Primacy of bottom-up effects on a butterflyfish assemblage

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Abstract.   The question of whether biological systems are maintained by top-down versus bottom-up drivers is a recurring one in ecology. It is a particularly important question to address in the management of coral reefs, which are at risk from a variety of anthropogenic stressors. Here, we explicitly test whether the abundance of different feeding guilds of coral-associated *Chaetodon* butterflyfishes are controlled by top-down or bottom-up drivers, and we assess the relative influence of all statistically significant drivers. We find that the abundance and species richness of *Chaetodon* butterflyfishes are predominately determined by bottom-up drivers. The abundance of corallivores is primarily driven by availability of branching and tabular live corals, whereas the abundance of generalists is most strongly influenced by a negative association with macroalgal cover. We also find evidence of weak top-down control on the abundance of corallivorous butterflyfish by gape-limited mesopredators, but no such effects on generalist butterflyfish. Our findings indicate that conservation of coral reefs for *Chaetodon* butterflyfishes must include management at a larger spatial scale in order to reduce the effect of coral reef stressors such as declining water quality and climate change, but should also include implementation of fisheries management tools in order to increase local herbivory.

Additional keywords: boosted regression trees, butterflyfish, *Chaetodon*, Coral Triangle, macroalgae, mesopredator.

Introduction

The question of whether biological systems are controlled by top-down (e.g. predation) versus bottom-up (e.g. availability of resources) processes is a difficult one to definitively answer, with much evidence for both cases (Estes *et al.* 1998; Pace *et al.* 1999; Richardson and Schoeman 2004; Ware and Thomson 2005; Myers *et al.* 2007; Frank 2008). The abundance and diversity of coral reef fishes are often thought to be largely controlled from the top-down, in part because of a rich history of apex-predator induced trophic cascades (Myers *et al.* 2007; Baum and Worm 2009; Ferretti *et al.* 2010; Rizzari *et al.* 2014), and in part because of the importance of herbivorous fishes and invertebrates in controlling macroalgal growth and in maintaining a coral-dominated system (Hughes 1994; Bellwood *et al.* 2006; Mumby *et al.* 2006; Hughes *et al.* 2007). However, some members of the reef ecosystem are likely to be moderated by bottom-up processes, in particular, availability of food and benthic habitat for resource-specialists (Munday *et al.* 1997; Pratchett *et al.* 2006; Emslie *et al.* 2011). Furthermore, both top-down and bottom-up processes operate within the potential constraints of larval supply (Doherty and Williams 1988;

Armsworth 2002; Sale 2004), which is highly variable in both space and time (Williams *et al.* 1994; Jones *et al.* 2009; Berumen *et al.* 2012; Harrison *et al.* 2012).

Misunderstanding the dominant regulatory processes in an ecosystem can have important consequences for its persistence, as conservation of different ecosystem drivers can require very different management actions. For example, preservation of top-down processes on coral reefs has been achieved with the implementation of no-take marine reserves (Mumby *et al.* 2006; Mumby *et al.* 2007; O'Leary *et al.* 2012) and fishing gear restrictions (Cinner *et al.* 2009). However, preservation of bottom-up processes requires management actions at a much larger spatial scale, such as changes to land-use practices to reduce sedimentation and nutrient enrichment (McCook 1999; Brodie *et al.* 2012), and identification of spatial refugia in the face of climate change (McClanahan *et al.* 2007; McLeod *et al.* 2010; Groves *et al.* 2012).

Reality is likely to be far more complex than this dichotomous approach, such that both bottom-up and top-down processes are actually involved in maintaining ecosystem processes and components (e.g. Power 1992; Brett and Goldman 1997; Cury
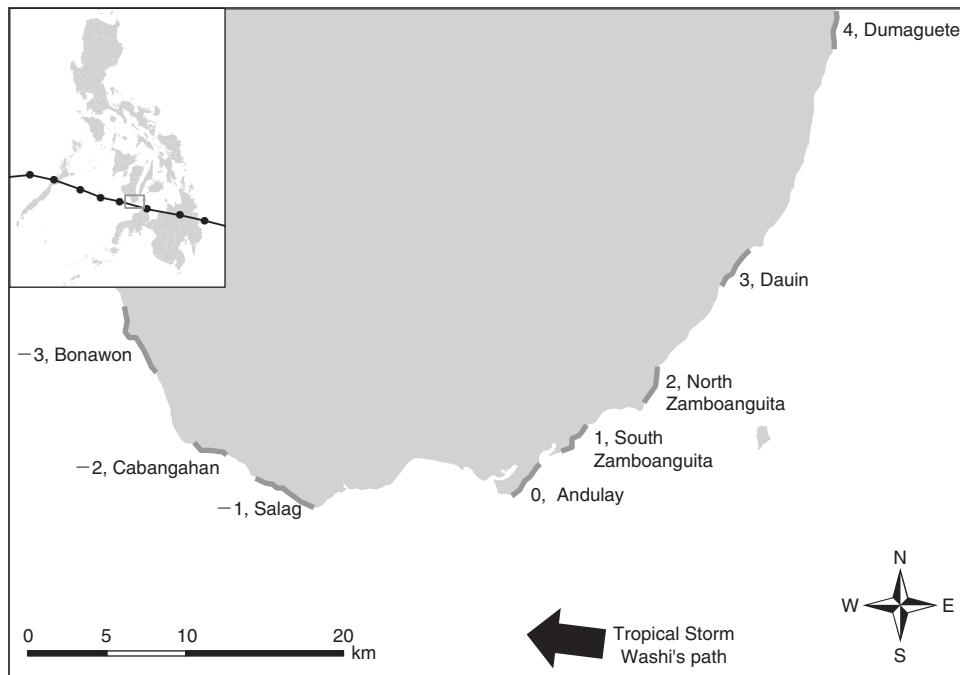
Fig. 1. Study region on the southern coast of Negros Oriental, in the Central Visayas region of the Philippines. Study sites are indicated in dark grey outline. Black arrow indicates the trajectory of Tropical Storm Washi. Inset: Philippines, including the path of Tropical Storm Washi (black), and study region (dark grey box). Tropical storm track data from United States Naval Research Laboratory Marine Meteorology Division (2011).

et al. 2000; Menge 2000). However, few studies have identified and quantified the relative influence of top-down and bottom-up processes on the abundance and diversity of coral reef fishes (but see Wilson *et al.* 2008), especially on the butterflyfishes (Chaetodontidae). The *Chaetodon* genus includes several distinct feeding guilds, which are generally assumed to be moderated solely by bottom-up processes, with obligate hard corallivores being most susceptible to changes in coral cover (Crosby and Reese 2005; Pratchett *et al.* 2006). However, reef fish populations are often strongly structured by mortality due to predation (Hixon 1991; Jones and McCormick 2002), which is particularly high immediately post-settlement and in juveniles (Webster 2002; Doherty *et al.* 2004; Almany and Webster 2006), and butterfly-fish should be no exception to this.

The primary aim of this study was to quantify the relative influence of the top-down and bottom-up biotic and abiotic variables affecting the abundance and species richness of *Chaetodon* butterflyfishes along an extensive coastline in the central Philippines that was recently impacted by a severe tropical storm. We used sheltered 'control' sites and sites that had a gradient of benthic assemblage compositions likely generated by distance from the storm path to distinguish and quantify the effects of benthos and predator abundance on the *Chaetodon* assemblage. We interpret our findings in the context of their implications for coral reef management techniques.

Materials and methods

Description of field sites

The southern coastline of Negros Oriental, in the central Philippines, is characterised by intermittent, shallow, fringing coral reefs with lagoonal seagrass or coral beds and occasional remnants of mangrove stands (Yambao *et al.* 2001; DeVantier *et al.* 2004). Tropical Storm Washi (local name: Sendong) traversed this region in December 2011, with devastating impacts on human communities and local ecosystems (Rasquinho *et al.* 2013).

A total of eight study sites were selected along the coast. The community of Andulay was very close to the path of Tropical Storm Washi and received the brunt of destructive winds and damaging waves on this coastline (Fig. 1), and is therefore designated as 'site zero.' The other seven study sites were distributed approximately evenly west (sheltered from the storm) and east (exposed to the storm) around site zero, and are identified numerically based on their relative distance from the storm's path (from −3 to +4, Fig. 1). Site 4 coincides with a large urban centre, Dumaguete. Irregularities in the distance between sites were due to lack of reef environments (e.g. between sites −1 and 0, Fig. 1), or to inaccessibility for political or logistical reasons (e.g. between sites 3 and 4, Fig. 1).

Field surveys

Surveys of the benthos, the *Chaetodon* assemblage and potential *Chaetodon* predator assemblages were carried out at each site between 17 September 2012 and 11 December 2012, ~1 year after Tropical Storm Washi's passage. Surveys were conducted on SCUBA on the reef crest and slope (3–15 m deep), as storm and cyclone effects are generally most distinctive on these reef zones (Harmelin-Vivien 1994). All benthivorous members of the *Chaetodon* genus and all predators >6-cm total length (TL) (certain members of the families Labridae, Lutjanidae,

Table 1.   Parameters and properties of the boosted regression tree models for the benthic assemblage and the *Chaetodon* assemblage
CBCT indicates branching and tabular corals, CMCE indicates massive and encrusting corals. Macroalgal cover was fourth-root transformed in order to reduce
the influence of a mean-variance relationship in the model residuals. No other dependent variables were transformed

Parameter	Distribution family	Learning rate	Tree complexity	Bag fraction	Optimal number of trees	Final number of variables	Adjusted D^2
CBCT cover	Gaussian	0.001	2	0.75	4050	2	45.7%
CMCE cover	Gaussian	0.001	2	0.75	6400	2	71.7%
Rubble cover	Gaussian	0.001	2	0.75	1700	2	47.9%
Macroalgal cover	Gaussian	0.001	2	0.75	6950	2	52.8%
Rock cover	Gaussian	0.001	2	0.75	8900	2	64.9%
Rugosity	Gaussian	0.001	2	0.75	4500	2	53.6%
Small predator abundance	Poisson	0.001	2	0.75	3150	2	52.0%
Large predator abundance	Poisson	0.001	2	0.75	1850	2	41.0%
Corallivore abundance	Poisson	0.001	2	0.75	4900	6	72.9%
Generalist abundance	Poisson	0.001	2	0.75	4350	5	54.9%
Chaetodon species richness	Gaussian	0.001	2	0.75	3350	5	62.2%

Pinguipedidae, Pseudochromidae, Serranidae, Scorpaenidae, and Synodontidae) were surveyed using 4 m wide, 50-m belt transects (200 m^2 per transect). Between 5 and 11 replicate transects were surveyed at each site, depending on the spatial extent of the reef zone and its benthic heterogeneity. Benthic characteristics were recorded every 0.5 m using the Point Intercept technique (English *et al.* 1994) on the return swim along each transect. An index of rugosity (as per Russ *et al.* 2005) was estimated at 10-m increments to provide a measure of benthic complexity.

Drivers of the benthic and predator assemblages

Boosted regression tree (BRT) models were built to assess spatial patterns, in particular the influence of position along the coast (i.e. distance from the storm) and survey depth, on the extent of major benthic components (branching and tabular live coral, massive and encrusting live coral, rubble, macroalgae, and rock), benthic complexity, and the abundance of small (6–10 cm TL) and large (>10 cm TL) predators. The small predator category (6–10 cm TL) was made up of mesopredators, which generally hunt for small prey items such as juvenile reef fishes within the reef matrix. Members of the large predator category (>10 cm TL) generally hunt for larger prey items above the reef matrix (Almany 2004). BRTs produce similar outputs to traditional regression-based techniques, but are arguably better suited to ecological studies as they accommodate non-linear relationships, identify and exclude unimportant variables, and can automatically model interactions (De'ath 2007; Elith *et al.* 2008). BRTs were built and fitted in RStudio (RStudio: Integrated Development Environment for R, ver. 0.98.978, Boston, MA, USA) using the *dismo* package (Elith *et al.* 2008), which is derived from the *gbm* package (Ridgeway 2007), but contains automated cross-validation and tree optimisation protocols. Because model output was reasonably insensitive to variation in key parameters, model parameters were derived to optimise biological meaningfulness and interpretability (Table 1). As such, tree complexity was limited to main effects and first-order interactions. A bag

fraction <1 introduced stochasticity into the model in order to prevent model over-fitting; model output therefore varied slightly each time it was run. The percent deviance explained by each model (adjusted D^2) is analogous to an adjusted R^2, which penalises models for the addition of extra variables that increase model explanatory power due to chance alone. Dependent variables were untransformed, with the exception of macroalgal cover, which was fourth-root transformed in order to reduce the magnitude of a mean-variance relationship in the model residuals.

Drivers of the Chaetodon *assemblage*

BRT models were built to explain *Chaetodon* species richness, as well as the abundance of members of the two most common *Chaetodon* feeding guilds: obligate hard corallivores and benthic generalists (Table 2), hereafter referred to as 'corallivores' and 'generalists' . Model parameters were similar to those used to model benthic components (Table 1). Predictor variables included depth and benthic components (branching and tabular live coral cover, massive and encrusting live coral cover, rubble cover, macroalgal cover, rock cover, and rugosity index), abundance of small (6–10 cm TL) predators, and abundance of large (>10 cm TL) predators. A simplification procedure was run to remove predictors that did not significantly improve the model (Elith *et al.* 2008; Harborne *et al.* 2012). Dependent variables did not require transformation.

Results

Drivers of the benthic and predator assemblages

BRT models containing only distance from the storm and depth as explanatory variables captured between 41 and 72% of the variation in the main benthic components and the predator assemblage (Table 1). Branching and tabular coral cover was best explained by depth, and massive and encrusting coral cover was best explained by distance from the storm (Table 3). Both types of coral cover exhibited complex non-linear relationships with distance from the storm, with high coral cover at sites

sheltered from the storm's impact (negative site numbers), a distinct low in coral cover at the site of the storm impact, and sequentially higher coral cover at each site further away from the storm impact (positive site numbers, Figs 1, 2*a*, *b*). Conversely, rubble cover was lowest at sheltered sites (negative site numbers), and exhibited a distinct peak near the site of the storm impact and gradual decline along the east-coast sites (positive site numbers, Figs 1, 2*c*). Macroalgal cover was also most strongly driven by position along the coast, in a complex spatial pattern with the highest peak in macroalgal cover at the site of the tropical storm (site 0, Fig. 2*d*). Rock cover was slightly more strongly explained by depth rather than position along the coast, but exhibited a clear decline between sites 1 and 4 (Fig. 2*e*). Rugosity (i.e. benthic complexity) was most strongly explained by position along the coast, with consistently high levels of rugosity at west coast sites, and a sharp decline along the east coast, between sites 1 and 4 (Fig. 2*f*). Patterns in the fitted function of each benthic component against depth approximated

Table 2.   Abundance of the benthic feeding members of the *Chaetodon* assemblage across the entire surveyed area (13 400 m^2)
Only hard corallivores and generalists were included in the statistical analyses due to low abundances of the other feeding guilds (soft corallivores and non-corallivores). Feeding guild classification as per Findley and Findley (2001) and Cole *et al.* (2008)

Species by guild	Abundance
Hard corallivores	212
C. baronessa	93
C. lunulatus	88
C. octofasciatus	10
C. ornatissimus	13
C. reticulatus	6
C. trifascialis	2
Generalists	198
C. adiergastos	10
C. auriga	3
C. citrinellus	10
C. lineolatus	1
C. lunula	9
C. rafflesi	6
C. speculum	2
C. vagabundus	149
C. xanthurus	8
Soft corallivores	39
C. melannotus	1
C. ocellicaudus	4
C. punctatofasciatus	34
Non-corallivores	7
C. selene	7

the reef profile in this region, with low complexity rock and macroalgal cover from 4 to 6 m, high complexity coral dominance (particularly branching and tabular morphologies) from 6 to 9 m, and intermediate to low complexity rubble and macroalgal dominance from 9 to 12 m (Fig. 2).

The predator assemblage was most strongly structured by depth (85.6% for small predators, Fig. 2*g*; 66.1% for large predators, Fig. 2*h*). Small predators were most common at depths >12 m, and large predators were most common at depths >8 m. Both sizes exhibited complex spatial patterns across the region: the abundance of small predators was particularly low at sites −1, 0, and 1 (Fig. 2*g*), whereas large predators appeared to be almost absent from the west coast (sites −3 to −1), and to increase in abundance from sites 0 to 2 (Fig. 2*h*).

Drivers of the *Chaetodon* assemblage

The *Chaetodon* assemblage was composed of 19 species of benthic feeding butterflyfish, and was numerically dominated by hard corallivores and generalists (Table 2). BRT models explained between 55 and 73% of the variation in the main *Chaetodon* feeding guilds, as well as species richness (Table 1). Relationships between explanatory and dependent variables were generally non-linear and frequently complex (Table 4, Fig. 3).

The abundance of corallivores was most strongly structured by the availability of branching and tabular live coral cover (Table 4, Fig. 3*a*). Corallivore abundance exhibited a non-linear increase with increasing branching and tabular live coral cover until ~15% coral cover, after which corallivore abundance showed no further increases (Table 4, Fig. 3*a*). Corallivore abundance was also structured by a strong negative relationship with macroalgal cover; the abundance of corallivores demonstrated a sharp and persistent decline in response to quite low levels of macroalgal cover (1–15%, Fig. 3*a*). The abundance of corallivores was also associated with intermediate levels of rock cover (20–30%), and intermediate depths (6–9 m, corresponding with the depth of the coral-rich reef crest and upper slope on reefs in this region, Fig. 2*a*, *b*). Corallivore abundance was also significantly associated with the abundance of small predators (6–10 cm TL), with increasing small predator abundance linked to decreased corallivore abundance (Fig. 3*a*). Corallivore abundance was also positively linked to the extent of massive and encrusting corals (Fig. 3*a*). Variables removed from the model due to lack of significance included rubble cover, benthic complexity, and the abundance of large predators (Table 4).

The abundance of generalists was significantly affected by five different explanatory variables, but most strongly by a negative relationship with macroalgal cover (Table 4, Fig. 3*b*). Generalists exhibited a sharp and persistent decline in response

Table 3.   Percentage deviance explained by each variable within the final Boosted Regression Tree model for each benthic component
CBCT indicates branching and tabular corals, CMCE indicates massive and encrusting corals. Macroalgal cover was fourth-root transformed in order to reduce the influence of a mean-variance relationship in the model residuals. No other dependent variables were transformed

Parameter	CBCT	CMCE	Rubble	Macroalgae	Rock	Rugosity	Small predators	Large predators
Distance from storm	41.7	81.5	81.3	62.1	46.1	62.0	14.4	33.9
Depth	58.3	18.5	18.7	37.9	53.9	38.0	85.6	66.1

to very low levels of macroalgal cover (1–5%, Fig. 3*b*). Generalists also exhibited a positive relationship with rock cover with beneficial and persistent effects of rock cover >20%, as well as a positive relationship with rugosity (Fig. 3*b*). The abundance of generalists had a complex and mostly negative relationship with the extent of branching and tabular corals, as well as a complex relationship with depth, with a peak between 9 and 11 m (Fig. 3*b*). Both measures of predator abundance were removed

from the model due to lack of significant explanatory power, as were rubble and massive and encrusting coral cover (Table 4).

Chaetodon species richness was most strongly explained by a complex relationship with depth, with a peak in species richness occurring between 9 and 12 m (Table 4, Fig. 3*c*). Species richness also demonstrated a strong negative relationship with macroalgal cover (Table 4, Fig. 3*c*). Weaker relationships with other variables included a positive relationship with rugosity.
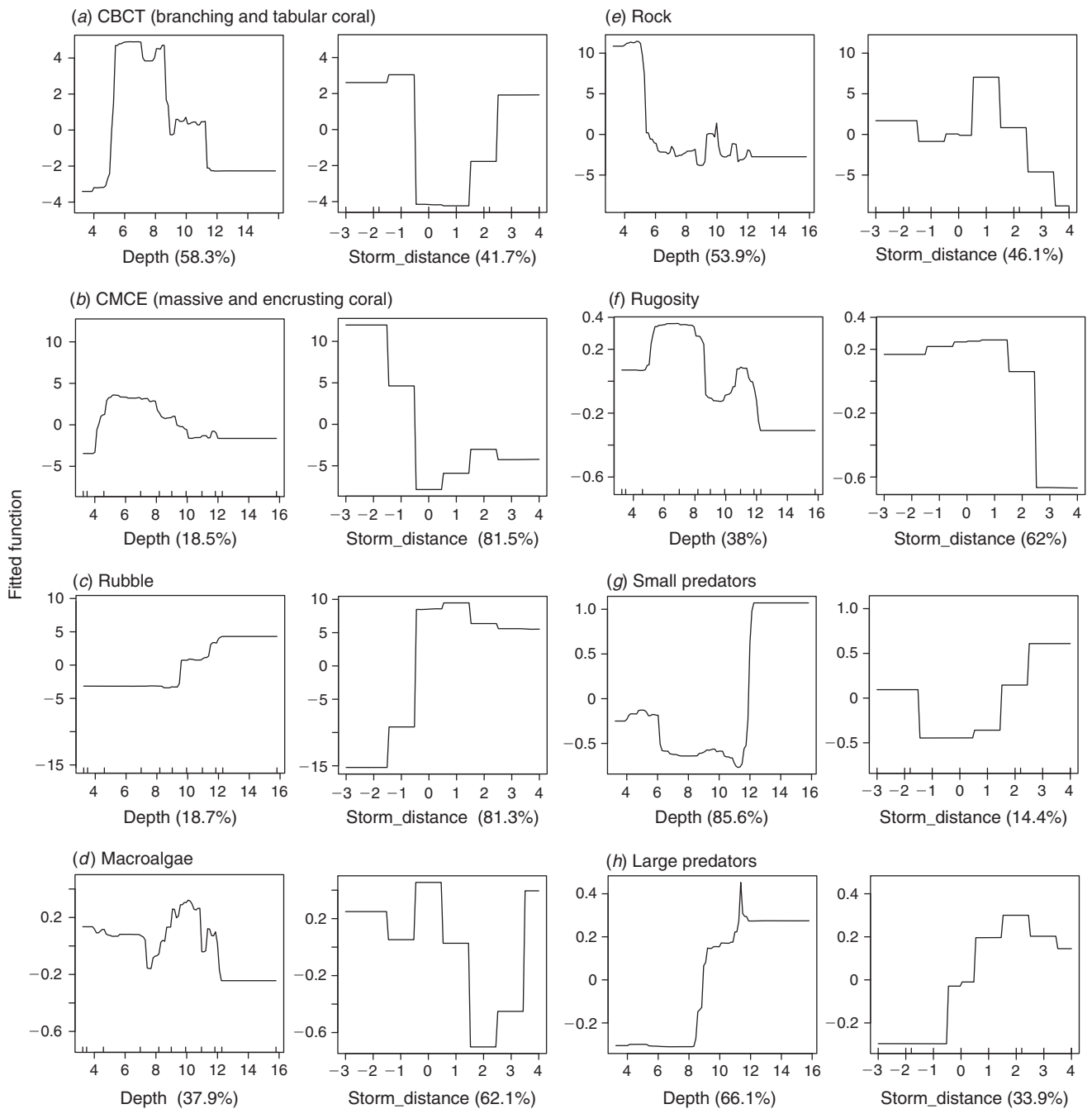

Fig. 2. Partial dependence functions for the two variables (distance from storm and depth) influencing the extent of each benthic component across the study region. (*a*) Branching and tabular live coral cover (CBCT), (*b*) massive and encrusting live coral cover (CMCE), (*c*) rubble cover, (*d*) fourth-root transformed macroalgal cover, (*e*) rock cover, (*f*) rugosity index, (*g*) abundance of small predators (6–10 cm), and (*h*) abundance of large predators (>10 cm).

Table 4. Percentage deviance explained by each variable within the final Boosted Regression Tree model for each descriptor of the *Chaetodon* assemblage

(+) Indicates a positive relationship, (−) indicates a negative relationship, (c) indicates a complex relationship, forward slashes (/) indicate variables that were removed from the model because BRT protocols rated them as non-contributors to the model

Parameter	Corallivore abundance	Generalist abundance	*Chaetodon* species richness
Depth	12.8 (c)	14.1 (c)	31.5 (c)
Branching and tabular coral (CBCT)	32.3 (+)	15.3 (c)	/
Massive and encrusting coral (CMCE)	8.0 (+)	/	/
Rock	16.6 (c)	19.8 (+)	14.1 (+)
Rubble	/	/	/
Macroalgae	18.2 (−)	35.0 (−)	25.8 (−)
Rugosity/benthic complexity	/	15.8 (+)	14.8 (+)
Small predator abundance	12.1 (−)	/	13.7 (−)
Large predator abundance	/	/	/

Species richness also exhibited a complex relationship with rock cover, with a peak in species richness at intermediate levels of rock cover (Fig. 3c), as well as a negative relationship with the abundance of small predators (Table 4, Fig. 3c). Both measures of live coral cover, as well as rubble and the abundance of large predators, did not significantly contribute towards explaining patterns of *Chaetodon* species richness (Table 4).

Discussion

In this study, we provide an assessment of both the effects of bottom-up and top-down processes on *Chaetodon* butterfly-fishes, and elucidate important ecological processes acting on this iconic coral reef taxon. Our results indicate that overall, the *Chaetodon* assemblage is most strongly structured by a few key bottom-up (habitat) variables. Depth, macroalgal cover, rugosity, rock cover, and the extent of branching and tabular corals consistently re-occur as the strongest predictors of *Chaetodon* abundance and species richness (Table 4, Fig. 3). Suitable habitat for corallivores appears to be algal-poor, intermediate-rocky reefs between 6 and 10 m deep, with at least 15% cover of branching and tabular corals (Fig. 3a). Suitable habitat for benthic generalists is algal-poor, rocky and rugose reefs between 9 and 12 m deep, with as little live coral cover as possible (Fig. 3b).

Our most striking finding was the strong negative effect of macroalgae on the butterflyfish assemblage. A negative relationship between macroalgae and reef fish abundance has generally been interpreted as a consequence of decreased live coral cover, without a direct cause-and-effect relationship between macroalgae and reef fish abundance (Done 1992; Hughes 1994; Mumby *et al.* 2006; Hughes *et al.* 2007). However, our results point to a considerable, and possibly more direct, negative algal effect on the butterflyfishes, particularly generalists, rather than simply a side effect of the loss of live coral cover. This is a concerning finding, given that increases in macroalgal cover are a common outcome of acute disturbances such as storm events, as well as of chronic stressors such as overfishing of herbivores, destructive fishing practices, sedimentation and nutrient enrichment (Hughes 1994; Hughes and Connell 1999; Nyström *et al.* 2000; Fabricius 2005; Knowlton and Jackson 2008), all of which are common stressors in this region (Gomez *et al.* 1994; Hoegh-Guldberg *et al.* 2009; McLeod *et al.* 2010; Burke *et al.* 2012).

We hypothesise that the strong negative effect of macro-algae on the *Chaetodon* butterflyfishes was the result of two main factors. The first factor is unattractive olfactory cues emitted by the algae, which could have deterred larval fish settlement. Larval-stage reef fishes use many olfactory cues to select suitable settlement habitat (Kingsford *et al.* 2002; Dixson *et al.* 2008; Coppock *et al.* 2013), with coral cues being significantly more attractive than algal cues for many coral reef fishes (Lecchini *et al.* 2013). The second factor is reduced foraging options, with increasing macroalgal cover reducing availability of both coral and non-coral invertebrate prey. An extensive review by Stella *et al.* (2011) on non-coral inverte-brate communities on coral reefs found that a high proportion of non-coral invertebrates were obligate coral associates (56%), with extremely high levels of specialisation (84% depended on just a single coral taxon, and predominantly fragile genera such as *Pocillopora* and *Acropora*). We therefore suggest that an increase in macroalgal cover may reduce the non-coral invertebrate community that generalist *Chaetodon* prey upon. However, neither of these factors can fully explain the low threshold levels (5% for generalists, 15% for corallivores) of the negative effect of macroalgal cover on butterflyfish abundance and species richness. The severity of the negative effects of macroalgal cover is surprising, and merits further investigation.

Although live coral (particularly branching and tabular morphologies) was an important predictor of corallivorous *Chaetodon* abundance, the benefits of branching and tabular coral cover on corallivore abundance were attained at only 15% cover of branching and tabular corals, which is much lower than has been found in other studies of deteriorated reef condition (Pratchett *et al.* 2006; Cheal *et al.* 2008). Furthermore, live coral cover exhibited a negative influence on generalist abundance, and was unrelated to overall *Chaetodon* species richness in this study. Research in other regions has found that live coral cover is an important predictor of *Chaetodon* species richness (in New Caledonia, Bozec *et al.* 2005; in the Chagos Archipelago, Graham 2007; and on the Great Barrier Reef, Halford *et al.* 2004; Pratchett *et al.* 2006; and Komyakova *et al.* 2013), and the difference with our study may be due in part to the high abundance of generalists in the *Chaetodon* assemblage in our study region relative to the previous studies (Table 2).
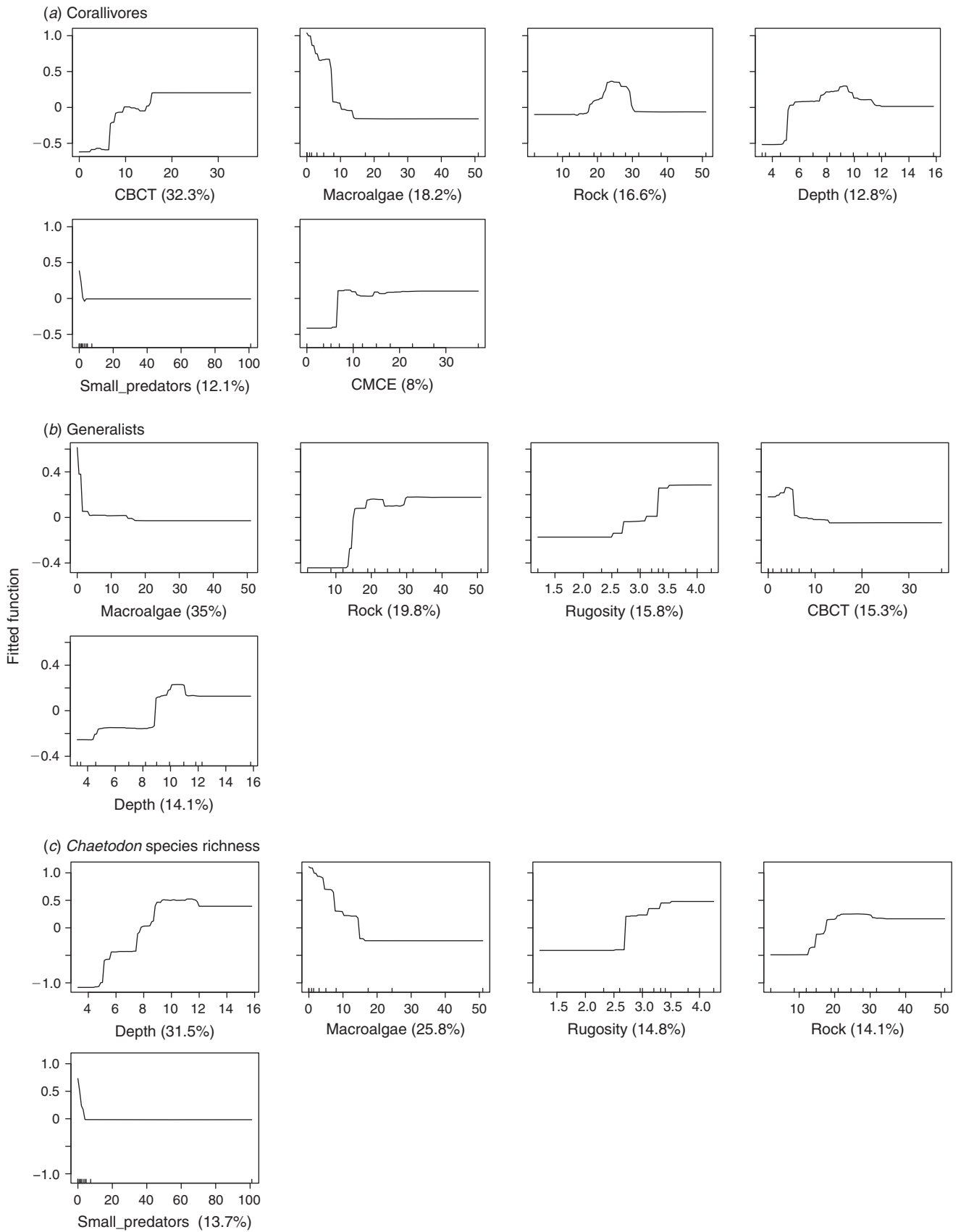
Fig. 3. Partial dependence functions for all variables significantly influencing (*a*) the abundance of corallivorous *Chaetodon*, (*b*) the abundance of generalist *Chaetodon*, and (*c*) *Chaetodon* species richness across the study region. Variables are presented in order of decreasing relative influence. CBCT indicates branching and tabular corals, CMCE indicates massive and encrusting corals.

Our results also contribute to growing evidence of the pre-eminence of measures of habitat complexity (e.g. rugosity and rock cover) over coral cover as a driver of butterflyfish abundance and diversity (Bozec *et al.* 2005; Graham *et al.* 2009; Tkachenko and Soong 2010). This may be particularly true in our study region, where high benthic complexity or rugosity was found at sites with high rock cover, and is therefore attributable to high levels of rugosity in the underlying dead coral and rocky reef structure (Fig. 2e, f) This underlying reef complexity is likely a major reason why our measure of rugosity was consistently high across most of the region, despite extremely low live coral cover and high rubble cover at the sites closest to the path of Tropical Storm Washi. The absence of a storm 'fingerprint' on the benthic complexity in our study may also be a consequence of the depth range of our surveys (3–15 m), with deeper areas being less vulnerable to storm damage, and sometimes experiencing increases in rugosity due to the displacement of massive corals and rocks from the upper reef slope to the lower reef slope during storms (Harmelin-Vivien 1994). This depth effect may explain why our results differ so strongly from studies on shallow reef slopes (6–9 m deep) on the Great Barrier Reef, which reported simultaneous reductions in live coral cover and benthic complexity as a result of physical storm damage (Emslie *et al.* 2008; Emslie *et al.* 2011; Emslie *et al.* 2014).

Some top-down control was suggested by the negative effect of small predators (6–10 cm) on the abundance of corallivorous butterflyfish and on overall *Chaetodon* species richness (Table 4, Fig. 3). Predators in this size range are considered mesopredators, and are largely responsible for the extremely high mortality seen in newly settled and juvenile reef fishes (Holmes and McCormick 2010; Feeney *et al.* 2012). It is therefore likely that the negative effect of mesopredators on butterflyfish abundance is occurring at these early life stages, during which small butterflyfish are still vulnerable to small, gape-limited predators. The vulnerability of newly settled and juvenile butterflyfish to predation is so strong that it is considered to be the main driver of the evolution and prevalence of false eyespots in juveniles of *Chaetodon* species (Neudecker 1989), whereas the large body size, lateral compression, extreme body depth, and long dorsal and anal spines on adult butterflyfish are thought to greatly limit predation risk for adult butterflyfishes (Hourigan 1989; Neudecker 1989). In addition, our data indicate that predation on *Chaetodon* juveniles is only significant for corallivorous species, and not for generalists. This is likely due to contrasting settlement site selection by members of the different feeding guilds, with dietary specialists such as corallivores needing to settle directly into deeper, coral-dominated habitats where they may be more prone to predation, whereas generalists can often settle into safer 'nursery' habitats such as shallow, rocky subtidal areas, and then carry out an ontogenetic shift onto deeper reef areas (Pratchett and Berumen 2008; Clark and Russ 2012) when they have outgrown the 'predation gauntlet' of mesopredators (Dahlgren and Eggleston 2000; Lecchini and Galzin 2005; Pratchett *et al.* 2008).

Our BRT models captured a great deal of the variation in *Chaetodon* abundances and species richness. However, there was still considerable unexplained variance in this system. Potentially the most important determinant of reef fish

abundances and diversity is larval supply (Williams *et al.* 1994; Armsworth 2002; Sale 2004), which we were unable to assess in this study. Although post-settlement habitat availability and preferences can strongly mediate adult abundances, they act on an initial pool of recruits that is not distributed evenly in space or time (Williams *et al.* 1994; Jones *et al.* 2009; Berumen *et al.* 2012; Harrison *et al.* 2012). Initial work to elucidate patterns of larval connectivity in this region (R. A. Abesamis, P. Saenz-Agudelo, L. P. C. Bernardo, M. L. Berumen, C. R. L. Jadloc, L. A. Solera, C. L. Villanoy, A. C. Alcala, and G. R. Rus, unpubl. data) will aid in understanding to what extent *Chaetodon* abundances are structured by larval supply versus post-settlement ecological factors such as those explored here.

While it is standard practice for ecological studies to assess and report the influence of a few key variables on a study species (Munday *et al.* 1997; Halford *et al.* 2004; Bozec *et al.* 2005; Pratchett *et al.* 2006; Graham 2007), it is much less common to quantify the relative influence of both bottom-up and top-down processes (but see Wilson *et al.* 2008). Exploring a much larger number of drivers, involving both bottom-up and top-down processes, is the only way to fully illustrate a complete ecological picture that can provide better information for management (e.g. Wilson *et al.* 2008). In this study, we identified that post-settlement *Chaetodon* abundance and species richness are overwhelmingly structured by bottom-up drivers. However, key benthic components such as live coral cover and macroalgal cover are themselves subject to both top-down (i.e. predation and herbivory respectively) and bottom-up (e.g. nutrient enrichment, environmental disturbances to benthos) influences, which makes management of coral reef systems particularly complex. This study contributes to growing evidence that coral reefs must be actively managed using a combination of bottom-up and top-down approaches, in which large-scale stressors such as sedimentation, nutrient enrichment, ocean acidification and sea-surface warming are addressed (Pandolfi *et al.* 2005; Veron *et al.* 2009; Brodie *et al.* 2012) to promote coral health and to reduce macroalgae-favouring conditions, while local-scale fisheries management is used to increase the abundance of herbivores (Mumby *et al.* 2006) and to control the abundance of mesopredators (Prugh *et al.* 2009).

Coral reef systems are especially vulnerable to multiple, interacting stressors, in which natural disturbance events are compounded by direct human activities and indirect climate-mediated stressors (Hughes *et al.* 2003; Veron *et al.* 2009; Hoegh-Guldberg 2011). However, their proximity to many of the world's poorest, most resource-dependent coastal nations (Hoegh-Guldberg *et al.* 2009; Burke *et al.* 2012) and their importance to the livelihoods of millions of people (Hoegh-Guldberg *et al.* 2009; Burke *et al.* 2012; Foale *et al.* 2013) means that their persistence will require careful and holistic management (Hoegh-Guldberg *et al.* 2009; McLeod *et al.* 2010; Burke *et al.* 2012). Management, in turn, must be informed by high-quality research that assesses and exposes the major drivers of abundance and diversity in coral reef systems.

Acknowledgements

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