading to species coexistence (e.g., niche partitioning, spatial heterogeneity, facilitation; (Adler et al., 2013; Chesson, 2000) that we did not implement in the model.

**Emergence:** All the model outputs (i.e., population % cover, number coral recruits m⁻², colony size distributions and eventually rugosity) emerge from the processes implemented and depend on the imposed environmental conditions (i.e., larvae connectivity, grazing pressure, hydrodynamics and thermal disturbance regime, sand input). The outputted percentage of sand cover (if included) results mostly from the imposed sand cover (but is it possible that not enough space is available to reach the desired cover). If the rugosity-grazing feedback process is activated (Figure 3.2), the percentage of reef grazed results from the sum of the % imposed (if the user decides to maintain a certain imposed grazing regime) and the % emerging from the complexity of the habitat created by coral colonies (see §C.7.1.2.2). Cell agents do not make decisions and their behaviour results from imposed deterministic or probabilistic rules.
Adaptation: Not implemented.
Objectives: Not implemented.
Learning: Not implemented.
Prediction: Not implemented.
Sensing: Not implemented.

Interactions: Agents on the edge of coral colonies and patches of algae interact directly with one another when competing for space. The outcome of a coral-coral interaction is determined by its specific pairwise outcome probabilities (or aggressiveness if the probability is not available for the species pair), the probability of coral-algae interactions are the same for all coral species, and algae-algae interactions result in a stand-off except when competing against crustose coralline algae. Branching and plating species also have the capacity to overtop other colonies and algae depending on their size (see §C.7.5). Agent also directly interact by occupied space, which prevents potential new recruits to settle.

Stochasticity: The model draws success or failure outcomes in several processes, based on probabilities that represent specific ecological phonemes or details. We used (i) grazing probabilities to represent the difference of palatability among algae functional groups (see §C.7.1.2); (ii) settlement probability to represent the differences of settlement suitability among substrate types (see §C.7.2.1.3); (iii) a surviving probability for the first few months of the life of new coral recruits in order to control recruitment rates without implementing the causes of new recruit mortality (see §C.7.2.1.3); (iv) coral-algae, algae-algae and published species-pair probabilities of interaction outcomes to represent the non-transitive and inconsistent nature of direct interactions between these organisms (see §C.7.5); (v) species-specific bleaching probabilities and a bleaching-induced probability of mortality to account for the complexity and variability of bleaching responses observed within populations (see §C.7.4); (vi) species-specific positively skewed density distributions of colony diameters to create coral colonies during the initialization of the reef (see §C.5.2.2). Finally, grazing and larval settlement and the placement of colonies and algae during the initialization of the reef happen randomly in space.
Collectives: Coral colonies are collectives of coral agents emerging from the growth of individual coral agents (new recruits). Agents being part of a same colony (i.e., alive, bleached and dead coral and algae on a colony) behave collectively when dislodged (see §C.7.3.1.2.a); living coral agents behave collectively when bleaching, dying from bleaching (see §C.7.4) and reproducing (see §C.7.2.1.1). Plating and branching corals can overtop other colonies and algae if their colony is large enough (see §C.7.5.2.2.b).

Observation: The model exports data that ecologists typically collect on the field to describe and understand patterns of community dynamics: (i) the percentage cover of each taxon (collected initially, after hydrodynamic and thermal disturbances and at the end of each time step and recorded in output/ PercentageCover/ PercentageCover_...csv), (ii) the mean number of recruits for each coral species m\(^{-2}\) (collected at the end of each time step and recorded in output/ NumberRecruits/ NumberRecruits_...csv), (iii) the planar area of each colony (collected initially, after hydrodynamic and thermal disturbances and at the end of each time step and recorded in output/ ColonyPlanarArea/ ColonyPlanarArea_... csv), and optionally (iv) the rugosity of the reef created by coral colonies and the associated % cover grazed due to the fish community (collected during the grazing process and recorded in output/ RugosityCoverGrazed/ RugosityCoverGrazed_...csv).

C.5. Initialization

The principal objective of the model is to simulate community dynamics as a function of species composition in different environmental scenarios. The composition and initial % cover for each coral species and algae functional group is imported from data/ Initial_benthic_composition.csv and communities can be selected using their unique communityNumber (or “Community Number” in the GUI). It is possible to define a % cover of bleached and dead coral species. Once the communityNumber is selected and the corresponding % cover imported, the grid is filled by creating agents. First, coral colonies are created at random locations, ordering the species from largest to smallest maximum colony diameter (this avoids having small colonies being enclosed by larger ones). Colonies are created by selecting an empty cell from the list of all available cells. A colony radius is then drawn from a species-specific size distribution (see §C.5.2) and
used to select all the neighboring cells present in the list. These cells are removed from the list, and a cell-agent is created in each one of them. Upon creation, each agent is associated to the *context* and *grid*, and is given its $x$ and $y$ coordinates; all agent forming a same colony share the same other variables (Table C1). The procedure continues until the cover occupied reaches the defined value and is repeated for each coral species. Similarly, patches of algae agents (of a 10 cm radius) are then created in the remaining available cells, one functional group at a time, until the inputted cover is reached. The remaining empty grid-cells are filled by creating barren ground agents and finally patches of sand are created by converting patches of barren grounds agents. The initial % cover of sand is imported from data/ Disturbance_sand.csv and it is associated to a certain environmental scenario, which can be selected using its unique disturbanceScenarioNumber (or “Disturbance Scenario” in the GUI; see §C.6).

Placing coral colonies randomly in space is probably a limitation as aggregation of colonies influence coral reef dynamics (Brito-Millán et al., 2019; Eynaud et al., 2016). Providing the option to define the initial spatial arrangement of the colonies could be part of future development of the model. So far, only Wakeford et al. (2008) implemented coral colonies spatial arrangements according to empirical data.

The number of agents created (i.e., the size of the *grid*) is defined by the parameters *reef_height* and *reef_width* (in cm).

**Related code:**

`coralreef2 / src / coralreef2 / CoralReef2Builder.java`

**C.5.1. Initialization of species cover**

**C.5.2. Initialization of colonies size and age**

**C.5.2.1 Background**

Colony size influences important processes such as colony fecundity (see §C.7.2.1), spatial competition (see §C.7.5) and mortality (see §C.7.3) (Connell et al., 2004; Hughes et al., 1992). Initializing colony size properly is consequently important. Size distributions of coral colonies are in nature positively skewed and approximate a symmetric distribution when log-transformed.
strategy—weedy species (i.e., short life cycle, high recruitment rate, small colony size) display positively skewed log-transformed distributions as opposed to stress resistant species (i.e., larger colonies, long life cycle, low recruitment rate; e.g., Meesters et al., 2001); and (ii) past disturbances having selective effects on certain colony sizes (e.g., Bauman et al., 2013).

The age of a colony also influences fecundity as young colonies need to reach maturity before sexually reproducing. However, colony size can vary enormously within individual colonies of a same cohort due to genetic and environmental differences. Because of its importance (regardless of age) on fecundity, competition and survival, colony size is considered a better predictor of coral fitness (Hughes, 1984).

C.5.2.2 Implementation

During the initialization of the reef, we draw colony diameters from species-specific colony size distributions. We generated these distributions using the following custom function:

\[
\text{nextSkewDistFun} <- \text{function}(\text{minVal}=0, \text{maxVal}, \text{skew}, \text{bias}, n=10000)\{
\text{range} <- \text{maxVal} - \text{minVal}
\text{mid} <- \text{minVal} + \text{range} / 2
\text{unitGaussian} <- \text{rnorm}(n, 0, 1)
\text{biasFactor} <- \exp(\text{bias})
\text{retval} <- \text{mid} + (\text{range} * (\text{biasFactor} / (\text{biasFactor} + \exp(-\text{unitGaussian/}\text{skew})) - 0.5))
\text{retval}
\}
\]

where \text{minVal} = \text{minimum} and \text{maxVal} = \text{maximum} colony diameter, \text{skew} and \text{bias} = \text{two parameters influencing the shape of the distribution}, and \text{n} = \text{sample size}. To generate the required species-specific size distributions, we predicted values for \text{bias} and \text{skew} as follow. We first defined \text{skew} and \text{bias} for eleven Caribbean species for which empirical size distributions were available based on data collected in Curaçao (Netherland Antilles) in 1996 (E. H. Meesters and R. P. M. Bak, personal communication, May 2017; Figure C2; Figure C3). We iteratively tried different values of \text{skew} and \text{bias} until the distributions visually matched the empirical ones.
The colony maximum diameter of these species spans a small range (11 to 250 cm) compared to the entire range of diameter found across all species (2 to 2000 cm). Consequently, we selected 20 additional species from the 798 species available in our coral traits imputed dataset (Appendix B), selecting ten with larger (706 to 2000 cm) and ten with smaller (2 to 8 cm) colony maximum diameter. We defined the values of skew and bias of these species assuming a positively skewed colony size distributions and higher skewness for species having larger maximum colony diameter (because reaching very large colonies is unlikely in the intense disturbance regimes that commonly affect reefs). We then fitted least-squares linear regressions for both skew and bias using maximum colony diameter as a predictive variable (Figure C4, Table C2). Finally, we predicted the skew and bias values of the 798 species (Figure C5).

Given that colony size and age are poorly correlated, there was no basis for establishing age based on the value of colony size drawn from the distributions. Thus, in all cases we set initial colony age at three years, which is the age at first maturity in the model (Appendix B; § C.7.2.1.1.a). The effect on recruitment is minor because we modeled colony fecundity as a function of the size of the colony; age being used only to determine when colonies recruited during simulation can start reproducing (§C.7.2.1).

Related code:
coralreef2 / src / coralreef2 / CoralReef2Builder.java
Figure C2. Size-class distributions of 11 Caribbean coral species (data collected in Curacao in 1996, E. H. Meesters and R. P. M. Bak, personal communication, May 2017).
Figure C3. Example of a visual comparison of colony size distributions between the real data (A, B) and the one obtained with the command `nextSkewDistFun` (C, D) for *Agaricia lamarcki* (n = 10,000). Real data were collected in Curaçao in 1996 (E. H. Meesters and R. P. M. Bak, personal communication, May 2017). We obtained the simulated distributions with bias = -1.9 and skew = 0.88.
Figure C4. Linear regression models for skew (A) and bias (B) expressed as a function of maximum colony diameter. Red circles are values of skew and bias manually obtained by comparison with empirical colony size class distributions (E. H. Meesters and R. P. M. Bak, personal communication, May 2017). Grey circles are the values of skew and bias we defined for the 20 species we added in order to increase the sample size and range of colony sizes. Also displayed are the least squares linear regression and the corresponding coefficient of determination.

Table C2. Parameters of the linear regression models for skew and bias expressed as a function of maximum colony diameter (log_{10}) (n = 31).

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters</th>
<th>Estimate</th>
<th>SE</th>
<th>R^2</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>skew</td>
<td>intercept</td>
<td>0.62</td>
<td>0.022</td>
<td>0.86</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>slope</td>
<td>0.14</td>
<td>0.010</td>
<td></td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>bias</td>
<td>intercept</td>
<td>0.59</td>
<td>0.094</td>
<td>0.96</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>slope</td>
<td>-1.20</td>
<td>0.044</td>
<td></td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Figure C5. Examples of modeled species-specific colony diameter distributions (n = 100,000). From top to bottom: Acropora nana (A, B), Acanthastrea echinata (C, D), Acropora longitcyathus (E, F), Acropora florida (G, H). Max value = maximum colony diameter.

C.6. Input data

Five predefined time series of input data are used to define the environmental context (Figure 3.2), and are characterized by a unique disturbanceScenarioNumber (or “Disturbance Scenario” in the GUI). The entire times series of a chosen scenario are imported upon initialization and the values used each time step are selected according to year. The time series define: (i) the hydrodynamic disturbance regime, in dislodgement mechanical threshold, which is a
dimensionless measure of the mechanical threshold imposed by waves and cyclones on coral colonies (see §C.7.3.1.1). The data is imported from data/Disturbance_cyclone.csv. We are not aware of any source for this data. Thermal stress intensity \((ii)\), in degree heating week, which is a measure of how much heat stress has accumulated in an area \((50 \times 50 \text{ km})\) over the past 12 weeks (it is calculated by adding up any temperature exceeding the bleaching threshold). The data is imported from data/Disturbance_bleaching.csv. For the model calibration (see §D.1 and §D.2.2), we downloaded real data from the US National Oceanic and Atmospheric Administration data server ERDDAP (Environmental Research Division's Data Access Program; coastwatch.pfeg.noaa.gov/erddap). The value of degree-heating weeks we imposed each time step was the maximum degree heating week value recorded during the corresponding periods. The \% of sand cover \((iii)\) is imported from data/ Disturbance_sand.csv. The \% of reef grazed \((iv)\) is imported from data/ Disturbance_grazing.csv. For the model calibration, we estimated grazing from population densities of Acanthuridae spp., Scaridae spp. and Diadema spp. using submodels we established from empirical data (see §D.2.3). The number of larvae per coral species m\(^{-2}\) coming from the regional pool \((v)\) is defined by the parameter connectivity (or “Connectivity” in the GUI) and is either imported from data/ Disturbance_larvalConnectivity.csv (if connectivity = “connectivityCSV”) or constant (if connectivity = any other value, see §C.7.2.1.2.b).

Related code:
coralreef2/src/coralreef2/CoralReef2Builder.java
coralreef2/src/coralreef2/InputData/BiodiversityData.java, Disturbance_bleaching.java, Disturbance_cyclone.java, Disturbance_grazing.java, Disturbance_larvalConnectivity.java, Disturbance_priority.java, Sand_cover.java.

C.7. Sub-models

All the related code for production of the following figures is in Manuscript/Rscripts/Appendix S2 - Overview Design concepts and Details.R.
C.7.1. Grazing

C.7.1.1 Background

The process of grazing is essential for maintaining reef ecosystems in a coral-dominated state (Mumby et al., 2007). The outcomes of coral-algae interactions are species- and context-specific (see §C.7.5.3), but coral species are in general disadvantaged by their slower growth rate when competing for space. Herbivores help corals by maintaining algae populations at low abundance and by influencing algal succession (Hixon and Brostoff, 1996; McClanahan, 1997). Reduction of grazing (due, for instance, to increased fishing) leads to algal populations increase, potentially exceeding the maximum grazing capacity (Williams et al., 2001), and allowing less palatable macroalgae to expand (Hay and Fenical, 1988). Negative feedbacks can then establish and maintain the ecosystem in an alternative stable and algae-dominated state. Alternatively, positive feedback processes help in maintaining the ecosystem in a coral-dominated state. The relationship between habitat complexity and grazing pressure is, for instance, one of the most important feedback process involved in reef resilience: coral colonies form complex structures that support a high diversity and biomass of herbivores, which enhances grazing pressure and favors coral growth and recruitment (Bozec et al., 2013; Mumby and Steneck, 2008; van de Leemput et al., 2016; Vergés et al., 2011).

Numerous species of herbivore graze on reefs, and they exhibit inter-class differences in grazing preference among algal functional groups (Steneck and Dethier, 1994). Sea urchin and nudibranch (Gastropoda) are for instance generalists and feed on most algae (Diaz-Pulido and McCook, 2008; Morrison, 1988). In contrast, fish species are generally more sensitive to allopathic defenses. Variation in allopathic sensitivity and behaviour between grazers leads to different algal population dynamics, depending on the identities of the most abundant herbivores. For example, sea urchin populations can maintain a benthic algal community in an intermediate succession stage (McClanahan, 1997), whereas parrotfishes and surgeon fishes strongly deflect the trajectory of algal succession, and territorial damsel-fishes merely slow the successional rate (Hixon and Brostoff, 1996). Herbivory also affects spatial patterning: contrary to fish, sea urchins have spatially constrained movements and create foraging “halos” which favor coral recruitment (Sandin and McNamara, 2012) and reef recovery (Eynaud et al., 2016). Finally, intense grazing regimes can have negative effects on corals by increasing bioerosion (Bellwood...
et al., 2004) and reducing coral recruitment rate (Sammarco, 1980).

Algae differ in their palatability. Despite high interspecific variability, generalities have been made for functional groups. Turf algae are considered highly edible: they are consumed by all grazers (Steneck and Dethier, 1994), and their presence under high grazing pressure is due to their fast growth rate rather than their resistance to grazing (Diaz-Pulido and McCook, 2008). In comparison, macroalgae have a larger and thicker structure, which provides resistance against small grazing fish and crustaceans (Hay, 1984; Mumby et al., 2007, but see Kuempel and Altieri, 2017). Allelopathic macroalgae (AMA) release secondary metabolites strong enough to significantly reduce their palatability (Hay and Fenical, 1988; Paul et al., 1990). In addition to secondary chemical compounds, *Halimeda* spp. have calcareous structure, which reduces further their edibility (Kuempel and Altieri, 2017; Lewis, 1986; McClanahan et al., 2002). Crustose coralline algae (CCA) can be considered poorly eatable because of their calcified and encrusting structure, which explain why its cover is usually positively correlated with grazing intensity (Belliveau and Paul, 2002; Steneck, 1997, 1986).

C.7.1.2 Implementation

C.7.1.2.1. General procedure

The proportion of the reef grazed at each time step is entered as an input variable and needs to be defined before the start of simulations. Values can be arbitrarily defined in case of an experiment. Simulating real grazing regimes can be achieved differently and depends on the type of data available. For instance, Mumby (2006) defined the percentage of the reef maintained in a cropped state as being proportional to *Scaridae* spp. (parrot fish) density and inversely proportional to rugosity. For the calibration of our model with the empirical data of the three sites in Martinique (Caribbean), we modeled grazing of fish (*Acanthuridae* spp. and *Scaridae* spp.) and urchins separately using published data (Appendix D).

The reef is grazed by randomly selecting circular patches of agents (29 agents at a time). Non-algae agents selected during the grazing process are qualified as “grazed”, and consequently cannot be converted into algae during the present time step. Algae agents successfully grazed are converted into the type of substratum they were covering (barren ground or dead coral) and are qualified as “grazed”. A selected algae agent avoids being grazed if its functional group-specific
distribution bounded between 0 and one. The grazing process is executed until the desired percentage of cover cropped is reached.

**Table C3.** Probabilities of being grazed of each algal functional group implemented in the model. We considered several values for calibration (Appendix D). Bold values are the ones providing best fit in at least one of the three Caribbean sites. More than one bold value are shown when different values maximised the fit in different sites. No bold values are shown when none of the values tested improved the fit.

<table>
<thead>
<tr>
<th>Functional groups</th>
<th>Probability of being grazed</th>
<th>Reasoning</th>
</tr>
</thead>
<tbody>
<tr>
<td>MA</td>
<td>0.3; 0.5; <strong>0.7</strong></td>
<td>Thicker structure</td>
</tr>
<tr>
<td>AMA</td>
<td><strong>0.3; 0.5</strong></td>
<td>Thicker structure, strong secondary metabolites</td>
</tr>
<tr>
<td>Halimeda</td>
<td><strong>0.3; 0.5; 1.0</strong></td>
<td>Thicker structure (calcareous), strong secondary metabolites</td>
</tr>
<tr>
<td>ACA</td>
<td>0.5; <strong>0.7; 1.0</strong></td>
<td>Thick structure (calcareous)</td>
</tr>
<tr>
<td>Turf</td>
<td>1.0</td>
<td>Thin structure</td>
</tr>
<tr>
<td>CCA</td>
<td>0.05; 0.1; 0.25; 0.5; 0.75</td>
<td>Harder structure (calcareous), encrusting</td>
</tr>
</tbody>
</table>

MA: macroalgae; AMA: allelopathic macroalgae; Halimeda: *Halimeda* spp.; ACA: articulate coralline algae; CCA: crustose coralline algae

C.7.1.2.1. The rugosity-grazing feedback process (optional)

If the procedure is activated (*Rugosity_Grazing* = TRUE), the % cover grazed obtained is added to the one imported from the file. We implemented the feedback process by linking the rugosity of the reef created by coral colonies to the abundance of herbivorous fish, which we then linked to the percentage of reef maintained in a grazed state during the duration of a time step. Each time the state of the community is updated, the model calculates the linear rugosity of the reef with Kubicek and Reuter's (2016) formula:

\[
Rugosity = \sqrt{\frac{S_{\text{uncovered}} + \sum_{i=1}^{n} S_{\text{colony } i}}{S_{\text{total}}}}
\]

where \(S_{\text{uncovered}}\) = the surface of the reef not covered by a coral colony, \(S_{\text{colony } i}\) = the surface of the \(i^{th}\) colony, \(n\) = the total number of colonies present and \(S_{\text{total}}\) = the surface of the reef (25 m\(^2\)). The
model calculates colony surface areas ($S_{colony,i}$) using geometric formulas defined for each growth (Table C5). We assumed that colonies with a planar surface area < 100 cm$^2$ do not contribute to reef rugosity.

Rugosity is then used to determine the density of herbivorous fish using the following empirically established relationship (Bozec et al., 2013):

$$\text{Density}_{\text{Fish}} = 19.74 \times (\text{Rugosity} - 1)$$

where $\text{Density}_{\text{Fish}} = \text{the density of herbivory fish (indiv.120 m}^2). \text{Note that Bozec et al. (2013) established the relationship with individual fish belonging to eight parrot fish species (Scaridae), which are the dominant herbivorous fish in the Caribbean (Table C4).}$

The model then converts fish density in g.m$^{-2}$ using the mean fish length of each species measured by Bozec et al. (2013) and the following length-weight relationships:

$$\text{Weight} = a \times \text{Length}^b$$

where $b = \text{the isometric growth in body proportions and } a = \text{a parameter describing body shape. Values for } a \text{ and } b \text{ (Table C4) are available in FishBase (Froese et al., 2014; Froese and Pauly, 2014).}$

Finally the model determines the proportion of reef grazed ($\text{Surface}_{\text{grazed}}$) from herbivorous fish density using a asymptotic model we defined from Williams and Polunin’s (2001) empirical data (Figure C6):

$$\text{Surface}_{\text{grazed}} = \frac{70 \times (\text{Density}_{\text{Fish}})^2}{\text{Density}_{\text{Fish}}^2 + 90}$$

where $\text{Density}_{\text{Fish}} = \text{fish density (g.m}^2). \text{Williams and Polunin, (2001) conducted field surveys in 19 Caribbean reefs and analyzed the relationship between the percentage cover cropped (i.e., covered by either turf, crustose coralline algae or bare substratum but not by macroalgae) and the density of Acanthuridae spp. and Scaridae spp. present. (Other grazers such as the sea urchin Diadema spp. were not present in high enough abundance to influence their results.)}$
Related code:
coralreef2 / src / coralreef2 / ContextCoralReef2.java

Table C4. Parrot fish density and body length (total length ≥ 4 cm) collected on the fore reef zone of Grovers Atoll by Bozec et al., (2013) and values for a and b parameters of the from the length-weight relationships (LWR) and available from FishBase (Froese and Pauly, 2014).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean density (indiv. 120 m²)</th>
<th>Mean body length (cm)</th>
<th>a</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scarus iserti</td>
<td>4.28</td>
<td>9.8</td>
<td>0.01096</td>
<td>3.02</td>
</tr>
<tr>
<td>Sparisoma aurofrenatum</td>
<td>2.41</td>
<td>13.4</td>
<td>0.01072</td>
<td>3.12</td>
</tr>
<tr>
<td>Sparisoma viride</td>
<td>1.12</td>
<td>24.0</td>
<td>0.01380</td>
<td>3.04</td>
</tr>
<tr>
<td>Sparisoma chrysopterum</td>
<td>0.37</td>
<td>26.7</td>
<td>0.01072</td>
<td>3.09</td>
</tr>
<tr>
<td>Sparisoma rubripinne</td>
<td>0.12</td>
<td>28.4</td>
<td>0.00933</td>
<td>3.04</td>
</tr>
<tr>
<td>Scarus taeniopterus*</td>
<td>0.04</td>
<td>16.7</td>
<td>0.01096</td>
<td>3.02</td>
</tr>
<tr>
<td>Scarus vetula</td>
<td>0.02</td>
<td>27.8</td>
<td>0.01445</td>
<td>3.04</td>
</tr>
<tr>
<td>Scarus coelestinus</td>
<td>&lt; 0.01 (0.005)**</td>
<td>40.0</td>
<td>0.01622</td>
<td>3.05</td>
</tr>
</tbody>
</table>

* values for a and b for Scarus taeniopterus were not available so we chose values for Scarus iserti because the two species have similar maximum total and common lengths.

** we attributed a density of 0.005 indiv.120 m-2 for Scarus coelestinus
Table C5. Formulae and values used to calculate the three dimensional surface area of colonies depending on their growth form (McWilliam et al., 2018b). Note that we corrected the formula for laminar (M. McWilliam, personal communication, July 2019).

<table>
<thead>
<tr>
<th>Growth from</th>
<th>Formula surface area</th>
<th>Parameter values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branching*</td>
<td>( \pi r^2 \left(N_b \left(2\pi r_b h_b + \pi r_b^2\right)\right))</td>
<td>( r_b = 1 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h_b = 10 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( N_b = 0.225 )</td>
</tr>
<tr>
<td>Tabular</td>
<td>See branching</td>
<td>( r_b = 0.5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h_b = 1 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( N_b = 2.5 )</td>
</tr>
<tr>
<td>Laminar</td>
<td>( 2\pi r \sqrt{r^2 + h_b^2} )</td>
<td>( h_b = 20 )</td>
</tr>
<tr>
<td>Massive</td>
<td>( 2\pi r^2 )</td>
<td>-</td>
</tr>
<tr>
<td>Corymbose</td>
<td>See branching</td>
<td>( r_b = 1 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h_b = 5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( N_b = 0.5 )</td>
</tr>
<tr>
<td>Digitate</td>
<td>See branching</td>
<td>( r_b = 2 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h_b = 5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( N_b = 0.2 )</td>
</tr>
<tr>
<td>Columnar</td>
<td>See branching</td>
<td>( r_b = 3 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h_b = 25 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( N_b = 0.05 )</td>
</tr>
<tr>
<td>Encrusting long upright</td>
<td>Encrusting + branching</td>
<td>( r_b = 0.5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h_b = 5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( N_b = 0.2 )</td>
</tr>
<tr>
<td>Encrusting</td>
<td>( \pi r^2 )</td>
<td>-</td>
</tr>
</tbody>
</table>

Parameters are: colony radius \( r \); branch radius \( r_b \); branch height \( h_b \); number of branches per cm\(^2\) \( N_b \).

* Coefficient values were obtained by averaging values for “complex” and “simple” branching.
Figure C6. Model defining the percentage of reef surface grazed as a function of herbivorous fish density. Grey circles are averaged surface of reefs maintained in a cropped state as a function of pooled Acanthuridae spp. and Scaridae spp. densities in 19 Caribbean reefs (Williams and Polunin 2001). The red line is the asymptotic model we defined: $y = \frac{70x^2}{90 + x^2}$.

C.7.2. Reproduction and recruitment

C.7.2.1 Implementation of coral reproduction

Coral recruits are composed of larvae produced locally and immigrating from the regional pool. The proportion of larvae immigrating from the regional pool depends on the parameter connectivity.

C.7.2.1.1 Coral larvae locally produced

a. Onset of spawning

Using a three, four or six-month time step allows to implement seasonality (i.e., wet and dry seasons) and a distinction between broadcast spawning and brooding species: the latter release eggs once every season as opposed to spawners, which reproduce only once a year. During a spawning event, all the colonies able to reproduce will release gametes simultaneously. This implementation is in accordance with the simplified generalization that brooding species have
multiple reproductive cycles through the year (Ritson-Williams et al., 2009) and spawning species only reproduce annually and in synchrony intra and interspecifically (Baird et al., 2009b). In reality, coral reproduction is more complex and diverse (e.g., Glynn et al., 2000). Importantly, the model offers the possibility to prioritise the onset of disturbances (i.e., cyclone and bleaching) and coral reproduction (Figure 3.2), as the timing of these different processes can be crucial for coral recruitment (Harrison and Wallace, 1990).

Juvenile colonies do not reproduce as they invest most of their energy into growth. We set the age at maturity of a colony at three years for all coral species. This value corresponds to the time needed for *Acropora millepora* colonies to become mature (Guest et al., 2014). The trait “age at maturity” certainly varies among species (Harrison and Wallace, 1990) but the only three other species for which this trait is available are *Coelastrea aspera* (4.5 yrs), *Goniastrea favulus* (5.5 yrs), *Platygyra sinensis* (6.5 yrs) (coraltraits.org; Madin et al., 2016). We chose the smallest value to avoid penalizing species that strategically invest into early onset of sexual reproduction and because the size of the colony is more important for determining colony fecundity (Hughes, 1984).

b. Calculation of the total number of oocytes produced on the reef ($O_t$)

The total number of oocytes produced in the reef for each species ($O_t$) is obtained with the formula:

$$O_t = \frac{f_p \times p_f}{C_a} \times \sum_{i=1}^{N} S_i \times p_{mi}$$

where $S_i$ = three-dimensional surface area of a colony, $p_{mi}$ = the proportion of mature polyps in this colony, $N$ = the total number of colonies in the population, $f_p$ = the trait *polyp fecundity*, $p_f$ = the proportion of female polyps in the population and $C_a$ = the trait *corallite area*.

The surface $S$ is obtained by summing the three-dimensional area of all the colonies of a given species. Given that vertical growth is not explicitly simulated in the model, these surface areas are obtained by calculating colony planar surface area ($S_p$) using geometric models defined for each coral growth form McWilliam and colleagues (2018) (Table C5; Figure C7). For simplification, the radius of each colony $r$ is estimated under the assumption that colonies’ planar areas are circular.
The proportion of mature polyps in a colony \( (p_m) \) varies interspecifically and increases with colony size (Álvarez-Noriega et al., 2016), and the proportion of the “sterile zone” (i.e., zone often situated at the extremities of the colonies, where polyps invest more in growth than reproduction) is bigger in smaller size colonies. Álvarez-Noriega and colleagues (2016) defined empirical models predicting polyp maturity probability as a function of growth form and colony planar surface area. They defined their models for eight coral species and four growth forms. This limited number of species and growth forms prevented the definition of a model for all 798 species or all nine growth forms used in our coral ABM. In consequence, we defined a single model by averaging the model parameters over the eight species (Table C6, Figure C8A). The parameterized model is:

\[
\text{logit}(p_m) = 8.626 + 1.682 \times \log_e(S_p)
\]

with the colony planar surface area \( (S_p) \) expressed in \( \text{m}^2 \). Several of the species in our set only reach small maximum colony sizes. Applying this model for them would underestimate their reproductive output. We consequently defined species-specific models by applying a correction coefficient \( (C_c) \) as follows:

\[
\text{logit}(p_m) = 8.626 + 1.682 \times \log_e(S_p + C_c)
\]

\[
C_c = \frac{\text{logit}(0.9) - 8.626}{1.682} - \log_e(S_{p_{\text{max}}})
\]

\[
S_{p_{\text{max}}} = \frac{\pi}{4} \times d_{\text{max}}^2
\]

with \( S_{p_{\text{max}}} = \) the maximum planar surface area the colony can reach \( (\text{m}^2) \) and \( d_{\text{max}} = \) the trait maximum colony diameter \( (\text{m}) \). We defined the correction coefficient \( \text{(correction}_c_{\text{of polypFecundity)} \) so that a polyp has 0.9 chance of being fecund when its colony has reached its maximum size. To be selected for this correction, a species must have a strictly positive \( C_c \), which corresponds to having \( S_{p_{\text{max}}} < 218.9 \text{ cm}^2 \) and \( d_{\text{max}} \leq \) smaller than 16.7 cm (Figure C8B). For comparison, the smallest species considered in Álvarez-Noriega and
colleagues (2016) (for which $d_{\text{max}}$ is known) is *Acropora nasuta*, which has a 80 cm colony maximum diameter, corresponding to a 5026.5 cm² circular planar surface area.

The proportion of female polyps in a colony (or female colonies in a population) $p_f$ depends on the species sexual system, which can be globally classified as “hermaphrodite” or “gonochore” (with numerous variations; Baird et al., 2009b). We chose $p_f = 1.0$ for hermaphrodites species and $p_f = 0.5$ for gonochoric species in order to consider the proportion of male polyps in a colony or male colonies in the population (both scenarios being observed in reality).

![Conversion of colony planar area into three-dimensional surface area using geometric models for each growth form (McWilliam et al., 2018b). The conversion necessitated considering the planar surface area of each colony as circular.](image)

**Figure C7.** Conversion of colony planar area into three-dimensional surface area using geometric models for each growth form (McWilliam et al., 2018b). The conversion necessitated considering the planar surface area of each colony as circular.
Table C6. Parameter values for the models defining the probability of a polyp to be fecund as a function of colony planar surface area (Álvarez-Noriega et al., 2016).

<table>
<thead>
<tr>
<th>Species</th>
<th>Growth form</th>
<th>Intercept</th>
<th>Slope</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>LCI</td>
<td>median</td>
<td>UCI</td>
</tr>
<tr>
<td>A. hyacinthus</td>
<td>tabular</td>
<td>4.022</td>
<td>5.908</td>
<td>8.345</td>
</tr>
<tr>
<td>A. cytherea</td>
<td>tabular</td>
<td>0.446</td>
<td>1.023</td>
<td>1.657</td>
</tr>
<tr>
<td>A. digitifera</td>
<td>digitate</td>
<td>7.309</td>
<td>11.507</td>
<td>17.142</td>
</tr>
<tr>
<td>A. spathulata</td>
<td>corymbose</td>
<td>5.933</td>
<td>9.496</td>
<td>14.107</td>
</tr>
<tr>
<td>G. pectinata</td>
<td>massive</td>
<td>0.802</td>
<td>7.036</td>
<td>14.169</td>
</tr>
<tr>
<td>G. retiformis</td>
<td>massive</td>
<td>2.796</td>
<td>4.966</td>
<td>7.423</td>
</tr>
<tr>
<td>Average</td>
<td>-</td>
<td>-</td>
<td>8.626</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure C8. Probability of a polyp to be mature depending on the size of the colony. Coloured lines (i.e., red, purple and yellow) in panel A displays the eight species-specific models established by Álvarez-Noriega and colleagues (2016); the black line in panels A and B represents the model obtained by averaging coefficient over the eight species. Panel B displays the 50 models we defined for the species reaching a maximum planar surface area inferior to 218.9 cm$^2$. The horizontal dashed line indicates 0.9 probability; it intercepts with individual grey lines when the colony of the corresponding species reaches its maximum planar area (assuming the latter is circular).

c. Calculation of the number of larvae produced on the reef ($L_c$)

The total number of competent larvae produced on the reef for each species ($L_c$) is given by:

$$L_c = O_t \times f_r \times (1 - p_r)$$

with $O_t =$ the number of oocytes produced, $f_r =$ the fertilization rate and $p_r =$ the predation rate.

Fertilization rate varies among species (Negri et al., 2007) and depends on gametes concentration (Nozawa et al., 2015; Oliver and Babcock, 1992), temperature and environmental conditions (Ritson-Williams et al., 2009). For simplicity, we chose $f_r = 0.5$, a value approximating the average fertilization rates measured in the field for Montipora digitata by Oliver and Babcock (1992). We attributed the same value for brooding species because no information is available for this mode of larval development. (Brazeau and Lasker, 1992, found a fertilization rate comprised between 5 and 25% in a brooding octocoral species.)
Predation of coral larvae by fish is considered as one of the major sources of larval mortality (Hamner et al., 1988; Pratchett et al., 2001; Westneat and Resing, 1988). Pratchett and colleagues (2001) estimated in a study conducted in Lizard Island (Great Barrier Reef) that between 20 and 36% of coral propagules released during a spawning event are consumed by reef fish. According to these results, we fixed predation rate $p_r = 0.3$. Larval predation by coral is also important (Fabricius and Metzner, 2004) but is considered during the settlement process (see §C.7.2.1.3). We did not implement the difference of palatability of coral propagules to fish (Baird et al., 2001) and corals (Fabricius and Metzner, 2004).

d. Calculation of the number of competent larvae settling on the reef ($L_s$)

The number of larvae settling in the reef ($L_s$) is determined by the number of viable larvae becoming competent before being flushed away from the reef (Connolly and Baird, 2010):

$$L_s = L_c \times p_s \times p_o$$

with $L_c =$ the number of competent larvae, $p_s =$ the proportion of the latter settling and $p_o =$ a proportional coefficient (i.e., the model parameter $otherProportion$; Appendix D) accounting for other factors potentially affecting the number of larvae locally settling.

The proportion of larvae settling $p_s$ is the proportion of larvae reaching competency while remaining on the reef. Figueiredo and colleagues (2013) modelled the relationship between time to motility ($t_m$, in days) and the proportion of competent larvae retained on the reef (and settling) for different retention times (using eight spawning species):

$$p_s = \alpha + \beta \times t_m$$

or

$$p_s = \alpha + \gamma \times e^{-\rho \times t_m}$$

with $\alpha, \beta, \gamma$ and $\rho$ being model parameters they empirically defined (Table C7). We chose the middle range value of 4.69 days as retention time for our simulations but other values for $retentionTime = 16.30, 10.24, 7.66, 6.97, 2.14, 1.5, 1.21, 0.90$ and $0.70$ days. Additionally, the
authors established a significant linear relationship between time to motility ($t_m$, in hours) and the trait *egg diameter* (i.e., $e_d$, μm, $n = 20$ spawning species), so that the $t_m$ value is species-specific:

$$t_m = 0.059 \times e_d + 0.067$$

For brooding species, larvae are matured and motile when released in the water (Gleason and Hofmann, 2011) so their time to motility equals zero.

The proportional coefficient $p_o$ is introduced to account for other potential factors, such as the proportion of non-viable oocytes or spawning disynchrony observed between individual colonies of a same species (Baird et al., 2000). Its value is 0.0001 and was obtained during the model calibration (Appendix D).

**Table C7.** Parameter values for the different models expressing the proportion of larvae retained in the reef ($p_s$) as a function of time to motility ($t_m$, in days) and retention time (Figueiredo et al., 2013).

<table>
<thead>
<tr>
<th>Retention time (d)</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\gamma$</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>16.3</td>
<td>0.801</td>
<td>-0.222</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>10.24</td>
<td>0.768</td>
<td>-0.247</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7.66</td>
<td>0.741</td>
<td>-0.267</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6.97</td>
<td>0.731</td>
<td>-0.274</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4.69</td>
<td>0.180</td>
<td>-</td>
<td>0.545</td>
<td>1.354</td>
</tr>
<tr>
<td>2.14</td>
<td>0.090</td>
<td>-</td>
<td>0.557</td>
<td>2.740</td>
</tr>
<tr>
<td>1.50</td>
<td>0.050</td>
<td>-</td>
<td>0.551</td>
<td>3.400</td>
</tr>
<tr>
<td>1.21</td>
<td>0.031</td>
<td>-</td>
<td>0.536</td>
<td>3.800</td>
</tr>
<tr>
<td>0.90</td>
<td>0.014</td>
<td>-</td>
<td>0.501</td>
<td>4.500</td>
</tr>
<tr>
<td>0.70</td>
<td>0.006</td>
<td>-</td>
<td>0.461</td>
<td>5.100</td>
</tr>
</tbody>
</table>

C.7.2.1.2. Larvae immigrating from the regional pool

Numerous processes and factors influence larval connectivity: distance between the reefs, oceanic currents, frictional forces of coastal topography, predation (Cowen and Sponaugle, 2009), mortality and loss of competency (Connolly and Baird, 2010). We defined the parameter
connectivity to determine the number of larvae immigrating to the focal reef. By setting connectivity = “noConnectivity”, the focal reef is totally isolated, and no larvae immigrate. By choosing connectivity = “connectivityCSV”, the model imports the number of larvae m\(^2\) (\(L_{sr}\)) for each coral species and each time step from coralreef2 / data / Disturbance_larvalConnectivity.csv. The time series of larvae density have to be defined manually beforehand and are associated to the parameter disturbanceScenarioNumber.

Alternatively, connectivity can be set to certain distance separating the focal “sink” reef from a fictional “source” reef: “high (5 km)”, “medium (10 km)”, “low (20 km)”, “isolated (100 km)” and “isolated (200 km)”. Each distance represents a certain number of alive and competent larvae m\(^2\) immigrating to the focal reef (\(L_{sr}\)). We made the following assumptions to determine the number and diversity of immigrating larvae: (i) the remote reef has the same species; (ii) the total number of larvae produced is shared equally between species; (iii) brooding species larvae are three times less abundant than spawning species larvae because their populations are usually more closed in comparison to spawning species populations (Doropoulos et al., 2015); (iv) only brooded larvae are produced during the non-reproductive season, in an amount equivalent to the number of brooded larvae produced during the reproductive season. We explain how we determined the number of alive and competent larvae m\(^2\) immigrating (\(L_{sr}\)) for each distance we considered in the following sections.

a. Number of larvae produced in the remote reef (\(L_{cr}\))
The total number of larvae produced on the remote reef (\(L_{cr}\)) is determined using the following assumptions: (i) the remote and focal reefs have the same surface area (\(S_r\), m\(^2\)); the remote reef (ii) produces \(10^6\) larvae m\(^2\) (Hall and Hughes, 1996; Pratchett et al., 2001) and (iii) has a 50% coral cover. We applied the same predation rate (\(p_r\)) with the focal reef:

\[
L_{cr} = 10^6 \times S_r \times 0.5 \times (1 - p_r)
\]

b. Number of larvae reaching the focal reef (\(L_{sr}\))
The number of larvae reaching the focal reef m\(^2\) (\(L_{sr}\)) is:

\[
L_{sr} = L_{cr} \times p_l \times p_{rf} \times p_{ac}
\]
with $L_{cr}$ = the total number of larvae produced on the remote reef m$^{-2}$, $p_l$ = the proportion of larvae leaving the remote reef, $p_{rf}$ = the proportion of larvae reaching the focal reef and $p_{ac}$ = the proportion of them being still alive and competent.

The proportion of larvae leaving the remote reef depends on retention time and time to motility (Figueiredo et al., 2013). We arbitrarily chose $p_l = 0.5$.

The proportion of larvae reaching the focal reef $p_{rf}$ depends on the distance separating the two reefs and the speed and direction of water currents. In Black's (1993) simulated experiment, between 0.1 and 10% of particles released from an upstream reef were captured by a downstream reef (they had the same size and were spaced by 19 km), depending on the orientation of the water current. We chose $p_{rf} = 1.0\%$, the most commonly observed proportion in the simulations. In the model, the distance 19 km corresponds to a “low level of connectivity” as it is the maximum reef spacing in the Great Barrier Reef (Black, 1993). Based on this value, we arbitrarily estimated the percentage of larvae reaching the focal reef for other levels of connectivity (Table C8).

While coral larvae are transported between reefs, their risk of losing competency and dying increases with time. Connolly and Baird (2010) established species-specific models for five species to predict the proportion of larvae in a cohort that are competent and alive as a function of time. We defined a unique “average model” for all the 798 species by averaging the coefficients (because five species was not enough to define species-specific coefficients using traits based predictive models; Table C9; Figure C9):

$$p_{ac}(t) = p_{alive}(t) \times p_{competent}(t)$$

$$p_{alive}(t) = e^{-(\lambda t)^\nu}$$

$$p_{competent}(t) = \begin{cases} 
0 & t > t_c \\
\frac{a(e^{-b(t-t_c)} - e^{-a(t-t_c)})}{a-b} & t > t_c 
\end{cases}$$

with $P_{competent}(t)$ and $P_{alive}(t)$ the proportions of competent and alive larvae, respectively, as a function of time $t$ (in days) and $t_c$ = the development time required before acquisition of competency. We chose velocity $= 0.15$ m.s$^{-1}$ (common value observed in the GBR, Brinkman et
al., 2002), we used the average model to determine the proportion of larvae still alive and competent $p_{ac}$ for the different levels of connectivity (Table C10).

Table C8. Proportion of larvae from the remote reef reaching the focal reef ($p_{rf}$) depending on the separation distance.

<table>
<thead>
<tr>
<th>Distance between reefs</th>
<th>$p_{rf}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>high (5 km)</td>
<td>0.5</td>
</tr>
<tr>
<td>medium (10 km)</td>
<td>0.1</td>
</tr>
<tr>
<td>low (20 km)</td>
<td>0.01</td>
</tr>
<tr>
<td>isolated (100 km)</td>
<td>0.001</td>
</tr>
<tr>
<td>isolated (200 km)</td>
<td>0.0001</td>
</tr>
<tr>
<td>not connected</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Figure C9. Prediction of the dispersal potential depending on time for five coral species (Connolly and Baird, 2010). The black line represents the prediction from the average model (i.e., we averaged the coefficients of the five species-specific models).
Table C9. Parameter values for the different models predicting the proportion of larvae alive ($P_{\text{alive}}$) and competent ($P_{\text{competent}}$) as a function of time (Connolly and Baird, 2010).

<table>
<thead>
<tr>
<th>Species</th>
<th>Competency model ($P_{\text{competent}}$)</th>
<th>Survival model ($P_{\text{alive}}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$a$ $b$ $t_c$</td>
<td>$\lambda$ $\nu$</td>
</tr>
<tr>
<td><strong>Acropora millepora</strong></td>
<td>0.180 0.050 3.239</td>
<td>0.043 0.57</td>
</tr>
<tr>
<td><strong>Acropora valida</strong></td>
<td>0.220 0.031 0.000</td>
<td>0.019 0.46</td>
</tr>
<tr>
<td><strong>Acropora gemmifera</strong></td>
<td>0.390 0.145 3.471</td>
<td>0.067 1.00</td>
</tr>
<tr>
<td><strong>Goniastrea retiformis</strong></td>
<td>0.580 0.096 0.000</td>
<td>0.087 1.00</td>
</tr>
<tr>
<td><strong>Platygyra daedalea</strong></td>
<td>0.390 0.099 2.937</td>
<td>0.060 0.72</td>
</tr>
<tr>
<td><strong>average</strong></td>
<td>0.352 0.084 1.929</td>
<td>0.055 0.75</td>
</tr>
</tbody>
</table>

Table C10. Proportion of larvae remaining alive and competent ($p_{ac}$) as a function of the distance between the remote and the focal reef. We defined the traveling time assuming 0.15 m.s$^{-1}$ current velocity and alignment of the reefs in the current direction. Also displayed is the corresponding number of larvae settling by squared meter of the focal reef ($L_{sr}$) and the corresponding values of the model parameter *connectivity*.

<table>
<thead>
<tr>
<th>Distance between reefs</th>
<th>connectivity</th>
<th>Duration journey (d)</th>
<th>$p_{ac}$</th>
<th>$L_{sr}$ (m$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 km</td>
<td>“high (5 km)”</td>
<td>0.39</td>
<td>0.40 *</td>
<td>35000.00</td>
</tr>
<tr>
<td>10 km</td>
<td>“medium (10 km)”</td>
<td>0.77</td>
<td>0.40 *</td>
<td>7000.00</td>
</tr>
<tr>
<td>20 km</td>
<td>“low (20 km)”</td>
<td>1.54</td>
<td>0.40 *</td>
<td>700.00</td>
</tr>
<tr>
<td>100 km</td>
<td>“isolated (100 km)”</td>
<td>7.72</td>
<td>0.38</td>
<td>66.50</td>
</tr>
<tr>
<td>200 km</td>
<td>“isolated (200 km)”</td>
<td>15.43</td>
<td>0.17</td>
<td>2.98</td>
</tr>
<tr>
<td>$\infty$</td>
<td>“noConnectivity”</td>
<td>-</td>
<td>0.0</td>
<td>0.00</td>
</tr>
<tr>
<td>-</td>
<td>“connectivityCSV”</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* At these distances, the larvae have reached the focal reef before being competent. We attributed the maximum proportion as we assumed these larvae remain and settle in the focal reef.
C.7.2.1.3. Larval settlement

a. Background
Larval settlement is complex as it varies inter-specifically and depends on environmental factors. Certain species produce larvae capable of habitat selection (Golbuu and Richmond, 2007; Harrington et al., 2004; Morse et al., 1988), which increases post-settlement survival (Ritson-Williams et al., 2009). Certain crustose coralline algae species attract larvae for settlement and induce larval development but others use anti-settlement strategies (Harrington et al., 2004; Price, 2010). Settlement success can also be specific to the coral-algae species associations (Ritson-Williams et al., 2010). Finally, additional factors such as topographic cues (Whalan et al., 2015), light exposure (Morse et al., 1988) and density-dependence (Doropoulos et al., 2017) influence the settlement process. In consequence, recruitment probability is highly variable, context and time dependent (Table C11).

Table C11. Proportions of larvae settling, metamorphosing and surviving ($P_{ss}$) in different laboratory experiments.

<table>
<thead>
<tr>
<th>$P_{ss}$ (%)</th>
<th>Substratum type</th>
<th>Duration</th>
<th>No. coral sp.</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>36 to 87</td>
<td>5 CCA sp.</td>
<td>1 day</td>
<td>3</td>
<td>(Morse et al., 1988)</td>
</tr>
<tr>
<td>67 to 91</td>
<td>4 CCA and 1 ACA sp. Rubble Coral skeleton</td>
<td>8 days</td>
<td>1</td>
<td>(Heyward and Negri, 1999)</td>
</tr>
<tr>
<td>0 to &gt; 60</td>
<td>Tile</td>
<td>2, 30, 60 days</td>
<td>2</td>
<td>(Nishikawa et al., 2003)</td>
</tr>
<tr>
<td>64.2; 57.2; 47.1</td>
<td>Tile</td>
<td>0, 20, 40 days</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>81.7, 59.9, 13.1</td>
<td>Tile</td>
<td>240 days</td>
<td>2</td>
<td>(Harrington et al., 2004)</td>
</tr>
<tr>
<td>24.2</td>
<td>1 CCA sp. Tile</td>
<td>2 CCA sp., rubble</td>
<td>24 hours</td>
<td>2</td>
</tr>
<tr>
<td>20.1 0</td>
<td>4 other CCA sp.</td>
<td>6 weeks</td>
<td>2</td>
<td>(Ritson-Williams et al., 2010)</td>
</tr>
</tbody>
</table>

CCA: crustose coralline algae; ACA: articulated coralline algae
b. Implementation

Larvae settle one after another randomly in the reef. Coral species do not differ in their capacity to settle. We defined the probability of recruitment \( p_{lr} \) as:

\[
p_{lr} = p_{ls} \times p_{lxs}
\]

with \( p_{ls} = \) the probability to successfully settle and \( p_{lxs} = \) the probability to survive during the number of months represented by a time step.

The probability to successfully settle \( p_{ls} \) depends on the type of substratum and was estimated to the best of our judgement (Table C12).

We defined \( p_{lxs} \) using Ritson-Williams and colleagues’ (2016) experimental results. The authors first let larvae of two brooding and two spawning species settle and metamorphose on tiles covered with a “preferred” crustose coralline algae species (\( Hydrolithon boergesenii \)) under laboratory conditions. They then placed the tiles in a reef and measured the proportion of new recruits surviving at different time intervals. We used their results (combining all four species) to fit a least-squares regression model that we used to predict the proportion of new recruits surviving after six months (Figure C10; Figure C11; Table C13).
Table C12. Probabilities of successful coral larvae settlement on different substrata.

<table>
<thead>
<tr>
<th>Substratum</th>
<th>$p_{ls}$</th>
<th>Justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>barren ground</td>
<td></td>
<td>We chose this mid value for all the suitable substratum types because of the high diversity of coral specificity toward CCA species and other substratum (Birrell et al., 2008), and the wide ranges of settlement success (Table C11), and insufficient knowledge.</td>
</tr>
<tr>
<td>dead coral</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>CCA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>sand</td>
<td>0.0</td>
<td>Sand does not provide a stable substratum for coral larvae to metamorphose</td>
</tr>
<tr>
<td>alive coral</td>
<td>0.0</td>
<td>Corals feed on larvae (Fabricius and Metzner, 2004)</td>
</tr>
<tr>
<td>bleached coral</td>
<td>0.0</td>
<td>Bleached corals rely on heterotrophy to compensate for the loss of the symbiont (Grottoli et al., 2006)</td>
</tr>
<tr>
<td>macroalgae turf</td>
<td>0.0</td>
<td>Pre-emption of space, and release of deleterious or lethal chemicals impede larval metamorphosis (Birrell et al., 2008)</td>
</tr>
<tr>
<td>AMA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACA</td>
<td>0.0</td>
<td>ACA do not provide a stable substratum for coral larvae to metamorphose</td>
</tr>
<tr>
<td>Halimeda</td>
<td>0.0</td>
<td>Halimeda is ephemeral so larvae settling die through shading (Nugues and Szmant, 2006)</td>
</tr>
</tbody>
</table>

CCA: crustose coralline algae; AMA: allelopathic macroalgae; ACA: articulate coralline algae
Figure C10. Proportion of larvae surviving after settlement as a function of time (from figure 8b in Ritson-Williams et al., 2016). Twelve and 20 replicate tiles (covered with the CCA Hydrolithon boergesenii) were used respectively for brooding (A. agaricites, Favia fragum) and spawning species (A. cervicornis, A. palamata). Each tile received initially three recruits of a same species. The grey symbols represent the mean percentage of surviving recruits by tile. The red line is the least-squares regression model we established, considering each point as a single observation (Table C13). The black dashed lines show the proportion of recruits at six months after settlement ($p_{18}$ = 0.18). Points have been offset slightly to improve visibility.

Figure C11. Residual diagnostic plots of the coral recruitment model we established based on Ritson-Williams and colleagues’ (2016) results (Figure C10): normal quantile plot (A) and residual plot (B) respectively show that the standardized residuals are normally and homogeneously distributed. Points in B have been offset slightly to improve visibility.
Table C13. Parameter values of the least-squares regression model we established based on Ritson-Williams and colleagues’ (2016) results: $y = \text{Intercept} + \text{Slope} \times 1/x$ (Figure C10; Figure C11).

<table>
<thead>
<tr>
<th>parameters</th>
<th>Estimate</th>
<th>SE</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>10.3</td>
<td>8.30</td>
<td>0.235</td>
</tr>
<tr>
<td>slope</td>
<td>43.3</td>
<td>15.67</td>
<td>0.015</td>
</tr>
</tbody>
</table>

Related code:
coralreef2 / src / coralreef2 / CoralReproduction.java

C.7.2.2 Algae reproduction

C.7.2.2.1. Implementation

Algal functional groups exhibit enormous variation in reproductive mode (i.e., sexual, asexual, vegetative), the onset of spawning, and the amount and types of propagules (e.g., Bellgrove et al., 2004). This, combined with a lack of data, prevented us from implementing algae reproduction processes. Instead, we simulated algal reproduction by converting all the ungrazed and available space (barren ground and dead coral skeleton) remaining after all the other processes have been simulated (Figure 3.2)—patches of algae agent with a five centimetres radius are created consecutively and at random locations, for each functional group of algae, until the available space (i.e., ungrazed dead coral and barren ground agents) is filled.

Related code:
coralreef2 / src / coralreef2 / ContextCoralReef2.java

C.7.3. Wave and cyclone damage

C.7.3.1 Damage on the coral community

C.7.3.1.1. Background
Waves and cyclones generate different types of damages: mechanical breakage, dislodgement, increase in sedimentation and turbidity, lower salinity and change in sea level (Harmelin-Vivien, 1994). Madin and Connolly (2006) defined the colony shape factor (CSF), a dimensionless measure of a colony’s mechanical vulnerability to hydrodynamic disturbances (e.g., waves and cyclones). The colony shape factor is expressed as a function of colony planar area and growth form and has to be compared with the dislodgement mechanical threshold (DMT), which represents the threshold imposed by a hydrodynamic disturbance. The dislodgement mechanical threshold depends on the intensity of the disturbance and the exposure of the reef. A colony is dislodged when its colony shape factor surpasses the dislodgement mechanical threshold. But for some species, dislodgement does not mean extirpation: branching species are the most susceptible to dislodgement but their capacity to fragment into small viable pieces enhances their survival rate (Madin et al., 2014). Asexual reproduction via fragmentation is even considered to be the main means of reproduction for some species (Harrison and Wallace, 1990; Hughes et al., 1992).

C.7.3.1.2. Implementation

a. Dislodgement

We used the colony shape factor to determine the dislodgement susceptibility of colonies, which is calculated for each colony according to Madin and Connolly’s (2006) model:

$$\ln(CSF) = \alpha + \beta \times \ln(S_{plan})$$

with $S_{plan} = \text{the colony planar surface area (m}^2)$. Madin and colleagues (2014) determined empirically $\alpha$ and $\beta$ for five of the nine growth forms implemented in the model. We consequently determined the parameter values for the remaining four growth forms using the best of our judgement. First, the mechanical vulnerability of encrusting and encrusting long upright colonies is independent of their size. The latter are slightly more susceptible to dislodge than the encrusting colonies because they produce vertical features, which create friction. Laminar growth forms are similar to table forms but tend to remain closer to the substratum, which confers slightly more resistance. Finally, columnar
colonies form thick vertical features, which are more resistant than laminar colonies but offer more friction than corymbose species (Table C14; Figure C12). Values of dislodgement mechanical threshold must be defined for each time step before starting the simulations (and imported from a file). During the cyclone process, the colony shape factor of each colony is calculated and a colony is dislodged the value surpasses the dislodgement mechanical threshold. Dislodgement is simulated by converting all the agents of the colony (i.e., alive or dead coral, algae recovering coral) into barren ground.

Table C14. Model parameters determining the colony shape factor of a colony as a function of its size and growth form (Madin et al., 2014). Values below the dashed lines were determined arbitrarily (see text, Figure C12).

<table>
<thead>
<tr>
<th>Morphology</th>
<th>$\beta$</th>
<th>$\alpha$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>branching</td>
<td>0.79</td>
<td>8.34</td>
<td>73</td>
</tr>
<tr>
<td>table_or_plate</td>
<td>0.39</td>
<td>4.47</td>
<td>76</td>
</tr>
<tr>
<td>corymbose</td>
<td>0.16</td>
<td>2.28</td>
<td>78</td>
</tr>
<tr>
<td>digitate</td>
<td>-0.04</td>
<td>1.25</td>
<td>68</td>
</tr>
<tr>
<td>massive</td>
<td>-0.23</td>
<td>-0.94</td>
<td>86</td>
</tr>
<tr>
<td>laminar</td>
<td>0.27</td>
<td>3.80</td>
<td>-</td>
</tr>
<tr>
<td>columnar</td>
<td>0.20</td>
<td>3.00</td>
<td>-</td>
</tr>
<tr>
<td>encrusting_long_upright</td>
<td>0.00</td>
<td>1.40</td>
<td>-</td>
</tr>
<tr>
<td>encrusting</td>
<td>0.00</td>
<td>1.00</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure C12. Colony shape factor as a function of colony planar area for different colony growth forms. Grey symbols represent a single colony and lines are fitted least-squares regression lines per growth forms (Madin et al., 2014). The coloured lines represents the model we implemented in the coral ABM for the growth forms not considered in Madin and colleagues 2014 (see text; Table C14).

b. Proportion of surviving branching fragments

We implemented the capacity of a branching colony to survive dislodgement by first defining the size of the fragment potentially surviving as a function of the disturbance intensity. We arbitrarily established a linear model assuming that half of the colony remains if dislodgement mechanical threshold = 120 and none of the colony survive if dislodgement mechanical threshold = 1 (Figure C13A). We then determined the survival probability of the fragment using Highsmith and colleagues’s (1980) results: they empirically defined a model predicting the proportion of surviving fragments of *Acropora palmata* (branching) as a function of their length. Their model predicts values superior to one when fragment length > 112 cm, so we used a similar but asymptotic model (Figure C13B). In case the fragment survives, the colony planar area is reduced accordingly to the proportion obtained by the previous model. The length of a fragmented colony is its diameter, assuming a circular planar area.
Figure C13. Models predicting the proportion of a branching colony remaining and potentially surviving as a function of dislodgement mechanical threshold (DMT, A) and the proportion of surviving fragments as a function of their length (B). The blue line in panel B corresponds to the empirical relationship established by Highsmith and colleagues (1980), the red line is the model we defined.

c. Sedimentation

There is no empirical model determining the amount of sediment cover generated by a cyclone of a given intensity. The amount of sediment at a given time step must be determined before launching a simulation (and imported from a file). Sedimentation is the last process simulated during a time step (Figure 3.2) and consists of adding or removing patches of sand (i.e., converting barren ground agents into sand agents or vice versa) until the desired cover is reached.

C.7.3.2 Damage on the algae community

C.7.3.2.1. Background

Hydrodynamic disturbances such as cyclones can dramatically affect the algal community (e.g., Blair et al., 1994). The loss of algae can be caused by three mechanisms: removal, burial or erosion of sediment supporting the community (Fourqurean and Rutten, 2004). All functional groups or taxa can be affected (e.g., Glynn, 1964) but there are notable variations between morphotypes: the loosely attached species with erect or sprawling habits are the most impacted
whereas encrusting species and those with firm or substantial attachment survive better (e.g., Blair et al., 1994, Fourquarean and Rutten, 2004). There are several examples of macroalgae being dramatically extirpated after a cyclone (> 75%; Blair et al., 1994; Fourquarean and Rutten, 2004; Lapointe et al., 2006). Turf and crustose coralline algae are in general less affected (Diaz-Pulido and McCook, 2008).

Cyclones can also facilitate the growth of certain functional groups by releasing nutrients and increasing available space, which favour fast growing and opportunistic species (Diaz-Pulido and McCook, 2008). For instance, Trichosolen spp. (which we classified as turf) are notorious for blooming and pre-empting freed space during the weeks following the disturbance (Littler and Littler, 1999; Pauly et al., 2011; Woodley et al., 1981). Finally, other earlier colonists organisms such as diatoms can overcome available space just after the disturbance (e.g., Diaz-Pulido et al., 2007).

C.7.3.2.2. Implementation

We defined cyclone response models for each functional group of algae based on the following assumptions: macroalgae, allopathic macroalgae, Halimeda spp. and articulated coralline algae are the most sensitive groups because they sustain the highest friction due to their height. In consequence they are totally extirpated under intense cyclone intensity (dislodgement mechanical threshold < 10). In comparison, turf algae are more resistant and maintain at least 10% of their cover under the highest intensity disturbance. Crustose coralline algae are the least affected because they offer less friction and are mostly impacted by sedimentation and abrasion due to rubble being moved around. In consequence, at least 20% of the initial cover remains even under the most intense cyclones (Figure C14; Table C15).
Table C15. Models and parameter values defined to determine the proportion of algal cover removed as a function of dislodgement mechanical threshold for each functional group of algae (Figure C14).

<table>
<thead>
<tr>
<th>Functional groups</th>
<th>Proportion algae cover removed ($P_{ar}$, %)</th>
<th>DMT ≤ 10</th>
<th>10 &lt; DMT &lt; $\alpha$</th>
<th>$\alpha$ ≤ DMT</th>
</tr>
</thead>
<tbody>
<tr>
<td>MA</td>
<td>$P_{ar} = -0.83 \times DMT + 108.33$</td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>AMA</td>
<td></td>
<td>100</td>
<td>$\alpha = 130$</td>
<td>0</td>
</tr>
<tr>
<td>ACA</td>
<td></td>
<td></td>
<td>$\alpha = 130$</td>
<td>0</td>
</tr>
<tr>
<td>Halimeda</td>
<td></td>
<td></td>
<td>$\alpha = 130$</td>
<td>0</td>
</tr>
<tr>
<td>Turf</td>
<td>$P_{ar} = -0.90 \times DMT + 99.00$</td>
<td>90</td>
<td>$\alpha = 110$</td>
<td>0</td>
</tr>
<tr>
<td>CCA</td>
<td>$P_{ar} = -1.00 \times DMT + 90.00$</td>
<td>80</td>
<td>$\alpha = 90$</td>
<td>0</td>
</tr>
</tbody>
</table>

DMT: dislodgement mechanical threshold; MA: macroalgae; CCA: crustose coralline algae; AMA: allelopathic macroalgae; ACA: articulate coralline algae

Figure C14. Proportions of algae removed from the reef depending on cyclone intensity (DMT) (Table C15).
C.7.4. Coral bleaching

C.7.4.1 Background

Coral bleaching is a stress-response corresponding to the expulsion by the host (i.e., the polyp) of its symbiodinium (i.e., “zooxanthellae”) because the latter realized reactive oxygen species (ROS) that are harmful for the host’s cells. The disruption of the symbiosis is due to diverse stressful environmental conditions (e.g., water cooling, pollution, reduced salinity), but most commonly because of a combination of temperature and irradiance increase and wind speed decrease (Brown, 1997). The bleaching process is complex and coral species show a high interspecific variability in the response: species can bleach and die, bleach and not die, not bleach and die or not bleach and not die (McClanahan, 2004). Further, for some species, the stress (i.e., bleaching or dying) is shared by only a subset of the polyps, as opposed to being shared by the whole colony (Baird and Marshall, 2002). This allows for a quicker recovery via vegetative growth (Glynn and Fong, 2006; Roff et al., 2014).

Such variation in the bleaching response is partially explained by the high fidelity of most coral species to one main type of symbiodinium (Hidaka, 2016) and the pronounced difference in thermotolerance between phylotypes of the latter (Swain et al., 2017). Interspecific functional differences of the host also contribute to the interspecific variation (Baird et al., 2009a). Coral species have developed diverse strategies to maintain a high fitness (Darling et al., 2012) and to cope with bleaching events (Wooldridge, 2014). Numerous bleaching resistance traits are potentially involved in the response. Evaluating their respective importance and developing predictive species-specific response models is a topical challenge (Carturan et al., 2018).

Typical tropical coral reefs are found in shallow oligotrophic waters. In consequence, most coral species depend significantly on symbiotic phototrophic sources of carbon (Yellowlees et al., 2008). Thus, bleaching results in starvation and eventually death of the polyp, colony or the population depending on the temporal and spatial scale of the disturbance (Baker et al., 2008; Hughes et al., 2018b). In case of a mild to moderate event, polyps usually recover their normal symbiont density a few months after they have bleached (e.g., Hughes and Grottoli, 2013; Jokiel and Coles, 1977; Rodrigues and Grottoli, 2007; Ward et al., 2000). It can however take more than eight months to recover normal levels of tissue biomass, lipid, protein and carbohydrate (e.g., Hughes and Grottoli, 2013; Rodrigues and Grottoli, 2007) as well as normal ratios between
heterotrophic and phototrophic carbon (Baumann et al., 2014). These affect coral growth and calcification rate. For instance, Goreau and Macfarlane (1990) and Mendes and Woodley (2002) measured a reduction of growth rate between 40 and 80% for severely bleached *M. annularis* colonies approximately six months after the bleaching event; Baird and Marshall (2002) found no growth for two species nine months after the event (Table C16). The effects on coral reproduction can last even longer (Table C17). For instance, nine months after the event, Ward and colleagues (2000) found that the fecundity was reduced by more than 50% for several species and Baird and Marshall (2002) observed a half reduction of the proportion of fecund colonies for *Acropora Hyacinthus*. In certain cases, severely bleached colonies did not complete gametogenesis one year later (Szmant and Gassman, 1990) or the number of full size gonads was still reduced after two years (Mendes and Woodley, 2002). Additionally, the reduced gametes concentration and sperm motility can decrease the fertilization rate during a mass spawning event, which further compromises coral recruitment (Omori et al., 2001).

**Table C16.** Examples of coral growth and calcification rates reduction after a bleaching event.

<table>
<thead>
<tr>
<th>Species</th>
<th>Growth rate reduction (%)</th>
<th>Bleaching event</th>
<th>Time post bleaching</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Montastrea annularis</em></td>
<td>60</td>
<td>Nov. 1987, Jamaica, strong</td>
<td>6 mo.</td>
<td>(Goreau and Macfarlane, 1990)</td>
</tr>
<tr>
<td><em>Acropora millepora</em></td>
<td>~100</td>
<td>Early 1998, GBR, strong</td>
<td>9 mo.</td>
<td>(Baird and Marshall, 2002)</td>
</tr>
<tr>
<td><em>A. hyacinthus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Montastraea annularis</em></td>
<td>40 to 80</td>
<td>Sept. 1995, Jamaica, ?</td>
<td>5 to 7 mo.</td>
<td>(Mendes and Woodley, 2002)</td>
</tr>
<tr>
<td><em>Porites compressa</em></td>
<td>89*</td>
<td>Experiment</td>
<td>1.5 mo.</td>
<td>(Rodrigues and Grottoli, 2006)</td>
</tr>
<tr>
<td></td>
<td>100*</td>
<td></td>
<td>4 mo.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>67*</td>
<td></td>
<td>8 mo.</td>
<td></td>
</tr>
<tr>
<td><em>Montipora capitata</em></td>
<td>80*</td>
<td>Experiment</td>
<td>1.5 mo.</td>
<td>(Rodrigues and Grottoli, 2006)</td>
</tr>
<tr>
<td></td>
<td>80*</td>
<td></td>
<td>4 mo.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>27*</td>
<td></td>
<td>8 mo.</td>
<td></td>
</tr>
</tbody>
</table>

*: calcification rate
Table C17. Examples of different effects of bleaching events on coral reproduction.

<table>
<thead>
<tr>
<th>Species</th>
<th>Effect on reproduction</th>
<th>Bleaching event</th>
<th>Time post bleaching</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora millepora</td>
<td>% reduction of fecund colonies</td>
<td>Early 1998, GBR, strong</td>
<td>9 months</td>
<td>(Baird and Marshall, 2002)</td>
</tr>
<tr>
<td>A. hyacinthus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montastraea annularis</td>
<td>No gametogenesis completed for severely bleached colonies</td>
<td>Sept. 1995, Jamaica</td>
<td>1 year</td>
<td>(Mendes and Woodley, 2002)</td>
</tr>
<tr>
<td>Acropora aspera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. humilis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. millepora</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. nobilis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. palifera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. pulchra</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. valida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montipora digitata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Symphyllia spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acropora aspera</td>
<td>% reduction of polyps / fecundity</td>
<td>March 1998, GBR, strong</td>
<td>6 weeks</td>
<td>(Ward et al., 2000)</td>
</tr>
<tr>
<td>A. millepora</td>
<td>% reduction of reproductive polyps</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. nobilis</td>
<td>% reduction of polyps / fecundity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. palifera</td>
<td>% reduction of reproductive polyps</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. pulchra</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. valida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acropora aspera</td>
<td>% reduction of polyps / fecundity</td>
<td>March 1998, GBR, strong</td>
<td>9 months</td>
<td>(Ward et al., 2000)</td>
</tr>
<tr>
<td>A. millepora</td>
<td>% reduction of reproductive polyps</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. nobilis</td>
<td>% reduction of polyps / fecundity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. palifera</td>
<td>% reduction of reproductive polyps</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. pulchra</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. valida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. nasuta</td>
<td>% reduction of fertilization rate</td>
<td>1998, Japan, strong</td>
<td>1 year</td>
<td>(Omori et al., 2001)</td>
</tr>
<tr>
<td>M. annularis</td>
<td>No gametogenesis completed</td>
<td>Summer 1987, Caribbean</td>
<td>1 year</td>
<td>(Szmant and Gassman, 1990)</td>
</tr>
</tbody>
</table>

GBR: Great Barrier Reef

C.7.4.2 Implementation

Implementing bleaching response consisted of three successive steps (i) defining a species-specific index of bleaching susceptibility (bleaching probability) using the bleaching response
index (Swain et al., 2016b) and bleaching resistance coral functional traits; (ii) establishing species-specific logistic bleaching probability models using the bleaching_probability as a parameter and degree heating week—a measure of the intensity of the bleaching event (Kayanne, 2017)—as predictor; (iii) defining a logistic mortality probability model, which also uses degree heating week as independent variable and determines the risk of a bleached colony to die. We only provide here the final sub-models obtained because the procedures produced a lot of statistical results and the three steps are related to one another. We refer the reader to Appendix E for more details.

C.7.4.2.1. The species-specific index of bleaching susceptibility

The final averaged beta regression model we defined to predict bleaching_probability for each of the 798 coral species is:

\[
cloglog(E(\text{bleaching
data_{i}})) = -1.242 + 0.187 \times \ln(\text{colony maximum diameter}_i) \\
- 0.123 \times \ln(\text{corallite area}_i) \\
+ 0.024 \times \ln(\text{growth rate}_i) \\
- 0.668 \times \ln(mRSC_i) \\
+ 0.024 \times \ln(\text{colony maximum diameter}_i) : \ln(\text{corallite area}_i) \\
+ 0.063 \times \ln(\text{colony maximum diameter}_i) : \ln(\text{growth rate}_i) \\
+ 0.001 \times \ln(\text{colony maximum diameter}_i)^2 \\
- 0.001 \times \ln(\text{corallite area}_i)^2 \\
- 0.034 \times \ln(\text{growth rate}_i)^2 \\
+ 0.135 \times \ln(mRSC_i)^2
\]

with bleaching_probability~ B(μ, ϕ) (i.e., beta distribution with mean μ and dispersion ϕ), E(bleaching_probability) = μ, VAR(bleaching_probability) = μ(1 - μ)/(1 + ϕ); ϕ = 4.267; mRSC= the trait microscopic reduced scattering coefficient (reduced_scattering_coefficient); growth rate = the diametral lateral growth rate (in mm.yr⁻¹) and not the growth_rate implemented in the model (see §C.7.5.1). See §E.1 for more details.
C.7.4.2.2. The species-specific bleaching probability models

The probability of a coral species $i$ to bleach ($P_{Bi}$) is expressed as a function of the thermal disturbance intensity ($DHW$), its bleaching susceptibility ($bleaching\_probability, IP_{Bi}$) relatively to the bleaching susceptibility of the other 797 species:

$$\logit(P_{Bi}) = \alpha + \beta_1 \times DHW + \gamma_i$$

$$\gamma_i = \frac{IP_{Bi} - \text{mean}(IP_B)}{\text{max}(IP_B) - \text{min}(IP_B)} \times \frac{DHW}{\varphi}$$

with $\logit()$ the logit transformation, $\alpha = -2.78$, $\beta_1 = 0.29$, $\text{mean}(IP_B) = 0.27$, $\text{min}(IP_B) = 0.06$, and $\text{max}(IP_B) = 0.60$ (the mean, maximum and minimum $bleaching\_probability$ among the 798 coral species, respectively) and $\varphi = 2$ (value calibrated; see Appendix D). See §E.2 for more details.

C.7.4.2.3. Bleaching-induced mortality probability model

The probability of a bleached coral colony to die ($P_{BD}$) depends on the intensity of the thermal disturbance ($DHW$):

$$P_{BD} = \frac{1}{1 + e^{-0.4 \times (DHW - 11.6)}}$$

The probability of mortality is multiplied by two in cases where the coral colony is already bleached when the bleaching event occurs. See §E.3 for more details.

C.7.4.2.4. Effect of bleaching on surviving colonies

Surviving bleached colonies have their growth rate divided by two during six months after the bleaching event and cannot reproduce for one year (this is monitored with $timeRecoveryBleaching$).
C.7.5. Growth and spatial competition

C.7.5.1 Growth

We simulated radial vegetative growth: agents on the edge of a colony or a patch (for algae) attempt to convert their neighbouring agents (outside of their colony or patch) within a certain radius \( r_{\text{random}} \). The latter is generated each attempt by first sampling a decimal number from the range \([0; r_{\text{max}}]\) and then rounding this number to the nearest inferior integer. We defined \( r_{\text{max}} \) (i.e., \textit{growth\_rate} in Table C1) for each taxon so that on averaged \( r_{\text{random}} \) equals a real growth rate (see Traits\_and\_imputation/ Datasets/ growthRate_randomRadiusConversion.xls). This procedure allows to simulate continuous growth rate in a space having a discrete dimension (here with one cm\(^2\) for minimum value). We verified the accuracy of the method in the hierarchically structure validation (see §F.2). A colony cannot grow larger than its species-specific maximum planar surface area = \( \pi \times (\text{maximum colony diameter} / 2)^2 \).

Related code:
coralreef2 / src / Disturbances / Bleaching.java

C.7.5.2 Competition between corals

C.7.5.2.1. Background

Coral species have different strategies when directly competing for space with one another: extension of mesentarial filaments, specialized sweep tentacles, extension of long polyps, production of mucus, production of cytotoxins and overgrowing or overtopping, depending on the size and shape of the colonies (Lang and Chornesky, 1990). Coral interactions are complex as the use of these diverse mechanisms differ greatly between species (Lang and Chornesky, 1990). Additionally, species respond differently to environmental factors and consequently the nature of their interactions can change depending on the type of habitat (Connell et al., 2004) or the geographic regions (e.g., Caribbean \textit{versus} Red Sea \textit{versus} GBR; Logan, 1984) or even between laboratory experiments and field observations (Logan, 1984). It is consequently challenging to establish a constant linear dominance ranking between species (Lang and
Chornesky, 1990). Recently, Precoda et al., (2017) established species-pair probabilities of interaction outcomes (i.e., winning, standoff and loosing) for 774 species based on a review of 2322 interactions. Fitting these outcomes of interaction to mixed-effect models, they found that (i) nearly 80% of the species triple interactions are transitive (purely and non-hierarchical combined), the rest being intransitive. They also found that corallite area explained most of the species’ competitive ability, followed by geographical range and growth form. However, random effect was greater than the trait effect, which can be due to pair-species idiosyncrasy, environmental heterogeneity or omission of important traits.

C.7.5.2.2. Implementation

a. Direct encounter
We used the output of Precoda and colleagues’s (2017) simulations to determine the outcome of an encounter between two coral species. After correcting nomenclature, their dataset contained 741 coral species. In case the species-pair is not present in this list, we used the trait aggressiveness, which represents the species-specific competitive ability of coral species when in contact with one another. We constructed aggressiveness by combining six ranking lists established empirically (Abelson and Loya, 1999; Connell et al., 2004; Dai, 1990; Lang, 1973; Logan, 1984; Sheppard, 1979) and using an iterative partial rank aggregation pivoting algorithm (IPRAPA; Swain et al., 2017; aggressiveness.R). The procedure allowed us to attribute an aggressiveness value to 116 species. We predicted the value for the rest of the 798 species with the random-forest trait data imputation (Appendix B).

The growth rate of a colony overgrowing another colony is reduced by being multiplied by a coefficient (growth rate reduction interaction) to account for the energy invested in the process. We calibrated the value of the coefficient with empirical datasets (Appendix D).

b. Overtopping colonies
Plating and branching colonies can overtop smaller other colonies, a strategy known as the “escape in height strategy” (Meesters et al., 1996; Swierts and Vermeij, 2016). The growth rate of an overtopping colony is unchanged, contrary to a direct encounter. The process requires the
planar cover of the overtopping colony to surpass the planar cover of the overtopped colony by the ratio $ratio\ overtop \ colony = 2$; value calibrated using empirical datasets (Appendix D).

To overtop encrusting and encrusting long upright colonies, branching and plating colonies have to surpass their height by 5 cm. The height of a non-encrusting colony is its radius, assuming a semi-spherical growth. The height of an encrusting colony = 2 cm (Table C18).

**Table C18.** Parameters and rules involved in the overtopping process of a branching or plating colony when growing over a coral colony of a patch of algae.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Value</th>
<th>Rule for overtopping</th>
</tr>
</thead>
<tbody>
<tr>
<td>$ratioAreaBranchingPlating_{OvertopColonies}$</td>
<td>2</td>
<td>$\frac{So}{Su} &gt; 2$</td>
</tr>
<tr>
<td>(value calibrated; Appendix 3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$height_{BigAlgae}$ (i.e., macroalgae, ACA, AMA, Halimeda)</td>
<td>30 cm</td>
<td>$\sqrt{\frac{So}{\pi}} &gt; 30 + 5$</td>
</tr>
<tr>
<td>$height_{Turf}$</td>
<td>10 cm</td>
<td>$\sqrt{\frac{So}{\pi}} &gt; 10 + 5$</td>
</tr>
<tr>
<td>$height_{CCA_EncrustingCoral}$</td>
<td>2 cm</td>
<td>$\sqrt{\frac{So}{\pi}} &gt; 2 + 5$</td>
</tr>
</tbody>
</table>

$So$: planar surface area of the overtopping branching or plating colony; $Su$: planar surface area of the overtopped colony; CCA: crustose coralline algae; ACA: articulated coralline algae; AMA: allopathic macroalgae algae.

c. Special cases

An agent (coral or algae) can grow over a dead coral colony without constraint. However, a coral colony is able to grow over a dead branching or plating colony only if the ratio of the planar surface areas of the two colonies is $ratio\ overtop\ colony$. Similarly, an encrusting (and encrusting long upright) coral agent can overgrow a dead branching or plating colony only if the difference of heights is $< 5$ cm.

To simulate “re-sheeting”, or “phoenix effect”, which is observed in species of different growth forms and enhances recovery rate (Glynn and Fong, 2006; Jordan-Dahlgren, 1992; Roff
et al., 2014), a coral colony can grow over dead coral agents of a same species one third faster than its normal growth rate (as polyps do not have to grow skeletons).

C.7.5.3 Competition between corals and algae

C.7.5.3.1. Background

Interactions between corals and algae are highly variable in mechanisms: overgrowth, shading, abrasion, chemical, space pre-emption, recruitment barrier, epithelial sloughing (McCook et al., 2001). In addition, certain algae can indirectly affect corals by contaminating their tissues with pathogenic bacteria (Barott et al., 2012a; Smith et al., 2006). The outcome of the competition depends on the life-history of the species competing and environmental factors such as herbivory, nutrient input and light level (McCook et al., 2001). Inhibition is usually reciprocal for both algae and corals (Jompa and McCook, 2002; McCook et al., 2001; Titlyanov et al., 2007).

The outcomes of these interactions are consequently difficult to generalize, even within functional groups (Jompa and McCook, 2003a), and are best considered at the level of species (Jompa and McCook, 2003b, 2002; Titlyanov et al., 2007). But doing so is challenging because of the difficulty to identify algae at the species level, their high plasticity, and the multispecies composition of algae assemblages (McCook et al., 2001).

More specifically, crustose coralline algae are in general inferior (Barott et al., 2012b) or equal (Vermeij et al., 2010) competitors against corals, regardless of the level of anthropogenic stresses (e.g., fishing or nutrient input) and little or no apparent stress is observed for the coral (Barott et al., 2012a, 2009). Observations for filamentous turf algae are varied. Turf has been described as a mixture of a large number of species that are poor competitors and have minor effect on corals (McCook et al., 2001; McCook, 2001), with however exceptions (e.g., Jompa and McCook, 2003a, 2003b). But if coral can overgrow turf assemblages, the input of nutrients can reverse the competitive dominance (Barott et al., 2012b; Vermeij et al., 2010, but see McCook, 2001).

Similarly varied observations were made for macroalgae: a variety of primarily upright macroalgae had minor effect on coral except for one species (Tanner, 1995), same for sargassum beds that have little or no competitive effects on understory corals (McCook, 1999).
Contrastingly, the creeping foliose brown alga *Lobophora variegata*, which is a common species in the GBR (Diaz-Pulido and McCook, 2008), is a markedly superior competitor against *Porites cylindrica* (Jompa and McCook, 2002). Finally, different macroalgae and turf assemblages can cause hypoxia to coral tissue in contact (Barott et al., 2012a, 2009) and can on average (both functional groups confounded) win the majority of their interactions with corals (Barott et al., 2009).

Recently, Brown and colleagues (2017) measured and categorized the interactions between different groups of corals and algae on the field. They found that (i) filamentous algae and cyanobacteria (i.e., turf) always won; (ii) crustose coralline algae and *Halimeda* spp. algae lost on average approximately 25% and 45% of their interactions, respectively; (iii) macroalgae won 80% of their interactions.

C.7.5.3.2. Implementation
a. Direct encounter
We defined probabilities of winning interactions (i.e., overgrowing) between coral and algae using Brown and colleagues’s (2017) results as well as additional unpublished results (K. T. Brown, personal communication, October 2017; Table C19). The growth rate of an algae overgrowing a coral colony is reduced by growth rate *reduction interaction* (see §C.7.5.2.2.a). (For comparison, De Ruyter van Steveninck et al., 1988 found that the growth rate of *Lobophora variegata*’s blades was reduced by approximately 35% when in contact with coral colonies.)

We did not implement the effect of colony size on the competitive ability against algae because of conflicting empirical results: Brown and colleagues (2017) found that small colonies are less affected; as opposed to Ferrari and colleagues (2012) who found the opposite and Bonaldo and Hay (2014), who did not observe a relationship.
Table C19. Functional groups of algae, their competitive outcome probability when competing with corals (based on K. T. Brown, personal communication, October 2017) and radial growth rates.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Description</th>
<th>Probability of winning against corals</th>
<th>Radial growth rate (mm.yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>macroalgae (MA)</td>
<td>Forms 30 cm high canopy (e.g., <em>Sargassum, Hydroclathrus</em>)</td>
<td>0.70</td>
<td>150</td>
</tr>
<tr>
<td><em>Halimeda</em> spp.</td>
<td>Calcified and non-aggressive macroalgae; forms 30 cm high canopy</td>
<td>0.15</td>
<td>150</td>
</tr>
<tr>
<td>allelopathic macroalgae (AMA)</td>
<td>Produces defensive chemicals; forms 30 cm high canopy (e.g., <em>Chlorodesmis</em>)</td>
<td>0.80</td>
<td>150</td>
</tr>
<tr>
<td>turf</td>
<td>Filamentous algae and cyanobacteria; forms 10 cm high canopy</td>
<td>1.00</td>
<td>250</td>
</tr>
<tr>
<td>articulate coralline algae (ACA)</td>
<td>Forms 30 cm high canopy (e.g., <em>Calliarthron tuberculatum</em>)</td>
<td>0.40</td>
<td>21</td>
</tr>
<tr>
<td>crustose coralline algae (CCA)</td>
<td>Encrusting, 2 cm high (e.g., <em>Porolithon onkodes</em>)</td>
<td>0.10</td>
<td>12</td>
</tr>
</tbody>
</table>

b. Overtopping colonies

Plating and branching colonies can overtop smaller other colonies, a strategy known as the “escape in height strategy” (Meesters et al., 1996; Swierts and Vermeij, 2016). The growth rate of an overtopping colony is unchanged, contrary to a direct encounter. The process requires the planar cover of the overtopping colony to surpass the planar cover of the overtopped colony by the ratio \( \text{ratio overtop colony} = 2 \); value calibrated using empirical datasets (Appendix D).

To overtop encrusting and encrusting long upright colonies, branching and plating colonies have to surpass their height by 5 cm. The height of a non-encrusting colony is its radius, assuming a semi-spherical growth. The height of an encrusting colony = 2 cm (Table C18).
C.7.5.4 Competition between algae

C.7.5.4.1. Background

Competition between algae is complex and the outcomes depend on \( (i) \) the nature of the competition: indirect (e.g., depletion of resources, pre-emption of space), direct (i.e., interference interactions), \( (ii) \) the traits and strategies involved (e.g., growth rate, size and shape, allelopathy) and \( (iii) \) the implication of other factors such as herbivory, nutrient concentration and disturbances (Olson and Lubchenco, 1990). Predicting the outcome between two algae species is challenging because of the difficulty to identify which mechanisms are involved in a specific interaction and the competition can be asymmetric (i.e., species use different mechanisms against one another; Olson and Lubchenco, 1990).

Among the algal functional groups defined in the model, crustose coralline algae is the only algae that can be generally considered as an inferior competitor against different macroalgae (e.g., McClanahan, 1997) and turf (e.g., Borowitzka et al., 1978; Kendrick, 1991).

C.7.5.4.2. Implementation

Except for crustose coralline algae, we considered algal functional groups as equal competitors and can consequently not overgrow each other. We defined \textit{prob cover crustose coralline algae} as the probability of crustose coralline algae to lose their interactions against other algae. We attempted to calibrate the parameter using the empirical dataset, but no value could be defined during the procedure (Appendix D). We consequently chose the smallest value considered (i.e., 0.1) in order to compensate for its lack of competitiveness in the model.

\textbf{Related code:}

coralreef2 / src / coraReef2 / agent / Agent.java
Appendix D. Chapter 3: Model calibration

The objective of this calibration is to define general parameter values, so the species simulated interact, recruit and respond to disturbances in an ecologically relevant manner. We calibrated twelve model parameters using empirical data describing the biodiversity and environmental context of three Caribbean reefs over time. For each site, we used the time series of the percentage cover of coral species and algae functional groups to define the initial size of each population in the simulations and to measure the fit between the percentage cover of the simulated and real populations. We used empirical time series of sand cover, degree heating weeks (DHW) and herbivorous fish and urchin densities to determine at each time step the amount of sand to input or output in the virtual reef, the intensity of the thermal stress and the grazing pressure respectively. Finally, we considered the occurrence and intensity of cyclones that affected the reefs during the period considered. We present here the empirical data used, their implementation and the design and results of the calibration. All the related code for production of the figures is in Manuscript / Rscripts / Appendix S3 - Model calibration.R.

D.1. Study sites and related data

We used data collected in three sites located in Martinique in the Caribbean: Fond Boucher (14° 39’ 21.07” N, 61° 09’ 38.98” W), Pointe Borgnesse (14° 26’ 48.74” N, 60° 54’ 12.72” W), and Ilet à Rats (14° 40’ 58.04” N, 60° 54’ 1.18” W) and Ilet à Rats (14°40’58.04"N; 60°54’1.18"W) between November 2001 and July 2011. For each site, we only considered a time period where all data were available.

The biodiversity data were collected by the Observatoire du Milieu Marin Martiniquais for the program Initiative Française pour les REcifs COralliens. Surveys were conducted biannually and describe the benthic, macroinvertebrates and fish communities at the species or genera levels (no data were available for 2010, Figure D1; Figure D2). The benthic community composition was assessed using a line-intercept transect method (LIT). One permanent 60-meter long transect was positioned along the reef crest at each site. The benthic groups recorded are: live coral, dead coral (bare dead coral substrate and fragments), sessile invertebrates (soft coral, sponges, zoanthids), algae (macroalgae, turf, cyanophycae, encrusting and erected calcareous algae) and
sand. They assessed the fish community structure at the same transect but over a 4 × 50 and 2 × 50 m belt transect for mobile and territorial species respectively. Urchin populations density were measured along three 1 × 50 m belt transects (Figure D2).

We downloaded values of degree-heating weeks for the corresponding location (collected twice every week at a 50 km resolution) from the US National Oceanic and Atmospheric Administration data server ERDDAP (Environmental Research Division's Data Access Program; coastwatch.pfeg.noaa.gov/erddap) (Figure D3). We identified cyclones tracks using the National Oceanic and Atmospheric Administration Historical Hurricane Tracks website (coast.noaa.gov/hurricanes). Hurricane Dean affected the reefs in August 2007 and its intensity changed from category one to two while passing over Martinique.

Related code:

Figure D1. Composition of the benthic communities in the three Caribbean sites. Vertical grey bars indicate the dates at which data were collected. The data were collected by the Observatoire du Milieu Marin Martiniquais for the program Initiative Française pour les REcifs Coralliens.
Figure D2. Population densities of herbivore fish and sea urchins (Diadema antillarum and Echinometra viridis combined) measured in the three Caribbean sites. Vertical grey bars indicate the dates at which data were collected. The data were collected by the Observatoire du Milieu Marin Martiniquais for the program Initiative Française pour les RÉcis Coralliens.

Figure D3. Evolution of the thermal stress in degree heating weeks affecting the three Caribbean sites (US National Oceanic and Atmospheric Administration’s data server ERDDAP).
D.2. Data implementation

D.2.1. Benthic cover

We manipulated the empirical data so it could be used in our six-month time step model. Biological data were collected at the end of the dry and wet seasons, which respectively span from December to May and from June to November. Measures of benthic cover were used in the calibration by being compared to the simulated cover values. We adjusted temporally the empirical cover data when necessary, so each measure would fall exactly six months after the previous one.

Sand cover was used to determine the target percentage at each time step (Figure D4). Small patches of barren ground agents were converted to sand or vice versa in case sand needed to be added or removed.

Figure D4. Level of sand cover to reach at each time step for three Caribbean sites.
D.2.2. Thermal stress and hydrodynamic regimes

The value of degree-heating weeks to impose during a time step is the maximum DHW value recorded during the corresponding period (Figure D5).

The intensity of hydrodynamic regimes is defined by the dislodgement mechanical threshold (DMT), a dimensionless measure of the mechanical threshold imposed by waves and cyclones (see §C.7.3.1; Madin and Connolly 2006). A lower value represents a more intense disturbance. For instance, Madin and Connolly (2006) estimated that cyclone Rona (category three) imposed a DMT approximately equal to 18 at the crest and 88 at the back of Lizard Island in February 1999. In comparison, they also estimated the DMT imposed by a “moderate cyclone” at the same locations: around 38 and 162 respectively at the crest and back of the reef. We had no information about the intensity of the hydrodynamic regimes other than the category of the hurricane Dean. Considering that the three sites are not directly in contact with the Atlantic Oceanic currents (Fond Boucher and Pointe Borgnesse are in the Caribbean side and Ilet à Rats is protected in a bight), we first arbitrarily attributed DMT values to the different disturbance regimes: 140 for waves, 120 for tropical storms (TS), 100 for hurricanes of category 1 (H1), 80 for H2, 60 for H3, 40 for H4 and 10 for H5. The sites having potentially different exposure to both wave and cyclone, we defined two additional hydrodynamic disturbance regimes by (1) subtracting 10 and (2) adding 10 to the DMT values at each time step (respectively cyclone\textsubscript{model1} and cyclone\textsubscript{model3} in Figure D5).
D.2.3. Grazing pressure estimation

We defined four models predicting the proportion of the reef maintained in a grazed state as a function of herbivore densities (Figure D6; Figure D8). Among the different species present in the datasets, we only considered Acanthuridae spp. and Scaridae spp. and sea urchins, as they are considered the most important herbivores in reefs (Steneck, 1988). We determined the fish grazing pressure using Williams and Polunin, (2001)’s empirical data. They conducted field surveys in 19 Caribbean reefs and analysed the relationship between the percentage cover cropped (i.e., covered by either turf, crustose coralline algae or bare substratum but not by macroalgae) and the density of Acanthuridae spp. and Scaridae spp. present. (Other grazers such as the sea urchin Diadema spp. were not present in high enough abundance to influence their results.) We combined abundances of the two genera and established a least-square linear regression between the total fish biomass and the percentage cover grazed (we considered “cropped” as equivalent to “grazed” in our model). The fish densities measured in Williams and Polunin, (2001)’s study do not reach the maximum values observed in the three Caribbean sites (Figure D2). In order to avoid predicting percentage values above 100, we defined two
asymptotic models approximating the linear regression but plateauing respectively at 90% and 70% for higher fish densities (Figure C6A):

\[ S_{G_{model1}} = \frac{90 \times D_F^2}{D_F^2 + 135} \]

\[ S_{G_{model2}} = \frac{70 \times D_F^2}{D_F^2 + 90} \]

where \( S_G \) = the surface of the reef grazed and \( D_F \) = the density of herbivore fish (g.m\(^{-2}\)). We excluded the possibility for the reef to be grazed at 100% because such a scenario is not realistic even at high fish densities (Paddack et al., 2006; Williams et al., 2001).

Similarly, we modeled urchin grazing using Sammarco’s (1980) data, who experimentally manipulated the density of the sea urchin \( Diadema antillarum \) (excluding other types of grazers) and analysed the relationship with algal cover (the author did not specify which functional groups the term includes) in a reef at Discovery Bay (Jamaica). We defined a least-squares linear regression model to predict the “percentage of reef grazed” (obtained by subtracting the percentage cover of algae from 100) with the density of \( D. antillarum \) (Figure D6). We log-transformed urchin density to meet the assumptions of normality and equal variance of the linear model (Figure D7). Both urchin species \( D. antillarum \) and \( Echinometra viridis \) were present in the three Caribbean reefs. We determined the urchin grazing pressure by pooling their respective abundances, assuming a similar function of the two species. This could potentially be a limitation as the two species have little niche overlap (McClanahan, 1999).

The total surface grazed is obtained by adding up the surface respectively grazed by fishes and urchins, which provides the grazing regimes grazing\(_{model1}\) and grazing\(_{model2}\) in Figure C8. We defined regimes grazing\(_{model3}\) and grazing\(_{model4}\) by subtracting 10 and 20 % to grazing\(_{model2}\) respectively.
Figure D6. Models defining the percentage of reef surface grazed as a function of herbivore density. Fish densities were measured in 19 Caribbean reefs (A, Williams and Polunin 2001). Also shown are the surface grazed averaged by site (grey circles), the significant least-squares regression line (black solid line; equation: $Y = 15.5 + 2.9X$) and the two asymptotic models we defined for modeling fish grazing pressure at higher fish densities (i.e., densities not observed in the study). Sea urchin densities were measured in a cage exclusion field experiment (B, Sammarco 1980). Grey circles are surface grazed averaged by site, black lines are least-squares regressions (black solid line; equation: $Y = 8.9 + 29.5X$). Dashed lines represent the 95% confidence bands.
Figure D7. Normal quantile plots (left column) and residual plots (right column) respectively verifying the assumptions of normality and equal variance distribution of the residuals of the least-squares linear regression models established to model fish (top row) and urchin grazing pressure (bottom row).

Figure D8. Percentage cover grazed imposed in the model at each time step for the three Caribbean sites.
D.3. Calibration

D.3.1. General procedure

We calibrated the model for each site independently and then conducted a between sites comparison of the parameter values that maximized model fit. A common approach for model calibration and validation is to divide the empirical data into a training and a test set. The model parameters are calibrated with the training set and the model generalizability is evaluated with the test set. Alternatively, resampling procedures can be used to train and test the model on the whole dataset iteratively (e.g., k-fold cross-validation). The time series we used were too short to be split and still allow for proper parameter calibration and model testing. Alternatively, we could have calibrated the model with one site and tested the model on the other sites. But we feared that model testing would not be satisfactory because of the paucity of the data describing the environmental context of the sites. By calibrating the model with the three datasets independently and then comparing the selected parameter values, we can dissociate between the parameters that can be generalized from those that need to be adjusted to a specific site. Alternatively, between-site differences in the parameter values offer the opportunity to question how relevant is the implementation of the related processes, if and how the implementation could be improved and if additional processes should be considered.

D.3.2. Sampling algorithm

All the possible combinations of parameter values are generated. Each parameter combination is interpretable as a point, whose parameter values are its coordinates in the parameter space. The algorithm we defined first selects the centroid, the most extreme parameter points, and the points situated at mid-distance between the centroid and the extreme points (1). A simulation with each parameter point is launched and replicated five times for each of the three Caribbean sites (2). The fit between the empirical and the simulated cover time series is measured using an objective
function. The algorithm then selects the ten points providing the best performance and samples around each of them to select the five closest (and not yet tested) points in the parameter space (3). Steps (2) and (3) are repeated one more time. Distance between points in the parameter space is measured using the Gower’s distance metric (Gower, 1971).

The objective function measures the performance of a given run by calculating the Euclidian distance between the empirical (coverEmp) and simulated cover time series (coverSim, averaged over five replicates), averaged over all the taxa:

$$\text{performance} = \frac{\sum_{j=1}^{N\text{taxa}} \frac{\sum_{t=t_{\text{end}}}^{t} (\text{coverEmp}_{j,t} - \text{coverSim}_{j,t})^2}{N\text{taxa}}}{N\text{taxa}}$$

where $j$ = a specific taxon, $N\text{taxa}$ = the last taxon, $t$ = a specific time step, $t_{\text{end}}$ = the last time step. Smaller values indicate better performance, zero being the minimum value and indicating perfect match.

In order to compare the performance of the runs to a second reference value, we generated for each empirical dataset a null distribution of performance values. These values are measures of performance between the empirical datasets and a randomized version of themselves. We randomized by rows (i.e., time periods) to keep the total taxa cover identical to the real data.

**D.3.3. Parameter selection and procedure**

Being limited by the number of simulations we could perform in a reasonable time, we decided to calibrate the model in several rounds of simulations, each round being composed of one or several of the following steps: (1) select a limited number of parameters, define several possible values (instead of ranges for continuous parameters) and generate all the possible combination of parameter values; (2) launch the previously described sampling algorithm; (3) analyse the results of the calibration to identify the parameter values providing the worst performance; (4) analyse the simulated time series of the runs having the best performance to identify the processes and associated parameters that could improve the performance of the model and decide on the new values to add; (5) generate a new set of all the possible combinations of parameter values with the new parameter values and without those being associated with the worst performance; finally
repeat (2), (3) and (4) and eventually (5) until results are satisfactory. Eventually (7), launch additional simulations with specific parameter values selected by the modeller. This “hands-on” calibration approach allows exploring specific parts of the parameter space potentially omitted by the algorithm or influencing specific processes that the modeller estimates to be relevant to act upon after having analysed previous results of the calibration. This human-directed search served to accelerate and guide the process, providing a faster convergence to the best parameter values.

We conducted in total four rounds of simulations. In round one, we selected only the parameters related to the different disturbance regimes (i.e., bleaching, cyclone and grazing models) and those whose value could not be found or estimated from the literature (i.e., growth rate reduction interaction, otherProportions, prob cover crustose coralline algae, ratio overtop colony, Table D1). We limited the number of possible parameter values to a maximum of five and generated the 4,860 possible parameter points, from which our algorithm sampled 357 points for each site. This first round of simulations showed that none of the fittest parameter points at one site were sampled in another site. This could have been due to either the sites having different intrinsic characteristics leading to different local optima, or our algorithm was omitting certain parts of the parameter space. We consequently selected 40 of the parameter points providing best performance in each site and launched simulations with the subset of these points that were not run in a given site. This resulted in implementing round two with 41, 49 and 38 additional parameter points for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively. None of these additional runs showed a better performance (Figure D9), confirming that the divergence in certain parameter values we observed between sites are due to intrinsic environmental differences. Analysis results at this stage revealed a consistently poorer performance of the simulations implementing values 0.01 and 0.001 of the parameter otherProportions (Figure D10). We consequently excluded these values in the next simulations. In addition, inspecting surface covers of the best fitted runs in each site revealed a poor match of the populations of algae. Grazing being one of the most important processes controlling these populations, we added more values to algae grazing probabilities. We then generated 2,592 additional combinations of parameter values from which the algorithm sampled 202 of them (round three). The analysis of the simulated cover at this stage revealed a consistent incapacity of crustose coralline algae to maintain its population in all three sites. We decided to improve its
persistence by enhancing its competitiveness against other algae (i.e., by adding the value 0.1 to \textit{prob cover crustose coralline algae}) and reducing its palatability (i.e., by adding the value 0.05 to \textit{prob grazing crustose coralline algae}). We launched the fourth round of simulations by generating 72 new parameter points with these new values and a subset of the other parameter values that consistently provided a better performance (i.e., \textit{bleaching model}: 3; \textit{cyclone model}: 1, 2, 3; \textit{grazing model}: 3, 4; \textit{growth rate reduction interaction}: 2, 4, 8; \textit{ratio overtop colony}: 2; \textit{prob grazing macroalgae}: 0.7; \textit{prob grazing allopatic macroalgae}: 0.3; \textit{prob grazing Halimeda}: 0.3, 0.5; \textit{prob grazing articulated coralline algae}: 0.7). We generated a total of 7716 different parameter combinations from which we sampled 672, 680 and 669 parameter points for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively.

Related code:

Table D1. Description of parameters calibrated and their respective values considered.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>bleaching model</td>
<td>value of the coefficient $\phi$ (see §E.2.2): a smaller $\phi$ increases the interspecific difference for the probability of bleaching when the thermal stress increases; a larger $\phi$ reduces this difference.</td>
<td>2; 3; 4</td>
</tr>
<tr>
<td>cyclone model</td>
<td>value of one of the three hydrodynamic regimes models displayed in Figure D5</td>
<td>1; 2; 3</td>
</tr>
<tr>
<td>grazing model</td>
<td>value of one of the four grazing regimes models displayed in Figure D6</td>
<td>1; 2; 3; 4</td>
</tr>
<tr>
<td>growth rate reduction interaction</td>
<td>lateral growth rate reduction coefficient to apply when one coral colony or an algae overgrows over other colonies or algae.</td>
<td>2; 3; 4; 6; 8</td>
</tr>
<tr>
<td>otherProportions</td>
<td>the coefficient $p_o$, which is used to reduce the number of larvae produced by all the colonies present in the reef (see §C.7.2.1.d)</td>
<td>0.0001; 0.001; 0.01</td>
</tr>
<tr>
<td>prob cover crustose coralline algae</td>
<td>probability that algae overgrow crustose coralline algae</td>
<td>0.10; 0.25, 0.50; 0.75</td>
</tr>
<tr>
<td>ratio overtop colony</td>
<td>ratio needed for a branching or plating colony to overtop smaller colonies</td>
<td>1.5; 2; 3</td>
</tr>
<tr>
<td>prob grazing macroalgae</td>
<td>probability of macroalgae being palatable</td>
<td>0.3; 0.5; 0.7</td>
</tr>
<tr>
<td>prob grazing allopathic macroalgae</td>
<td>probability of allopathic macroalgae being palatable</td>
<td>0.3; 0.5</td>
</tr>
<tr>
<td>prob grazing Halimeda</td>
<td>probability of <em>Halimeda</em> spp. being palatable</td>
<td>0.3; 0.5; 1.0</td>
</tr>
<tr>
<td>prob grazing articulated coralline algae</td>
<td>probability of articulated coralline algae being palatable</td>
<td>0.5; 0.7; 1.0</td>
</tr>
<tr>
<td>prob grazing crustose coralline algae</td>
<td>probability of crustose coralline algae being palatable</td>
<td>0.05; 0.1; 0.2; 0.3; 1.0</td>
</tr>
</tbody>
</table>
D.4. Results

Performance values are bounded between 28 and 10 (where lower values are better) and are all below the lower 95% confidence limit of the null distribution of performance values (Figure D9). This shows that despite the model complexity, the high number of parameters, and the uncertainty around them, the model outputs population dynamics significantly closer to the real data as compared to randomly generated ones. The best performance values converged toward 10 in the three Caribbean sites (minimum values with standard error are 10.93 ± 3.677, 10.89 ± 2.872, 10.39 ± 3.119 for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively) and were obtained during round three and four of the calibration (Figure D9). The first 257 points in round one were sampled uniformly in the parameter space, and expectedly show the highest ranges of performance values. The ranges from runs 258 to 357 narrow down drastically as sampling happened around the points providing best performance but the lower limits stayed constant. In round two, running in one site the combinations of parameter values that provided best performance in other sites increased the lower limit slightly for Fond Boucher, importantly for Pointe Borgnesse, and increased the higher limit for Ilet à Rats. The addition of alternative values for the probabilities of grazing the different groups of algae in round three lowered the lower range limits in all three sites. Finally, our attempt to support crustose coralline algae populations by increasing its competitiveness and reducing its palatability in round four, did not change further the range of performance values (Figure D9), as crustose coralline algae cover remained quasi absent even in the runs having the best performance (Figure D14; Figure D15; Figure 3.3).

For six parameters, the same value was the most commonly observed among the best fitted runs in the three sites: bleaching model (2), grazing model (4), otherProportions (0.0001), ratio overtop colony (2, Figure D10), and to a lesser extent prob grazing macroalgae (0.7) and prob grazing articulated coralline algae (0.7, Figure D11).

Three parameters have contrasting values between sites: growth rate reduction interaction (8 for Fond Boucher and Ilet à Rats and 2 for Pointe Borgnesse), prob grazing allopathic macroalgae (0.3 for Pointe Borgnesse and either 0.3 or 0.5 for the other two sites), prob grazing Halimeda (0.5 for Pointe Borgnesse and 0.3 for Ilet à Rats). The differences observed for prob grazing allopathic macroalgae and prob grazing Halimeda (Figure D11) could suggest that the
accurate value for both parameters lies between 0.3 and 0.5. The small growth rate reduction value calibrated at Pointe Borgnesse compared to the two other sites could be due to the difference of turf abundance. Probably less turf-coral direct interactions occur at Pointe Borgnesse because turf is less abundant and shares its dominance with allogalae (Figure D14; Figure D15; Figure 3.3). Turf has the fastest growth rate among algae and coral species and is the most competitive algae when competing with corals. As a result, a higher growth rate reduction value might be necessary for coral populations to persist in Fond Boucher and Ilet à Rats compared to Pointe Borgnesse. These differences in the values providing best performance for these three parameters could be caused by contrasting algae growth rates between sites due to either different species composing the functional groups or differences in grazing regimes that we did not capture or other processes not implemented (e.g., effects of nutrient concentrations on growth rate).

Lastly, values considered for three parameters did not influence performance: cyclone model, prob cover crustose coralline algae and prob grazing crustose coralline algae. Two reasons might explain why none of the three hydrodynamic disturbance regimes simulated influence performance: (i) the coral species present were either too resistant or (ii) they did not reach a colony size large enough to be dislodged. Colony dislodgement due to cyclones and waves is determined from colony planar area and growth form (see §C.7.3.1). Several of the dominant species in the three sites are massive (i.e., P. astreoides, O. faveolata, O. annularis, O. franksi) and could withstand even the hardest regime (i.e., model 3 in Figure D5). The other relatively abundant species have more vulnerable growth forms and their fragility increases with colony size (i.e., branching: M. mirabilis, P. furgata; digitate: M. decactis; laminar: A. agaricites). Possibly, spatial competition in the model prevented these species from reaching colony sizes large enough to be dislodged even under the most intense regime.

Analysing the distribution of the combinations of parameter values with their associated performance in the parameter space reveals one unique global optimum in each site as the parameter combinations having the highest performance are clustered together (Figure D12). The parameters that influence performance the most in all sites are grazing model, and otherProportions, growth rate reduction interaction (respectively arrow number 3, 5 and 4 in Figure D12). The probabilities of grazing the different algae clearly dissociate runs generated during round one and two from the ones generated during rounds three and four: in the latter,
higher values of *prob grazing macroalgae* and lower values of *prob grazing allopathic macroalgae*, *Halimeda*, *articulated coralline algae* and *crustose coralline algae* were implemented (respectively arrow number 8, 9, 10, 11 and 12 in Figure D12). When compared all together, the combination of parameter values providing best performance in sites Fond Boucher and Ilet à Rats overlap (Figure D13). Pointe Borgnesse performance optimum is distant from the other sites due to opposite calibrated values for *growth rate reduction interaction* (Figure D10; arrow number 4 in Figure D13).

**Figure D9.** Evolution of the performance (smaller values show better performance) as a function of the order at which runs were launched for the three Caribbean sites (n = 672, 680 and 669 for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively). Each grey dot represents the performance of a given parameter combination (averaged over five replicates). The 20 parameter points showing the best performance are shown in red. The vertical dashed lines separate the simulations launched respectively in round one, two, three and four. The horizontal black lines and grey areas show the mean and 95% confidence intervals of the null distributions of performance values (n = 1000).
Figure D10. Performance comparison of all the combinations of parameter values simulated for six of the twelve parameters calibrated (n = 672, 680 and 669 for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively). Grey circles represent the performance of a unique parameter combination (averaged over five replicates). Smaller values show better performance. Black dots and error bars show the mean ± standard error by parameter value. Red circles show the 20 parameter combinations providing the best performance.
Figure D11. Performance comparison of all the combinations of parameter values simulated for six of the twelve parameters calibrated (n = 672, 680 and 669 for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively). Grey circles represent the performance of a unique parameter combination (averaged over five replicates). Smaller values show better performance. Black dots and errors bars show the mean ± standard error by parameter value. Red circles show the 20 parameter combinations providing the best performance.
Figure D12. Projection in the parameter space of the combinations of parameter values selected during the calibration for each site (n = 672, 680 and 669 for Fond Boucher, Pointe Borgnesse and Ilet à Rats respectively). Arrows indicate parameter loading; numbers designate parameters (coordinates values are displayed on the top and right sides): (1) bleaching model; (2) cyclone model; (3) grazing model; (4) growth rate reduction; (5) other Proportions; (6) prob cover crustose coralline algae; (7) ratio overtop colony; (8) prob grazing macroalgae; (9) prob grazing allopathic macroalgae; (10) prob grazing Halimeda; (11) prob grazing articulated coralline algae; (12) prob grazing crustose coralline. Light yellow to red colour gradient indicates the performance values from lower to higher performance (averaged over five replicates). The 20 parameters points showing the best performance are circled in black.
Figure D13. Projection in the parameter space of the combinations of parameter values selected during the calibration all sites confounded (n = 2021). Arrows indicate parameter loading; numbers designate parameters (coordinates values are displayed on the top and right sides): (1) bleaching model; (2) cyclone model; (3) grazing model; (4) growth rate reduction; (5) otherProportions; (6) prob cover crustose coralline algae; (7) ratio overtop colony; (8) prob grazing macroalgae; (9) prob grazing allopathic macroalgae; (10) prob grazing Halimeda; (11) prob grazing articulated coralline algae; (12) prob grazing crustose coralline. Grey dots represent individual combinations of parameter values. Circles highlight the 20 combinations providing best performance in each site.
Figure D14. Comparison between empirical and simulated taxa cover for the combination of parameter values providing the best performance for site Fond Boucher. Solid lines in the simulated time series are the mean percentages cover (averaged over five replicates) and the shaded areas show the standard error. The right panels display the cover difference between simulated and empirical time series.
Figure D15. Comparison between empirical and simulated taxa cover for the combination of parameter values providing the best performance for site Pointe Borgnesse. Solid lines in the simulated time series are the mean percentages cover (averaged over five replicates) and the shaded areas show the standard error. The right panels display the cover difference between simulated and empirical time series.
Appendix E. Chapter 3: Implementation of the bleaching response

The objective of this appendix is to show how we determined species-specific coral bleaching response models. We first defined an index of bleaching susceptibility expressed as a function of coral bleaching resistant traits. We then used this index to create species-specific logistic functions determining the bleaching probability of a colony as a function of thermal stress intensity. We parameterized these functions using an empirical dataset reporting impacts of bleaching events recorded in the Caribbean. Finally, we defined a non-species-specific logistic model determining the probability of bleaching-induced mortality as a function of thermal stress intensity. All the related code for the statistical analyses and production of figures is in Manuscript / Rscripts / Appendix S4 - Implementation bleaching response.R.

E.1. Species-specific index of bleaching susceptibility

E.1.1. General procedure

Our goal was to define an intrinsic (i.e., independent of environmental conditions) index of bleaching susceptibility expressed as a function of bleaching resistance traits. We established a statistical model between an empirical measure of bleaching susceptibility (dependent variables) and functional-traits (independent variables) on a subset of the 798 coral species for which the dependent variables had been measured. We then used the model to predict the bleaching susceptibility index value for the 798 coral species.

The dependent variable we selected is the bleaching response index (taxon-BRI), which represents the species-specific average percentage cover that bleached or died during an event. It was obtained for 374 taxa (304 if only considering species level values and after correcting for species names) from 2036 records concerning 316 sites, between 1982 and 2006 by Swain and colleagues (2016c). 65% of the Taxon-BRI value is determined by intrinsic factors (i.e., coral biology), 6% by extrinsic factors (i.e., environmental conditions) and 29% by measurement uncertainty (Swain et al., 2016c).
Coral bleaching is a complex process involving numerous resistant traits. We initially selected five traits based on the number of species for which the traits were measured and on the degree to which they are implicated in the bleaching process: (i) colony maximum diameter, (ii) growth rate, (iii) microscopic reduced scattering coefficient, (iv) growth forms and (v) corallite area (Carturan et al., 2018). We used the imputed traits dataset in order to avoid having missing predictor values.

We generated numerous beta regression models, defined the confidence set (i.e., the subset of models being the most supported by the data), averaged the latter and predicted the index values for the 798 species.

**E.1.2. Data exploration**

We first converted the taxon-BRI’s interval from [0,100] to ]0,1[. We then logit-transformed the taxon-BRI_{0,1}, as appropriate when modeling a proportional dependent variable (Warton and Hui, 2011). We log-transformed the numerical traits in order to reduce the skewness of their distributions and improve linearity of their association with taxon-BRI_{0,1} (Figure E1).

The independent variables do show significant covariation (Figure E2): colony maximum diameter with corallite area (Spearman $r_s = -0.21, P < 0.001$), growth form (Spearman $r_s = -0.18, P < 0.01$), growth rate (Spearman $r_s = 0.25, P < 0.001$) and microscopic reduced scattering coefficient (Spearman $r_s = 0.33, P < 0.001$); corallite area with growth form (Spearman $r_s = 0.55, P < 0.001$), growth rate (Spearman $r_s = -0.73, P < 0.001$); and growth form with growth rate (Spearman $r_s = -0.75, P < 0.001$). These covariations need to be considered when defining the full model (see §E.1.3). (We produced Figure E2 using the pairs.panels function from the R package psych 1.8.3.3; Revelle 2017).
Figure E1. Relationships between the taxon-BRI \textsubscript{0.11} (logit-transformed) and the five bleaching resistance traits initially selected (n = 304). Black lines are smoothing splines and are used for visual aid. Growth forms are ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Each gray circle represents the trait value averaged by species, the black points are the averaged trait value over all the species by category (E), and the error bars extend to ± one standard error.
Figure E2. Correlation analyses between the bleaching resistance traits used in the full regression model (n = 304): colony maximum diameter (CMD), coralline algae (CA), growth forms (GF), growth rate (GR), and microscopic reduced scattering coefficient (mRSC). Growth forms are ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Black points represent the trait value averaged by species, the red line is the locally estimated scatterplot smoothing fit and the grey area it 95% confidence interval. The upper panels show the values of the Spearman’s rank correlation coefficient. Asterisks indicate the test statistics’ significance: *P<0.05; **P<0.01; ***P<0.001.

E.1.3. Beta regression

Proportional data often display asymmetric distributions, which contradict the normality assumption required in classic regression models. Contrastingly, beta regression models allow for the prediction of response variables having any unimodal distribution in the interval ]0,1[ (i.e., “beta” distributions; Ferrari and Cribari-Neto 2004). Beta density distributions are defined
by two parameters: the mean $\mu$ and the precision parameter $\phi$ and are mathematically expressed as $B(\mu, \phi)$. Obtaining the final beta regression model requires following several steps: (i) define the “global” model, (ii) remove the observations (species) that are too influential on the model parameters (based on the Cook’s distance), (iii) chose the appropriate link function for $\mu$, (iv) chose the appropriate link function for $\phi$, (v) define the confidence set of models (i.e., data dredging), and eventually (vi) average these models. These steps are described in detail below:

The initial “global” model:
We first defined the “global” (also referred as “full”) model by including as predictors all the bleaching resistance traits at the first and second degree polynomials as well as their significant interactions based on Figure E2. We chose the logit link function as the initial link function for the “location” submodel (i.e., to model the mean $\mu$) because the logit function is appropriate for modelling proportional data (Warton and Hui, 2011). We chose a constant $\phi$ to model dispersion. We used the `betareg` function of the R package `betareg 3.1-0` (Cribari-Neto and Zeileis, 2010) to define the beta regression models. The global model is:

$$
\text{logit}(E(\text{taxon-BRI}_{[0,1]})) = \alpha + \beta_1 \times \ln(\text{colony maximum diameter})_i \\
+ \beta_2 \times \ln(\text{corallite area})_i \\
+ \beta_3 \times \ln(\text{growth rate})_i \\
+ \beta_4 \times \ln(mRSC)_i \\
+ \beta_5 \times \text{growth form}_i \\
+ \beta_6 \times \ln(\text{colony maximum diameter})_i : \ln(\text{corallite area})_i \\
+ \beta_7 \times \ln(\text{colony maximum diameter})_i : \text{growth form}_i \\
+ \beta_8 \times \ln(\text{colony maximum diameter})_i : \ln(\text{growth rate})_i \\
+ \beta_9 \times \ln(\text{colony maximum diameter})_i : \ln(mRSC)_i \\
+ \beta_{10} \times \ln(\text{corallite area})_i : \text{growth form}_i \\
+ \beta_{11} \times \ln(\text{corallite area})_i : \ln(\text{growth rate})_i \\
+ \beta_{12} \times \text{growth form}_i : \ln(\text{growth rate})_i \\
+ \beta_{13} \times \ln(\text{colony maximum diameter})_i^2 \\
+ \beta_{14} \times \ln(\text{corallite area})_i^2 \\
+ \beta_{15} \times \ln(\text{growth rate})_i^2
$$
with \( \text{taxon-BRI}_{0.1 bloggers} \sim B(\mu_i, \phi) \) (i.e., beta distribution with mean \( \mu_i \) and dispersion \( \phi \)), \( E(\text{taxon-BRI}_{0.1 bloggers}) = \mu_i \), \( \text{VAR}(\text{taxon-BRI}_{0.1 bloggers}) = \mu_i(1 - \mu_i)/(1 + \phi) \), \( \alpha \) the intercept, \( \varepsilon_i \) the residual associated with the \( i^{\text{th}} \) observation (i.e., species) and \( \beta_j \) the respective coefficient for each of the bleaching resistance traits.

**Removal of influential observations**

We used the Cook’s distance (Cook, 1977) to identify observations (i.e., species) being the most influential on the model parameters. Observations with a Cook’s distance superior to one should be removed (Johnson and Omland 2004 and reference therein). We conserved all of the observations because none of them had a large Cook’s distance (Figure E3). We calculated the Cook’s distance using the `cooks.distance` function from the package `stats` (R Core Team, 2017).

**Figure E3.** Cook’s distance of the species (n=304) for the global beta regression model.

**Selection of the link function for \( \mu \)**

Different link functions can be used to model the distribution of the response variable (e.g., logit, loglog, etc.). We created a global beta regression for each of the link functions available in the
function *betareg* (Figure E4). We then selected the link function based on (1) fit maximization—
assess with the adjusted $R^2$ and the Akaike information criterion (AIC)—and (2) the distribution
argued that AIC should be used over the adjusted $R^2$ in model selection because the latter does
not account for the complexity of the model (i.e., the parsimony principal). However, in our
situation, all the model candidates have the same complexity (i.e., number of predictors). It is
consequently relevant to also consider this measure of fit. We assessed the homoscedasticity of
the residuals by comparing Pearson residuals against predicted values (Figure E5). Finally, we
assessed the distribution of the residuals by plotting the Pearson residuals against normal
quantiles (Figure E6).

Each version of the global model satisfies the assumptions of homogeneity (Figure E5) and
normality (Figure E6) of the residual distribution and no model seems to perform better in these
aspects. We chose the model implementing the *cloglog* link function as it provides the highest fit
($R^2 = 0.23$; Figure E4).

![Figure E4](image-url)

**Figure E4.** Associations between the observed and predicted values for different versions of the
global model. Each version implements a different link function to estimate the parameter $\mu$
($n=304$). Also displayed are the pseudo $R^2$, the Akaike information criterion (AIC) and the
identity line.
Figure E5. Associations between Pearson’s residuals and predicted values for the different versions of the global model. Each version implements a different link function to estimate the parameter $\mu$ (n=304).
Figure E6. Half-normal plot with simulated envelopes for the different versions of the global model. Each version implements a different link function to estimate the parameter $\mu$ (n=304).

Selection of the link function for $\phi$
We implemented each factor individually with a given link function (i.e., $identity$, $log$, $sqrt$) and compared the resulting models with the one implementing $\phi$ as a constant using a likelihood-ratio test (Cribari-Neto and Zeileis, 2009). None of the models obtained yielded a significant $P$-value. We consequently kept $\phi$ as a constant. The likelihood-ratio test was performed with the `lrtest` function from the R package `lmtest` (Zeileis and Hothorn, 2002).

Model selection
We generated 504 submodels (i.e., models implementing a subset of the global model’s predictors, excluding models with only the second order of the polynomial for a given predictor)
and selected the 95% confidence set of models using the Akaike weight (Johnson and Omland, 2004). The procedure selected 65 nested models. The predictors $\ln(\text{colony maximum diameter})$ and $\ln(\text{corallite area})$ are present in all the models whereas growth form is not present in any of them (Table E1; Table E2). We used the `dredge` function for generating and ranking the different models and the `get.models` function for selecting the confidence set; both functions come from the R package `MuMIn` 1.40.0 (Bartón, 2017).

**Table E1.** Summary of the bleaching resistance traits (predictors) for the averaged beta regression model (from the 65 models of the 95% confidence set). The relative importance of each predictor is calculated as a sum of the Akaike weights over all of the models in which the term appears.

<table>
<thead>
<tr>
<th>Bleaching resistance traits</th>
<th>Relative importance</th>
<th>No. models where present</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\ln(\text{colony maximum diameter})$</td>
<td>1.00</td>
<td>65</td>
</tr>
<tr>
<td>$\ln(\text{corallite area})$</td>
<td>1.00</td>
<td>65</td>
</tr>
<tr>
<td>$\ln(\text{mRSC})$</td>
<td>1.00</td>
<td>65</td>
</tr>
<tr>
<td>$\ln(\text{growth rate})$</td>
<td>0.59</td>
<td>49</td>
</tr>
<tr>
<td>$\ln(\text{colony maximum diameter}): \ln(\text{corallite area})$</td>
<td>0.57</td>
<td>37</td>
</tr>
<tr>
<td>$\ln(\text{colony maximum diameter}): \ln(\text{growth rate})$</td>
<td>0.22</td>
<td>23</td>
</tr>
<tr>
<td>$\ln(\text{colony maximum diameter})^2$</td>
<td>0.27</td>
<td>29</td>
</tr>
<tr>
<td>$\ln(\text{corallite area})^2$</td>
<td>0.58</td>
<td>37</td>
</tr>
<tr>
<td>$\ln(\text{mRSC})^2$</td>
<td>0.26</td>
<td>29</td>
</tr>
<tr>
<td>$\ln(\text{growth rate})^2$</td>
<td>0.20</td>
<td>21</td>
</tr>
</tbody>
</table>
Table E2. Summary statistics of the ten best models (out of 65) belonging to the 95% confidence set (link function: cloglog).

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>logLik</th>
<th>AIC</th>
<th>delta</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1/2/8/9*</td>
<td>6</td>
<td>169.759</td>
<td>-327.517</td>
<td>0.000</td>
<td>0.073</td>
</tr>
<tr>
<td>1/2/5/8</td>
<td>6</td>
<td>169.742</td>
<td>-327.484</td>
<td>0.033</td>
<td>0.071</td>
</tr>
<tr>
<td>1/2/3/5/8</td>
<td>7</td>
<td>170.434</td>
<td>-326.868</td>
<td>0.649</td>
<td>0.052</td>
</tr>
<tr>
<td>1/2/5/8/9</td>
<td>7</td>
<td>170.284</td>
<td>-326.568</td>
<td>0.950</td>
<td>0.045</td>
</tr>
<tr>
<td>1/2/3/8/9</td>
<td>7</td>
<td>170.005</td>
<td>-326.011</td>
<td>1.506</td>
<td>0.034</td>
</tr>
<tr>
<td>1/2/3/5/8/9</td>
<td>8</td>
<td>171.000</td>
<td>-326.000</td>
<td>1.517</td>
<td>0.034</td>
</tr>
<tr>
<td>1/2/3/8/9/10</td>
<td>8</td>
<td>170.948</td>
<td>-325.896</td>
<td>1.622</td>
<td>0.032</td>
</tr>
<tr>
<td>1/2/8</td>
<td>5</td>
<td>167.844</td>
<td>-325.689</td>
<td>1.829</td>
<td>0.029</td>
</tr>
<tr>
<td>1/2/3/5/6/8</td>
<td>8</td>
<td>170.825</td>
<td>-325.650</td>
<td>1.867</td>
<td>0.029</td>
</tr>
<tr>
<td>1/2/4/5/8</td>
<td>7</td>
<td>169.793</td>
<td>-325.585</td>
<td>1.932</td>
<td>0.028</td>
</tr>
</tbody>
</table>

*Each number corresponds to a predictor: \( \ln(\text{colony maximum diameter}) \) (1); \( \ln(\text{corallite area}) \) (2); \( \ln(\text{growth rate}) \) (3); \( \ln(\text{colony maximum diameter})^2 \) (4); \( \ln(\text{corallite area})^2 \) (5); \( \ln(\text{growth rate})^2 \) (6); \( \ln(\text{mRSC})^2 \) (7); \( \ln(\text{mRSC}) \) (8); \( \ln(\text{colony maximum diameter}) \times \ln(\text{corallite area}) \) (9);

**Model averaging**

We averaged the parameter values to obtain the final model. The procedure provides parameter values obtained from (i) the “natural average”, or “conditional average”, which we refer as the “subset model” (i.e., the parameter estimate is averaged only from the parameter values of the model in which it is present) and (ii) the “zero method” or “full average”, which we refer as the “full model” (i.e., zeros are replaced as values of parameters in the models where the variable is not present). We used the “subset model” in order to avoid shrinking the factors not present in all the models (Grueber et al., 2011) but we also present the results of the “full model” for comparison (Figure F7; Figure F8; Figure F9; Figure F10; Figure F11). The averaged “subset” model coefficients are presented in (Table E3). The diagnostic plots of the Pearson residuals for both models are presented in Figure F7.

For both models, residuals are evenly distributed along each predictor (Figure F7; Figure F8) and their normality is acceptable (Figure F9). Diagnostic residuals plots are similar between the “subset” and the “full” models.

We averaged the models using the `model.avg` function from the R package MuMIn. We obtained the pseudo-R\(^2\) value by squaring the correlation between linear predictors and the
cloglog-transformed $\text{BRI}_{[0,1]}$ (Ferrari and Cribari-Neto, 2004). We used the Pearson’s coefficient as measure of correlation.

**Table E3.** Estimates of the parameters of the averaged “subset” beta regression model (link function: cloglog).

| Model’s parameters                                         | Estimate | Std. Error | z value | Pr(>|z|) |
|------------------------------------------------------------|----------|------------|---------|----------|
| (Intercept)                                                | -1.242   | 1.0273     | 1.209   | 0.227    |
| $\ln(\text{coli}ne \text{y maximum diameter})$           | 0.187    | 0.1470     | 1.274   | 0.203    |
| $\ln(\text{corallite area})$                              | -0.123   | 0.0806     | 1.527   | 0.127    |
| $\ln(mRSC)$                                                | -0.668   | 0.8174     | 0.817   | 0.414    |
| $\ln(\text{growth rate})$                                 | 0.024    | 0.2937     | 0.081   | 0.936    |
| $\ln(\text{coli}ne \text{y maximum diameter}) : \ln(\text{corallite area})$ | 0.024    | 0.0226     | 1.061   | 0.289    |
| $\ln(\text{coli}ne \text{y maximum diameter}) : \ln(\text{growth rate})$ | 0.063    | 0.0707     | 0.886   | 0.376    |
| $\ln(\text{coli}ne \text{y maximum diameter})^2$         | 0.001    | 0.0252     | 0.053   | 0.958    |
| $\ln(\text{corallite area})^2$                            | -0.001   | 0.0061     | 1.582   | 0.114    |
| $\ln(mRSC)^2$                                              | 0.135    | 0.3497     | 0.386   | 0.699    |
| $\ln(\text{growth rate})^2$                               | -0.034   | 0.0440     | 1.000   | 0.317    |
| $\phi$                                                     | 4.267    | 0.3360     | 12.697  | <0.001   |
| Pseudo $R^2$                                               | **0.122**|            |         |          |
Figure E7. Relationship between Pearson residuals of the averaged “subset” beta regression model and predicted values (A), and each of the potential bleaching resistant traits (B to F) (n = 304). Growth forms are ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Each gray circle represents the trait value averaged by species, the black points are the averaged trait value over all the species by category (E), and the error bars extend to ± one standard error.
Figure E8. Relationship between Pearson residuals of the averaged “full” beta regression model and predicted values (A), and each of the potential bleaching resistant traits (B to F) (n = 304). Growth forms are ranked from the most complex to the simplest: branching, table/plate, corymbose, digitate, laminar, columnar, massive, encrusting long upright, encrusting. Each gray circle represents the trait value averaged by species, the black points are the averaged trait value over all the species by category (E), and the error bars extend to ± one standard error.
Intrinsic probability of bleaching

We then obtained the intrinsic probability of bleaching for each of the 798 species using the final averaged beta regression model (Figure E10; Figure E11).
Figure E11. Comparison of distributions between the observed (taxon-BRI\_0,1) and the predicted (intrinsic probability of bleaching) response variable (A) and the extrapolated intrinsic probability of bleaching (n = 798, B) for the averaged “full” beta regression model.

E.2. Species-specific bleaching probability models

E.2.1. Dataset

Eakin and colleagues (2010) established an empirical linear model linking the mean proportion of colony bleaching within a reef and the intensity of the thermal stress expressed in degree heating weeks (DHW; the product of °C above the highest monthly mean sea-surface temperature for a location and its duration in weeks during the most recent 12-week period; coralreefwatch.noaa.gov; Kayanne 2017). The relationship is based on 2575 bleaching surveys in the Caribbean between June 2005 and February 2006. Eakin and colleagues (2010) combined percentages of coral cover bleached and colonies bleached (i.e., the proportion of colonies bleached over the total number of colonies) to define the “mean coral bleached (% )”. They looked at the association between the mean coral bleached (%) and (i) the “observed DHW” and (ii) the “2005 annual maximum DHW”.

For consistency with our agent-based model, we only considered the cover bleached as the dependent variable. We used the “observed DHW” as the independent variable because the bleaching response usually happens within the weeks following the onset of the disturbance.
E.2.2. Generalized linear mixed model

The global model

We defined a binomial generalized linear mixed model (GLMM) using a logistic link function to model the association between bleached coral cover (“cover bleached”) and DHW. We considered each observation in Eakin and colleagues’ (2010) dataset as a single data point (several observations were made at a same site and date). We defined the variable “time” as the number of days elapsed since the earliest sampling date in Eakin and colleagues’ (2010) dataset (i.e., the first sampling date corresponds to day one). We established an initial model with DHW as fixed effect and site and time as random effects:

\[
\text{logit}(\mathbb{E}(\text{cover bleached}_{ijk})) = \alpha + \beta_1 \times \text{DHW}_i + \text{site}_j + \text{time}_k
\]

where = \alpha the intercept, \text{DHW}_i = the fixed effect associated to the coefficient \beta_1 and the \text{i}^{th} observation; \text{site}_j and \text{time}_k = the random intercepts associated to the \text{j}^{th} site and \text{k}^{th} time unit, respectively, with \text{site}_j \sim N(0,\sigma_{\text{site}}^2) and \text{time}_k \sim N(0,\sigma_{\text{time}}^2) (i.e., \text{site}_j and \text{time}_k are normally distributed, with a mean of zero and variance \sigma_{\text{site}}^2 and \sigma_{\text{time}}^2 respectively).

Model selection

We tested the significance of each random effect individually using a likelihood ratio test to compare the goodness of fit of the first model with a model excluding alternatively site and time. The test showed that both site (\chi^2 = 14.56, P < 0.001) and time (\chi^2 = 14.56, P = 0.004) contribute significantly to the goodness of fit of the model. We used the function \text{glmer} from the R package \text{lme4} 1.1-15 (Bates et al., 2015) to create the model and \text{lrmtest} from the R package \text{lmtest} 0.9-35 (Zeileis and Hothorn, 2002) for the likelihood ratio test.

Model validation

Residuals of logistic regressions are by nature curvilinear, not normally distributed and heteroscedastic. Residuals diagnostic plots are in consequence used to detect strong disqualifying patterns. No such patterns are found with the model: (i) no strong curvilinear trends are observed between the Pearson residuals and the fitted values; (ii) deviance residuals do not deviate greatly.
from normality; (iii) the distribution of residuals is not strongly heteroscedastic; (iv) there are no outliers (Figure E12).

**Figure E12.** Diagnostic plots of the generalized linear mixed model (n = 1216). Black lines are smoothing splines and are used for visual aid.

*Model parameters*

The parameters of the generalized linear mixed model are presented in Table E4 and the fit of the model is displayed in Figure E13.

**Table E4.** Parameters values of the generalised linear mixed model (binomial distribution and logit link function). The model as fitted on Eakin and colleagues’ (2010) dataset.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Fixed effects</th>
<th>Random effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
</tr>
<tr>
<td>α (intercept)</td>
<td>-2.78</td>
<td>0.191</td>
</tr>
<tr>
<td>β_i (DHW)</td>
<td>0.29</td>
<td>0.026</td>
</tr>
</tbody>
</table>
Figure E13. Relationship between the proportion of cover bleached in reefs and degree heating week (DHW). Grey circles represent individual observations (n = 1216) in a given site at a certain time (Eakin et al., 2010). The grey lines are the logistic regression curves of the general linear mixed model for each combination of sites and time (i.e., random effects; n = 771). The red curve is the logistic regression without random effects (y = 1/(1+exp(2.78 - 0.29×DHW)).

Species-specific bleaching response

We first defined the species-specific probability of bleaching ($P_B$) using the “intrinsic probability of bleaching” ($IP_B$) and the logistic regression model defined in previous sections. We defined a species-specific logistic response function by adding the coefficient $\gamma_i$ as an intercept to the model. The coefficient $\gamma_i$ is the standardized distance between $IP_{Bi}$ and the averaged $IP_B$, so that the set of logistic regressions is centered around the GLM we established previously (i.e., red line in Figure E13). The model for the $i^{th}$ species can be expressed as:

$$\text{logit}(P_{Bi}) = \alpha + \beta_1 \times \text{DHW} + \gamma_i$$

where $\alpha$ and $\beta_1$ = the coefficients of the logistic regression established previously (Table E4). We defined $\gamma_i$ as being (1) only dependent on $IP_B$, or (2) also dependent on DHW so that the difference of response between species increases with DHW:
\[ \gamma_i = \frac{IP_{Bl} - \text{mean}(IP_B)}{\text{max}(IP_B) - \text{min}(IP_B)} \]  

(1)

\[ \gamma_i = \frac{IP_{Bl} - \text{mean}(IP_B)}{\text{max}(IP_B) - \text{min}(IP_B)} \times \frac{DHW}{\varphi} \]  

(2)

with \( \text{mean}(IP_B) = 0.27, \text{min}(IP_B) = 0.06, \text{and max}(IP_B) = 0.60 \) and are the mean, maximum and minimum bleaching probability among the 798 coral species, respectively. The coefficient \( \varphi \in ]0, +\infty[ \); we chose \( \varphi \in \{2,3,4\} \) as three reasonable values (Figure E14) and \( \varphi = 2 \) provided better fit with the empirical data during the model calibration (Appendix D).

**Figure E14.** Species-specific logistic bleaching responses with \( \gamma_i \) being independent of DHW (A), dependent of DHW and \( \varphi = 4 \) (B), \( \varphi = 3 \) (C) and \( \varphi = 2 \) (D). Grey circles are individual sampling proportions of coral cover bleached (n = 1216) from Eakin and colleagues’ (2010) dataset. The solid red line represents the logistic regression fitting these observations (\( y = 1/(1+\exp(2.78-0.29\times\text{DHW})) \)). Blue lines represent the response of each 798 coral species.
E.3. Bleaching-induced mortality probability model

We define here another model to determine the probability that a bleached colony dies from the stress. Eakin and colleagues’ (2010) dataset does not allow to capture the relationship between the degree-heating weeks and the resulting percentage of dead coral cover. We consequently could not define a species-specific probability of mortality. Instead, we defined a unique logistic mortality response assuming the probability equals 0 for no stress (0 °C-week) and 0.85 for a high stress (16 °C-week, Figure E15). This latter value corresponds to the proportion of mortality in the most affected part of the Great Barrier Reef after the bleaching event of 2016 (ARC Center of Excellence For Coral Reef Studies, 2016), for which degree heating week reached 16 °C-week (Hughes et al., 2017b). The formula is:

\[
P_{BD} = \frac{1}{1 + e^{-0.4 \times (DHW - 11.6)}}
\]

The probability of mortality is multiplied by two in cases where the coral colony is already bleached when the bleaching event occurs.

Figure E15. General mortality response of a bleached coral colony as a function of degree-heating weeks (DHW) \((y = 1 / (1 + \exp(-0.4 \times (x - 11.6))))\).
Appendix F.  Chapter 3: Hierarchically structured validation

We present here the hierarchically structured validation of our coral agent-based model, a procedure proposed by Kubicek and colleagues (2015) to further validate complex models. The goals are to show that the processes are implemented in an ecologically relevant manner, to discuss about eventual unexpected outputs, and more generally, to deeply understand the model behaviors. The procedure consists in assessing the correctness of each process implemented, starting from those happening at the lowest scales, to those affecting the whole system. Each process can be assessed differently: visual and qualitative inspection of patterns, expert knowledge or using statistical comparison with independent data.

The processes of the model we assessed here are: (i) vegetative growth, (ii) recruitment, (iii) responses to disturbances (i.e., resistance and recovery), (iv) larval connectivity and (v) grazing. Additionally, (vi) competition is assessed simultaneously with (iii), (iv) and (v) because competition outcomes are context dependent. For each process, we defined expectations based on ecological knowledge. We then compared the model outputs to these expectations and discuss the results. We based several of the expectations using Grime’s (1977) classification of life-history strategies into competitive, stress-tolerant and ruderal (or weedy) functional groups. Darling and colleagues’ (2012) adapted this classification to coral species: competitive species have large branching or plating growth forms able to overtop other colonies, fast growth rates, and low resistance to hydrodynamics and thermal disturbances; stress-tolerant species have resistant domed morphologies (e.g., massive growth form), slow growth rates and high fecundity; weedy species have for principal characteristic a small colony size and a brooding mode of larval development (weedy species tend to show a diversity of values in the other traits).

Related code:
Manuscript / Rscripts / Appendix S5 - Hierarchically structured validation.R
Simulations / Rscripts / Hierarchically_structured_validation_Input_dataset.R,
F.1. Definition of the functional space

We compared coral interspecific functionality with the following traits: (i) aggressiveness; (ii) colony maximum diameter; (iii) corallite area; (iv) egg diameter; (v) polyp fecundity; (vi) growth rate; (vii) mode of larval development; (viii) sexual system; (ix) bleaching probability; (x) growth form. We converted categorical traits into numerical traits, so each dimension is continuous. For mode of larval development (vii), we attributed one to spawner and negative one to brooder and for sexual system (ix), we attributed one to hermaphrodite and negative one to gonochore.

We represented growth form (x) with two continuous dimensions, which are the first two principal components we obtained using our implemented relations between growth form and the three following processes: reproduction, resistance to cyclones and competition (see §C.7.2.1.1, §C.7.3.1.2 and §C.7.5, respectively). We first attributed a numerical value to each growth form for each of the three processes. For reproduction, we used the ratio between colony surface and planar area; for resistance to cyclones, we used the slope of the relationship between colony shape factor and colony planar area (on the logarithm scale) (Table C14); for competition, we attributed one to growth forms allowing to overtop (i.e., branching and plating) and zero otherwise. We then conducted the principal component analysis (Figure F1).
**Figure F1.** Principal component analysis used to quantify growth form on continuous dimensions. Grey dots represent growth forms and red arrows represent the load the different process-related variables (see text for details).

**F.2. Vegetative growth and spatial saturation**

**F.2.1. Objective and procedure**

Because the model smallest spatial scale is one cm$^2$, and taxa’s growth rates have decimals, we implemented vegetative growth by sampling radius values within species-specific intervals and converting agents within this radius, so that continuous averaged growth rates emerge (see §C.7.5.1). Here we verified that (i) population growth rates (i.e., value averaged over all colony’s growth rates) equals the species’ growth rate, and (ii) colony growth is constrained by the amount of available surrounding space.

We disabled all processes except vegetative growth (i.e., no reproduction, disturbance, larvae connectivity, grazing and algae invasion). The reef contained only one species at a time, which initially covered 30% of total area. We ran simulations for 20 years and measured growth rate at
the beginning, the middle and the end. Each time we calculated the averaged individual colony planar growth rates over three years. We calculated population growth rate by averaging colony’s growth rates over all the colonies present. We repeated the procedure with three coral species having different growth rates (Figure F2). We avoided selecting branching or plating species so the colonies cannot overtop each other.

**Figure F2.** Principal component analysis of the coral functional space (shown with the first two principal components) and the three species selected to assess growth rate and space saturation processes: *Acropora pulchra* (red square; fast: 65.5 mm.yr\(^{-1}\)); *A. polystoma* (blue diamond; medium: 37.3 mm.yr\(^{-1}\)); *A. gemmifera* (green circle; slow: 12.0 mm.yr\(^{-1}\)). Each grey dot represents one of the 798 species. The black arrow represents the load of the trait growth rate.

### F.2.2. Expected patterns

At first, colonies are small and most of them separated from each other. Population growth rate should consequently approximate species growth rate. As colonies grow, space becomes saturated, colonies touch each other, and population growth rate should decrease until eventually reaching zero. Fastest species should saturate the space more rapidly.

### F.2.3. Results

Expectations are met: at the beginning of the simulation, population growth rates approximated species growth rates (Figure F4; left column). As colonies grew, space became saturated (Figure
F3) and population growth rates decreased until eventually reaching zero for the fastest species (Figure F4).

**Figure F3.** Space saturation due to the vegetative growth of a unique coral species in absence of any other processes (colonies are distinguished by different shades of purple). We took screen shots of the 2 × 2 m² at different time intervals.
Figure F4. Effect of space saturation on coral colony growth rate saturation for three coral species, growing in a monospecific reef: *Acropora pulchra* (red square); *A. polystoma* (blue diamond) and *A. gemmifera* (green circle). The implemented growth rate (growth rate\textsubscript{imp}) corresponds to the values found in the literature. The dashed lines indicate no growth.
F.3. Recruitment and spatial saturation

F.3.1. Objective and procedure

Here we verified that population recruitment rate depends on the (i) species fecundity, (ii) mode of larval development (brooding species reproduce more often than spawning species), (iii) surface covered, (iv) size distribution of the colonies (because smaller colonies have a lower proportion of mature polyps; see C.7.2.1.1), and (v) amount of available space for settlement.

We kept the same model configuration as in the previous section and enabled coral reproduction. The reef was occupied by only one coral species at a time, which initially covers 10% of the reef. We ran simulations for 20 years and recorded number of new coral recruits and percentage cover each time step (six months). We compared results between three species having different life history strategies, based on Darling and colleagues' (2012) classification: (1) competitive Acropora gemmifera, (2) weedy Agaricia tenuifolia, (3) stress-tolerant Echinophyllia orpheensis (Figure F5). We replicated the simulations five times for each species.

To easily compare species fecundity, we defined “colony fecundity” (number of eggs cm$^{-2}$ of colony planar surface area) such as:

\[
\text{colony fecundity} = \frac{\text{polyp fecundity} \times \text{ratio}_{3D/2D} \times \text{coefficient}_{sexual\ system}}{\text{corallite area}}
\]

with

\[
\text{coefficient}_{sexual\ system} = \begin{cases} 0.5 \text{ for gonochore} \\ 1.0 \text{ for hermaphrodite} \end{cases}
\]

The coefficient ratio$_{3D/2D}$ is the colony surface area divided by the colony planar surface area, based on the geometric formulae we used (Table C5) and assuming that planar surface area is circular.
**Figure F5.** Principal component analysis of the coral functional space (shown with the first two principal components) and the three species selected to assess recruitment rate and space saturation processes: *Acropora gemmifera* (competitive, red dot in square); *Agaricia tenuifolia* (weedy, green dot in diamond); *Echinophyllia orpheensis* (stress-tolerant, blue dot in circle). Each grey dot represents one of the 798 species, colored dots are species classified either as competitive (red), weedy (green), stress-tolerant (blue) generalist (black) by Darling et al., (2012). Arrows indicate trait loadings; numbers correspond to: (1) aggressiveness; (2) colony maximum diameter; (3) corallite area; (4) egg diameter; (5) polyp fecundity; (6) growth rate; (7) mode of larval development; (8) sexual system; (9) bleaching probability; (10) growth form PC1; (11) growth form PC2.
Figure F6. Functional characteristics of the three species selected to assess recruitment rate and space saturation processes (from left to right: competitive in red, weedy in green and stress-tolerant in blue). Each vertex of the web corresponds to a trait: (1) colony maximum diameter ($\log_{10}$); (2) egg diameter (mm); (3) colony fecundity (no. eggs.cm$^{-2}$, $\log_{10}$); (4) mode of larval development; (5) growth rate ($\log_{10}$). The colored polygons situate the trait value of the species in the range of values spanned by the 798 species, with highest values at the extremities and lowest values near the center of the web.

F.3.2. Expected patterns

At the beginning of the simulation, the percentage cover occupied is low and the colonies are smaller. Recruitment rate should increase as surface cover increase and colonies become larger and more fecund. After the population reaches a certain percentage cover, available space becomes more limited and recruitment rate decreases. The increase and decrease in recruitment rate should be proportional to growth rate because colonies reach larger sizes, higher fecundity and fill up available space faster. The initial colony size distribution, which depends on species’ maximum colony diameter (see §C.5.2), and colony fecundity are positively associated with recruitment rate.

F.3.3. Results

Expectations are met. An increase followed by a decrease in recruitment is observed for *A. tenuifolia* (weedy) and *E. orpheensis* (stress-tolerant) but not for *A. gemmifera* (competitive), whose recruitment only decreased (Figure F7). All three species have similar colony fecundity (trait 3 in Figure F6) but *A. gemmifera* has by far the highest colony maximum diameter (trait 1


in Figure F6). Consequently, its initial colony size distribution is characterized by fewer but larger colonies, with one colony belonging to $[10^4,10^{4.7}]$ and one to $[10^{4.7},10^5]$ cm$^2$; in comparison, the other species’ colonies are all $< 10^4$ cm$^2$ (Figure F8). Larger colonies containing a higher proportion of fecund polyps (see §C.7.2.1.1.b), A. gemmifera was able to recruit more the first year (Figure F7; Figure F8). In combination with a higher growth rate (trait 5 in Figure F6), the species was able to fill up the available space more rapidly (i.e., in six years). Stress-tolerant species E. orpheeensis had initially a few more of the largest colonies compared to weedy A. tenuifolia (Figure F8), which is due to its slightly higher maximum colony diameter and results in a higher initial number of recruits (Figure F7). It surpassed the weedy species’ maximum recruitment rate because it filled up space less rapidly. Indeed, the weedy species has a slightly faster vegetative growth rate (trait 5 in Figure F6) and reproduced twice a year due to its brooding model of larval development.

This section shows that colony size influences importantly recruitment rate. Consequently, expressing probability of polyp fecundity as a function of colony size in a non-species-specific model (see §C.7.2.1.1) is a potentially important limitation of the model. Future improvement should consist in defining realistic species-specific models, providing that empirical data and evidences will be available.
Figure F7. Recruitment rate and space saturation for three coral species, growing in a monospecific reef: *Acropora gemmifera* (competitive, red dot in square); *Agaricia tenuifolia* (weedy, green dot in diamond); *Echinophyllia orpheensis* (stress-tolerant, blue dot in circle). Each symbol indicates the cover and number of recruits measured at a given time interval. Simulations were replicated five times. Trend lines are shown for visual aid. Also displayed is the species radial growth rate.
Figure F8. Initial Colony size-frequency distributions of the three species grown in a monospecific reef for the recruitment rate and space saturation simulations. Frequencies were averaged over five replicates.
F.4. Disturbance intensity

F.4.1. Objective and procedure

Here we verified that coral species fitness depends on their functional characteristics and the intensity of the disturbance regimes defining their environment. In particular, we want to identify the mechanisms generating the results and assess their ecological relevance.

We enable all the processes in the simulations. The reef was occupied by three coral species having different life history strategies, macroalgae, turf and crustose coralline algae, all covering initially 10% of the reef. We exposed the community to four different disturbance regimes, from low to high wave exposure (DMT_{background}) and bleaching intensity (DHW_{bleaching}): (1) DMT_{background} = 120 and DHW_{bleaching} = 0 °C-weeks; (2) DMT_{background} = 100 and DHW_{bleaching} = 5 °C-weeks; (3) DMT_{background} = 80 and DHW_{bleaching} = 10 °C-weeks; (4) DMT_{background} = 60 and DHW_{bleaching} = 15 °C-weeks. The other two factors are kept constant: grazing at 50% and larval connectivity at “medium (10 km)” levels (7000 larvae.m$^{-2}$). We ran simulations for 20 years with a bleaching event happening at year seven. We replicated each treatment five times.

Because functional diversity is another factor influencing the model’s outputs, we did the experiment with two different coral communities, which we assembled by selecting species from Western Atlantic and Eastern Pacific (Figure F9; Figure F10).
Figure F9. Principal component analyses of the coral functional space (shown with the first two principal components) and the three species selected to assess response to disturbances, larval connectivity, grazing and competition. Species from the Western Atlantic (left) are: *Acropora palmata* (competitive, red dot in square); *Madracis pharensis* (weedy, green dot in diamond); *Orbicella annularis* (stress-tolerant, blue dot in circle). Species from the Eastern Pacific (right) are: *Pocillopora elegans* (competitive, red dot in square); *P. damicornis* (weedy, green dot in diamond); *Porites lutea* (stress-tolerant, blue dot in circle). Each grey dot represents one of the 798 species, colored dots are species classified either as competitive (red), weedy (green), stress-tolerant (blue) or generalist (black) by Darling and colleagues (2012). Arrows indicate trait loadings; trait numbers correspond to: (1) aggressiveness; (2) colony maximum diameter; (3) corallite area; (4) egg diameter; (5) polyp fecundity; (6) growth rate; (7) mode of larval development; (8) sexual system; (9) bleaching probability; (10) growth form PC1; (11) growth form PC2.
Figure F10. Functional characteristics of the species selected to assess recruitment rate and space saturation processes (the Western Atlantic and Eastern Pacific species are respectively at the top and bottom; from left to right: competitive in red, weedy in green and stress-tolerant in blue). Each vertex of the web corresponds to a trait: (1) colony maximum diameter (log\(_{10}\)); (2) egg diameter (mm); (3) colony fecundity (no. eggs.cm\(^{-2}\), log\(_{10}\)); (4) mode of larval development (i.e., one for spawner, zero for brooder); (5) growth rate (log\(_{10}\)); (6) aggressiveness; (7) bleaching susceptibility; (8) growth for PC1 (i.e., resistance to hydrodynamics disturbances and capacity to overtop), (9) growth form PC2 (i.e., 3D to 2D surface ratio). The colored polygons situate the trait value of the species in the range of values spanned by the 798 species, with highest values at the extremities and lowest values near the center of the web.

F.4.2. Expected patterns

Under low wave exposure, we expect the community to be dominated by the competitive species because of its faster growth rate and its capacity to overtop smaller colonies due to its potentially large and branching colonies. As wave intensity increases, the colonies of the competitive species are dislodged once they reach a certain size, preventing them from overtopping other
colonies and providing more space to the other two species. Contrastingly, the cover of the stress-tolerant species should increase because of the high resistance of its colonies, which should become larger and more fecund. Finally, the fate of the weedy species under higher waves exposure depend on its capacity to compete with the other species. Competition can take different forms and involves different traits: (i) direct in the case of physical contact between colonies (aggressiveness and growth rate are involved), (ii) indirect, via competition with algae (growth rate and growth form are involved), pre-emption of available space due to (iii) vegetative growth (growth rate and growth form are involved), and (iv) via recruitment (polyp fecundity and size, growth form, mode of larval development and sexual system are involved).

The bleaching event happening at year seven should affect more the species having the highest susceptibility, which in the model depends on the traits growth rate, corallite area (i.e., polyp size), microscopic reduced-scattering coefficient, and maximum colony diameter (Appendix E). If the most bleaching susceptible species is the one dominating the community, we expect a switch of species composition after the bleaching event. However, such a change in species assembly dependents on the intensity of the thermal stress, the level of larval connectivity and the amount of available space for larvae to settle (which also depends on grazing pressure).

F.4.3. Results

Western Atlantic

The competitive species (A. palmata, in red) dominated the community under lower wave exposure (Figure F11). Having higher growth rate (trait 5 in Figure F10), its colonies rapidly pre-empted space and reached larger colony sizes, which hampered the other two species from growing and recruiting. In addition, many of its colonies were large enough to overtop other smaller colonies (Figure F12). By occupying a high surface cover and owning most of the largest colonies, A. palmata recruited importantly (Figure F11). The colony fecundity of the other two species is not superior enough to compensate for their slower growth rate (trait 3 in Figure F10).

Under more intense wave regimes, A. palmata’s largest colonies were systematically dislodged (Figure F13) due to the low resistance of branching growth forms (trait 8 in Figure F10). Its cover consequently decreased and weedy species M. pharensis became the most abundant species under the highest wave exposure (Figure F11) because of the wave-resistance
of its digitate growth form and its relatively fast growth rate (respectively trait 8 and 5 in Figure F10). Reaching larger colonies, *M. pharensis* recruited more and could not be overtopped by *A. palmata* (Figure F13). Being more aggressive, *M. pharensis* also won most of its interactions with *A. palmata* (trait 6 in Figure F10).

Despite being the most resistant and aggressive species (respectively traits 8 and 6 in Figure F10), the stress-tolerant species *O. annularis* was only able to persist due to external larval supply (Figure F11). Its lower growth rate compared to the other two species (trait 5 in Figure F10) was a disadvantage for several reasons. First, *O. annularis* grows over less available surface when directly competing for space with the other coral species. Second, corals also compete against algae, especially with turf, which is the most dominant algae in the model (e.g., Figure F20; Figure F25). Turf has the fastest growth rate and wins 100% of its interactions with corals (see §C.7.5.3). Under the grazing regime imposed in these simulations (50%), *O. annularis* lost more surface in its competition with turf than it gained by growing vegetatively. Third, *O. annularis* recruited less (Figure F11) because of the smaller sizes of its colonies (Figure F12; Figure F13).

The bleaching disturbance happening at year seven affected coral species accordingly to their thermal sensitivity (Figure F10)—*A. palmata* cover decreased dramatically, even after a mild event, whereas *M. pharensis* and *O. annularis* were less affected in comparison (Figure F11). Recruitment rate increased just after the bleaching event because numerous dead colonies provided suitable larval settlement substrate.

Species recovered pre-cover level approximately one year after the disturbance, which is faster than the five to ten years usually observed in real ecosystems (Pratchett et al., 2009 but see Diaz-Pulido et al., 2009). This is due to the high and constant number of larvae coming from the regional pool (7000 larvae m⁻²). In reality, an intense bleaching event (> 10 C°-weeks) would affect large geographic areas and consequently reduce larval supply and recovery rates (e.g., Hughes et al., 2019). If needed, the number of coral larvae to input at each time step can be defined before launching simulations.
Figure F11. Evolution of cover (top) and number of recruits (bottom) of the three coral species from Western Atlantic (red for the competitive Acropora palamata, green for the weedy Madracis pharensis, blue for the stress-tolerant Orbicella annularis and black for total coral cover) for different disturbance regimes. The black arrow indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; shaded areas at the top show ± SE; individual symbols at the bottom show the number of recruits at a given time for one replicate.
**Figure F12.** Colony size-frequency distributions of the Western Atlantic species at the lowest wave exposure (DMT_{background} = 120) and with no thermal disturbance (DHW_{bleaching} = 0 °C-weeks). Colonies with a colony planar area = 1 cm² are not displayed.

**Figure F13.** Colony size-frequency distributions of Western Atlantic species at the highest wave exposure (DMT_{background} = 60) and thermal disturbance (DHW_{bleaching} = 15 °C-weeks). Colonies with a colony planar area = 1 cm² are not displayed.

*Eastern Pacific*
The competitive species *P. elegans* dominated the community regardless of the intensity of the disturbance regime (Figure F14). Its cover decreased under higher wave regimes, but the species could recruit more than the two other species. The three species coexisted under the highest wave regime—weedy species *P. damicornis* reached a stable population size and structure and the cover of the stress-tolerant species *P. lutea* slowly increased (Figure F16).

The competitive species dominated the weedy species because of its mode of larval development—*P. elegans* is a spawning species and receives three times more larvae from the regional pool compared to *P. damicornis* (see §C.7.2.1.2), which explains its higher recruitment rate (Figure F14). Other traits played a minor role in the competition between the two species because of their high functional similarity (Figure F10).

The stress-tolerant species *P. lutea* did not establish permanently other than under the highest wave regime because of its lower growth rate and colony fecundity compared to the competitive species (respectively traits 5 and 3 in Figure F10). Unable to reach larger colony sizes (Figure F15), *P. lutea*’s population persisted because of the high input of larvae from the regional pool (Figure F14). Under the highest wave regime, the two other branching species could not reach large colony size (Figure F16), leaving more space to *Porites lutea*’s resistant colonies to grow (trait 8 in Figure F10). Having more large colonies (Figure F16), *P. lutea* recruitment rate slightly increased (Figure F14).

The three species have a similar bleaching susceptibility (trait 7 in Figure F10) and were similarly affected by the thermal disturbance (Figure F14). Compared to the two other species, *P. lutea* failed to rapidly recover pre-disturbance cover after bleaching because of its slow growth rates (traits 5 in Figure F10).
Figure F14. Evolution of the cover (top) and the number of recruits (bottom) of the three coral species from Eastern Pacific (red for the competitive *Pocillopora elegans*, green for the weedy *Pocillopora damicornis*, blue for the stress-tolerant *Porites lutea* and black for total coral cover) for different disturbance regimes. The black arrow indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; shaded areas at the top show ± standard error; individual symbols at the bottom show the number of recruits at a given time for one replicate.
Figure F15. Colony size-frequency distributions of the Eastern Pacific species at the lowest wave exposure (DMT<sub>background</sub> = 120) and with no thermal disturbance (DHW<sub>bleaching</sub> = 0 C°-weeks). Colonies with a colony planar area = 1 cm<sup>2</sup> are not displayed.

Figure F16. Colony size-frequency distributions of the Eastern Pacific species at the highest wave exposure (DMT<sub>background</sub> = 60) and thermal disturbance (DHW<sub>bleaching</sub> = 15 C°-weeks). Colonies with a colony planar area = 1 cm<sup>2</sup> are not displayed.
F.5. Connectivity

F.5.1. Objective and procedure

Here we assessed how larval connectivity influences coral population dynamics. We enabled all the processes and used the same coral species, and the same initial percentage cover as in the previous section. We ran simulations for 20 years and triggered the bleaching event at year seven. We exposed the communities to five different levels of larval connectivity: (i) “no connectivity”, (ii) “isolated (100 km)” (66.5 larvae.m⁻²), (iii) “low (20 km)” (700.0 larvae.m⁻²), (iv) “medium (10 km)” (7000 larvae.m⁻²); (v) “high (5 km)” (35000 larvae.m⁻²). We kept constant grazing pressure, wave exposure and bleaching intensity (50%, DMT_{background} = 80, DHW_{bleaching} = 10 C°-weeks, respectively).

F.5.2. Expected patterns

Recruitment rate depends on the number of larvae settling in the reef and the amount of available space. The number of larvae a population produces locally depends on (i) the surface cover occupied, (ii) the size of the colonies, and (iii) the species investment in sexual reproduction. Corals have different strategies enhancing local recruitment rate, such as high colony fecundity, multiple reproductive cycles per year (a strategy mostly observed in brooding species, Ritson-Williams et al., 2009), and brooding larvae (which are ready to settle just after realise). Under no or low larval connectivity, species having one or several of these strategies have an advantage recovering from a disturbance and maintaining their population under stressful conditions (provided they are resistant enough). Under higher larval connectivity, the capacity to self-recruit locally is less critical because larval supply is not uniquely supported by local populations. Other traits become more important, such as growth rate and the capacity to overtop other colonies in protected locations and resistance to disturbances in more exposed ones.
F.5.3. Results

Western Atlantic

There was a clear contrast in species dominance between low and high larval connectivity (Figure F17). Under no or low connectivity, weedy species *M. pharensis* competitively excluded the other two species, mainly because it was better at recruiting locally. *Madracis pharensis* could reproduce twice a year and all its larvae remained in the reef because of its brooding mode of larval development. Contrastingly, *A. palmata* and *O. annularis* reproduce once a year and only a portion of their larvae remains in the reef. This proportion depends on water retention time (4.69 days) and time to motility of the larvae, which is determined by egg diameter (see §C.7.2.1.1.d). With relatively large egg diameter (trait 2 in Figure F10), only one third of *A. palmata* and *O. annularis* remained in the reef.

Despite its higher growth rate, the competitive species *A. palmata* became competitively excluded because of its lower aggressiveness, colony fecundity, and resistance to waves (respectively traits 6, 3 and 8 in Figure F10). In comparison, the stress-resistant species *O. annularis* resisted better because of its higher aggressiveness but was eventually excluded because it was incapable of recruiting (Figure F17) and could not compensate for the cover loss in its competition with turf.

Under higher connectivity, producing a large number of larvae was not the most important strategy and *A. palmata* competitively excluded the other two species (Figure F17) because of its faster growth rate and its capacity to overtop smaller colonies (see §F.4.3 for more details).

*Madracis pharensis* and *A. palmata* recovered rapidly after bleaching under low and high connectivity, respectively, by using different strategies. *Madracis pharensis* is the least bleaching susceptible species (trait 7 in Figure F10) and consequently lost less than 50% cover after the disturbance; its unbleached surviving colonies were able to reproduce every six months after bleaching. Contrastingly, *A. palmata* was much more impacted and recovered due to the high input of larvae and its fast growth rate.
Figure F17. Evolution of cover (top) and number of recruits (bottom) of the three coral species from Western Atlantic (red for the competitive Acropora palamata, green for the weedy Madracis pharensis, blue for the stress-tolerant Orbicella annularis and black for total coral cover) for different larval connectivity levels. The black arrow indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; shaded areas at the top show ± standard error; individual symbols at the bottom show the number of recruits at a given time for one replicate.
Some of the results observed with this community contrast importantly with the ones described previously. Under no or low larval connectivity, the weedy species *P. damicornis* was not the dominant species, despite being also the only brooder species in the community. Instead, the stress-tolerant species *P. lutea* who competitively excluded both *P. damicornis* and the competitive species *P. elegans* (Figure F18). The superior competitiveness of *P. lutea* here is explained by its much higher resistance to waves (trait 8 in Figure F10). Both *P. damicornis* and *P. elegans* have branching colonies, which are dislodged by waves after reaching a certain size. *Porites lutea*, on the other hand, has massive colonies can sustain strong wave regimes, especially as they become larger. In contrast with the previous example, the capacity to recruit locally does not play an important role, and the recruitment rates remained low for all three species (Figure F18). The cover occupied by *P. lutea* increased mainly because of the vegetative growth of its colonies (Figure F19).

Under higher levels of larval connectivity, the competitive species excluded the other two species (Figure F18) for different reasons. *Pocillopora damicornis* was outcompeted because of its lower recruitment rate compared to the spawning species, while *P. lutea* has a lower growth rate and colony fecundity (traits 5 and 3 in Figure F10).
**Figure F18.** Evolution of the cover (top) and the number of recruits (bottom) of the three coral species from Eastern Pacific (red for the competitive *Pocillopora elegans*, green for the weedy *Pocillopora damicornis*, blue for the stress-tolerant *Porites lutea* and black for total coral cover) for different larval connectivity levels. The black arrow indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; shaded areas at the top show ± standard error; individual symbols at the bottom show the number of recruits at a given time for one replicate.
Figure F19. Colony size-frequency distributions of the Eastern Pacific species with no larval connectivity. Colonies with a colony planar area = 1 cm$^2$ are not displayed.

F.6. Grazing intensity

F.6.1. Objective and procedure

Here we assessed the effect of grazing intensity on populations dynamics of both corals and algae. We enabled all the processes and used the same coral species, and initial percentage cover as in the previous section. We ran simulations for 20 years and triggered a bleaching event at year seven. We exposed the community to five different grazing regimes: 10, 30, 50, 70 and 90% reef cover permanently grazed. We kept constant larval connectivity, wave exposure and bleaching intensity (7000 larvae.m$^{-2}$, DMT$_{background}$ = 80 and DHW$_{bleaching}$ = 10 C$^\circ$-weeks, respectively).

F.6.2. Expected patterns

A decrease of grazing pressure usually leads to an increase of algal biomass and cover and a decrease in coral cover (e.g., Suchley and Alvarez-Filip, 2017). The recovery of the coral
community after a pulse disturbance should also be affected by a reduction of grazing intensity because less suitable space is available for vegetative growth and larval settlement (e.g., Steneck et al., 2014). Under prolonged insufficient grazing, new feedback processes establish and coral reefs switch to an alternative stable state dominated by algae (Mumby, 2009).

Under high grazing pressure, the algae community should be dominated principally by crustose coralline algae, because few herbivores species can consume its encrusting tissue. Turf algae can also persist in a cropped state, because their fast growth rate can compensate for their usually high palatability (e.g., McClanahan, 1997). With lower grazing pressure, a higher cover of turf cover and establishment of large macroalgae should be observed. Once established, these macroalgae can persist because of their lower palatability to many herbivores and higher longevity (Steneck and Dethier, 1994).

After a pulse disturbance, such as cyclone or bleaching, the available space is usually filled first by turf, followed by crustose coralline algae or macroalgae depending on the intensity of the grazing regime (McClanahan et al., 2009). The recovery of the coral community depends on the grazing regime, the coral cover surviving the pulse disturbance and larval connectivity (Birrell et al., 2008). A high grazing pressure should provide enough available cover for corals to recover via vegetative growth and recruitment, provided that enough colonies survived locally and/or enough external larvae settle in the reef. Under more moderate grazing pressure, the fate of the coral community is uncertain because a pulse disturbance can push the ecosystem into an alternative stable state dominated by algae. Even under substantial grazing pressure, a strong reduction of coral cover can lead to a large increase of algae cover, overwhelming herbivores (“dilution of herbivory”) and allowing macroalgae to establish permanently (Mumby et al., 2007; Williams et al., 2001).

Predicting coral population dynamics in a community exposed to variable grazing regimes requires to consider coral-algae interactions at the species level because of the high functional diversity of the two taxa (even within functional groups), and the diverse mechanisms they use to compete (see §C.7.5.3.1). Certain coral traits play a role in these interactions. Large colonies are for instance, less likely shaded or overtopped than smaller ones. Branching colonies entangles erected macroalgae and are consequently less affected by whiplash (McCook et al., 2001). Plating and branching colonies can overtop algae and avoid direct contact (“escape in height strategy”). Fast rates of calcification and tissue regeneration allow to outcompete certain algae.
(e.g., Diaz-Pulido et al., 2009). On the other hand, species having fast growth rates and small polyp size (i.e., characteristics of most competitive species) seem to be less competitive against many algae, potentially because of their limited capacity to increase heterotrophy (Steneck et al., 2014). Finally, disease-susceptible species seem to be more affected by allopatic algae (Bonaldo and Hay, 2014). Despite these coral traits being important to consider, coral-algae competitive outcomes might depend more on the functional characteristics of the algae (Diaz-Pulido and McCook, 2008).

F.6.3. Results

Western Atlantic

As expected, we observed an algae and coral-dominated states under low and high grazing regimes, respectively (Figure F20). Under the lowest grazing pressure, fewer coral colonies surpassed 100 cm² (Figure F22) and the coral community relied essentially on external larval supply (Figure F21). Under higher grazing pressure, more coral colonies reached larger sizes due to the increase of available space (Figure F23; Figure F24). Coral recruitment rate was the highest at intermediate grazing level (Figure F21) because space was saturated by algae and coral colonies under the lowest and highest regimes, respectively. Finally, there was no hysteresis (as attested by the approximate equality between coral cover and surface grazed) because we did not implement feedback processes (Figure F20).

Turf dominated the algae community regardless of grazing pressure (Figure F20). Despite being the most palatable algae (see §C.7.1.2), turf has the highest radial growth rate (250 mm.yr⁻¹) and consequently over-competed the other algae by pre-empting space more rapidly. In the model, all algae (except crustose coralline algae) cannot overgrow each other (see §C.7.5.4.2). Macroalgae failed to establish because its lower palatability did not compensate for the difference in growth rate. In future, we can aim at solving the issue by, for instance, allowing macroalgae to overgrow turf or implementing a process of transition from turf to macroalgae similar to the one implemented by Mumby et al., (2007). Crustose coralline algae failed to establish under all grazing regimes partly because of its very low radial growth rate (12 mm.yr⁻¹). We attempted to enhance crustose coralline algae competitiveness during the calibration by lowering its probabilities of being grazed and being covered by other algae but with no real improvement (see Appendix D). In addition, crustose coralline algae is an inferior competitor
against corals (see §C.7.5.3.2) and is a favorable substrate for coral settlement (see §C.7.2.1.3.b). Preventing crustose coralline algae from being grazed and overgrown by other algae or increasing its competitiveness against corals are solutions to investigate in future to help it reach realistic cover occupancy.

The available space created by bleaching-induced coral mortality was filled primely by coral recruits (Figure F21) rather than algae (Figure F20). This happened because coral recruitment precedes growth and algae invasion during a time step (Figure 3.2), which favors coral recovery, especially under high larval connectivity. Unfortunately, the model structure does not allow to implement these two processes simultaneously. Reducing further the competitiveness of coral recruits against algae could however solve the issue.

The competitive species A. palmata dominated the coral community under low to moderate grazing pressure (10 to 50%), because of its higher growth and recruitment rates (Figure F21). As discussed previously, algae indirectly mediate coral-coral competition in the model (see §F.4.3). There are more coral-algae interactions under lower grazing pressures, and A. palmata’s colonies can compensate better for the cover lost to algae due to their growth rate. In addition, A. palmata recruits more than (i) the brooding species M. pharensis because three times more larvae arrive form the regional pool and (ii) O. annularis because of a much higher growth rate, allowing A. palmata to reach more fecund colony sizes (Figure F22; Figure F23). Under higher grazing regimes (70 to 90%), A. palmata was over-competed by the weedy species M. pharensis (Figure F20), because of the relatively high wave exposure of the site and the higher resistance of M. pharensis’ colonies (trait 8 in Figure F10). Precisely, A. palmata’s colonies were dislodged once reaching 66.7 cm² whereas M. pharensis’ colonies were only limited by their colony maximum diameter (Figure F24). In addition, a lower algae cover implies a higher number of coral-coral interactions and A. palmata gradually conceded space to the other two species because it is the least aggressive species (trait 6 in Figure F10). The population of the stress-tolerant species O. annularis was stable because it is the most resistant and aggressive species but also the slowest.
Figure F20. Evolution of cover of the three coral species from Western Atlantic (top: red for the competitive Acropora palamata, green for the weedy Madracis pharensis, blue for the stress-tolerant Orbicella annularis and black for total coral cover) and algae (bottom: light green for turf, dark green for macroalgae and orange for CCA) for different grazing intensities. The black arrows indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; shaded areas at the top show ± standard error.
Figure F21. Evolution number of recruits of the three coral species from Western Atlantic (red for the competitive *Acropora palamata*, green for the weedy *Madracis pharensis*, blue for the stress-tolerant *Obricella annularis* and black for total coral cover) for different grazing intensities. The black arrows indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; individual symbols show the number of recruits at a given time for one replicate.
Figure F22. Colony size-frequency distributions of the Western Atlantic species at lowest grazing pressure (i.e., 10%). Colonies with a colony planar area = 1 cm$^2$ are not displayed.

Figure F23. Colony size-frequency distributions of the Western Atlantic species at intermediate grazing pressure (i.e., 50%). Colonies with a colony planar area = 1 cm$^2$ are not displayed.
Colony size-frequency distributions of the Western Atlantic species at highest grazing pressure (i.e., 90%). Colonies with a colony planar area = 1 cm$^2$ are not displayed.

**Eastern Pacific**

The results with the Eastern Pacific community are similar on many aspects to the previous results: turf and corals dominated under low and high grazing pressure, respectively (Figure F25); coral recruitment was higher at intermediate grazing levels (Figure F26); the increased available space after the disturbance was filled by coral recruits mainly; the competitive coral species *P. elegans* dominated the coral community under lower grazing regimes. Under higher grazing pressure, however, the stress-tolerant species *P. lutea* over-competed the other two species (Figure F25). Both *P. elegans* and the weedy species *P. damicornis* have branching colonies, which are dislodged once reaching a certain size. *Porites lutea* consequently progressively gained more surface cover by reaching higher colony size (Figure F27).
Figure F25. Evolution of cover of the three coral species from Eastern Pacific (red for the competitive *Pocillopora elegans*, green for the weedy *Pocillopora damicornis*, blue for the stress-tolerant *Porites lutea* and black for total coral cover) and algae (bottom: light green for turf, dark green for macroalgae and orange for CCA) for different grazing intensities. The black arrows indicate when the bleaching event occurred. Solid lines represent mean values over five replicates; shaded areas at the top show ± standard error.
Figure F26. Evolution number of recruits of the three coral species from Eastern Pacific (red for the competitive *Pocillopora elegans*, green for the weedy *Pocillopora damicornis*, blue for the stress-tolerant *Porites lutea* and black for total coral cover) for different grazing intensities. The black arrows indicates when the bleaching event occurred. Solid lines represent mean values over five replicates; individual symbols show the number of recruits at a given time for one replicate.
Figure F27. Colony size-frequency distributions of the Eastern Pacific species at highest grazing pressure (90%). Colonies with a colony planar area = 1 cm$^2$ are not displayed.

F.7. Summary

The hierarchically structured validation showed that our implementation of the processes we selected yields ecologically relevant patterns. The patterns for vegetative growth and recruitment rate as a function of percentage cover and colony size distribution matched our expectations. The dynamics we observed at the community level are harder to validate with certainty because we, ecologists, cannot predict precisely population dynamics because of to our lack of understanding of the numerous processes at play and their interactions. However, we provided ecologically relevant explanations for the emergent community dynamics we observed. For each factor tested (i.e., disturbance, grazing, connectivity), we could explain population dynamics considering simultaneously (i) functional differences among species, (ii) colony size distributions and (iii) the environmental context. The variations and magnitudes of the different variables we measured (i.e., % cover, number of recruits m$^{-2}$, colony size distributions) do not contrast with what we would expect in real systems. These proves that our model combines adequately functional traits and demographic approaches.

The validation procedure also revealed where the model can be improved. We summarize here the two main anomalies we observed. First, coral communities recovered pre-disturbance cover
in one year, even in the most intense disturbance regime scenario. There are three modifications we could do: (1) reduce larval supply from the regional pool after the disturbance, (2) reduce coral larvae competitiveness against algae, and (3) implement feedback processes. Second, the algae community was dominated by turf algae, irrespectively of the grazing intensity. We could reduce turf competitiveness by decreasing the palatability of the other algae.
Chapter 3: Global sensitivity analysis

G.1. Method

We did a global sensitivity analysis on each of the three versions of the model that we calibrated with the Caribbean sites (Appendix D). The goal was to estimate the model sensitivity during a process of recovery after a strong pulse-disturbance. We followed the recommendations of Prowse and colleagues (2016) for sampling the parameter space, choosing the number of replicates and the emulator and for the assessment of sampling sufficiency.

Related code:
- Manuscript / Rscripts / Appendix S6 - Global sensitivity analysis.R
- Simulations / Rscripts / Global_sensitivity_analysis.R and
- Hierarchically_structured_validation_functions.R.

G.1.1. Parameters, range of values and sampling

We selected ten of the twelve parameters considered in the calibration (we did not include cyclone model and grazing model because we used these to select site-specific disturbance regimes and are consequently not intrinsic model parameters; see Appendix D). We added six parameters having potentially important effects in the execution of ecological processes implemented, and whose values are uncertain (Table G1). We defined for each parameter a range of continuous values centred on the nominal values (the calibrated values in the case of the ten first parameters) and we defined the size of the range considering the type of parameter (e.g., proportion, coefficient) and the results of the calibration (i.e., the range is wider when more than one value provided the best fitness during calibration). We then drew a Latin hypercube sample ($n = 1000$) from the resulting parameter space using the randomLHS function from the R package lhs 0.16 (Carnell, 2018).
G.1.2. Simulations

We ran the simulations for 10.5 years, with a bleaching event happening at year four at an intensity of 12 °C-weeks. We kept constant grazing pressure (50%), wave hydrodynamic regime (dislodgement mechanical threshold = 120, which is equivalent to strong wave regimes that colonies experience at the reef crest), and larval input from regional pool (700 larvae m\(^{-2}\)). We defined the initial benthic composition as the one observed in the Caribbean sites during the first assessment. We ran each of the 1000 simulations only once (no replicate) as recommended by Prowse and colleagues (2016).

G.1.3. Response variables

We assessed model sensitivity for five different, ecologically relevant response variables: (i) coral cover (total coral cover at 10.5 years); (ii) difference cover (difference between total coral cover at 10.5 years and that just after the bleaching event); (iii) evenness (Pielou’s evenness at 10.5 years); (iv) richness (number of coral species having > 1% cover at 10.5 years) and (v) recruits (total number of coral recruits m\(^{-2}\) at 10.5 years).

G.1.4. Emulators

We determined the influence of each parameter on the variability of the response variables by fitting boosted regression trees in the \textit{gbm.step} function from the R package \textit{dismo} 1.1-4 (Hijmans et al., 2017), setting the learning rate to 0.01, the bag fraction to 0.75, the tree complexity to 3, and optimized the number of fitted trees based on 10-fold cross-validation. We assumed a Gaussian error distribution for each of the five response variables.

G.1.5. Estimation of sampling sufficiency

We estimated the sufficiency of the sample size by fitting boosted regression trees to random subsamples \((n = 100, 250, 500, 750)\) from the \(n = 1000\) set of parameter points generated. With higher sample sizes, we expected the influence of the parameters on the response variables to converge toward the same values. The difference of influence values for two consecutive sample sizes should consequently decrease as sample size increases. To measure the difference of the
parameters’ influence between two samples, we used De’ath's (2012) measure of community turnover:

\[ D_\beta = e^{\sum_{j=1}^{2} \sum_{i=1}^{s} \frac{p_{ij} \ln (p_{ij})}{2} - \sum_{i=1}^{s} p_{i} \ln (p_{i})}\]

where \( j \) = one of the two consecutive samples, \( i \) = one of the model parameters, \( s \) = the total number of parameters, \( p_{ij} \) = the influence of parameter \( i \) obtained with sample \( j \), and \( p_{i} \) = the averaged value between \( p_{i1} \) and \( p_{i2} \). \( D_\beta \) decreases asymptotically toward 1 as the parameters’ influence converges towards equality. We considered that the sample size was sufficient if we observed \( D_\beta \) asymptoting towards 1.
Table G1. Description of parameters used in the global sensitivity analysis and their respective ranges for each site (FB = Fond Boucher; PB = Pointe Borgnesse; IR = Ilet à Rats).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Nominal value</th>
<th>Sampling interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>bleaching diff response</td>
<td>value of the coefficient ( \varphi ) (see §E.2.2): a smaller ( \varphi ) increases the interspecific difference for the probability of bleaching when the thermal stress increases; a larger ( \varphi ) reduces this difference</td>
<td>3</td>
<td>[2.5,3.5]</td>
</tr>
<tr>
<td>growth rate reduction interaction</td>
<td>lateral growth rate reduction coefficient to apply when a coral colony or algae overgrows other colonies or algae</td>
<td>8 for FB, IR 2 for PB</td>
<td>[6,10] for FB, IR [1,5] for PB</td>
</tr>
<tr>
<td>otherProportions</td>
<td>coefficient ( p_o ) reduces the number of larvae produced by all the colonies present in the reef (see §C.7.2.1.1.d)</td>
<td>0.0001</td>
<td>[0.00005,0.00015]</td>
</tr>
<tr>
<td>prob cover crustose coralline algae</td>
<td>probability that algae overgrow crustose coralline algae</td>
<td>0.1, 0.25, 0.5, 0.75</td>
<td>[0,0.05]</td>
</tr>
<tr>
<td>ratio overtop colony</td>
<td>ratio needed for a branching or plating colony to overtop smaller colonies</td>
<td>2</td>
<td>[1.1,3]</td>
</tr>
<tr>
<td>prob grazing macroalgae</td>
<td>probability of macroalgae being palatable</td>
<td>0.7 for FB, PB 0.5, 0.7 for IR</td>
<td>[0.5,0.9]</td>
</tr>
<tr>
<td>prob grazing allopatic macroalgae</td>
<td>probability of allopatic macroalgae being palatable</td>
<td>0.3, 0.5 for FB, IR 0.3 for PB</td>
<td>[0.2,0.6] for FB, IR [0.1,0.5] for PB</td>
</tr>
<tr>
<td>prob grazing Halimeda</td>
<td>probability of Halimeda spp. being palatable</td>
<td>0.5 for PB 0.3 for IR</td>
<td>[0.2,0.7] for PB [0.1,0.5] for IR</td>
</tr>
<tr>
<td>prob grazing articulated coralline algae</td>
<td>probability of articulated coralline algae being palatable</td>
<td>0.7</td>
<td>[0.5,0.9]</td>
</tr>
<tr>
<td>prob grazing crustose coralline algae</td>
<td>probability of crustose coralline algae being palatable</td>
<td>0.05, 0.1, 0.2, 0.3</td>
<td>[0.01,0.1]</td>
</tr>
<tr>
<td>Parameters</td>
<td>Description</td>
<td>Nominal value</td>
<td>Sampling interval</td>
</tr>
<tr>
<td>----------------------------------</td>
<td>------------------------------------------------------------------------------</td>
<td>---------------</td>
<td>-------------------</td>
</tr>
<tr>
<td><em>height big algae</em></td>
<td>height in cm of macroalgae, allopathic macroalgae and articulated coralline algae</td>
<td>30</td>
<td>[20,50]</td>
</tr>
<tr>
<td><em>height turf</em></td>
<td>height in cm of turf</td>
<td>10</td>
<td>[5,15]</td>
</tr>
<tr>
<td><em>height crustose coralline algae encrusting coral</em></td>
<td>height in cm of crustose coralline algae, encrusting and encrusting long upright corals</td>
<td>2</td>
<td>[0.5,4]</td>
</tr>
<tr>
<td><em>prob settle crustose coralline algae</em></td>
<td>probability of a coral larvae to settle successfully on crustose coralline algae agents</td>
<td>0.5</td>
<td>[0.2,0.8]</td>
</tr>
<tr>
<td><em>prob settle barren ground</em></td>
<td>probability of a coral larvae to settle successfully on barren ground agents</td>
<td>0.5</td>
<td>[0.2,0.8]</td>
</tr>
<tr>
<td><em>prob settle dead coral</em></td>
<td>probability of a coral larvae to settle successfully on dead coral agents</td>
<td>0.5</td>
<td>[0.2,0.8]</td>
</tr>
</tbody>
</table>
G.2. Results

The parameters with the most important effects on the response variables were growth rate reduction interaction and otherProportions (Figure G1). They were followed by prob settle barren ground, prob settle dead coral, and in certain sites prob grazing articulated macroalgae and prob grazing Halimeda. The remaining six parameters did not have an important influence.

*Growth rate reduction interaction* mediates the impact that a superior taxon has on an inferior taxon when in direct competition by reducing the surface conceded. Consequently, higher growth rate reduction interaction is expected to increase evenness and richness in the case of coral-coral interactions. Algae such as turf, allopathic macroalgae and Halimeda spp. are stronger competitors compared to corals, so higher parameter values reduced their competitive advantage, which should have increased coral cover and difference cover. Number of recruits is expected to be positively correlated as well due to higher coral cover. As expected, growth rate reduction interaction was positively correlated with all response variables in all three sites, except for evenness at Pointe Borgnesse. This is explained by a nonlinear relationship between evenness and growth rate reduction interaction (i.e., the relationship is negative for growth rate reduction interaction $< 3.5$ and positive when $\geq 3.5$) and a range of smaller parameter values used for Pointe Borgnesse (Table G1; Figure G2).

The parameter otherProportions directly controls the number of larvae locally produced—higher values increase the proportion of competent larvae potentially setting in the reef. As expected, the parameter was positively correlated with coral cover, cover difference and number of coral recruits. It was negatively correlated with richness and evenness because higher values favoured a few (brooding) species that outcompeted most other species mainly because of a higher recruitment rate (Figure G3).

The probabilities of grazing algae were counterintuitively associated negatively with the response variables. These probabilities define the inter-algae difference of palatability and have to be compared to the grazing probability of turf algae, which was constant $= 1$. Increasing the grazing probability of algae consequently reduced the grazing pressure on turf, which affected coral colonies because turf is the most competitive algae with corals. There were between-site differences in the influence of some of these parameters: prob grazing allopathic macroalgae and prob grazing Halimeda had a stronger influence at Pointe Borgnesse and Ilet à Rats,
respectively. These discrepancies arose because of the different ranges of values used between sites (Table G1)—a range of smaller values (e.g., prob grazing allopathic macroalgae at Pointe Borgnnesse) allowed the corresponding population of algae to have a higher cover (Figure G4) and consequently, to influence the response variables more. Likewise, prob grazing macroalgae, prob grazing articulated coralline algae and prob grazing articulated coralline algae had little effect on the response variables because these algae occupied smaller portions of substratum (Figure G4).

Similar to other Proportions, the probabilities to settle on dead coral, barren ground and crustose coralline algae influence coral recruitment rate. We therefore expected them to be positively correlated with coral cover, difference cover, and number recruits, and negatively with evenness and richness. We observed these expected patterns with prob settle barren ground and prob settle dead coral, but crustose coralline algae cover was too low to allow prob settle crustose coralline algae to have had an effect (Figure G4).

The remaining parameters did not have much influence on the response variables because their implication in processes depended on certain population or community structures. In particular, height big algae and height turf did not have an effect because most of the branching colonies did not reach large enough sizes to overtop these algae, even under the lowest heights of algae (Figure G5). Likewise, branching colonies were too small to overtop other colonies, which prevented ratio overtop colony from affecting the response variables. Height crustose coralline algae encrusting coral and prob cover crustose coralline algae did not have an effect because crustose coralline algae was not abundant enough (Figure G4) and there was only one encrusting coral species present (only at Fond Boucher) and its cover remained close to zero (Figure G6).

Lastly, bleaching diff response (Φ) had no effect on the response variables because in most simulations, most coral species had such small population sizes that they had little effect on the response variables (e.g., averaging species cover at 10.5 years over the 1000 simulations revealed that only one or two coral species had a mean cover > 5%), and because the difference of bleaching susceptibility between the few dominant species was small with the range of values we defined for bleaching diff response (Figure G7).

Finally, we are confident that our sampling effort was sufficient because the measure of stability converged towards 1 for all five response variables and all three sites (Figure G8).
**Figure G1.** Influence (%) of each model parameter (rows) on each of the five response variables (columns), for each site: Fond Boucher (FB), Pointe Borgnesse (PB) and Ilet à Rats. Red and blue colours represent positive and negative relationships between parameters and response variables, respectively. Colour saturation indicates the amount of influence of parameters.
**Figure G2.** Relationship between the parameter *growth rate reduction interaction* and *evenness* predicted by the fitted boosted regression trees (fitted function) for each site (FB = Fond Boucher; PB = Pointe Borgnesse; IR = Îlet à Rats). Fitted functions are centred by subtracting their mean from each value.

**Figure G3.** Example of a comparison of the effect of lower (left panels, red) and higher (right panels, blue) values of *otherProportions* on individual coral species cover (top panels) and number of recruits m⁻² at Fond Boucher. Each line represents the cover or number of recruits of one coral species (*n* = 12 species). The black dashed line in the top panels shows the 1% cover threshold below which species were not accounted for richness (at 10.5 yrs).
Figure G4. Comparison of algae cover between sites (FB = Fond Boucher; PB = Pointe Borgnesse; IR = Ilet à Rats). Each line represents the algal cover of one simulation; the dashed black line shows the averaged cover over all the simulations ($n = 1000$).
**Figure G5.** Examples of colony size distributions of branching species by sites (FB = Fond Boucher; PB = Pointe Borgnesse; IR = Ilet à Rats) at 8 years. Each red line represents a species’ colony size distribution in one simulation; each plot shows 100 distributions that we randomly selected among the 1000 simulations. Horizontal black lines display the minimum colony planar area necessary to achieve for a colony to overtop the corresponding algae (CCA = crustose coralline algae; the line for big algae falls outside of the plots).
Figure G6. Cover of the encrusting coral species present at Fond Boucher. Each line represents the cover of one simulation \((n = 1000)\).

Figure G7. Bleaching probability of the most abundant species for the two extreme \(\phi (= \varphi\), the bleaching diff response) in each site (FB = Fond Boucher; PB = Pointe Borgnesse; IR = Ilet à Rats). We calculated the mean abundance at 10.5 years over the 1000 simulations and selected the \(n\) species with a mean percentage cover > 1%. The vertical dashed line shows the intensity of the thermal perturbation imposed in the simulations (12 °C-weeks).
Figure G8. Measures of stability (turnover) between two consecutive sample sizes (i.e., 100-250; 250-500; 500-750; 750-1000) for each response variable and site (FB = Fond Boucher; PB = Pointe Borgnesse; IR = Îlet à Rats).
Appendix H.  Chapter 4: Supporting information

H.1. Experimental design

H.1.1. Functional traits

We assembled communities by selecting species from a list of 798 functionally realistic and distinct species, whose missing trait values were imputed by (Appendix B). We selected the species depending on their position in the functional space, which we defined with the following traits: (1) colony maximum diameter (cm); (2) colony complexity; (3) dislodgement susceptibility; (4) bleaching susceptibility; (5) colony fecundity; (6) mode of larval development; (7) growth rate (diametral growth; mm.yr\(^{-1}\)); (8) overtop capacity. We provide below details about the traits not present in coraltraits.org (Madin et al., 2016a).

*Colony complexity*: The square root of the ratio between the area and planar area of a colony, measured when colony planar area = 1000 cm\(^2\) (Figure H1). We used McWilliam and colleagues’ (2018) geometric formulas and assumed circular planar areas (Table C5).

![Figure H1](image)

*Figure H1*. *Colony complexity* (Y axis) measured at colony planar surface area = 1000 cm\(^2\) for each growth forms (vertical dashed line; columnar: 4.99; corymbose: 4.16; branching: 4.11; digitate: 3.88; tabular: 3.13; encrusting long upright: 2.07; laminar: 1.46; massive: 1.41; encrusting: 1.00). We calculated colony surface area using geometric formulas (McWilliam et al., 2018b) and assumed circular planar areas.
Dislodgement susceptibility: The slope of the colony shape factor—a dimensionless measure of colony’s mechanical vulnerability (Madin and Connolly, 2006)—and colony planar area (on the log scale) for each growth form (Figure C12; Table C14). Slopes for laminar, columnar, encrusting and encrusting long upright are not empirically defined so we used the values estimated in §C.7.3.1.

Bleaching susceptibility: The species-specific coefficient of bleaching susceptibility defined from the growth rate, colony maximum diameter, corallite area and microscopic reduced scattering coefficient (Appendix E).

Mode of larval development: We attributed one to spawner and negative one to brooder.

Colony fecundity: The number of eggs produced per planar surface area (no. eggs cm⁻² of colony planar area), defined as:

\[
\text{colony fecundity} = \frac{\text{polyp fecundity} \times \text{ratio}_{3D/2D} \times \text{coefficient}_{\text{sexual system}}}{\text{corallite area}}
\]

with

\[
\text{coefficient}_{\text{sexual system}} = \begin{cases} 
0.5 & \text{for gonochore} \\
1.0 & \text{for hermaphrodite}
\end{cases}
\]

where corallite area = the area occupied by a polyp, and polyp fecundity = the number eggs or gametes contained in one polyp (coraltraits.org), ratio_{3D/2D} = the ratio between the surface area and the planar surface area of the colony, which we calculated for each growth form using geometric formulas (McWilliam et al., 2018b).

Overtop capacity: The capacity of branching and plating colonies to overtop small colonies. We attributed one to branching and plating growth forms and zero otherwise.
H.1.2. Definition of the functional space

After log_{10}-transforming colony maximum diameter, colony complexity, colony fecundity and growth rate to reduce the skewness of the distribution of these traits, we did a scaled principal component analysis and retained the four first principal components (89.7% of variance explained), which defined the functional space from where we sampled communities (Figure H2).

![Figure H2](image)

**Figure H2.** Functional space we defined to sample coral species (n = 978; grey dots), using the following traits: (1) colony maximum diameter; (2) colony complexity; (3) dislodgement susceptibility; (4) bleaching susceptibility; (5) colony fecundity; (6) mode of larval development; (7) growth rate; (8) overtop capacity.

H.1.3. Community assemblage

Using the Euclidean distance, we divided the functional space in different units: (i) one large unit containing all the species; (ii) $2^4 = 16$ medium units, each one covering two third of each dimension; (iii) $3^4 = 81$ small units, each one covering one third of each dimension (Figure H3). Each unit is characterized by its centroid and 16 vertices. We defined an algorithm that assembles communities of nine species in each unit, centered around the centroid and evenly spread out in space. The algorithm executed the following steps: (i) find the species the closest from the 16 vertices, calculate the functional richness (FRic) of all the possible communities of
nine species and select the one having the highest value; (ii) remove the selected species; (iii) repeat steps (i) and (ii) until less than nine species remained in the unit. In case only one or two communities were formed in a small unit, and at least four species remained unselected, the algorithm completed the community by selecting already-selected species that were the closest from the centroid. In case a small unit contained initially between one to eight species, the algorithm completed the community by selecting the external species that were the closest from the centroid.

A total of 789 different communities were created (88, 596 and 105 in the large, medium and small units, respectively), and 36 out of 81 small units did not contain any species. The algorithm then selected $n = nine$, six and three communities in each large, medium and small unit, respectively, by executing the following steps: (i) determine the range of FRic values present in the unit, (ii) divide the range in $n - 1$ portions of equal Euclidian distance; (iii) select the communities having FRic values the closest from the extremities of each portion. Finally, we manually added seven communities in the large unit and between one and three communities in 14 medium unites in order to obtain more even distributions of FRic values. The final procedure yielded a total of 245 communities (19, 160 and 66 in the large, medium and small units, respectively), which spanned a wide range of FRic values (Figure H4) and located in diverse places in the functional space (Figure H5).

**Figure H3.** Illustration of the functional space partition into units from which species were sampled in order to assemble 245 functionally distinct communities. We sampled species for the 4-dimensional space defined by the first four principal components created obtained by conducting a principle component analysis on the original height dimensional functional trait space.
Figure H4. Distribution of functional richness (FRic) of the 245 communities of nine species sampled in the large, medium and small units.
**Figure H5.** Example of communities created by sampling communities of nine species from the functional space at different locations and with different functional richness (FRic; values untransformed). Each dot represents one of the 798 species; red dots indicate the species belonging to the same community.
Figure H6. Overview of the analysis pipeline and example of expected results. The plot on the left shows the functional space represented by the first three principal components of the PCA (PC1, PC2, PC3); grey and red dots represent the entire trait dataset (798 species) and the nine species comprising an example community, respectively (we model 245 communities in total). The volume occupied by the community ($FRic$; log-transformed and scaled) and the coordinates of its centroids (black cross) along PC1 and PC2 (i.e., PC.1, PC.2) are the independent variables. The middle plots show the percent cover through time (± standard error) of individual coral species (coloured lines) and cumulative percentage cover (black lines) for the bleaching and cyclone scenarios (the disturbance was triggered at year = 4); red arrows represent the dependent variables resilience cover, resistance cover and recovery cover (rugosity is not displayed). We averaged each dependent variable between the two scenarios and fitted linear models. The right panel shows several possible relative influences of interaction between a given measure of resilience ($resilience_j$), $FRic$ and one of the two centroid variables.
coordinates ($PC.i$), as well as their related direction of effect. The green, blue and purple lines represent cases where we set $PC.i$ to the 1st, 2nd (median) and 3rd quartile of $PC.i$'s distribution across the entire sample ($n = 245$), respectively.
### H.2. Results

Table H1. Parameter estimates and 95% confidence limits of the best full generalised linear model with gamma distribution and log link function fitted for resilience after excluding four outliers from the dataset (n = 241, df = 233; pseudo $R^2 = 0.71$; McFadden’s pseudo $R^2 = 0.39$; AICc = 409.49; $FRic$ = functional richness, log-transformed and scaled; $PC.1$ and $PC.2$ = first two principal components of the communities’ centroids in the functional space, scaled).

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Estimate</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
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<tr>
<td>intercept</td>
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<tr>
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<td>0.212</td>
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</tr>
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<td>$FRic:PC.1:PC.2$</td>
<td>-0.02</td>
<td>-0.085</td>
<td>0.051</td>
</tr>
</tbody>
</table>
Table H2. Parameter estimates and 95% confidence limits of the “full” averaged generalised linear model with gamma distribution and log link function fitted for resilience rugosity (n = 241; pseudo $R^2 = 0.71$; McFadden’s pseudo $R^2 = 0.38 \pm 0.001$; four models are in the 95% confidence set; $FRic =$ functional richness, log-transformed and scaled; $PC.1$ and $PC.2 =$ first two principal components of the communities’ centroids in the functional space, scaled).

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Estimate</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
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<td>0.306</td>
</tr>
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<td>$PC.1:PC.2$</td>
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<tr>
<td>$FRic:PC.1:PC.2$</td>
<td>-</td>
<td>-</td>
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Figure H7. Diagnostic plots with the deviance residuals of the best full generalised linear model with gamma distribution and log link function fitted for resilience rugosity on the complete dataset (n = 245; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
**Figure H8.** Diagnostic plots with the deviance residuals of the best full generalised linear model with gamma distribution and log link function fitted for *resilience* *rugosity* after excluding four outliers from the dataset (n = 241; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
Table H3. Parameter estimates and 95% confidence limits of the best full beta regression model fitted for *resilience cover* (n = 245; df = 233; pseudo $R^2 = 0.1$; McFadden’s pseudo $R^2 = -1.15$; AICc = -644.53; *FRic* = functional richness, log-transformed and scaled; *PC.1* and *PC.2* = first two principal components of the communities’ centroids in the functional space, scaled).

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Estimate</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
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<tr>
<td><strong>Mean model (mu; Cauchit link function):</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>intercept</td>
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<td><em>PC.1</em></td>
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<tr>
<td>intercept</td>
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<td>-0.541</td>
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Table H4. Parameter estimates and 95% confidence limits of the “full” averaged beta regression model fitted for resilience cover (n = 245; pseudo $R^2 = 0.10$; McFadden’s pseudo $R^2 = -1.15 \pm 0.001$; two models are in the 95% confidence set; $FRic$ = functional richness, log-transformed and scaled; $PC.1$ and $PC.2$ = first two principal components of the communities’ centroids in the functional space, scaled).

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<tr>
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<td>intercept</td>
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<td>1.605</td>
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Figure H9. Diagnostic plots with standardized weighted residuals 2 of the best full beta regression model fitted for resilience cover (n = 245; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
Figure H10. Results and predictions of the “full” averaged beta regression model fitted for Resilience cover (= the total proportion of coral cover 10 years after the pulse disturbance, averaged between the bleaching and cyclone scenarios). Grey (a, c) and black arrows (e) represent the loadings of the first and second principal components of the initial weighted community centroids (PC.1 and PC.2, respectively); OC = overtop capacity; MLD = mode of larval development; GR = growth rate; CF = colony fecundity; DS = dislodgement susceptibility; CMD = colony maximum diameter; CC = colony complexity; BS = bleaching susceptibility. Black circles (b, d, e) show the communities’ initial functional richness (FRic, log-transformed and scaled) and position along PC.1 and PC.2; we
used these communities (n = 245) to predict resilience (red to blue colour ramp) in the entire parameter space (we set FRic, PC.1 and PC.2 to their median value in e, d and b, respectively). The yellow symbols designate the communities presented in Figure 4.5.
**Table H5.** Parameter estimates and 95% confidence limits of the best full beta regression model fitted for resistance cover after excluding one outlier from the dataset (n = 244; df = 228; pseudo $R^2 = 0.67$; McFadden’s pseudo $R^2 = -1.99$; AICc = -528.72; $FRic$ = functional richness, log-transformed and scaled; $PC.1$ and $PC.2$ = first two principal components of the communities’ centroids in the functional space, scaled).

<table>
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<th>Estimate</th>
<th>2.5%</th>
<th>97.5%</th>
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<td>Mean model ($mu$; loglog link function):</td>
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<td>$FRic$</td>
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<td>-0.482</td>
<td>-0.112</td>
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<td>$PC.1$</td>
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<td>$PC.2$</td>
<td>-0.05</td>
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<tr>
<td>$FRic:PC.1$</td>
<td>-0.10</td>
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<td>0.080</td>
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<tr>
<td>$FRic:PC.2$</td>
<td>-0.37</td>
<td>-0.563</td>
<td>-0.176</td>
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<tr>
<td>$PC.1:PC.2$</td>
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<tr>
<td>$FRic:PC.1:PC.2$</td>
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<td>-0.137</td>
<td>0.266</td>
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Table H6. Parameter estimates and 95% confidence limits of the “full” averaged beta regression model fitted for resistance cover (n = 244; pseudo $R^2 = 0.69$; McFadden’s pseudo $R^2 = -1.95 \pm 0.009$; 62 models are in the 95% confidence set; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Estimate</th>
<th>Confidence limits</th>
</tr>
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<tbody>
<tr>
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<tr>
<td>Mean model (mu; loglog link function):</td>
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<tr>
<td>intercept</td>
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<td>0.329</td>
</tr>
<tr>
<td>FRic</td>
<td>-0.04</td>
<td>-0.081</td>
</tr>
<tr>
<td>PC.1</td>
<td>0.30</td>
<td>0.251</td>
</tr>
<tr>
<td>PC.2</td>
<td>0.08</td>
<td>0.032</td>
</tr>
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<td>-0.027</td>
</tr>
<tr>
<td>FRic:PC.2</td>
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<td>-0.059</td>
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<tr>
<td>PC.1:PC.2</td>
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<td>-0.046</td>
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<td>Precision model (phi; log link function):</td>
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<tr>
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<td>FRic:PC.2</td>
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<td>PC.1:PC.2</td>
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<tr>
<td>FRic:PC.1:PC.2</td>
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<td>-0.063</td>
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</table>
**Figure H11.** Diagnostic plots with standardized weighted residuals 2 of the best full beta regression model fitted for resistance cover on the complete dataset (n = 245; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
Figure H12. Diagnostic plots with standardized weighted residuals 2 of the best full beta regression model fitted for resistance cover after excluding one outlier from the dataset (n = 244; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
Figure H13. Results and predictions of the “full” averaged beta regression model fitted for Resistance cover (= 1 - the proportional reduction of total coral cover caused by the pulse disturbance, averaged between the bleaching and cyclone scenarios). Grey (a, c) and black arrows (e) represent the loadings of the first and second principal components of the initial weighted community centroids (PC.1 and PC.2, respectively); OC = overtop capacity; MLD = mode of larval development; GR = growth rate; CF = colony fecundity; DS = dislodgement susceptibility; CMD = colony maximum diameter; CC = colony complexity; BS = bleaching susceptibility. Black circles (b, d, e) show the communities’ initial functional richness (FRic, log-transformed and scaled) and position along PC.1 and PC.2; we
used these communities (n = 245) to predict resilience (red to blue colour ramp) in the entire parameter space (we set FRic, PC.1 and PC.2 to their mean value in e, d and b, respectively). The yellow symbols designate the communities presented in Figure 4.5.
Table H7. Parameter estimates and 95% confidence limits of the full linear model fitted for recovery cover ($n = 245$; $df = 237$; pseudo $R^2 = 0.75$; McFadden’s pseudo $R^2 = 0.19$; AICc = 1472.04; $FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).}

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Estimate</th>
<th>Confidence limits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<tr>
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<td>$FRic:PC.2$</td>
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<td>$FRic:PC.1:PC.2$</td>
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Table H8. Parameter estimates and 95% confidence limits of the full linear model fitted for recovery cover with exponential variance structured applied to FRic (n = 245; df = 237; pseudo $R^2 = 0.74$; McFadden’s pseudo $R^2 = 0.20$; AICc = 1459.14; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).

<table>
<thead>
<tr>
<th>Explanatory variables</th>
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<th>97.5%</th>
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<tbody>
<tr>
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<tr>
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<td>3.000</td>
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<tr>
<td>PC.1</td>
<td>-7.32</td>
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<td>PC.2</td>
<td>0.03</td>
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<td>$\delta$ (varExp)</td>
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Table H9. Parameter estimates and 95% confidence limits of the “full” averaged linear model fitted for recovery cover with exponential variance structured applied to FRic (n = 245; pseudo $R^2 = 0.74$; McFadden’s pseudo $R^2 = 0.20 \pm 0.000$; three models are in the 95% confidence set; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Estimate</th>
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<th>97.5%</th>
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<td>FRic:PC.2</td>
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<td>PC.1:PC.2</td>
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<td>$\delta$ (varExp)</td>
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<td>0.193</td>
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Figure H14. Diagnostic plots with Pearson residuals of the full linear model fitted for recovery cover (n = 245; \(FRic\) = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
Figure H15. Diagnostic plots with normalised residuals of the full linear model fitted for recovery cover and applying exponential variance structured to FRic (n = 245; FRic = functional richness, log-transformed and scaled; PC.1 and PC.2 = first two principal components of the communities’ centroids in the functional space, scaled).
Figure H16. Results and predictions of “full” averaged linear model fitted for recovery cover (= the rate of recovery during the first three years after the disturbance; in % cover yr\(^{-1}\); averaged between the bleaching and cyclone scenarios) and applying varExp variance structured to FRic. Grey (a, c) and black arrows (e) represent the loadings of the first and second principal components of the initial weighted community centroids (PC.1 and PC.2, respectively); OC = overtop capacity; MLD = mode of larval development; GR = growth rate; CF = colony fecundity; DS = dislodgement susceptibility; CMD = colony maximum diameter; CC = colony complexity; BS = bleaching susceptibility. Black circles (b, d, e) show the communities’ initial functional richness (FRic, log-transformed and scaled) and position along PC.1 and PC.2; we used these communities (n = 245) to predict resilience (red to blue...
colour ramp) in the entire parameter space (we set FRic, PC.1 and PC.2 to their mean value in e, d and b, respectively). The yellow symbols designate the communities presented in Figure 4.5.

Figure H17. Effect of the feedback process between reef rugosity and grazing pressure for the bleaching scenario: high reef rugosity generates high grazing pressure, which enhances total coral cover. Each line represents total percentage coral cover through time (left panel) or cover grazed (right panel) in one community, averaged over five replicates (n = 245).
Figure H18. Effect of the feedback process between reef rugosity and grazing pressure for the cyclone scenario: high reef rugosity generates high grazing pressure, which enhances total coral cover. Each line represents total percentage coral cover through time (left panel) or cover grazed (right panel) in one community, averaged over five replicates (n = 245).
Figure H19. Correlation among species (n = 798) between bleaching and dislodgement susceptibility. Each gray circle represents the trait value averaged by species. The horizontal dashed line indicates the mean bleaching susceptibility. Dislodgement susceptibility is growth form-specific (Figure C12). Also shown is the Spearman’s rank correlation statistic ($r_s$) and associated significance level (*** corresponds to $P < 0.001$) and a loess line for visual aid.
**Figure H20.** Correlations among species (n = 798) between the competitive trait *overtop capacity* and *colony complexity* (effect trait), *dislodgement* and *bleaching susceptibilities* (resistance traits) and *growth rate* (mm yr\(^{-1}\); log\(_{10}\)-transformed) and *colony fecundity* (no. eggs cm\(^{-2}\) of colony planar area; log\(_{10}\)-transformed) (recovery traits). Each gray circle represents the trait value averaged by species; boxes delimit 1st and 3rd quartiles, whiskers extend to 1.5 × IQR, thick vertical lines represent group medians, black circles represent group means. Also shown the Glass’ rank biserial correlation statistic (*r_g*) and associated 95% confidence intervals.