

# Reef flattening effects on total richness and species responses in the Caribbean

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## Summary

1. There has been ongoing flattening of Caribbean coral reefs with the loss of habitat having severe implications for these systems. Complexity and its structural components are important to fish species richness and community composition, but little is known about its role for other taxa or species-specific responses.

2. This study reveals the importance of reef habitat complexity and structural components to different taxa of macrofauna, total species richness, and individual coral and fish species in the Caribbean.

3. Species presence and richness of different taxa were visually quantified in one hundred 25-m<sup>2</sup> plots in three marine reserves in the Caribbean. Sampling was evenly distributed across five levels of visually estimated reef complexity, with five structural components also recorded: the number of corals, number of large corals, slope angle, maximum sponge and maximum octocoral height. Taking advantage of natural heterogeneity in structural complexity within a particular coral reef habitat (*Orbicella* reefs) and discrete environmental envelope, thus minimizing other sources of variability, the relative importance of reef complexity and structural components was quantified for different taxa and individual fish and coral species on Caribbean coral reefs using boosted regression trees (BRTs).

4. Boosted regression tree models performed very well when explaining variability in total (82.3%), coral (80.6%) and fish species richness (77.3%), for which the greatest declines in richness occurred below intermediate reef complexity levels. Complexity accounted for very little of the variability in octocorals, sponges, arthropods, annelids or anemones. BRTs revealed species-specific variability and importance for reef complexity and structural components. Coral and fish species occupancy generally declined at low complexity levels, with the exception of two coral species (*Pseudodiploria strigosa* and *Porites divaricata*) and four fish species (*Halichoeres bivittatus*, *H. maculipinna*, *Malacoctenus triangulatus* and *Stegastes partitus*) more common at lower reef complexity levels. A significant interaction between country and reef complexity revealed a non-additive decline in species richness in areas of low complexity and the reserve in Puerto Rico.

5. Flattening of Caribbean coral reefs will result in substantial species losses, with few winners. Individual structural components have considerable value to different species, and their loss may have profound impacts on population responses of coral and fish due to identity effects of key species, which underpin population richness and resilience and may affect essential ecosystem processes and services.

**Key-words:** biodiversity, conservation, degradation, relief, topography

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## Introduction

The number and variety of species is considered a fundamental component of ecosystem structure and function (Naeem & Li 1997; Loreau *et al.* 2001; Hooper *et al.* 2005), and complex coral reefs are among the most species-diverse marine habitats (Huston 1985; Jackson 1991; Gray 1997). Within habitats, species-rich areas may show greater resilience to disturbance (Peterson, Allen & Holling 1998; Bellwood & Hughes 2001), and consequently, 'hot spots' of high species richness are often prioritized for conservation efforts (e.g. Myers *et al.* 2000; Hughes, Bellwood & Connolly 2002; Roberts *et al.* 2002; Mora *et al.* 2003), although this may not always be appropriate (Wilson *et al.* 2006). However, biological diversity is widely under threat (Gaston 2000; Knowlton & Jackson 2008), and its loss may have severe consequences for reef systems (Sebens 1994).

Corals and fishes are the most studied coral reef organisms. Akin to birds in terrestrial systems (Stattersfield *et al.* 1998), fishes are often used as a focal group to investigate trends in species richness because they are speciose, widely distributed and easily observed (Allen 2008; Mumby *et al.* 2008). However, they may not always be a good proxy for other taxa (e.g. Sutcliffe *et al.* 2012) and may not contribute greatly to overall diversity (Fisher *et al.* 2015). The pool of available species on reefs is determined by a combination of large-scale processes such as latitude, temperature, habitat area or environmental stability (Fraser & Currie 1996; Bellwood & Hughes 2001; Mora *et al.* 2003; Parravicini *et al.* 2013) as well as small-scale variations in the local environment. Stochastic processes such as recruitment (Sale 1991) may drive local fish species richness and abundance, but habitat structure appears to mediate much of the post-settlement patterns (Syms & Jones 2000) through species-specific habitat preferences or modification of competition and predation (Hixon & Menge 1991; Hixon & Beets 1993; Beukers & Jones 1997; Almany 2004; Grabowski, Hughes & Kimbro 2008). Habitat structure has been shown repeatedly to be important to coral reef fish and has received increasing attention (Graham & Nash 2013). This has largely been driven by the threat ongoing loss of structural complexity on Caribbean coral reefs (Alvarez-Filip *et al.* 2009) poses to biodiversity and reef habitats (e.g. Chong-Seng *et al.* 2012). However, there is a paucity of studies on other taxa or the response of individual species or families to changes in reef structural complexity (Graham & Nash 2013; Pratchett, Hoey & Wilson 2014).

Measures of habitat structure on coral reefs are often reduced to a single aggregate measure such as chain and tape measures of rugosity (Risk 1972), visually estimated complexity (e.g. Polunin & Roberts 1993), compound habitat (e.g. Gratwicke & Speight 2005b) and PCA scores (e.g. Chong-Seng *et al.* 2012), or recently digital terrain models (e.g. Pittman *et al.* 2007; Pittman, Costa & Battista 2009; Costa *et al.* 2014). However, a single measure

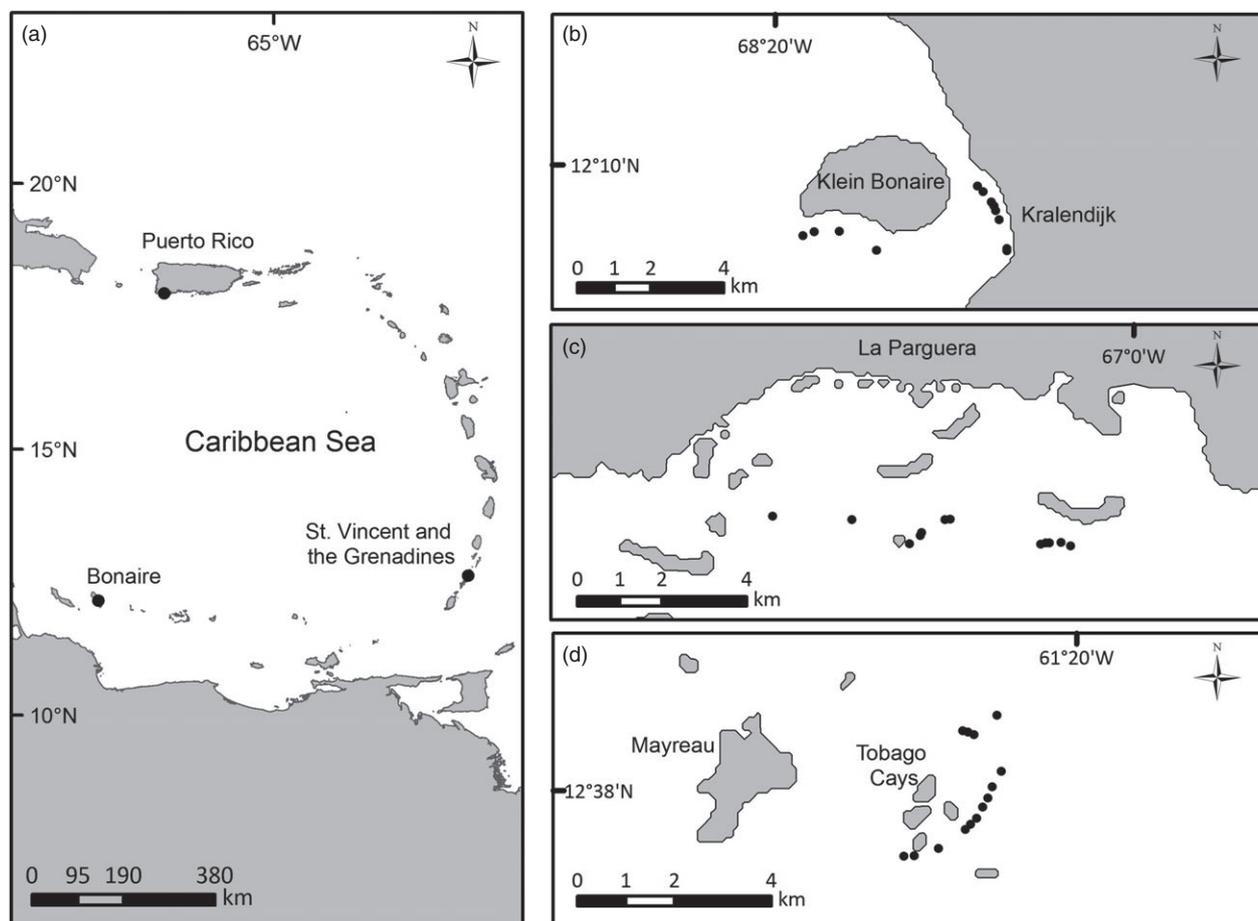
is unlikely to capture all the variability in complexity; habitat complexity has been defined as incorporating both complexity and the abundance of individual structural components (McCoy & Bell 1991), and they can have separate effects on assemblages (Beck 2000). Thus, a range of individual structural components have been investigated on reefs including vertical relief, frequency of tall corals, coral morphology and the amount of holes/refuge (McCormick 1994; Friedlander & Parrish 1998; Gratwicke & Speight 2005a,b; Wilson, Graham & Polunin 2007; Harborne, Mumby & Ferrari 2012; Graham & Nash 2013). Multiple measures of topographic complexity and structural components may be required to elucidate individual species relationships (e.g. Beck 2000; Harborne, Mumby & Ferrari 2012).

Reef complexity acts on fish species richness in concert with other covariates such as wave exposure or depth, and the effects of complexity may be difficult to separate (Jennings, Boullé & Polunin 1996; Graham *et al.* 2009; Chong-Seng *et al.* 2012; Wilson *et al.* 2012; Graham & Nash 2013). This study takes advantage of natural spatial heterogeneity in structural complexity within small geographic areas within a discrete environmental envelope (Chollett *et al.* 2012) and a particular habitat type (*Orbicella* reefs) to reduce spatiotemporal confounding. This facilitates the elucidation of the relative importance of reef complexity (within 25-m<sup>2</sup> plots) and five structural components (the number of corals, number of large corals, slope angle, maximum sponge and maximum octocoral height) to (i) total richness on coral reefs, (ii) richness of different macrofauna taxa and (iii) individual coral and fish species occupancy.

## Materials and methods

The presence of reef macrofauna was recorded on reefs with different levels of topographic complexity in three marine reserves in the Caribbean: Bonaire National Marine Park (BON), La Parguera Natural Reserve in south-west Puerto Rico (PR) and the Tobago Cays Marine Park in St. Vincent and the Grenadines (SVG; Fig. 1). These locations were selected due to well-developed reefs with a range of topographic complexity levels, with surveys in Bonaire and SVG in established marine reserves with low levels of exploitation and infrequent physical disturbance from hurricanes (Chollett *et al.* 2012), while the marine protected area in PR has long-term commercial and recreational fishing (Appeldoorn *et al.* 1992; Valdés-Pizzini & Schäfer-Umpierre 2014).

Species presence was quantified in twenty 25-m<sup>2</sup> plots at each of five levels of reefscape complexity in each country (100 plots total per country). Surveys were conducted in the same reef system within each country in order to minimize other sources of variability (e.g. physical conditions, fishing pressure), in the same reef habitat in sheltered areas (prevailing wind direction from the east in all cases, with all reefs sheltered by either land or windward reefs). The maximum distance between surveys was 5.5 km in Bonaire, 6.9 km in PR and 3.6 km in SVG. Plots were haphazardly situated in areas of uniform complexity at least 10 m from a boundary between different complexity levels or from other



**Fig. 1.** Survey locations: (a) in eastern Caribbean, (b) west coast of Bonaire, (c) La Parguera, south-west Puerto Rico, and (d) Tobago Cays in St. Vincent and the Grenadines.

plots, on coral fore-reefs at depths of 5–15 m (mean  $10.15 \pm 0.14$  SE  $n = 300$ ).

Reefscape complexity was visually estimated on a scale of 1 (flat, little relief) to 5 (highly complex with high vertical relief and overhangs) following Polunin & Roberts (1993). A single complexity value was assigned by two experienced surveyors (SPN and CSD) to avoid observer bias, and each plot was photographed to ensure continuity of complexity estimates by enabling post-survey standardization based on the range of reefscape complexity from all plots surveyed (see Appendix S1, supporting information, for examples of each complexity level). Visual estimates of complexity have been widely employed (e.g. Polunin & Roberts 1993; Jennings, Boullé & Polunin 1996; Wilson, Graham & Polunin 2007), are strongly correlated with coral reef fish richness (Wilson, Graham & Polunin 2007) and incorporate aspects of complexity such as caves and overhangs (Polunin & Roberts 1993) that chain and tape surface rugosity estimates (e.g. Risk 1972) may fail to accurately reflect. Visually estimating complexity also allowed plots to be rapidly categorized and selected prior to disturbing motile faunal communities. Three divers characterized the faunal communities and one recorded structural complexity components.

Plots were delineated with tape measures in a 'T' shape, after first recording larger, more mobile fish species (SPN) 2.5 m either side of the first 5-m tape as it was deployed following the depth contour. Each plot half was then carefully searched for fish (by S Newman

and C Dryden) and arthropods (by C Dryden), emergent annelids, anemones, molluscs and flatworms (by S Newman), and then corals, echinoderms, sponges, octocorals, zoanthids, antipatharians and corallimorphs (by S Williams). Unknown species were photographed for later identification. Survey time was greater in more complex plots due to greater surface area and the necessity to thoroughly search for cryptic species, with total plot survey times varying between 10 and 20 min.

In addition to visual assessment of reefscape complexity (hereafter referred to as just 'reef complexity', while 'complexity' refers to the overall ecological concept), five structural components (Table 1) were recorded (by C Sanchez) to characterize the aspects of complexity (*sensu* McCoy & Bell 1991) which can have separate effects on assemblages (Beck 2000). Numbers of live corals larger than 4 cm in diameter ('*no. corals*') and of large corals (>50 cm height, '*no. large corals*') provided metrics independent of the reef complexity scale representing different aspects of coral density that may be important predictors of fishes (e.g. Harborne, Mumby & Ferrari 2012). Maximum octocoral height ('*octocoral max height*') has been used to describe octocoral communities (Lasker & Coffroth 1983) and was recorded in each plot because soft corals may contribute to structural complexity (Dustan, Doherty & Pardede 2013). Maximum sponge height in the plot ('*sponge max height*') was included because sponges can also act as ecosystem engineers and provide biogenic structures in otherwise low relief habitats (e.g. McClintock *et al.* 2005) and may

**Table 1.** Summary of predictors (mean  $\pm$  standard error and range) used in boosted regression tree models

Variable	Description	Mean	Range
Country	Categorical location of sample	na	na
Reef complexity	Visually estimated complexity	na	1–5
No. corals	Number of live coral colonies in plot	163.1 $\pm$ 4.5	11–400
No. large corals	Number of corals taller than 50 cm	6.7 $\pm$ 0.4	0–32
Sponge max height	Maximum vertical height of sponge (cm)	32.4 $\pm$ 1.8	0–211
Octocoral max height	Maximum vertical height of octocoral (cm)	87.4 $\pm$ 2.9	0–229
Slope angle	Estimated angle of underlying reef slope (degrees)	27.4 $\pm$ 1.3	0–80

enhance fish species richness. ‘*Slope angle*’ was visually estimated in degrees from the horizontal plane at each plot edge perpendicular to the reef slope and averaged, and was included as a predictor due to flatter reef areas typically having less coral development (e.g. Jones & Chase 1975). The requirements of a fish species for different aspects of architectural complexity were expected to remain the same regardless of location, and thus, ‘*country*’ was included as a fixed effect in the analysis to account for any covariates that were not included in these models, despite best efforts to minimize other sources of variability by surveying within a discrete coral habitat and environmental envelope.

#### MODELLING APPROACH

Relationships between species richness of different taxonomic groups and reef complexity and structural components, and the relative importance of each complexity variable, were examined using boosted regression trees (BRTs). This technique can accommodate continuous, categorical or missing variables, can model nonlinear and complex relationships, and may outperform GLM and GAM approaches in terrestrial (Elith *et al.* 2006) and marine systems (Leathwick *et al.* 2006). Separate BRT models were fitted predicting the total number of species present (including all taxonomic groups; see Appendix S2), for separate taxonomic groups (corals, fishes, arthropods, octocorals, annelids, echinoderms and anemones) and the presence of each coral and fish species, in R (v2.15.3, www.R-project.org; R Development Core Team 2013), using the ‘gbm’ package (Ridgeway 2013) and functions from Elith, Leathwick & Hastie (2008). Individual species were only modelled if they were present in more than 20 plots (of 300 sampled) to avoid modelled relationships based on sparse presence data. All models were fitted to allow interactions using a tree complexity of 5, a bag fraction of 0.6 and a learning rate of 0.003 or 0.001 to minimize predictive deviance and maximize performance. Interaction values indicate the relative departure from a purely additive effect, with zero indicating no interaction. The predictor variables ‘sponge height’, ‘octocoral height’ and ‘number of corals’ were excluded from models of sponge, octocoral and coral richness, respectively, due to the direct relationship between predictor and response. The ‘number of large corals’ was included as a predictor because it was more independent of coral species richness as coral size distributions tend to be right-skewed (Bak & Meesters 1999). Predictor variables that increased variance and reduced model performance were dropped using the ‘gbm.step’ function from Elith, Leathwick & Hastie (2008).

Ten-fold cross-validation (CV) was used to identify the optimum number of trees (1000–2650 for taxonomic group models and 250–2350 for individual species models) and to test the model on randomly withheld portions of data (Hastie, Tibshirani & Friedman 2001), with all data used to fit each model. BRTs

tend to overfit training data (Elith, Leathwick & Hastie 2008; Leathwick *et al.* 2008) so model performance was based on predictions of data withheld during CV, and predictive deviance expressed as a percentage of the null deviance for each group. For models predicting individual species occurrence, an additional measure of performance was the area under the receiver operator characteristic curve (AUC; Hanley & McNeill 1982). AUC values estimate how well-fitted values discriminate between observed presences and absences, with values ranging from 0.5 (no better than random) to 1.0 (perfect discrimination). Here, models with AUC scores >0.8 are considered very good and >0.9 excellent (following Hosmer & Lemeshow 2000). The relative importance of each predictor variable was estimated using formulae developed by Friedman (2001) and script within the R package ‘gbm’, based on the number of times a variable was selected for splits and weighted by the squared improvement of the model and averaged over all trees (Friedman & Meulman 2003). This was then scaled to 100, with higher numbers indicating stronger influence on the response variable. Here, partial dependence plots (where all other predictors are kept at their mean) are presented for the four most important predictors in models where complexity predictors explain at least 40% of the total variability in a taxon’s species richness or a species occurrence. Plots include 95% confidence intervals for each predictor determined from 100 bootstrap replicates using a function written by the authors.

#### Results

Across all countries, 418 species were identified, with fishes comprising 34%, sponges 22%, corals 12% and arthropods and octocorals each 8% of total species (Table 2). In total, 143 fish species (80 genera, 41 families)

**Table 2.** Number of identified species in each taxonomic group in rank order of abundance in total and in each country with percentage of grand total in parentheses. Total richness includes all other taxa plus identified corallimorphs, flatworms and zoanthids

	Total	Bonaire	Puerto Rico	SVG
Fishes	143 (34)	104 (73)	86 (60)	105 (73)
Sponges	90 (22)	67 (74)	67 (74)	70 (78)
Corals	49 (12)	35 (71)	40 (82)	33 (67)
Arthropods	35 (8)	17 (49)	25 (71)	27 (77)
Octocorals	33 (8)	18 (55)	30 (91)	29 (88)
Annelids	16 (4)	11 (69)	14 (88)	15 (94)
Echinoderms	10 (2)	7 (70)	6 (60)	7 (70)
Anemones	9 (2)	7 (78)	7 (78)	4 (44)
Grand total:	418	280 (67)	292 (70)	314 (75)

were recorded, with 104 fish species in Bonaire (60 genera, 33 families), 86 fish species in PR (51 genera, 28 families) and 105 fish species in SVG (64 genera, 37 families). Due to their low occurrence and diversity, flatworms (two species), antipatharians (one species) and corallimorphs (two species) were excluded from further individual analysis, while molluscs were excluded from analysis due to the absence of some species-level data.

#### IMPORTANCE OF COMPLEXITY TO DIFFERENT TAXA

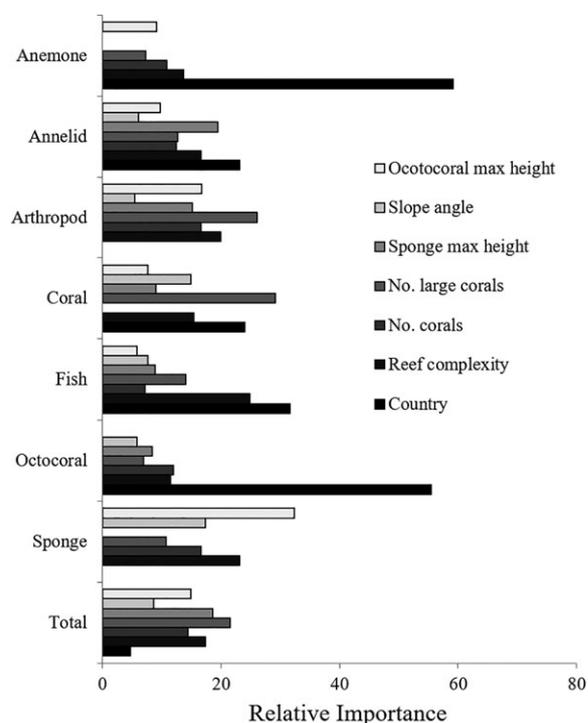
Boosted regression tree predictive deviance was greatest for total richness (82.3%), octocoral (81.7%), coral (80.6%), fish (77.3%) and anemone species richness (57.9%, Table 3). BRTs explained very little variability in annelid, arthropod or sponge richness (Table 3), and complexity predictors accounted for little of the variability in octocoral and anemone richness (Fig. 2). Reef complexity and number of large corals were in the top four predictors for fish, corals and total richness (Fig. 3), but their relative importance varied (Fig. 2) and fitted functions were mostly nonlinear and complex (Fig. 3).

The model predicting total species richness explained the greatest variability (82.3%) revealing the importance of habitat structural complexity to the total species richness of coral reef ecosystems in the Caribbean (Table 3). The fitted functions (Fig. 3a) reveal total species richness was greatest in plots with more than 10 large corals (per 25 m<sup>2</sup>) with tall sponges (> ~75 cm) and octocorals (>100 cm). Total species richness was greatest at reef complexity level 4 (mean 70.7 ± 1.3 SE species), although there was little variation among levels 3–5, but total richness declined considerably at lower complexity levels (complexity 1: mean 50.1 ± 1.3 SE and complexity 2: 60.8 ± 1.3 species, Fig. 3a). Interactions were small and non-significant, suggesting predictors acted in an additive manner.

Coral species richness was greatest in areas with more than 15 large corals per plot, increased almost linearly with slope angle, and was lowest in SVG (Fig. 3b). Coral species richness was slightly higher at reef complexity level three, and declined greatly at lowest reef complexity, while confidence intervals at high complexity levels indicate increased variability in coral species richness

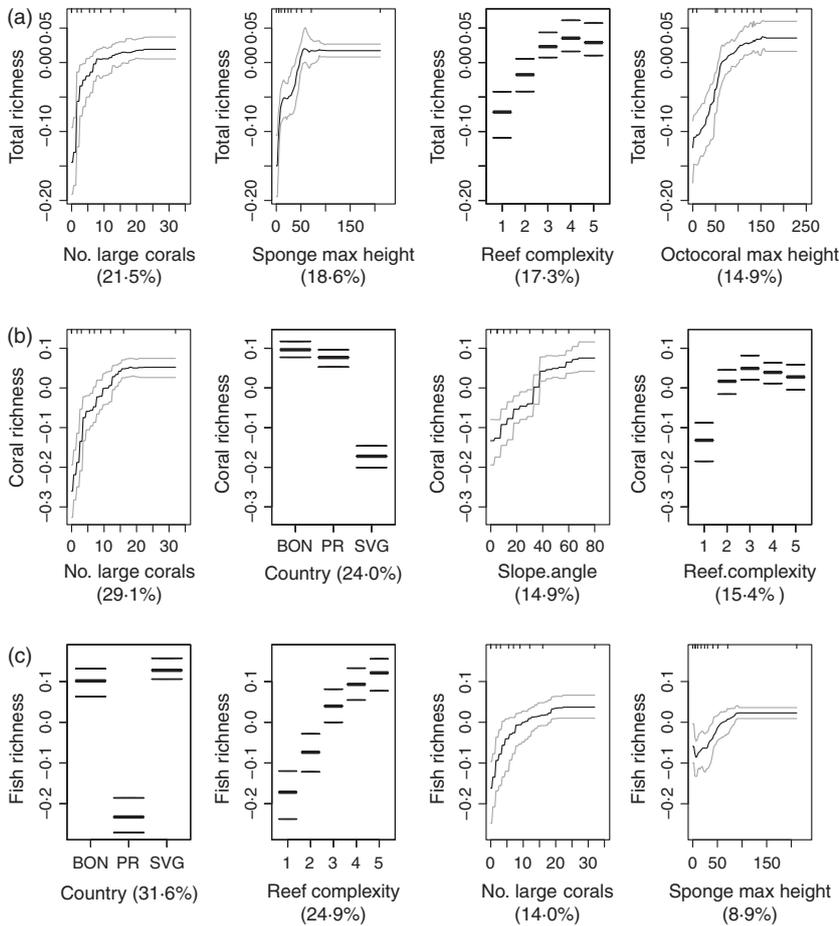
**Table 3.** Predictive performance of boosted regression tree (BRT) models relating richness of different reef taxa to reef complexity and location. Table variables indicate the learning rate, optimum number of trees fitted, the mean residual deviance of the model, the percentage deviance using 10-fold cross-validation (how good the model is a predicting left out or unknown data) and the percentage total deviance explained by each model

Taxonomic group	Learning rate	No. of trees	Model residual deviance	CV residual deviance (SE)	Total deviance (%)
Anemone	0.005	1000	0.35	0.43 (0.05)	57.9
Annelid	0.001	2150	0.49	0.58 (0.06)	29.6
Arthropod	0.001	1250	0.83	0.99 (0.06)	21.3
Coral	0.005	1450	0.27	0.43 (0.04)	80.6
Octocoral	0.005	2550	3.18	1.05 (0.11)	81.7
Fish	0.005	1250	0.56	0.43 (0.09)	77.3
Sponge	0.005	1500	1.29	1.09 (0.09)	35.9
Total	0.005	2650	0.47	1.03 (0.09)	82.3



**Fig. 2.** Relative influence (%) of complexity variables predicting richness of different taxa on Caribbean reefs. Total richness includes all listed taxa plus anemones, flatworms, antipatharians and corallimorphs (see Appendix S2 for full species list). Note octocoral and sponge height, and number of corals were not used in models predicting octocoral, sponge and coral richness, respectively; all other absent bars indicate variable dropped from final model.

(Fig. 3b). Reef complexity and country had the greatest relative influence on fish species richness (Fig. 2), with fish species richness lowest in PR (Fig. 3c). Fish species richness was highest in Bonaire and SVG, at high reef complexity levels, where there were more than 15 large corals per plot and with sponges over 75 cm tall (note fitted functions in Fig. 3c). Fish species richness declined below reef complexity level three, and confidence intervals indicate a greater variability in the number of fish species at lower levels of complexity (Fig. 3c), despite even sampling across reef complexity levels. A small but significant interaction existed between country and reef complexity



**Fig. 3.** Functions fitted for the four most important predictor variables (ranked by percentage relative influence left to right) by BRT models relating (a) total species richness, (b) coral species richness and (c) fish species richness to reef complexity variables and location. Total richness was calculated as the sum of all species of fishes, corals, sponges, octocorals, anemones, annelids, arthropods, flatworms, antipatharians and corallimorphs (see Appendix S2 for full species list). See Table 1 for descriptions of *x*-axes parameters. A common scale is used on the vertical axis for all plots. Fitted lines represent the mean estimate (black) and 95% confidence intervals (grey) based on 100 bootstrap replicates. Rug plots show distribution of data in deciles of the *x*-axis variable.

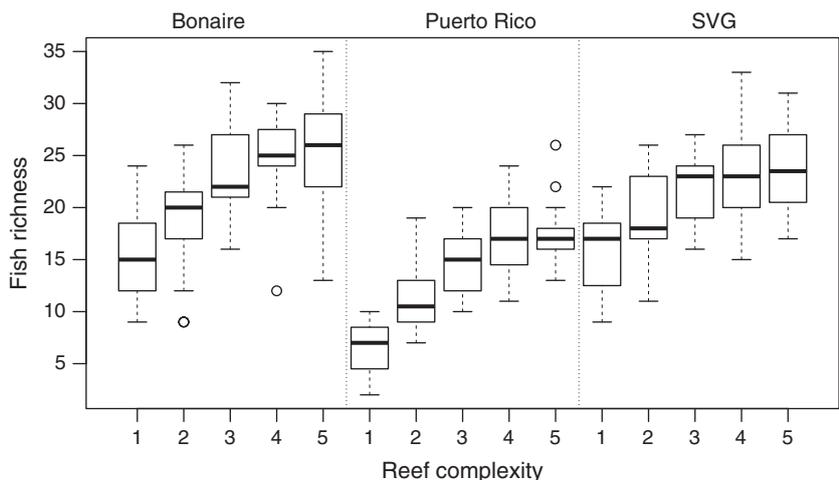
(1-95) with fish species richness at low complexity in Bonaire and SVG equal to fish species richness at high reef complexity sites in PR (Fig. 4).

**SPECIES RELATIONSHIPS**

*Coral species presence*

The presence of 23 of 51 coral species was modelled (45%, see Table S1 for all species models), with two

species not modelled due to presence in over 95% of surveyed plots (*Millepora alcicornis* and *Porites asteroides*), while other non-modelled species were in <20% of plots. Models explained over 40 % of the total deviance in 19 coral species (Table 4) with excellent performance (area under receiver operator characteristic curve, AUC score > 0.90; Table S1). As a single predictor, country had the greatest relative importance across all coral species (mean 35.6 %, range 7.0–66.6%), but combined reef complexity and structural components accounted for on



**Fig. 4.** Relationship between fish species richness and complexity (1: low, 5: high; visually assessed) in protected areas in Bonaire and St. Vincent and the Grenadines (SVG) and in a heavily fished area in Puerto Rico, in the Caribbean.

average 64.4% of the explained variance across all coral species (range: 33.4–93.0%, Table 4).

Reef complexity was retained as a significant predictor for 17 coral species (Table 4) and had the greatest relative importance of all the complexity predictors across all species modelled (average 17.7%). The importance of reef complexity varied with coral species and was the most important complexity predictor for the presence of *Orbicella faveolata* (53.7%), *Agaricia agaricites* (36.9%), *Orbicella annularis* (29.7%) and *Porites furcata* (23.1%), which contribute greatly to complexity on Caribbean coral reefs. Relationships between coral species presence and reef complexity were highly variable in shape and were frequently nonlinear (see Fig. S1 for the four most important functions for each coral species). Many coral species showed dramatic declines in occurrence at low reef complexity levels (complexity level one or two), with only two species showing greater occupancy at low complexities (*P. strigosa* and *P. divaricata*). Five coral species showed a peak in occurrence at high complexity (*Agaricia lamarcki*, *Madracis auretenra*, *O. annularis*, *O. faveolata*, *Scolymia cubensis*) although this only accounted for large amounts of predicted deviance for *Orbicella* corals. Four coral species showed peaks at intermediate reef complexity level three (*Colpophyllia natans*, *Montastraea cavernosa*, *Orbicella franksi* and *P. porites*; Fig. S1).

The number of large corals was the second most important complexity predictor averaged across all modelled species (17.3%), but was retained in models for only 11 of the 19 species (Table 4). The number of large corals was the most important predictor of *M. auretenra* (39.8%), *O. franksi* (37.2%) and *O. annularis* (26.5%, Table 4). Octocoral maximum height was the only complexity

predictor retained in all coral species models, although on average the relative influence (15.7%) was lower than that of reef complexity and the number of large corals. The relationship between coral occurrence and octocoral maximum height varied with species, with occurrence of seven species showing a clear increase (*A. agaricites*, *C. natans*, *Eusimilia fastigiata*, *O. faveolata*, *P. divaricata*, *P. furcata*, *P. strigosa*) and three species decreasing with increasing maximum octocoral height (*A. lamarcki*, *O. annularis*, *O. franksi*; see Fig. S1).

Coral species presence was commonly lower when maximum sponge height was low (e.g. <50 cm, see fitted functions in dependence plots in Fig. S1). The exceptions to this were two species (*P. furcata*, *P. porites*) which had a negative relationship with increasing maximum sponge height. Slope angle exhibited a positive relationship with coral species presence when retained as a significant predictor (Fig. S1).

#### Fish species presence

The presence of 54 of the 143 fish species identified was modelled with respect to reef complexity (38%, see Table S2), with all other species not modelled due to low occurrence (observed in <20% of plots). Models explained over 40% of the total deviance for 28 fish species (Table 5), and performance was generally excellent with no species model AUC score < 0.80 and AUC scores > 0.90 for 40 fish species (74% of modelled fish species, Table S2). As a single predictor, country had the greatest relative importance across all coral species (mean 31.8%, range 0–79.7%), but combined reef complexity and structural components accounted for on average

**Table 4.** Total deviance and percentage relative importance of reef complexity and structural components to coral species presence calculated using boosted regression tree models (see Table S1 for model details). Only species modelled with total explained deviance >40% are reported. See Fig. S1 for functions for all coral species modelled. Empty cells indicate non-significant variable dropped from model

Species	Total deviance	Reef complexity	No. large corals	Sponge max height	Octocoral max height	Slope angle	Country
<i>Agaricia agaricites</i>	45.98	36.93			21.10		41.97
<i>Agaricia lamarcki</i>	40.81	11.03	10.47	11.88	14.69	26.93	25.00
<i>Colpophyllia natans</i>	41.36	18.30	29.97	8.07	25.12	6.86	11.67
<i>Eusimilia fastigiata</i>	60.41			11.13	13.84	12.46	62.56
<i>Madracis auretenra</i>	57.91	9.67	39.85	12.07	17.48	9.44	11.50
<i>Madracis decactis</i>	68.97	9.53		7.50	4.66	11.74	66.57
<i>Madracis pharensis</i>	66.79	4.75	9.73	7.99	5.36	7.20	64.97
<i>Meandrina memorialis</i>	66.65	5.90	9.09	5.76	4.70	12.42	62.13
<i>Montastraea cavernosa</i>	55.76	15.54	7.60	19.75	12.63	17.24	27.24
<i>Orbicella annularis</i>	47.65	29.74	26.49		18.37		25.40
<i>Orbicella faveolata</i>	42.92	53.70	9.27	19.27	10.02		7.73
<i>Orbicella franksi</i>	42.92	14.30	37.15	11.66	11.90	18.03	6.97
<i>Porites divaricata</i>	49.75	11.46		7.78	20.42	15.71	44.63
<i>Porites furcata</i>	55.23	23.13		14.76	14.59		47.52
<i>Pseudodiploria labyrinthiformis</i>	40.67			36.78	25.88		37.35
<i>Pseudodiploria strigosa</i>	46.38	18.16	6.92	11.54	23.87	8.47	31.05
<i>Scolymia cubensis</i>	73.38	18.63			27.91	27.18	26.28
<i>Siderastrea siderea</i>	43.73	13.41		20.77	18.88	20.38	26.55
<i>Stephanocoenia intersepta</i>	56.05	4.45	4.14	10.09	7.20	25.63	48.48

68.2% of the explained variance across all coral species (range: 20.3–100%, Table 5). Variability in fish species richness with complexity may be driven by identity effects, revealed by individual species relationships.

The number of corals, maximum octocoral height and reef complexity were the most commonly retained complexity predictors of individual fish species presence, with the number of corals and number of large corals having on average the greatest relative influence across all species (17.1% each; Table 5). The number of corals had the greatest relative influence on the occurrence of the wrasses *H. bivittatus* (slippery dick), *H. maculipinna* (clown wrasse), *H. pictus* (rainbow wrasse) and *T. bifasciatum* (blueheaded wrasse), the saddled blenny *M. triangulatus* and the longfin damsel *Stegastes diencaeus* (Table 5), with all species exhibiting negative relationships with increasing number of corals (see Fig. S2 for the four most important functions for all modelled fish species). The number of large corals was a significant predictor of 18 fish species and was the most important complexity predictor and exhibited a positive relationship with the presence of *Coryphopterus lipernes* (peppermint goby, 40.4%), *Neoniphon marianus* (longjaw squirrelfish, 39.6%), *Chromis cyanea* (blue chromis, 30.6%), *Mulloidichthys martinicus* (yellow goatfish, 21.8%) and *Stegastes planifrons* (threespot damsel, 17.8%, Table 5; see Fig. S2 for dependence plots).

Reef complexity was an important predictor for *Malacoctenus boehlkei* (diamond blenny, 30.1%), *Gramma loreto* (fairy basslet, 25.1%), *H. bivittatus* (25.0%) and *M. triangulatus* (20.2 %; Table 4). Fifteen of the modelled fish species showed clear patterns in presence with complexity, but relationships were highly variable in shape (see Fig. S2). Seven species exhibited an increase in occupancy at higher reef complexities, four species increased at lower complexity levels (*H. maculipinna*, *H. bivittatus*, *M. triangulatus* and *S. partitus* bicoloured damsel) and four species showed highest occupancy at intermediate complexity level 3 (*M. boehlkei*, *T. bifasciatum*, *S. diencaeus* and *Scarus taeniopterus* princess parrotfish; Fig. S2).

Maximum octocoral height had high relative influence (Table 5), although often exhibited a negative relationship with fish species presence with a few exceptions such as *Sparisoma viride* (stoplight parrotfish) and *M. boehlkei*. Maximum sponge height was most important to the presence of the sponge-dwelling yellowline goby (*Gobiosoma horsti*, 34.82%). Slope angle was less important for fish species presence than for corals, with an average relative influence of 12.5%. Slope angle was most important for the blackbar soldierfish (*Myripristis jacobus*, 38.6%) which had higher occupancy on steeper sloped plots (Fig. S2).

**Table 5.** Total deviance and percentage relative importance of reef complexity and structural components to fish species presence calculated using boosted regression tree models (see Table S2 for model details). Only species modelled with total explained deviance >40% are reported. See Fig. S2 for functions for all coral species modelled. Empty cells indicate non-significant variable dropped from model

Species	Total deviance	Reef complexity	No. large corals	No. of corals	Sponge max height	Octocoral max height	Slope angle	Country
<i>Cephalopholis cruentatus</i>	50.89	18.67	14.89	8.92	8.62	5.44		43.46
<i>Chromis cyanea</i>	57.08	4.88	30.58	10.60	6.86	4.45	10.52	32.12
<i>Chromis multilineata</i>	46.95		7.88	15.14	10.14	16.41	8.13	42.30
<i>Clepticus parrae</i>	43.97	20.81	18.33	17.22	11.56	13.48	7.19	11.41
<i>Coryphopterus dicrus</i>	47.12			14.21		11.29	15.48	59.02
<i>Coryphopterus eidolon</i>	69.85		6.63	12.26	11.88		22.69	46.54
<i>Coryphopterus hyalinus</i>	58.37	9.75	9.02	7.58	7.01	6.74	7.53	52.37
<i>Coryphopterus lipernes</i>	64.70	3.03	40.44	13.17	7.64	4.15	7.65	23.91
<i>Gnatholepis thompsoni</i>	47.05	7.40	5.53	8.52	15.18	7.51	9.85	46.00
<i>Gobiosoma horsti</i>	54.25	12.02			34.82	16.07	14.93	22.16
<i>Gramma loreto</i>	66.34	25.14	20.63	7.25	11.16		7.52	28.29
<i>Halichoeres bivittatus</i>	69.53	24.96		48.16	6.22	20.65		
<i>Halichoeres garnoti</i>	50.74			7.97	12.34			79.69
<i>Halichoeres maculipinna</i>	49.71	17.20		22.11				60.69
<i>Halichoeres pictus</i>	55.24	3.75	9.88	22.22	12.38	30.05	5.10	16.62
<i>Malacoctenus boehlkei</i>	43.94	30.10				39.73		30.17
<i>Malacoctenus triangulatus</i>	53.96	20.16		36.22		22.33		21.29
<i>Mulloidichthys martinicus</i>	58.84	15.68	21.84		20.98	13.40	16.79	11.31
<i>Myripristis jacobus</i>	47.15	5.91	18.14	12.57	12.63	7.84	38.64	4.28
<i>Neoiphon marianus</i>	54.48		39.64	20.95		19.77		19.64
<i>Scarus taeniopterus</i>	50.37	11.00	9.64	17.75		6.57	12.89	42.15
<i>Sparisoma atomarium</i>	50.92	10.30	13.08	16.05	6.60	10.56	14.12	29.28
<i>Sparisoma viride</i>	43.28	17.86		19.77	7.78	43.71		10.88
<i>Stegastes adustus</i>	53.91	13.32	8.89	15.32	12.44	13.92	12.80	23.31
<i>Stegastes diencaeus</i>	45.20	16.41		29.47		24.35		29.78
<i>Stegastes partitus</i>	59.20	14.82		10.82	10.89	18.50	6.96	38.02
<i>Stegastes planifrons</i>	67.25	12.06	17.79	15.38	4.98	5.95	5.44	38.40
<i>Thalassoma bifasciatum</i>	41.53	16.22	14.64	17.95		23.86		27.33

## Discussion

This study elucidates relationships between reef complexity and multiple structural components and the richness of multiple taxa, and of an estimate of total faunal richness, on Caribbean coral reefs. Substantially lower total, coral and fish species richness below intermediate reef complexity levels highlights the key functional role of architectural complexity on Caribbean coral reefs, and the need to maintain structure above a critical threshold. This threshold is similar to the visually estimated reef complexity level at which reefs demonstrated an increased capacity for recovery following disturbance (Graham *et al.* 2015). This study also reveals many fish and coral species occupancy relationships with architectural complexity for the first time. Species-specific relationships with complexity and structural components on Caribbean reefs suggest ongoing reductions in reef complexity (Alvarez-Filip *et al.* 2009) will lead to the extirpation of some species with few winners and likely predictable shifts in fish community composition that affect essential ecosystem processes and services (Mumby, Hastings & Edwards 2007; Jackson *et al.* 2014; Pratchett, Hoey & Wilson 2014), which underpin population richness and resilience.

Many studies investigating relationships between reef complexity and species richness focus on a single taxon and include samples across multiple habitats to generate a gradient of complexity, therefore also incorporate variable environment effects (e.g. Jennings, Boullé & Polunin 1996; Graham *et al.* 2009; Chong-Seng *et al.* 2012; Wilson *et al.* 2012). Here, using the same surveyors and confining surveys within a single habitat type (*Orbicella* sp. dominated reefs) allows greater insight, albeit with some caveats, of what might happen if reefs in the Caribbean continue to experience declines in structural complexity (Alvarez-Filip *et al.* 2009).

At mid-to-high reef complexity levels, high total species richness reflected that of fish and corals, but levelled off likely due to a more homogeneously diverse habitat (Kovalenko, Thomaz & Warfe 2012). At low reef complexity levels, lower total species richness was mitigated by increasing sponge richness, which are more diverse than corals in the Caribbean (Diaz & Rützler 2001). Although BRTs failed to predict useful amounts of deviance in arthropod, octocoral, sponge, annelid, echinoderm or anemone species richness related to reef complexity, complexity may still be important to these faunal groups because data were predominantly confined to emergent diurnal non-cryptic macrofauna. Furthermore, despite detailed searches and an even sampling protocol, poor relationships with complexity may reflect the size of species being investigated and the scale at which complexity was measured (McCormick 1994; Wilson, Graham & Polunin 2007) and additional work is required to better understand complexity relationships with these understudied taxa (Graham & Nash 2013). Importantly, these taxa contributed as many species to the total richness on the

studied coral reefs (193 species) as fishes and corals combined (192 species, Table 2), with fish and coral contributions to overall reef diversity quite small (Fisher *et al.* 2015). High sponge richness can be an indicator of bioerosion (e.g. Carballo *et al.* 2013), but structure-building sponges provide essential habitat for several fish and invertebrate species (Diaz & Rützler 2001) and their direct and indirect contribution to total species richness on Caribbean coral reefs should not be undervalued. Although the present study considered the maximum height of sponges, in future it may be worthwhile enumerating the number of sponges to assess their effect on species richness and community composition, especially considering sponges may play an important role on future reefs (Norström *et al.* 2009; Bell *et al.* 2013).

The importance of reef complexity and structural components on Caribbean coral reefs to total species richness was supported by the low relative importance of location in the model. Country was retained as a significant predictor for many taxa and species, although reef complexity and structural components combined regularly accounted a greater proportion of the total explained deviance. For individual taxa, a country effect may be due in part to geographical variability in the pool of available species due to life-history traits or local disturbance regimes. For example, low coral species richness in SVG may be due to high self-recruitment and low upstream connectivity (Holstein, Paris & Mumby 2014), while low fish species richness at all complexity levels in PR could be due to overfishing (Appeldoorn *et al.* 1992) or habitat disturbance (Valdés-Pizzini & Schärer-Umpierre 2014). The only notable interaction modelled by BRTs revealed a non-additive decline in fish species richness in areas of low complexity and within the reserve in PR. The shape of the relationship between fish species richness and reef complexity was similar in all countries, suggesting reduced fish species richness at all reef complexity levels in PR was greater than just the loss of commercially fished species. A multivariate analysis is underway to elucidate differences in community structure with respect to habitat structural complexity and disturbance. The extent of overfishing may have important ramifications on diversity (Worm *et al.* 2006), and loss of some fishery-targeted species, particularly parrotfish (Mumby, Hastings & Edwards 2007; Jackson *et al.* 2014), may cause population-wide declines in fish species richness, which has implications for ecosystem functioning (Loreau *et al.* 2001; Hooper *et al.* 2005).

Rarely explored species-specific relationships with complexity can help elucidate the spatial patterns in species richness on Caribbean reefs. Coral and fish species richness were expected to covary and show significant relationships with complexity (e.g. Pittman, Costa & Battista 2009), with the carbonate skeleton of corals creating the complex structure that fish respond to due to increased habitat and refuge (Hixon & Menge 1991; Hixon & Beets 1993; Beukers & Jones 1997; Almany 2004). As ecosystem

engineers, the species of coral is important (Alvarez-Filip *et al.* 2011a) and the loss of complexity in the Caribbean has been attributed to a loss of key ecosystem engineers and a shift to less complex 'weedy' coral species (Alvarez-Filip *et al.* 2011b; Yakob & Mumby 2011). Unsurprisingly, most coral species declined at lowest reef complexity, with only *P. strigosa* (smooth brain coral) and *P. divaricata* (thin finger coral) occupancy greater at low complexity levels. Coral species richness was very low at the lowest complexity but was relatively uniform at all other complexity levels, in contrast to the increase in coral richness with complexity reported by Alvarez-Filip *et al.* (2011a). This difference may be due in part to the dominance of *Orbicella* sp. at higher complexity in the present study, or due to differences in sampling methodology and site selection. Reef complexity had the greatest relative importance for complex massive (*Orbicella* spp., *Montastraea* sp.), foliose and plate corals (*Agaricia* sp.) that add to complexity through vertical relief or provision of overhangs. However, interestingly, the loss of complexity may also impact some coral species that do not contribute to complexity, with reef complexity important to *S. cubensis* due to preference for low-light areas under overhangs or among *Orbicella* colonies.

Interpreting this analysis as a space for time substitution in the context of Caribbean region-wide declines in coral cover (Gardner *et al.* 2003; Schutte, Selif & Bruno 2010; Jackson *et al.* 2014) and reef complexity (Alvarez-Filip *et al.* 2009), these findings suggest substantial declines in many fish species. Individual structural components have considerable value to different species, and their loss may have profound impacts on fish communities and associated ecosystem services, with small non-fisheries-targeted species such as wrasses, blennies and damsels among the few species likely to profit. Conservation of species richness alone may not always be appropriate (e.g. Wilson *et al.* 2006) as species identity and conservation goals are important, but conservation of reef structure may benefit ongoing functioning of coral reefs threatened by disturbance (Graham *et al.* 2015). Sampling *Orbicella* reefs which tend to have the highest benthic and fish diversity in the Caribbean (Mumby *et al.* 2008), and which retain substantial complexity, may overestimate the effects of persistent loss in habitat structure at metapopulation scales. As such, these findings should be treated as optimistic predictions because degrading habitat would be expected to have a population-wide influence, reducing the likelihood of further colonization and reducing ecosystem resilience to disturbance (Peterson, Allen & Holling 1998; Bellwood & Hughes 2001), and associated ecosystem processes and services.

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## Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.k5t1> (Newman *et al.* 2015).

## References

- Allen, G.R. (2008) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation, Marine and Freshwater Ecosystems*, **18**, 541–556.
- Almany, G.R. (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia*, **141**, 105–113.
- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R. & Gill, J.A. (2009) Flattening of Caribbean coral reefs, region-wide declines in architectural complexity. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 3019–3025.
- Alvarez-Filip, L., Dulvy, N.K., Côté, I.M., Watkinson, A.R. & Gill, J.A. (2011a) Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications*, **21**, 2223–2231.
- Alvarez-Filip, L., Gill, J.A., Dulvy, N.K., Perry, A.L., Watkinson, A.R. & Côté, I.M. (2011b) Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs*, **30**, 1051–1060.
- Appeldoorn, R., Beets, J., Bohnsack, J., Bolden, S., Matos, D., Meyers, S. *et al.* (1992) *Shallow Water Reef Fish Stock Assessment for the US Caribbean*. NOAA Technical Memorandum NMFS-SEFSC-304, 70 pp.
- Bak, R.P.M. & Meesters, E.H. (1999) Population structure as a response of coral communities to global change. *American Zoologist*, **39**, 56–65.
- Beck, M.W. (2000) Separating the elements of habitat structure, independent effects of habitat complexity and structural components on rocky intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **249**, 29–49.
- Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W. & Webster, N.S. (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology*, **19**, 2613–2624.
- Bellwood, D.R. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science*, **292**, 1532–1534.
- Beukers, J.S. & Jones, G.P. (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia*, **114**, 50–59.
- Carballo, J.L., Bautista, E., Nava, H., Cruz-Barraza, J.A. & Chávez, J.A. (2013) Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecology and Evolution*, **3**, 872–886.
- Chollett, I., Mumby, P.J., Müller-Karger, F.E. & Hu, C. (2012) Physical environments of the Caribbean Sea. *Limnology and Oceanography*, **57**, 1233–1244.
- Chong-Seng, K.M., Mannering, T.D., Pratchett, M.S., Bellwood, D.R. & Graham, N.A.J. (2012) The influence of coral reef benthic condition on associated fish assemblages. *PLoS One*, **7**, e42167.
- Costa, B., Taylor, C., Kracker, L., Battista, T. & Pittman, S.J. (2014) Mapping reef fish and the seascape: using acoustics and spatial modelling to guide coastal management. *PLoS One*, **9**, e85555.
- Diaz, M.C. & Rützler, K. (2001) Sponges, an essential component of Caribbean coral reefs. *Bulletin of Marine Science*, **69**, 535–546.
- Dustan, P., Doherty, O. & Pardede, S. (2013) Digital reef rugosity estimates coral reef habitat complexity. *PLoS One*, **8**, e57386.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Fisher, R., O'Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E. *et al.* (2015) Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology*, **25**, 500–505.
- Fraser, R.H. & Currie, D.J. (1996) The species richness-energy hypothesis in a system where historical factors are thought to prevail, coral reefs. *The American Naturalist*, **148**, 138–159.

- Friedlander, A.M. & Parrish, J.D. (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, **224**, 1–30.
- Friedman, J.H. (2001) Greedy function approximations, a gradient boosting machine. *Annals of Statistics*, **29**, 1189–1232.
- Friedman, J.H. & Meulman, J.J. (2003) Multiple additive regression trees with application in epidemiology. *Statistics in Medicine*, **22**, 1365–1381.
- Gardner, T.A., Côte, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Grabowski, J.H., Hughes, A.R. & Kimbro, D.L. (2008) Habitat complexity influences cascading effects of multiple predators. *Ecology*, **89**, 3413–3422.
- Graham, N.A.J. & Nash, K.L. (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, **32**, 315–326.
- Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, **518**, 94–97.
- Graham, N.A.J., Wilson, S.K., Pratchett, M.S., Polunin, N.V.C. & Spalding, M.D. (2009) Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. *Biodiversity and Conservation*, **18**, 3325–3336.
- Gratwicke, B. & Speight, M.R. (2005a) Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series*, **292**, 301–310.
- Gratwicke, B. & Speight, M.R. (2005b) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, **66**, 650–667.
- Gray, J.S. (1997) Marine biodiversity, patterns, threats and conservation needs. *Biodiversity and Conservation*, **6**, 153–175.
- Hanley, J.A. & McNeill, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.
- Harborne, A.R., Mumby, P.J. & Ferrari, R. (2012) The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental Biology of Fishes*, **94**, 431–442.
- Hastie, T., Tibshirani, R. & Friedman, J.H. (2001) *The Elements of Statistical Learning, Data Mining, Inference, and Prediction*. Springer-Verlag, New York.
- Hixon, M.A. & Beets, J.P. (1993) Predation, prey refuges and the structure of coral-reef fish assemblages. *Ecological Monographs*, **63**, 77–101.
- Hixon, M.A. & Menge, B.A. (1991) Species diversity, prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology*, **39**, 178–200.
- Holstein, D.M., Paris, C.B. & Mumby, P.J. (2014) Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. *Marine Ecology Progress Series*, **499**, 1–18.
- Hooper, D.U., Chapin, F.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005) Effects of biodiversity on ecosystem functioning, a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*, 2nd edn. John Wiley & Sons, New York. 375 pp.
- Hughes, T.P., Bellwood, D.R. & Connolly, S.R. (2002) Biodiversity hotspots, centres of endemism and the conservation of coral reefs. *Ecology Letters*, **5**, 775–784.
- Huston, M.A. (1985) Patterns of species diversity on coral reefs. *Annual Review of Ecology, Evolution and Systematics*, **16**, 149–177.
- Jackson, J.B.C. (1991) Adaptation and diversity of reef corals. *BioScience*, **41**, 475–482.
- Jackson, J.B.C., Donovan, M.K., Cramer, K.L. & Lam, W. (2014) *Status and Trends of Caribbean Coral Reefs, 1970–2012*. 306 pp. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
- Jennings, S., Boullé, D.P. & Polunin, N.V.C. (1996) Habitat correlates of the distribution and biomass of Seychelles' reef fishes. *Environmental Biology of Fishes*, **46**, 15–25.
- Jones, R.S. & Chase, J.A. (1975) Community structure and distribution of fishes in an enclosed high island lagoon in Guam. *Micronesica*, **11**, 127–148.
- Knowlton, N. & Jackson, J.B.C. (2008) Shifting baselines, local impacts, and global change on coral reefs. *PloS Biology*, **6**, e54.
- Kovalenko, K.E., Thomaz, S.M. & Warfe, D.M. (2012) Habitat complexity: approaches and future directions. *Hydrobiologia*, **685**, 1–17.
- Lasker, H.R. & Coffroth, M.A. (1983) Octocoral distributions at Carrie Bow Cay, Belize. *Marine Ecology Progress Series*, **13**, 21–28.
- Leathwick, J.R., Elith, J., Francis, M.P., Hastie, T. & Taylor, P. (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand, an analysis using boosted regression trees. *Marine Ecology Progress Series*, **321**, 267–281.
- Leathwick, J.R., Elith, J., Chadderton, W.L., Rowe, D. & Hastie, T. (2008) Dispersal, disturbance and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. *Journal of Biogeography*, **35**, 1481–1497.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001) Biodiversity and ecosystem functioning, current knowledge and future challenges. *Science*, **294**, 804–808.
- McClintock, J.B., Amsler, C.D., Baker, B.J. & van Soest, R.W.M. (2005) Ecology of Antarctic marine sponges, an overview. *Integrated Computational Biology*, **45**, 359–368.
- McCormick, M.I. (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series*, **112**, 87–96.
- McCoy, E.D. & Bell, S.S. (1991) Habitat structure, the evolution and diversification of a complex topic. *Habitat Structure, the Physical Arrangement of Objects in Space* (eds E.D. McCoy, S.S. Bell & H.R. Mushinsky), pp. 3–27. Chapman & Hall, London.
- Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. & Ludsin, S.A. (2003) Patterns and processes in reef fish diversity. *Nature*, **421**, 933–936.
- Mumby, P.J., Hastings, A. & Edwards, E.J. (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature*, **450**, 98–101.
- Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A. *et al.* (2008) Coral reef habitats as surrogates of species, ecological functions and ecosystem services. *Conservation Biology*, **22**, 941–951.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature*, **390**, 507–509.
- Newman, S.P., Meesters, E.H., Dryden, C.S., Williams, S.M., Sanchez, C., Mumby, P.J. *et al.* (2015) Data from: Reef flattening effects on total richness and species responses in the Caribbean. *Dryad Digital Repository*, doi: <http://dx.doi.org/10.5061/dryad.k5tg1>.
- Norström, A.V., Nyström, M., Lokrantz, J. & Folke, C. (2009) Alternative states on coral reefs: beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series*, **376**, 295–306.
- Parravicini, V., Kulbicki, M., Bellwood, D.R., Friedlander, A.M., Arias-Gonzalez, J.E., Chabanet, P. *et al.* (2013) Global patterns and predictors of tropical reef fish species richness. *Ecography*, **36**, 1254–1262.
- Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity and scale. *Ecosystems*, **1**, 6–18.
- Pittman, S.J., Costa, B.M. & Battista, T.A. (2009) Using lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *Journal of Coastal Research*, **SI53**, 27–38.
- Pittman, S.J., Christensen, J., Caldwell, C., Menza, C. & Monaco, M. (2007) Predictive mapping of fish species richness across shallow-water seascapes of the U.S. Caribbean. *Ecological Modelling*, **204**, 9–21.
- Polunin, N.V.C. & Roberts, C.M. (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series*, **100**, 167–176.
- Pratchett, M.S., Hoey, A.S. & Wilson, S.K. (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Current Opinion in Environmental Sustainability*, **7**, 37–43.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Ridgeway, G. (2013) *GBM, Generalised Boosted Regression Models Version 2.1*. <http://CRAN.R-project.org/package=gbm>.
- Risk, M.J. (1972) Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin*, **153**, 1–6.
- Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E. *et al.* (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **295**, 1280–1284.
- Sale, P.F. (1991) *The Ecology of Fishes on Coral Reefs*. Academic Press, London.
- Schutte, V.G.W., Selif, E.R. & Bruno, J.F. (2010) Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series*, **204**, 115–122.

- Sebens, K.P. (1994) Biodiversity on coral reefs, what are we losing and why? *American Zoologist*, **34**, 115–133.
- Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998) *Endemic Bird Areas of the World. Priorities for Biodiversity Conservation*. Birdlife Conservation Series 7. Birdlife International, Cambridge.
- Sutcliffe, P.R., Pitcher, C.R., Caley, M.J. & Possingham, H.P. (2012) Biological surrogacy in tropical seabed assemblages fails. *Ecological Applications*, **22**, 1762–1771.
- Syms, C. & Jones, G.P. (2000) Disturbance, habitat structure and the dynamics of a coral reef fish community. *Ecology*, **81**, 2714–2729.
- Valdés-Pizzini, M. & Schärer-Umpierre, M. (2014) People, habitats, species, and governance: an assessment of the social-ecological system of La Parguera, Puerto Rico. 111 pp. Interdisciplinary Center for Coastal Studies, University of Puerto Rico, Mayagüez, Puerto Rico.
- Wilson, S.K., Graham, N.A.J. & Polunin, N.V.C. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on reefs. *Marine Biology*, **151**, 1069–1076.
- Wilson, K.A., McBride, M.F., Bode, M. & Possingham, H.P. (2006) Prioritizing global conservation efforts. *Nature*, **440**, 337–340.
- Wilson, S.K., Babcock, R.C., Fisher, R., Holmes, T.H., Moore, J.A.Y. & Thomson, D.P. (2012) Relative and combined effects of habitat and fishing on reef fish communities across a limited fishing gradient at Ningaloo. *Marine Environmental Research*, **81**, 1–11.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., *et al.* (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–790.
- Yakob, L. & Mumby, P.J. (2011) Climate change induces demographic resistance to disease in novel coral assemblages. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 1967–1969.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Examples of visually assessed levels of complexity.

**Appendix S2.** Species lists by taxonomic group, with common names where used.

**Table S1.** Predictive performance of boosted regression tree (BRT) models relating coral species presence to reef complexity and location.

**Table S2.** Predictive performance of boosted regression tree (BRT) models relating fish species presence to reef complexity and location.

**Fig. S1.** Fitted functions for the four most important predictor variables relating presence of coral species to complexity and location calculated using Boosted Regression Tree models (see Tables S1 and S2).

**Fig. S2.** Fitted functions for the four most important predictor variables relating presence of fish species to complexity and location calculated using Boosted Regression Tree models (see Tables S3 and S4 for model details).