

A modified trait-based framework for assessing the resilience of ecosystem services provided by coral reef communities

BRUNO S. CARTURAN,^{1,2,†} LAEL PARROTT,^{1,2,3} AND JASON PITHER^{1,2,3}

¹*Department of Biology, University of British Columbia, Okanagan Campus, 1177 Research Road, Kelowna, British Columbia V1V 1V7 Canada*

²*Institute for Biodiversity, Resilience, and Ecosystem Services, University of British Columbia, Okanagan Campus, 1177 Research Road, Kelowna, British Columbia V1V 1V7 Canada*

³*Department of Earth, Environmental and Geographic Sciences, University of British Columbia, Okanagan Campus, 1177 Research Road, Kelowna, British Columbia V1V 1V7 Canada*

Citation: Carturan, B. S., L. Parrott, and J. Pither. 2018. A modified trait-based framework for assessing the resilience of ecosystem services provided by coral reef communities. *Ecosphere* 9(5):e02214. 10.1002/ecs2.2214

Abstract. Climate change and other anthropogenic disturbances are having dramatic impacts on tropical coral reefs and the ecosystem services they provide. Anticipating change in ecosystem services is a pressing challenge that requires understanding how species respond to an environmental change, and how they contribute to ecosystem services. Building on analogous efforts by plant ecologists, we propose a trait-based framework that aims to predict the resistance and recovery of coral ecosystem services against both pulse and press disturbances. The framework involves identifying effect, resistance, and recovery traits across coral species and using these to ascertain how species might (1) contribute to a service, (2) resist disturbance, and (3) recover after the disturbance. By identifying trait functional overlaps and quantifying correlations among the trait types, the framework can yield a better understanding of the potential mechanistic links between community assembly, ecosystem dynamics, and ecosystem functioning. We demonstrate the utility of the framework by applying it to a virtual scenario, implemented via simulation, in which habitat provisioning is the focal ecosystem service, and cyclones and bleaching events are the disturbances of interest. This demonstration required us to assemble an extensive dataset of relevant traits—a process that revealed key gaps in the coral trait database and in our understanding of coral functional ecology. The framework can provide predictive power for the resilience of ecosystem services and can also help identify crucial knowledge gaps, research objectives, and strategies for applying a trait-based approach to advancing coral reef science and conservation.

Key words: coral community; ecosystem service; effect, resistance and recovery framework; functional traits; resilience; trait correlations; trait functional overlap.

Received 19 March 2018; revised 28 March 2018; accepted 30 March 2018. Corresponding Editor: Hunter Lenihan.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

†E-mail: bruno.carturan@alumni.ubc.ca

INTRODUCTION

Coral reefs provide numerous ecosystem services (Moberg and Folke 1999), the total value of which is estimated to be more than \$352,000 ha⁻¹.yr⁻¹ (Costanza et al. 2014). The provisioning of an architecturally complex habitat that supports a high diversity of fish and macroinvertebrates (Graham and Nash 2013,

Fabricius et al. 2014) is arguably the most important ecosystem service provided by coral communities; numerous activities, such as fishing and tourism, are directly dependent on coral biodiversity (Wells et al. 2006, Teh et al. 2013, Rogers et al. 2014). The future of coral reef ecosystems and the habitat they provide is the source of serious concern (Bellwood et al. 2004, Bridge et al. 2013). Numerous pulse (e.g.,

cyclone, bleaching, crown of thorn) and press disturbances (e.g., fishing, pollution, acidification) are taking their toll (Pendleton et al. 2016), as are natural disturbance regimes (e.g., cyclones and warm events) whose intensity is increasing due to climate change (Hoegh-Guldberg and Bruno 2010).

The percentage cover of corals is decreasing worldwide (Gardner et al. 2003, Bruno and Selig 2007), and numerous reefs have been permanently lost. Less exposed or more resilient reefs potentially experience reassembly owing to immigration, range shifts, and asymmetrical species response to disturbances (Graham et al. 2014). Nevertheless, changes in coral species composition likely alter the delivery of ecosystem services because of the unique contributions of many species (Alvarez-Filip et al. 2013). For instance, the cumulative effects of disturbances in the Caribbean during recent decades have caused coral communities to switch from a dominance of large and complex *Acropora* species to simpler massive and small, weedy species. Consequently, the architectural complexity of the reefs is being reduced (Alvarez-Filip et al. 2009), which in turn affects the abundance, diversity, and trophic structure of the associated fish community (Rogers et al. 2014). Similar shifts in the functional composition of coral communities are observed in other parts of the globe (Darling et al. 2013, Denis et al. 2017). Managing ecosystem functions (among which are services), and in particular the provisioning of habitat, is a pressing challenge that requires a better understanding of the mechanisms linking disturbance, diversity, and functions (Graham 2014, Oliver et al. 2015).

A functional traits approach can help to establish these links (McGill et al. 2006, Cadotte et al. 2011) and has led to a better understanding of the mechanisms determining community assembly (e.g., Kraft et al. 2015), ecosystem functioning (e.g., Cadotte 2017), and resilience (e.g., O'Brien et al. 2014). It can also yield predictive capability (Cadotte et al. 2015). Lavorel and Garnier (2002), and subsequently Suding et al. (2008), have 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.,

traits involved in ecosystem functions) and response traits (i.e., traits implicated in response against disturbances). If a trait is involved in both the response and the 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 has been 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).

The consideration of functional traits for understanding aspects of coral species ecology has a long history (e.g., Porter 1976, Sheppard 1979, Chappell 1980, Highsmith 1981), but only recently have coral ecologists advocated adopting a more systematic trait-based approach (Madin et al. 2016b). We believe that adopting a trait-based response-effect framework for coral communities would not only advance our understanding of the mechanisms linking disturbances to ecosystem functions, but would also help identify key knowledge gaps and priorities for research.

Here, we build on the framework developed by Suding et al. (2008) by distinguishing between resistance traits and recovery traits, in order to consider these two components of resilience (McClanahan et al. 2012). We start by presenting our effect-resistance-recovery traits framework. We then illustrate its applicability by focusing on habitat provisioning, a key ecosystem service provided by corals. We review the literature to identify relevant traits, and to ascertain their influence on (1) the habitat provisioning function, (2) the resistance against cyclones or bleaching events, and/or (3) in recovery processes. Based on our findings, we assemble an extensive database of trait data, drawing from the coraltraits.org database (<https://coraltraits.org>; Madin et al. 2016a) and from the primary literature. Using these data, we then quantify correlations and overlaps (i.e., functional redundancies) 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 resilience in habitat provisioning by corals. Lastly, we discuss the different benefits the framework could provide to coral reef science.

THE EFFECT-RESISTANCE-RECOVERY TRAITS FRAMEWORK

The effect-response traits framework defined by Suding et al. (2008) relies on the assumption that functional traits determine ecosystem functions and community response to disturbances (Fig. 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 (1) effect traits and their correlations with response traits, and (2) 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; Fig. 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.

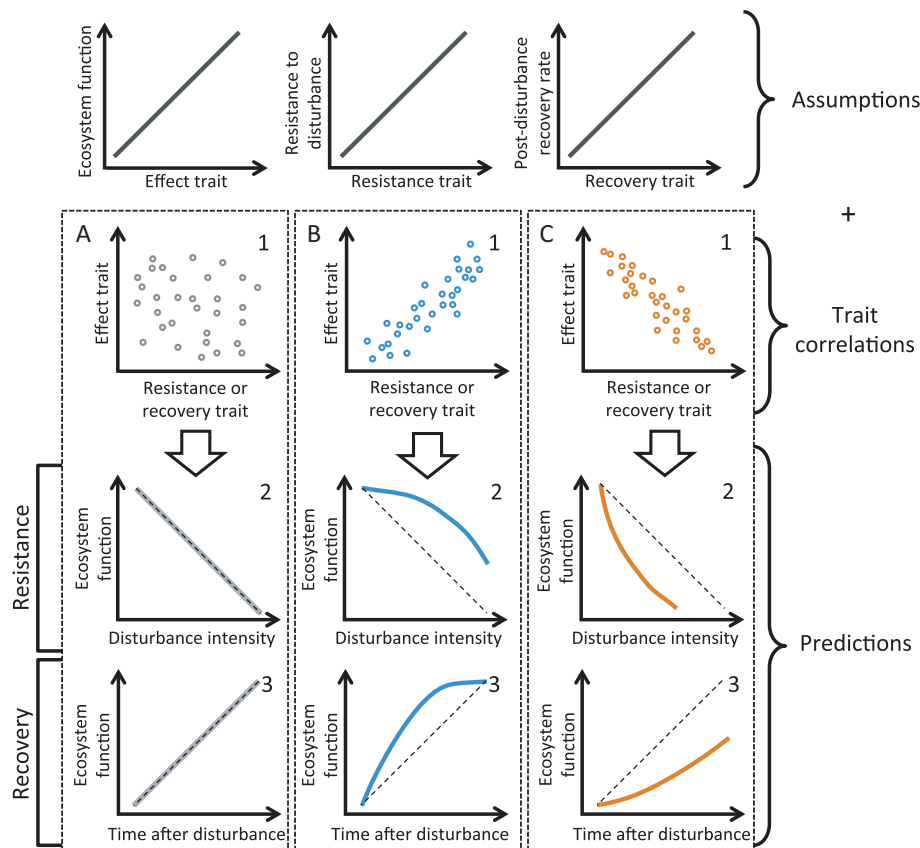


Fig. 1. The effect-resistance-recovery traits framework: Assumptions about traits’ roles in an ecosystem process (top row) and correlations between effect and resistance or recovery traits (A1, B1, C1) allow for predicting the resistance and the recovery of the function against a disturbance. Solid lines 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).

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 Fig. 1). With no correlation between effect and resistance traits (Fig. 1A1), the provisioning of function will decline (Fig. 1A2) or recover as expected with the null model (Fig. 1A3). When effect and resistance traits are positively correlated (Fig. 1B1; i.e., the most resistant species contribute most to the function), we can expect a smaller change in the ecosystem function (Fig. 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; Fig. 1B3). In these cases, the level of function will surpass null model expectations. When effect and resistance traits are negatively correlated (Fig. 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 (Fig. 1C2). The function is considered non-resistant. We also expect a slower recovery of function in this scenario (Fig. 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 (1) synthesizing knowledge and assumptions about traits and their respective roles in effect, resistance, and recovery, (2) quantifying associations among traits, and (3) demonstrating our capacity to predict the resilience of an ecosystem function using the framework and the available data. Lastly, (4) we discuss the benefits of applying this framework and how it helps prioritize future research efforts.

MATERIALS AND METHODS

All data processing and analysis as well as simulations were conducted using R (version 3.4.0, R-Core Team 2017). 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>).

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 (Appendix S1: Table S1). 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.marine-species.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 Appendix S1: Table S1.

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. (2016b).

Trait association 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 (10,000 permutations) to test the null hypothesis of no difference in the average maximum colony diameter among brooders and spawners. We used a χ^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).

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 1) and the trait functional overlaps and correlations we quantified (Fig. 2; Appendix S1: Figs. S2–S4) can be used to predict the resilience of an ecosystem function (cf. Fig. 1). Details of the model are presented in the Appendix. 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 (1) the disturbances only affect the focal community; (2) 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; (3) 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 was 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 (Fig. 1B1), the recovery of the function is expected to be faster, on average, than under the null model outcomes (Fig. 1B3).

RESULTS

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 1). Fourteen of the 25 traits were excluded from our correlation analyses for one or more of the following reasons: (1) Data were available for too few species (e.g., age and size at maturity, colony fecundity, HSP concentration, MAAs); (2) 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); (3) the measurements were too imprecise (e.g., generation length—out of the 695 species for which information is available, 673 have a 10-yr generation length); (4) no consistent methods for measuring the trait have been established (e.g., capacity to

Table 1. Coral functional traits involved in the habitat provisioning function, resistance, and recovery against disturbances (cyclone and coral bleaching).

Functional trait	Type			Explanation	No. sp	Used here	References
	Eff.	Res.	Rec.				
Age and size at maturity			Both	Later maturity causes lower post-disturbance recruitment rates, but there is a trade-off between starting reproduction early, while being still very vulnerable	3 for age; 7 for size	No	Hughes (1984), Hall and Hughes (1996)
Capacity of fragment regeneration			Cyc	Reduced mortality rate, increased recovery rate	Proxy?	No	Highsmith (1982)
Colony fecundity			Both	Higher fecundity implies higher potential offspring	12	No	Álvarez-Noriega et al. (2016)
Corallite area		Blea		Proxy for energy reserves (?)	713	Yes	van Woesik et al. (2012a), Darling et al. (2012)
Colony maximum diameter	Hab			Enhance heterotrophy by determining the range size of prey	307	Yes	Houlbrèque et al. (2009)
				Colonies with more complex morphologies contribute more to the architectural complexity			Darling et al. (2017)
		Cyc		Colonies with more complex morphologies tend to be more fragile as they grow bigger; opposite for simpler ones			Madin and Connolly (2006), Madin et al. (2014)
		Blea		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”	307	Yes	Porter (1976), Kim and Lasker (1998), Houlbrèque et al. (2009), van Woesik et al. (2012b), Wooldridge (2014)
Egg size			Both	Smaller eggs have a shorter time to motility which favors local recruitment	25	No	Figueiredo et al. (2013)
				Bigger egg implies more lipid reserves and so higher probability of recruitment (not proven for coral)			Álvarez-Noriega et al. (2016) and references therein
Energy reserves		Blea		Reduces coral susceptibility, increases recovery rates and facilitates acclimation	8	Yes	Anthony et al. (2009), Grottole et al. (2014)
Fluorescent pigment concentration		Blea		Provides photoprotection, but not under higher temperature (?)	22	Yes	Salih et al. (1998), Baird et al. (2009a), Hidaka (2016)
Generation length			Both	Older colonies are more fertile	845	No	Hall and Hughes (1996)
				Shorter generation length increases recovery rate (weedy species)			Ritson-Williams et al. (2009)
Growth form	Hab			More complex morphologies contribute more to the architectural complexity	816	Yes	Darling et al. (2017)
			Cyc	More complex morphologies are more fragile	816	Yes	Madin and Connolly (2006), Madin et al. (2014)
			Blea	Modulates thickness of boundary layer and so mass transfer	816	Yes	van Woesik et al. (2012b)
		Modulates DIC diffusion from water to symbiont	Wooldridge (2014)				
				Mediates predation rate (heterotrophy) depending on S/V ration and “shading effect”			Porter (1976), Kim and Lasker (1998), Houlbrèque et al. (2009)
Growth rate		Blea	Both	Rapid recovery of free space	125	Yes	Highsmith (1982), Guest et al. (2016)

(Table 1. *Continued*)

Functional trait	Type			Explanation	No. sp	Used here	References
	Eff.	Res.	Rec.				
Heat-shock proteins concentration (HSP)		Blea		HSPs act as molecular chaperones, which maintain protein structure and cell function, particularly following stress	?	No	Baird et al. (2009a), Fitt et al. (2009)
Heterotrophy		Bea		Allows to meet the required DME despite the loss of the symbiont	Proxy?	No	Grottoli et al. (2006), Houlbrèque et al. (2009), Levas et al. (2016)
Metabolic rate (respiration rate)		Blea		Corals with low growth rates and high metabolic rates acclimatize more effectively	20	Yes	Gates and Edmunds (1999) but see Jokiel and Coles (1990)
Mode of larval reproduction			Both	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	313	Yes	Ritson-Williams et al. (2016) and references therein Figueiredo et al. (2013), Keith et al. (2015)
Mucus production		Blea		Mucus (polysaccharide) has a solar screening protection role and reduces photoinhibition.	?	No	Fitt et al. (2009), Wooldridge (2009)
MAAs		Blea		Absorb UV and functions as an antioxidant	?	No	Yakovleva et al. (2004)
Physiological integration		Blea		Influences the patchiness of bleaching and induced tissue mortality on the colony	Proxy?	No	Baird and Marshall (2002)
Microscopic reduced-scattering coefficient ($\mu'_{s,m}$)		Blea		Influences light-scattering and so the endosymbiont light environment	93	Yes	Marcelino et al. (2013), Swain et al. (2016a)
Reproduction frequency			Both	Reproducing during one or two short periods per year increases fertilization rate, saturates predators but is more risky against environmental stochasticity	?	No	Harrison and Wallace (1990)
Reproductive investment			Both	Eggs with more energy reserve are more likely to be recruited (?)	?	No	Not investigated for corals
Symbiont acquisition			Both	Larvae obtaining the symbiont vertically can have more energy and so can survive disperse further	?	No	Baird et al. (2009b), Gleason and Hofmann (2011)
Symbiont density		Blea		Higher amount of ROS produced in case of the disruption of photosystem II	35	Yes	Cunning and Baker (2013), Wooldridge (2014)
Tissue thickness		Blea		Mediates shading protection to endosymbiont Mediates DIC diffusion	20	Yes	Stimson et al. (2002), Baker et al. (2008) Wooldridge (2014)

Notes: The table shows the type of process (effect, Eff.; resistance, Res.; recovery, Rec.), function (habitat provisioning, Hab), and disturbance (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 concentrations were assessed using lipid and chlorophyll *a* concentrations, respectively. DME, daily metabolic energy; DIC, dissolved inorganic carbon (CO₂ and HCO₃⁻); ?, data are either anecdotal, or sparse, or not available; Proxy?, data might not be quantifiable and would require finding a proxy trait; MAAs, myco-sporine-like amino acids.

generate viable fragments, mucus production, physiological integration); or (5) 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).

REVIEW OF FUNCTIONAL TRAITS AND ASSOCIATED ASSUMPTIONS

Effect traits involved in the habitat provisioning function

Structural complexity is a key reef attribute and is estimated either visually (Wilson et al.

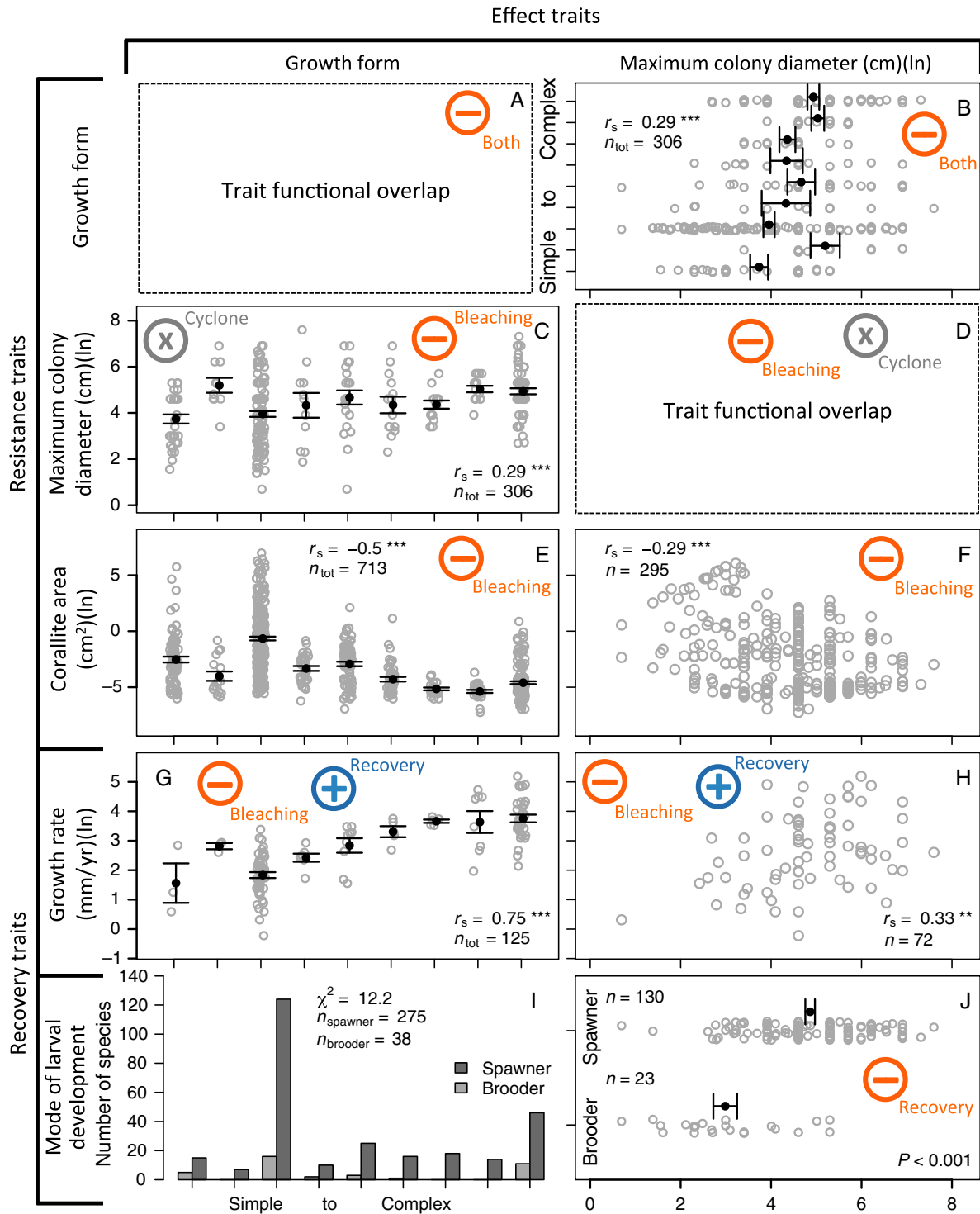


Fig. 2. Associations between effect, resistance, and recovery traits. The colored circles with a blue positive or an orange negative sign, respectively, refer to a positive or a negative relationship between effect and resistance or recovery and correspond to the color system in Fig. 1. For example, the positive correlation between maximum colony diameter and growth rate implies a negative correlation between effect and bleaching resistance

(Fig. 2. *Continued*)

(H): Species reaching bigger sizes contribute more to the habitat complexity, and species with faster growth rates are more bleaching sensitive (Table 1; Appendix S1: Fig. S1D). There is trait functional overlap when a trait is involved in both the effect and the response (A, D). The gray 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 gray circle represents the trait value averaged by species, the black point is the averaged trait value over all the species by category, and the error bars extend to \pm one standard error (SE). Statistical tests used are as follows: Spearman's rank correlation (r_s) (B, C, E, F, G, H); contingency test (χ^2) (I); permutation test (J). Asterisks indicate the test statistics' significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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 1). Complex growth forms are particularly important for juvenile and small size fish species (Wilson et al. 2006, Emslie et al. 2008) 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. 2011, 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 hispidose), 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.

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 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 to 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 CO₂ of the zooxanthellae and reduce the external supply of dissolved inorganic carbon (i.e., CO₂ and HCO³⁻; Wooldridge 2014). An insufficient provisioning of CO₂ 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 (1) increasing the heterotrophic carbon supply to the symbiont, (2) protecting the symbiont against radiation in order to reduce its demand in CO₂, (3) reducing symbiont density, (4) increasing heterotrophy to compensate for the loss of the symbiont, and/or (5) actively repairing the damage caused by ROS. Correspondingly, numerous functional traits are potentially involved (Table 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 vs. 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: (1) a positive correlation with maximum colony diameter (Appendix S1: Fig. S1B; Spearman $r_s = 0.34$;

$n = 155$; $P < 0.001$), which could be explained by a decrease in 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); (2) a negative correlation with corallite area (Appendix S1: Fig. S1C; 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 1); (3) a positive association with growth rate (Appendix S1: Fig. S1D; 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 (Marshall and Baird 2000, Graham et al. 2006). 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 (Appendix S1: Fig. S5; Spearman $r_s = -0.22$; $n = 17$; $P = 0.399$) or with the taxon-BRI (Appendix S1: Fig. S1E; 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 (Appendix S1: Table S1). Lastly (4), and in contrast to expectations, we observed only a weak association between growth form and the taxon-BRI (Appendix S1: Fig. S1A; 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 as follows: (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; Porter 1976, Kim and Lasker 1998), 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 CO₂ (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 *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 (Appendix S1: Fig. S1H; 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 (≤ 30 ; Appendix S1: Fig. S1).

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 1).

Recovery via asexual reproduction.—Coral regrowth can allow for faster recovery than sexual reproduction (Highsmith 1982, Guest et al. 2016). 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., 5–10 yr). 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: (1) larval production, (2) settlement success, and (3) 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, Alvarez-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 lecithotrophic 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 2008). Under unfavorable conditions (i.e., stressful environment, isolation), brooders are considered better suited for local sexual recruitment (Szmant 1986, Edinger and Risk 1995, Keith et al. 2015). 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 (Vermeij 2005, Jones et al. 2009, Figueiredo et al. 2013, Torda et al. 2013) 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 (CCA) 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).

QUANTIFYING TRAIT ASSOCIATIONS

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 1, Fig. 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 (Fig. 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: (1) maximum colony diameter (Fig. 2B, C; Spearman $r_s = 0.29$; $n = 306$; $P < 0.001$)—more complex morphologies tend to reach bigger diameters; (2) corallite area (Fig. 2E; Spearman $r_s = -0.50$; $n = 713$; $P < 0.001$)—more complex morphologies have smaller corallites; (3) tissue thickness (Appendix S1: Fig. S2B; Spearman $r_s = -0.60$; $n = 20$; $P = 0.005$)—more complex morphologies have thinner tissue; (4) growth rate (Fig. 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 (Appendix S1: Fig. S2E; Spearman $r_s = -0.11$; $n = 93$; $P = 0.298$) and symbiont density (Appendix S1: Fig. S2C; Spearman $r_s = -0.23$; $n = 35$; $P = 0.183$) do not show a correlation with growth form complexity. The small sample sizes (usually less than 10 species per morphological group) associated with the remaining three resistance traits—respiration rate, chlorophyll *a* concentration, and lipid content—preclude meaningful analysis (Appendix S1: Fig. S2A, D, F).

Maximum colony diameter is significantly negatively correlated with corallite area (Fig. 2F; Spearman $r_s = -0.294$; $n = 295$; $P < 0.001$) and growth rate (Fig. 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 (Appendix S1: Fig. S2K; Spearman $r_s = 0.22$; $n = 51$; $P = 0.115$); symbiont density (Appendix S1: Fig. S2I, Spearman $r_s = 0.10$; $n = 23$; $P = 0.634$), or not enough data were available for the analysis to be informative (Appendix S1: Fig. S2G, H, J, L).

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

(Fig. 2J; permutation test; 10,000 permutations; $P < 0.001$). We found no differences between spawners and brooders for growth form (Fig. 2I; χ^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 (Fig. 2G, H).

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.

Description of the simulated coral community

The information described above informed the parameterization of our simulation model (see Appendix S1), including the trait characteristics of the three virtual coral species, which are visualized in Fig. 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

(Fig. 2C; Appendix S1: Fig. S3B), smaller polyps (Fig. 2E, F; Appendix S1: Fig. S3A, C), and faster growth rates (Fig. 2G, H; Appendix S1: Fig. S1D). 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 (Fig. 2J; Appendix S1: Fig. S4A) 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 (Fig. 2B; Appendix S1: Fig. S3B) and its smaller polyps (Appendix S1: Fig. S3A, C). Compared to Species 1, Species 2 recovers much more slowly via vegetative growth (Fig. 2G; Appendix S1: Fig. S3D) but equally via larval recruitment because it too is a spawner (Appendix S1: Fig. S4B). 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 (Fig. 2C; Appendix S1: Fig. S1B) and larger corallites (Fig. 2F; Appendix S1: Fig. S1C). It has a faster growth

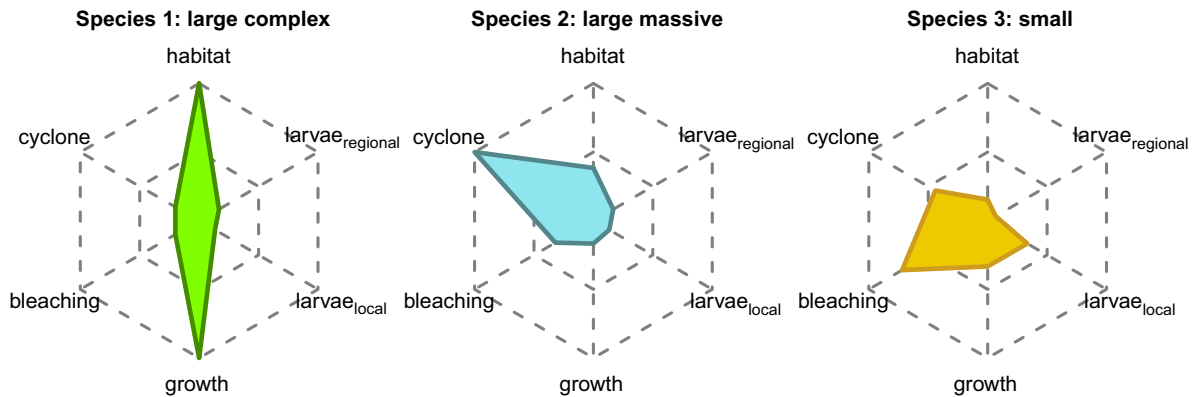


Fig. 3. Functional characteristics of the three species defined in the model. Each vertex of the web corresponds to a process: contribution to the habitat provisioning function, capacity to recover via recruitment of larvae regionally and locally produced and via vegetative growth, resistance to bleaching events and cyclones. The colored 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 (Appendix S1: Table S4) 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.

rate than Species 2 but slower than Species 1 (Fig. 2G). Finally, it is a brooding species (Fig. 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.

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 (Fig. 4A, G). The habitat provisioning function decreases faster in relation to disturbance intensity than expected based on the null model outcomes (Fig. 4A, G). This is because the colonies contributing the most to the function have a higher probability of being extirpated (case corresponding to Fig. 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 (Fig. 4E, F). Larval connectivity has only a small influence on the recovery rate (Fig. 4B, C). In the case of a more intense perturbation, most of the remaining habitat is supported by Species 2 (Fig. 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 (Fig. 4H, K). In consequence, the rate of recovery of the function is strongly influenced by connectivity (Fig. 4H, L). In contrast, species 3 is less affected by isolation (Fig. 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 (Fig. 3; Appendix S1: Table S3). 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 (Fig. 1B3).

The major difference of the bleaching response compared to a cyclone scenario (Appendix S1: Fig. S8) is the low resistance of Species 2, which results in a higher vulnerability of the

habitat (only Species 3 colonies are resistant; Appendix S1: Fig. S8A, 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 (Fig. 3; Appendix S1: Table S3). Consequently, Species 2 almost fails to recover in the case of high disturbance intensity and low larval connectivity (Appendix S1: Fig. S8L).

DISCUSSION AND CONCLUSION

Suding et al. (2008)'s 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 et al. (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 (Tables 1 and 2) and the relationships between many traits and

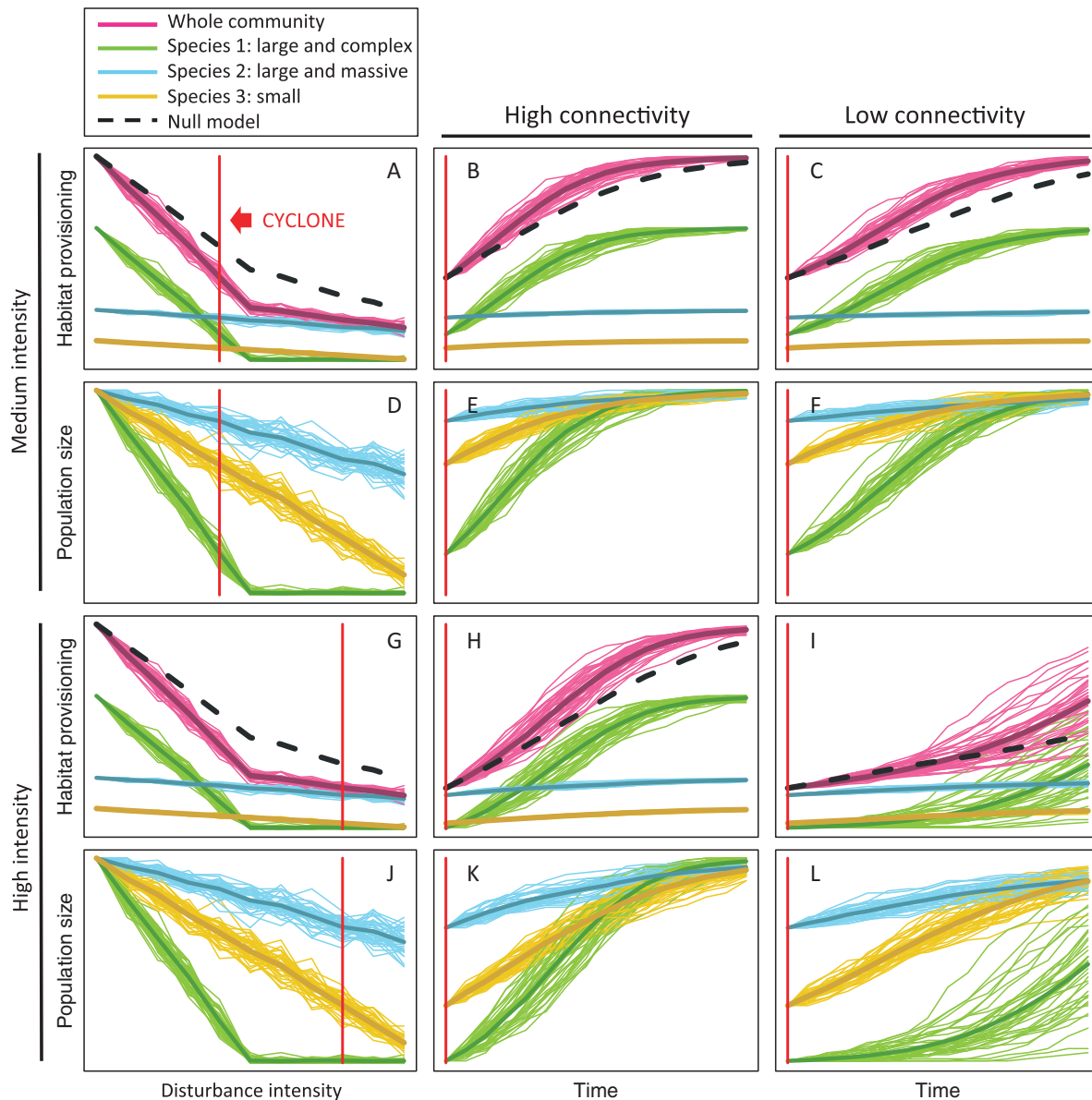


Fig. 4. Expected resistance (left column) and recovery rate (middle and right columns) of the coral community defined in the model, expressed as population size (panels D, E, F, J, K, L) and the habitat provisioning function it provides (panels A, B, C, G, H, I) against cyclone disturbances, under different 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 Fig. 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 Appendix S1: *Qualitative mechanistic model*). 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.

Table 2. Summary of the associations of effect traits with resistance and recovery traits related to the habitat provisioning function, cyclone, and coral bleaching disturbances.

Functional traits	Resistance	Recovery	Effect traits	
			Growth form	Maximum colony diameter
Growth form	Yes		Negative (C2, cyclone) Negative (C2, Bleaching)	Negative (C2, cyclone) Negative (C2, Bleaching)
Colony maximum diameter	Yes		Dual (B2, C2, cyclone)† Negative (C2, Bleaching)	Dual (B2, C2, cyclone)† Negative (C2, Bleaching)
Corallite area	Yes		Negative (C2, Bleaching)	Negative (C2, Bleaching)
Chlorophyll <i>a</i> concentration	Yes		Not enough data (Bleaching)	Not enough data (Bleaching)
Dark respiration	Yes		Not enough data (Bleaching)	Not enough data (Bleaching)
Lipid content	Yes		Not enough data (Bleaching)	Not enough data (Bleaching)
Microscopic reduced-scattering coefficient ($\mu'_{s,m}$)	Yes		None (A2, Bleaching)	None (A2, Bleaching)
Symbiont density	Yes		Not enough data (Bleaching)	Not enough data (Bleaching)
Tissue thickness	Yes		Not enough data (Bleaching)	Not enough data (Bleaching)
Growth rate	Yes	Yes	Negative (C2, Bleaching)	Negative (C2, Bleaching)
Growth rate		Yes	Positive (B3)	Positive (B3)
Mode of larval development		Yes	None (A3)	Negative (C3)

Note: 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; cf. Fig. 1).

† Combination of a positive and a negative correlation: Larger massive colonies are more resistant to cyclone, as opposed to colonies with complex growth forms.

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: (1) to gain a better understanding of relationships between traits and processes, (2) to make accurate, quantitative predictions about ecosystem functioning, (3) to identify key traits for gap-filling the coral trait database, and (4) to improve management of coral communities.

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 et al. (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 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 (Tables 1 and 2) such that multi-trait models can be developed to better predict species-specific performance.

Integrative 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 et al. (2008)'s 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 et al. (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 et al. (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 service provided by a population by using the appropriate effect traits.

Identify 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 (1) selecting a set of relevant and easy to measure functional traits, and (2) 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 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). Before investing in measuring these traits on a larger number of species, we should first determine whether 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 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 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 2014), multivariate imputation by chained equations (MICE), missForest (Penone et al. 2014), and the hierarchical Bayesian approach BHPMF (Schrodtt et al. 2015).

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 services 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. 2017). 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. 2017). 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. 2015, 2017) 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. 2017). 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 services, their resilience (i.e., resistance and recovery), and their complementarity with the other species already present locally.

ACKNOWLEDGMENTS

Constructive feedback from Robert Lalonde, Eugenia M. Sampayo, two anonymous reviewers, and the handling editor is gratefully acknowledged. JP and LP acknowledge financial support from the Natural Sciences and Engineering Research Council of Canada (Discovery Grants program), the Canadian Foundation for Innovation (CFI), and The University of British Columbia.

LITERATURE CITED

- Alvarez-Filip, L., J. P. Carricart-Ganivet, G. Horta-Puga, and R. Iglesias-Prieto. 2013. Shifts in coral-assembly composition do not ensure persistence of reef functionality. *Scientific Reports* 3:3486.
- Alvarez-Filip, L., N. K. Dulvy, I. M. Côté, A. R. Watkinson, and J. A. Gill. 2011. Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications* 21:2223–2231.
- Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* 276:3019–3025.
- Álvarez-Noriega, M., A. H. Baird, M. Dornelas, J. S. Madin, V. R. Cumbo, and S. R. Connolly. 2016. Fecundity and the demographic strategies of coral morphologies. *Ecology* 97:3485–3493.
- Anthony, K. R. N., M. O. Hoogenboom, J. A. Maynard, A. G. Grottoli, and R. Middlebrook. 2009. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Functional Ecology* 23:539–550.
- Anthony, K. R. N., et al. 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. *Global Change Biology* 21:48–61.
- Baird, A. H., R. Bhagooli, P. J. Ralph, and S. Takahashi. 2009a. Coral bleaching: the role of the host. *Trends in Ecology and Evolution* 24:16–20.

- Baird, A. H., J. R. Guest, and B. L. Willis. 2009b. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* 40:551–571.
- Baird, A. H., and P. A. Marshall. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* 237:133–141.
- Baker, A. C., P. W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* 80:435–471.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Berkelmans, R., and M. J. H. van Oppen. 2006. The role of zooxanthellae in the thermal tolerance of corals: a “nugget of hope” for coral reefs in an era of climate change. *Proceedings of the Royal Society B: Biological Sciences* 273:2305–2312.
- Bozec, Y. M., L. Alvarez-Filip, and P. J. Mumby. 2015. The dynamics of architectural complexity on coral reefs under climate change. *Global Change Biology* 21:223–235.
- Bridge, T. C. L., T. P. Hughes, J. M. Guinotte, and P. Bongaerts. 2013. Call to protect coral reefs. *Nature Climate Change* 3:528–530.
- Brown, B. E. 1997. Coral bleaching: causes and consequences. *Coral Reefs* 16:129–138.
- Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2:e711.
- Cadotte, M. W. 2017. Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters* 20:989–996.
- Cadotte, M. W., C. A. Arnillas, S. W. Livingstone, and S. E. Yasui. 2015. Predicting communities from functional traits. *Trends in Ecology and Evolution* 30:510–511.
- Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48:1079–1087.
- Chappell, J. 1980. Coral morphology, diversity and reef growth. *Nature* 286:249–252.
- Connell, J. H., T. P. Hughes, C. C. Wallace, J. E. Tanner, K. E. Harms, and A. M. Kerr. 2004. A long-term study of competition and diversity of corals. *Ecological Monographs* 74:179–210.
- Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67:461–488.
- Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S. J. Anderson, I. Kubiszewski, S. Farber, and R. K. Turner. 2014. Changes in the global value of ecosystem services. *Global Environmental Change* 26:152–158.
- Cunning, R., and A. C. Baker. 2013. Excess algal symbionts increase the susceptibility of reef corals to bleaching. *Nature Climate Change* 3:259–262.
- Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. McClanahan, I. M. Côté, and D. Bellwood. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.
- Darling, E. S., N. A. J. Graham, F. A. Januchowski-Hartley, K. L. Nash, M. S. Pratchett, and S. K. Wilson. 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36:561–575.
- Darling, E. S., T. R. McClanahan, and I. M. Côté. 2013. Life histories predict coral community disassembly under multiple stressors. *Global Change Biology* 19:1930–1940.
- Davies, K. F., B. A. Melbourne, C. D. James, and R. B. Cunningham. 2010. Using traits of species to understand responses to land use change: birds and livestock grazing in the Australian arid zone. *Biological Conservation* 143:78–85.
- DeAngelis, D. L., and V. Grimm. 2014. Individual-based models in ecology after four decades. *F1000Prime Reports* 6:6.
- Denis, V., L. Ribas-Deulofeu, N. Sturaro, C. Y. Kuo, and C. A. Chen. 2017. A functional approach to the structural complexity of coral assemblages based on colony morphological features. *Scientific Reports* 7:1–11.
- Doropoulos, C., S. Ward, G. Roff, M. González-Rivero, and P. J. Mumby. 2015. Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. *PLoS ONE* 10:1–23.
- Dove, S. 2004. Scleractinian corals with photoprotective host pigments are hypersensitive to thermal bleaching. *Marine Ecology Progress Series* 272:99–116.
- Edinger, E. N., and M. J. Risk. 1995. Preferential survivorship of brooding corals in a regional extinction. *Paleobiology* 21:200–219.
- Edmunds, P. J., et al. 2014. Evaluating the causal basis of ecological success within the scleractinia: an integral projection model approach. *Marine Biology* 161:2719–2734.
- Emslie, M. J., A. J. Cheal, H. Sweatman, and S. Delean. 2008. Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 371:177–190.

- Fabricius, K. E., G. De'ath, S. Noonan, and S. Uthicke. 2014. Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proceedings of the Royal Society B: Biological Sciences* 281:8.
- Figueiredo, J., A. H. Baird, and S. R. Connolly. 2013. Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. *Ecology* 94:650–659.
- Fitt, W. K., et al. 2009. Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. *Journal of Experimental Marine Biology and Ecology* 373:102–110.
- Forrest, J. R. K., R. W. Thorp, C. Kremen, and N. M. Williams. 2015. Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *Journal of Applied Ecology* 52:706–715.
- Fountain-Jones, N. M., S. C. Baker, and G. J. Jordan. 2015. Moving beyond the guild concept: developing a practical functional trait framework for terrestrial beetles. *Ecological Entomology* 40:1–13.
- Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224:1–30.
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–960.
- Gates, R. D., and P. J. Edmunds. 1999. The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* 39:30–43.
- Gleason, D. F., and D. K. Hofmann. 2011. Coral larvae: from gametes to recruits. *Journal of Experimental Marine Biology and Ecology* 408:42–57.
- Glynn, P. W., and S. B. Colley. 2008. Survival of brooding and broadcasting reef corals following large scale disturbances: Is there any hope for broadcasting species during global warming? *Proceedings of the 11th International Coral Reef Symposium*: 7–11.
- Golbuu, Y., and R. H. Richmond. 2007. Substratum preferences in planula larvae of two species of scleractinian corals, *Goniastrea retiformis* and *Stylaraea punctata*. *Marine Biology* 152:639–644.
- Graham, N. A. J. 2014. Habitat complexity: Coral structural loss leads to fisheries declines. *Current Biology* 24:R359–R361.
- Graham, N. A. J., J. E. Cinner, A. V. Norström, and M. Nyström. 2014. Coral reefs as novel ecosystems: embracing new futures. *Current Opinion in Environmental Sustainability* 7:9–14.
- Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326.
- Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. P. Bijoux, and J. Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences USA* 103:8425–8429.
- Grimm, V., and S. Railsback. 2005. *Individual-based modeling and ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Grottoli, A. G., L. J. Rodrigues, and J. E. Palardy. 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature* 440:1186–1189.
- Grottoli, A. G., M. E. Warner, S. J. Levas, M. D. Aschaffenburg, V. Schoepf, M. McGinley, J. Baumann, and Y. Matsui. 2014. The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Global Change Biology* 20:3823–3833.
- Guest, J. R., et al. 2016. Coral community response to bleaching on a highly disturbed reef. *Scientific Reports* 6:1–10.
- Hall, V. R., and T. P. Hughes. 1996. Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* 77:950–963.
- Harmelin-Vivien, M. L. 1994. The effects of storms and cyclones on coral reefs: a review. *Journal of Coastal Research* 12:211–231.
- Harrison, P. L., and C. C. Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. Pages 132–207 in Z. Dubinsky, editor. *Ecosystems of the world 25: coral reefs*. Elsevier Science Publishers B.V, Amsterdam, The Netherlands.
- Hidaka, M. 2016. Life history and stress response of scleractinian corals. Pages 1–24 in H. Kayanne, editor. *Coral reef science, strategy for exosystem symbiosis and coexistence with humans under multiple stresses*. Coral Reef. Springer, Tokyo, Japan.
- Highsmith, R. C. 1981. Coral bioerosion: damage relative to skeletal density. *American Naturalist* 117:193–198.
- Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7:207–226.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528.
- Holbrook, S. J., A. J. Brooks, and R. J. Schmitt. 2002. Variation in structural attributes of patch-forming

- corals and in patterns of abundance of associated fishes. *Marine and Freshwater Research* 53:1045–1053.
- Hoogenboom, M. O., and S. R. Connolly. 2009. Defining fundamental niche dimensions of corals: synergistic effects of colony size, light, and flow. *Ecology* 90:767–780.
- Houlbrèque, F., C. Ferrier-Pagès, C. Ferrier-page, and F. Houlbre. 2009. Heterotrophy in tropical scleractinian corals. *Biological Reviews* 84:1–17.
- Howells, E. J., V. H. Beltran, N. W. Larsen, L. K. Bay, B. L. Willis, and M. J. H. Van Oppen. 2012. Coral thermal tolerance shaped by local adaptation of photosymbionts. *Nature Climate Change* 2:116–120.
- Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *American Naturalist* 123:778–795.
- Hughes, T. P., D. Ayre, and J. H. Connell. 1992. The evolutionary ecology of corals. *Trends in Ecology and Evolution* 7:292–295.
- Hughes, T. P., and J. H. Connell. 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography* 44:932–940.
- Hughes, T. P., et al. 2017. Coral reefs in the Anthropocene. *Nature* 546:82–90.
- Hume, B. C. C., C. D. Angelo, E. G. Smith, J. R. Stevens, J. Burt, and J. Wiedenmann. 2015. *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. *Scientific Reports* 5:8562.
- Jokiel, P. L., and S. L. Coles. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–162.
- Jones, G. P., G. R. Almany, G. R. Russ, P. F. Sale, R. S. Steneck, M. J. H. Van Oppen, and B. L. Willis. 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307–325.
- Keith, S. A., E. S. Woolsey, J. S. Madin, M. Byrne, and A. H. Baird. 2015. Differential establishment potential of species predicts a shift in coral assemblage structure across a biogeographic barrier. *Ecography* 38:1225–1234.
- Kim, K., and H. R. Lasker. 1998. Allometry of resource capture in colonial cnidarians and constraints on modular growth. *Functional Ecology* 12:646–654.
- Klumpp, K., and J. F. Soussana. 2009. Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. *Global Change Biology* 15:2921–2934.
- Koide, R. T., C. Fernandez, and G. Malcolm. 2014. Determining place and process: functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytologist* 201:433–439.
- Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences* 112:797–802.
- Kubicek, A., C. Muhando, and H. Reuter. 2012. Simulations of long-term community dynamics in coral reefs – How perturbations shape trajectories. *PLoS Computational Biology* 8:e1002791.
- Kubicek, A., and H. Reuter. 2016. Mechanics of multiple feedbacks in benthic coral reef communities. *Ecological Modelling* 329:29–40.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Lavorel, S., and K. Grigulis. 2012. How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology* 100:128–140.
- Lavorel, S., et al. 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science* 24:942–948.
- Levas, S., A. G. Grotoli, V. Schoepf, M. Aschaffenburg, J. Baumann, J. E. Bauer, and M. E. Warner. 2016. Can heterotrophic uptake of dissolved organic carbon and zooplankton mitigate carbon budget deficits in annually bleached corals? *Coral Reefs* 35:495–506.
- Long, M., K. J. Berry, and P. W. Mickle. 2010. Multiway contingency tables: Monte Carlo resampling probability values for the Chi-squared and likelihood-ratio tests. *Psychological Reports* 107:501–510.
- Luck, G. W., A. Carter, and L. Smallbone. 2013. Changes in bird functional diversity across multiple land uses: interpretations of functional redundancy depend on functional group identity. *PLoS ONE* 8:e63671.
- Madin, J. S., A. H. Baird, M. Dornelas, and S. R. Connolly. 2014. Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecology Letters* 17:1008–1015.
- Madin, J. S., and S. R. Connolly. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* 444:477–480.
- Madin, J. S., et al. 2016a. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data* 3:160017.

- Madin, J. S., et al. 2016b. A trait-based approach to advance coral reef science. *Trends in Ecology and Evolution* 31:419–428.
- Magris, R. A., E. A. Tremblay, R. L. Pressey, and R. Weeks. 2015. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. *Ecography* 38:1–16.
- Marcelino, L. A., et al. 2013. Modulation of light-enhancement to symbiotic algae by light-scattering in corals and evolutionary trends in bleaching. *PLoS ONE* 8:e61492.
- Marshall, P. A., and A. H. Baird. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155–163.
- Massel, S. R., and T. J. Done. 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs* 12:153–166.
- McClanahan, T. R. 2004. The relationship between bleaching and mortality of common corals. *Marine Biology* 144:1239–1245.
- McClanahan, T. R., et al. 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE* 7:e42884.
- McCook, L. J., et al. 2010. Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences* 107:18278–18285.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Meesters, E. H., I. Wesseling, and R. P. M. Bak. 1996. Partial mortality in three species of reef-building corals and the relation with colony morphology. *Bulletin of Marine Science* 58:838–852.
- Minden, V., and M. Kleyer. 2011. Testing the effect-response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science* 22:387–401.
- Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29:215–233.
- Nelson, H. R., C. D. Kuempel, and A. H. Altieri. 2016. The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere* 7:1–14.
- Newman, S. P., E. H. Meesters, C. S. Dryden, S. M. Williams, C. Sanchez, P. J. Mumby, and N. V. C. Polunin. 2015. Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology* 84:1678–1689.
- O'Brien, M. J., S. Leuzinger, C. D. Philipson, J. Tay, A. Hector, M. J. O'Brien, S. Leuzinger, C. D. Philipson, J. Tay, and A. Hector. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4:710–714.
- Oliver, T. H., et al. 2015. Biodiversity and resilience of ecosystem functions. *Trends in Ecology and Evolution* 30:673–684.
- Pendleton, L. H., O. Hoegh-Guldberg, C. Langdon, and A. Comte. 2016. Multiple stressors and ecological complexity require a new approach to coral reef research. *Frontiers in Marine Science* 3:36.
- Penone, C., et al. 2014. Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution* 5:1–10.
- Pey, B., et al. 2014. Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic and Applied Ecology* 15:194–206.
- Plass-Johnson, J. G., M. H. Taylor, A. A. Husain, M. C. Teichberg, and S. C. A. Ferse. 2016. Non-random variability in functional composition of coral reef fish communities along an environmental gradient. *PLoS ONE* 11:e0154014.
- Porter, J. W. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *American Society of Naturalists* 110:731–742.
- R-Core Team. 2017. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rinkevich, B. 2014. Rebuilding coral reefs: Does active reef restoration lead to sustainable reefs? *Current Opinion in Environmental Sustainability* 7:28–36.
- Risk, M. J. 1972. Fish diversity on a coral reef in The Virgin Islands. *Atoll Research Bulletin* 153:1–6.
- Ritson-Williams, R., S. Arnold, N. Fogarty, R. S. Steneck, M. Vermeij, and V. J. Paul. 2009. New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithsonian Contributions to the Marine Sciences* 38:437–457.
- Ritson-Williams, R., S. Arnold, and V. Paul. 2016. Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. *Marine Ecology Progress Series* 548:127–138.
- Roff, G., S. Bejarano, Y.-M. M. Bozec, M. Nugues, R. S. Steneck, and P. J. Mumby. 2014. Porites and the Phoenix effect: unprecedented recovery after a mass coral bleaching event at Rangiroa Atoll, French Polynesia. *Marine Biology* 161:1385–1393.
- Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* 24:1000–1005.
- Salih, A., O. Hoegh-Guldberg, and G. Cox. 1998. Photoprotection of symbiotic dinoflagellates by fluorescent pigments in reef corals. *Proceedings of the*

- Australian Coral Reef Society 75th Anniversary Conference, Heron Island October 1997:217–230.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Schrodft, F., et al. 2015. BHPMF – a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Global Ecology and Biogeography* 24:1510–1521.
- Sheppard, C. R. C. 1979. Interspecific aggression between reef corals with reference to their distribution. *Marine Ecology Progress Series* 1:237–247.
- Silverstein, R. N., R. Cuning, and A. C. Baker. 2015. Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Global Change Biology* 21:236–249.
- Solé-Senan, X. O., A. Juárez-Escario, I. Robleño, J. A. Conesa, and J. Recasens. 2017. Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services by Mediterranean arable plants. *Agriculture, Ecosystems and Environment* 247:255–264.
- Stanley, G. D., and S. D. Cairns. 1988. Constructional azooxanthellate coral communities: an overview with implications for the fossil record. *Palaios* 3:233–242.
- Stat, M., E. Morris, and R. D. Gates. 2008. Functional diversity in coral-dinoflagellate symbiosis. *Proceedings of the National Academy of Sciences USA* 105:9256–9261.
- Stimson, J., K. Sakai, and H. Sembali. 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. *Coral Reefs* 21:409–421.
- Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M. L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14:1125–1140.
- Swain, T. D., J. Chandler, V. Backman, and L. Marcelino. 2017. Consensus thermotolerance ranking for 110 Symbiodinium phylotypes: an exemplar utilization of a novel iterative partial-rank aggregation tool with broad application potential. *Functional Ecology* 31:172–183.
- Swain, T. D., et al. 2016a. Skeletal light-scattering accelerates bleaching response in reef-building corals. *BMC Ecology* 16:10.
- Swain, T. D., J. B. Vega-Perkins, W. K. Oestreich, C. Triebold, E. DuBois, J. Henss, A. Baird, M. Siple, V. Backman, and L. Marcelino. 2016b. Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Global Change Biology* 22:2475–2488.
- Swenson, N. G. 2014. Phylogenetic imputation of plant functional trait databases. *Ecography* 37:105–110.
- Szmant, A. M. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5:43–53.
- Tanner, J. E., T. P. Hughes, and J. H. Connell. 1994. Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* 75:2204–2219.
- Teh, L. S. L., L. C. L. Teh, and U. R. Sumaila. 2013. A global estimate of the number of coral reef fishers. *PLoS ONE* 8:e65397.
- Torda, G., P. Lundgren, B. L. Willis, and M. J. H. Van Oppen. 2013. Revisiting the connectivity puzzle of the common coral *Pocillopora damicornis*. *Molecular Ecology* 22:5805–5820.
- Underwood, J. N., L. D. Smith, M. J. H. H. Van Oppen, and J. P. Gilmour. 2007. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology* 16:771–784.
- van Oppen, M. J. H., J. K. Oliver, H. M. Putnam, and R. D. Gates. 2015. Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences* 112:1–7.
- van Oppen, M. J. H., et al. 2017. Shifting paradigms in restoration of the world's coral reefs. *Global Change Biology* 23:1–12.
- van Woesik, R., E. C. Franklin, J. O'Leary, T. R. McClanahan, J. S. Klaus, and A. F. Budd. 2012a. Hosts of the Plio-Pleistocene past reflect modern-day coral vulnerability. *Proceedings of the Royal Society B: Biological Sciences* 279:2448–2456.
- van Woesik, R., A. Irikawa, R. Anzai, and T. Nakamura. 2012b. Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. *Coral Reefs* 31:633–639.
- Vermeij, M. J. A. 2005. Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. *Marine Ecology Progress Series* 295:123–133.
- Warton, D. I., and F. K. C. Hui. 2011. The Arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:03–10.
- Wells, S., C. Ravilious, and E. Corcoran. 2006. In the front line: shoreline protection and other ecosystem services from mangroves and coral reefs. United Nations Environmental Programme—World Conservation Monitoring Centre, Cambridge, UK.
- Wilson, S. K., N. A. J. Graham, and N. V. C. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151:1069–1076.

- Wilson, S. K., N. A. J. Graham, M. S. Pratchett, G. P. Jones, and N. V. C. Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Global Change Biology* 12:2220–2234.
- Wooldridge, S. A. 2009. A new conceptual model for the enhanced release of mucus in symbiotic reef corals during “bleaching” conditions. *Marine Ecology Progress Series* 396:145–152.
- Wooldridge, S. A. 2014. Differential thermal bleaching susceptibilities amongst coral taxa: re-posing the role of the host. *Coral Reefs* 33:15–27.
- Yakovleva, I., R. Bhagooli, A. Takemura, and M. Hidaka. 2004. Differential susceptibility to oxidative stress of two scleractinian corals: antioxidant functioning of mycosporine-glycine. *Comparative Biochemistry and Physiology – B Biochemistry and Molecular Biology* 139:721–730.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2214/full>