Newman SP, Meesters EH, Dryden CS, Williams SM, Sanchez C, Mumby PJ, Polunin NVC.

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***Journal of Animal Ecology* 2015, 84(6), 1678-1689.**

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

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Running headline: Coral reef complexity and species richness

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 macro-fauna, 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 25m^2 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 minimising 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. BRT 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.

Keywords biodiversity, conservation, relief, topography, degradation

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 'hotspots' of high species richness are often prioritised for conservation efforts (e.g. Myers et al. 2000; Roberts et al. 2002; Hughes, Bellwood & Connolly 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 and 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 et al. 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 et al. 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). The present 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 spatio-temporal confounding. This facilitates the elucidation of the relative importance of reef complexity (within 25 m^2 plots) and five structural components (the number of corals, number of large corals, slope angle, maximum sponge and maximum octocoral height) to 1) total richness on coral reefs, 2) richness of different macrofauna taxa, and 3) individual coral and fish species occupancy.

Methods

Presence of reef macrofauna were 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 Puerto Rico has long-term commercial and recreational fishing (Appeldoorn et al. 1992; Valdés-Pizzini & Schärer-Umpierre 2014).

Species presence was quantified in twenty 25 m^2 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 minimise other sources of variability (e.g. physical conditions, fishing pressure etc.), in the same reef habitat in sheltered areas (prevailing wind direction from the East in all cases, with all reefs sheltered either by land or windward reefs).

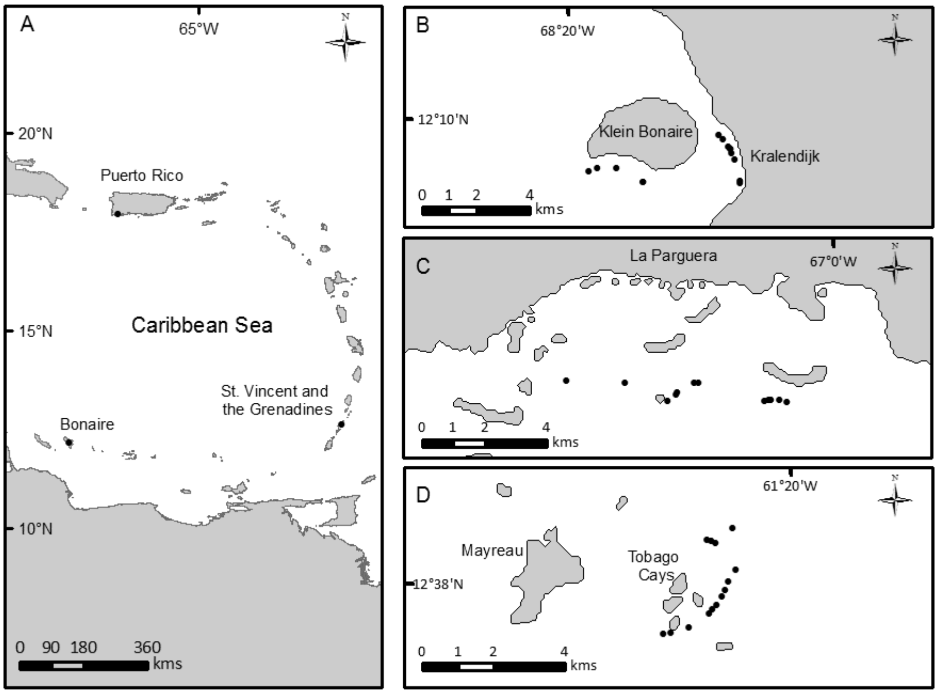


Figure 1 Survey locations: A) in eastern Caribbean, B) west coast of Bonaire, C) La Parguera, south-west Puerto Rico and D) Tobago Cays in St. Vincent and the Grenadines.

The maximum distance between surveys was 5.5 km in Bonaire, 6.9 km in Puerto Rico, 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 plots, on coral fore-reefs at depths of 5-15 m (mean 10.15 ± 0.14 S.E. 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 standardisation based on the range of reefscape complexity from all plots surveyed (see Supporting Information Appendix S1 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 categorised and selected prior to disturbing motile faunal communities. Three divers characterised 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 minutes.

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 characterise aspects of complexity (*sensu* McCoy & Bell 1990) 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 et al. 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 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 was 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 minimise other sources of variability by surveying within a discrete coral habitat and environmental envelope.

Table 1 Summary of predictors (mean ± 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 ± 4.5	11 - 400
No. large corals	Number of corals taller than 50 cm	6.7 ± 0.4	0 - 32
Sponge max height	Maximum vertical height of sponge (cm)	32.4 ± 1.8	0 - 211
Octocoral max height	Maximum vertical height of octocoral (cm)	87.4 ± 2.9	0 - 229
Slope angle	Estimated angle of underlying reef slope (degrees)	27.4 ± 1.3	0 - 80

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 non-linear 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 Supporting Information Appendix 2), 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 2004) 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 minimise predictive deviance and maximise 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 to 2650 for taxonomic group models and 250 to 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 over-fit training data (Elith, Leathwick & Hastie 2008; Leathwick et al 2008) so model performance was based on predictions of data withheld during cross-validation, 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 & McNeil 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 and 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 %, arthropods and octocorals each 8 % of total species (Table 2). In total, 143 fish species (80 genera, 41 families) were recorded, with 104 fish species in Bonaire (60 genera, 33 families), 86 fish species in Puerto Rico (51 genera, 28 families) and 105 fish species in SVG (64 genera, 37 families). Due to their low occurrence and diversity, flatworms (2 species), antipatharians (1 species), and corallimorphs (2 species) were excluded from further individual analysis, while molluscs were excluded from analysis due to absence of some species-level data.

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)

Importance of complexity to different taxa

BRT 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 non-linear and complex (Fig. 3).

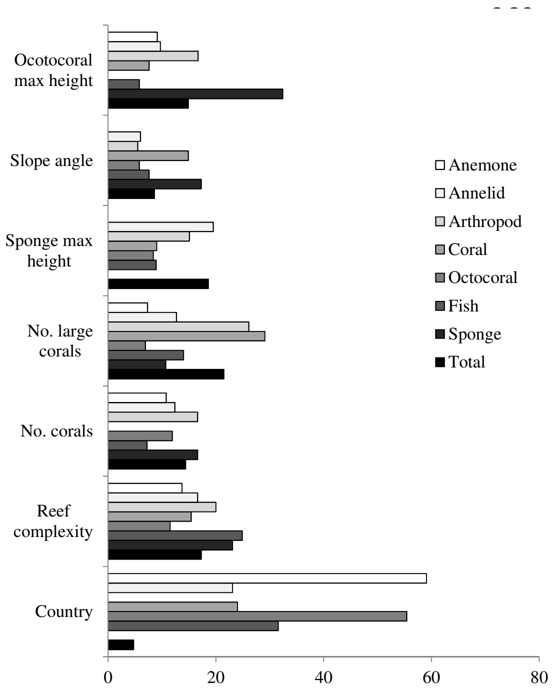


Figure 2 Relative influence (%) of complexity variables predicting richness of different taxa on Caribbean reefs. Total richness includes all listed taxa plus anemones, flatworms, antipatharians and corallimorphs (see Appendix S2 for full species list). Note ocotocoral and sponge height, and number of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

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

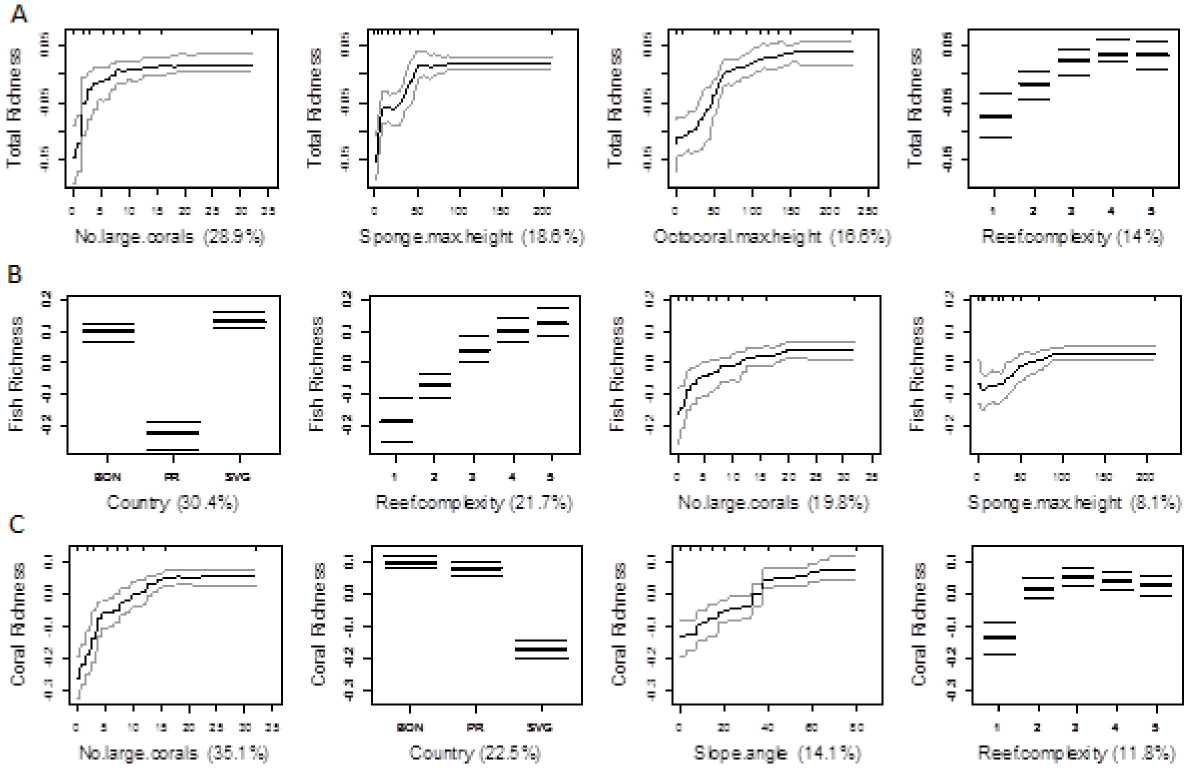
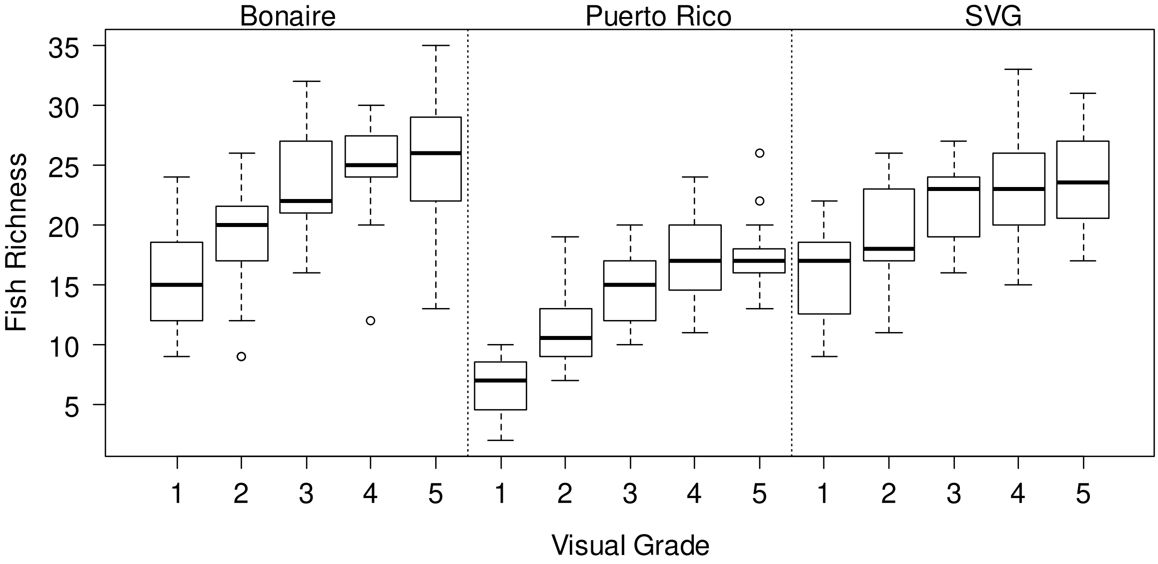


Figure 3 Functions fitted for the four most important predictor variables (ranked by percentage relative influence left to right) by BRT models relating (A) total species richness, (B) coral species richness and (C) fish species richness to reef complexity variables and location. Total richness was calculated as the sum of all species of fishes, corals, sponges, octocorals, anemones, annelids, arthropods, flatworms, antipatharians and corallimorophs (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.

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^2) with tall sponges (> ~75 cm) and octocorals (> 100 cm). Total species richness was greatest at reef complexity level 4 (mean 70.7 ± 1.3 S.E. 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 (Fig. 3b). Reef complexity and country had the greatest relative influence on fish species richness (Fig. 2), with fish species richness lowest in Puerto Rico (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 (1.95) with fish species richness at low complexity in Bonaire and SVG equal to fish species richness at high reef complexity sites in Puerto Rico (Fig. 4).

Figure 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.



Species relationships

Coral species presence

Presence of 23 of 51 coral species were 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 less than 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 average 64.4 % of the explained variance across all coral species (range: 33.4 – 93.0 %, Table 4).

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 Figure S1for 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
Agaricia agaricites	45.98	36.93			21.10		41.97
Agaricia lamarcki	40.81	11.03	10.47	11.88	14.69	26.93	25.00
Colpophyllia natans	41.36	18.30	29.97	8.07	25.12	6.86	11.67
Eusmilia fastigiata	60.41			11.13	13.84	12.46	62.56
Madracis auretenra	57.91	9.67	39.85	12.07	17.48	9.44	11.50
Madracis decactis	68.97	9.53		7.50	4.66	11.74	66.57
Madracis pharensis	66.79	4.75	9.73	7.99	5.36	7.20	64.97
Meandrina memorialis	66.65	5.90	9.09	5.76	4.70	12.42	62.13
Montastraea cavernosa	55.76	15.54	7.60	19.75	12.63	17.24	27.24
Orbicella annularis	47.65	29.74	26.49		18.37		25.40
Orbicella faveolata	42.92	53.70	9.27	19.27	10.02		7.73
Orbicella franksi	42.92	14.30	37.15	11.66	11.90	18.03	6.97
Porites divaricata	49.75	11.46		7.78	20.42	15.71	44.63
Porites furcata	55.23	23.13		14.76	14.59		47.52
Pseudodiploria labyrinthiformis	40.67			36.78	25.88		37.35
Pseudodiploria strigosa	46.38	18.16	6.92	11.54	23.87	8.47	31.05
Scolymia cubensis	73.38	18.63			27.91	27.18	26.28
Siderastrea siderea	43.73	13.41		20.77	18.88	20.38	26.55
Stephanocoenia intersepta	56.05	4.45	4.14	10.09	7.20	25.63	48.48

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 non-linear (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 (*Pseudodiploria strigosa* and *Porites 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*, *O. 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 *Madracis auretenra* (39.8 %), *Orbicella 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 franksii*; see Fig. S1).

Coral species presence was commonly lower when maximum sponge height was low (e.g. less than 50 cm, see fitted functions in dependence plots in Fig. S1). The exceptions to this were two species (*P. furcata*, *P. porities*) 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

Presence of 54 of the 143 fish species identified were modelled with respect to reef complexity (38 %, see Table S2), with all other species not modelled due to low occurrence (observed in less than 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 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 *Halichoeres bivittatus* (slippery dick)*, H. maculipinna* (clown wrasse)*, H. pictus* (rainbow wrasse) and *T. bifasciatum* (blueheaded wrasse), the saddled blenny *Malacoctenus 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).

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 Figure 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**
Cephalopholis cruentatus	50.89	18.67	14.89	8.92	8.62	5.44
Chromis cyanea	57.08	4.88	30.58	10.60	6.86	4.45
Chromis multilineata	46.95		7.88	15.14	10.14	16.41
Clepticus parrae	43.97	20.81	18.33	17.22	11.56	13.48
Coryphopterus dicrus	47.12			14.21		11.29
Coryphopterus eidolon	69.85		6.63	12.26	11.88	
Coryphopterus hyalinus	58.37	9.75	9.02	7.58	7.01	6.74
Coryphopterus lipernes	64.70	3.03	40.44	13.17	7.64	4.15
Gnatholepis thompsoni	47.05	7.40	5.53	8.52	15.18	7.51
Gobiosoma horsti	54.25	12.02			34.82	16.07
Gramma loreto	66.34	25.14	20.63	7.25	11.16	
Halichoeres bivitattus	69.53	24.96		48.16	6.22	20.65
Halichoeres garnoti	50.74			7.97	12.34	
Halichoeres maculipinna	49.71	17.20		22.11		
Halichoeres pictus	55.24	3.75	9.88	22.22	12.38	30.05
Malacoctenus boehlkei	43.94	30.10				39.73
Malacoctenus triangulatus	53.96	20.16		36.22		22.33
Mulloidichthys martinicus	58.84	15.68	21.84		20.98	13.40
Myripristis jacobus	47.15	5.91	18.14	12.57	12.63	7.84
Neoiphon marianus	54.48		39.64	20.95		19.77
Scarus taeniopterus	50.37	11.00	9.64	17.75		6.57
Sparisoma atomarium	50.92	10.30	13.08	16.05	6.60	10.56
Sparisoma viride	43.28	17.86		19.77	7.78	43.71
Stegastes adustus	53.91	13.32	8.89	15.32	12.44	13.92
Stegastes diencaeus	45.20	16.41		29.47		24.35
Stegastes partitus	59.20	14.82		10.82	10.89	18.50
Stegastes planifrons	67.25	12.06	17.79	15.38	4.98	5.95
Thalassoma bifasciatum	41.53	16.22	14.64	17.95		23.86

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 %), *Neoiphon 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. bivitattus* (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. bivitattus, M, triangulatus, Stegastes 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).

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 et al. 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, that 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 and 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 Puerto Rico 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 Puerto Rico. 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 Puerto Rico 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 co-vary 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 *Psuedodiploria strigosa* (smooth brain coral) and *Porites 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 *Scolymia cubensis* due to preference for low-light areas under overhangs or amongst *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 effects of persistent loss in habitat structure at meta-population 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 colonisation and reducing ecosystem resilience to disturbance (Peterson, Allen & Holling 1998; Bellwood & Hughes 2001), and associated ecosystem processes and services.

Acknowledgements

The research was funded by the European Commission 7th Framework programme (P7/2007-2013; grant 244161). We are grateful to the fisheries departments, organisations and individuals who provided permissions or assistance in Bonaire (STINAPA, Dive Friends Bonaire, Lizard Inn), Puerto Rico (M Carlo and J Kubaryk of University of Puerto Rico at Mayagüez), and St. Vincent and the Grenadines (Fisheries: Mr Ryan, C Isaacs; Tobago Cays Marine Park: O Harvey; Kings Landing: M James; G Adams). Special thanks to A Moleta of Ultramarine for logistical support in SVG, and to the helpful comments of the anonymous reviewers.

Data Accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.k5tg1

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. *Oceologia*, 141, 105-113.

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. & Côte, I.M. (2011b) Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs*, 30, 1051-1060.

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 B*, 276, 3019-3025.

Appeldoorn, R., Beets, J., Bohnsack , J., Bolden, S., Matos, D., Meyers, S., Rosario, A., Sadovy, Y. & Tobias, W. (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*, doi: 10.1111/gcb.12212

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.

Brieman, L., Friedman, J.H., Olshen, R.A. & Stone, C.J. (1984) *Classification and regression trees*. Wadsworth International Group, Belmont, CA, USA.

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(8), 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(1), 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(2), e57386.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettman, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips., S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.R., Soberón, J., Williams, S., Wisz, M. & Zimmerman, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802-813.

Fisher, R., O'Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E. & Caley, M.J. (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. *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., 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 III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning, a consensus of current knowledge. *Ecological Monographs*, 75(1), 3-35.

Hosmer, D.W. & Lemeshow, S. (2000) *Applied logistic regression, 2nd ed.* John Wiley & Sons, New York. 375pp.

Hughes, T.P., Bellwood, D.R. & Connolly, S.R. (2002) Biodiversity hotspots, centres of endemicity 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, Ecolution and Systematics*, 16, 149-177.

Jackson, J.B.C. (1991) Adaptation and diversity of reef corals. *BioScience*, 41(7), 475-482.

Jackson, J.B.C., Donovan, M.K., Cramer, K.L. & Lam, W. (2014) *Status and trends of Caribbean coral reefs, 1970-2012*. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland. 306pp.

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(2), 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., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (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.

Mora, C. (2008) A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B*, 275, 767-773.

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., Holmes, K.E., Kappel, C.V., Micheli, F. & Sanchirico, J.N. (2008) Coral reef habitats as surrogates of species, ecological functions and ecosystem services. *Conservation Biology*, 22(4), 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., Polunin, N.V.C. (2015) Data from: Reef flattening effects on total richness and species responses in the Caribbean. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.5ktg1

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.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R. & Jackson, J.B.C. (2003) Global trajectories of the longterm decline of coral reef ecosystems. *Science*, 301, 955-958.

Parravicini, V., Kulbicki, M., Bellwood, D.R., Friedlander, A.M., Arias-Gonzalez, J.E., Chabanet, P., Floeter, S.R., Myers, R., Vigliola, L., D’Agata, S. & Mouillot, D. (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., Christensen, J., Caldow, 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.

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.

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.

Ridgeway, G. (2004) GBM, generalised boosted regression models version 2.1.

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., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C. & Werner, T.B. (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.

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. Interdisciplinary Center for Coastal Studies, University of Puerto Rico, Mayagüez, Puerto Rico, 111pp.

Wilson, K.A., McBride, M.F., Bode, M. & Possingham H.P. (2006) Prioritizing global conservation efforts. *Nature*, 440, 337-340.

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, 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.

Yacob. L. & Mumby, P.J. (2011) Climate change induces demographic resistance to disease in novel coral assemblages. *Proceeding of the National Academy of Science USA*, 108. 1967-1969.

Supporting Information

The following Supporting Information is available for this article online.

Appendix S1 Examples of visually assessed levels of complexity

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

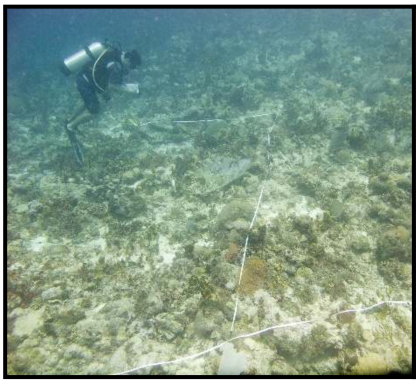
Table S1 Predictive performance of boosted regression tree (BRT) models relating coral species presence to reef complexity and location. Table variables indicate the frequency of occurrence (percentage of 300 plots a species was present in), model learning rate, optimum number of trees fitted with all models with a learning rate of 3 (allowing for interactions), the mean residual deviance of the model, the mean deviance using 10-fold cross validation (CV), and the total deviance explained by each model. AUC scores (area under receiver operator character curve) provide a discrimination of probabilities between presence and absence samples, with values >0.8 considered here very good and >0.9 excellent.

Figure 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). Plots are presented for models with a percentage total explained deviance >40 %. Less than four plots for a species is due to non-significant variables dropped from the model. Note predictor names are as Table 1, “visual” stands for visually estimated ‘reef complexity’.

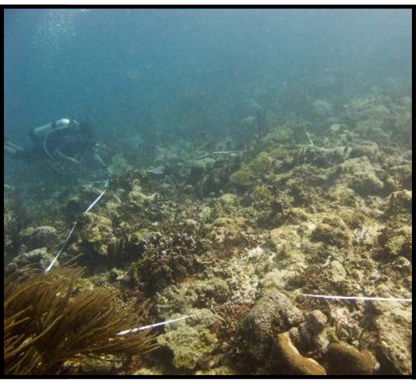
Table S2 Predictive performance of boosted regression tree (BRT) models relating coral fish species presence to reef complexity and location. Table variables indicate the frequency of occurrence (percentage of 300 plots a species was present in), learning rate, optimum number of trees fitted with all models with a learning rate of 3 (allowing for interactions), the mean residual deviance of the model, training data correlation, the mean deviance using 10-fold cross validation (CV), and the total deviance explained by each model. AUC scores (area under receiver operator character curve) provide a discrimination of probabilities between presence and absence samples, with values >0.8 considered here very good and >0.9 excellent.

Figure 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). Plots are presented for models with a percentage total deviance explained >40 %. Less than four plots for a species is due to non-significant variables dropped from the model. Note predictor names are as Table 1, “visual” stands for visually estimated ‘reef complexity’.

Appendix S1: Examples of visually assessed levels of complexity



Grade 1: No or very low vertical relief



Grade 2: Low relief

Grade 3: Moderately complex

Grade 4: Very co
with numerous fi

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

Anemone species list

Species	Common Name
Actinoporus elegans	Elegant anemone
Aiptasia tagetes	Pale anemone
Bartholomea annulata	Corkscrew anemone
Bartholomea lucida	Knobby anemone
Condylactis gigantea	Giant Anemone
Epicystis crucifer	Beaded anemone
Lebrunia coralligens	Hidden anemone
Lebrunia danae	Branching anemone
Phymanthis crucifer	Beaded anemone
Ragactis lucida	Knobby Anemone
Stichodactyla helianthus	Sun anemone
Unidentified brown anemone	Unidentified brown anemone

Annelid species list

Species	Common Name
Anamobaea orstedii	Split-Crown Feather duster
Anamobaea spp.	Ghost Feather Duster
Bispira brunnea	Social Feather Duster
Bispira variegata	Variegated Feather Duster
Branchiomma nigromaculata	Black-Spotted Feather Duster
Eupolymnia spp.	Spaghetti Worm
Hermodice caranculata	Bearded Fireworm
Hypsicomus spp	Ruffled Feather Duster
Loimia medusae	Medusa Worm
Megalomma spp.	Shy Feather Duster
Notaulax nudicollis	Brown Fanworm
Notaulax occidentalis	Yellow Fanworm
Pomatostegus stellatus	Star Horseshoe Worm
Protula spp.	Red-Spotted Horseshoe Worm
Sabellastarte magnifica	Magnificent Feather duster
Spirobranchus giganteus	Christmas Tree Worm

Arthropod species list

Species	Common Name
Alpheus spp.	Snapping Shrimp
Brachycarpus biunguiculatus	Two Claw Shrimp
Calcinus cadenati	Orangeclaw Hermit
Carpilius corallinus	Batwing Coral Crab
Lysmata rathbuinae	Hidden Cleaner Shrimp

Lysmata wurdemanni	Peppermint Shrimp
Mithrax cinctimanus	Banded Clinging Crab
Mithrax forceps	Red-Ridged Clinging Crab
Mithrax pilosus	Hairy Clinging Crab
Mithrax sculptus	Green Clinging Crab
Mithrax spinosissimus	Channel Clinging Crab
Mithrax verrucosus	Paved Clinging Crab
Mysidium spp	Mysid Shrimp
Neogonodactylus curacaoensis	Dark Mantis
Paguristes cadenati	Red Reef Hermit
Paguristes erythrops	Red Banded Hermit
Paguristes punticeps	White Speckled Hermit
Panulirus argus	Caribbean Spiny Lobster
Panulirus guttatus	Spotted Spiny Lobster
Pelia mutica	Cryptic Teardrop Crab
Percnon gibbesi	Nimble Spray Crab
Periclimenes or Neopontonides	Sea Plume Shrimp
Periclimenes pedersoni	Pederson Cleaner Shrimp
Periclimenes rathbunae	Sun Anenome Shrimp
Periclimenes yucatanus	Spotted Cleaner Shrimp
Phimochirus holthuisi	Red-Striped hermit
Phimochirus operculatus	Polkadotted hermit
Plumnus floridanus	Plumed Hairy Crab
Podochela spp.	Neck Crab
Scyllarides aequinoctialis	Spanish Lobster
Stemocionopus furcatus coelata	Furcate Spider Crab
Stenopus hispidus	Banded Coral Shrimp
Stenopus scutellatus	Golden Coral Shrimp
Stenorynchus seticornis	Yellowline Arrow Crab
Thor amboinesis	Squat Anenome shrimp

Coral species list

Species	Common Name
Acropora cervicornis	Staghorn coral
Acropora palmata	Elkhorn coral
Agaricia agaricites	Lettuce coral
Agaricia fragilis	Fragile saucer coral
Agaricia grahamae	Graham’s sheet coral
Agaricia humilis	
Agaricia lamarcki	Lamarck’s sheet coral
Agaricia tenuifolia	
Colpophyllia natans	Boulder brain coral
Dendrogyra cylindrus	Pillar coral

Dichocoenia stokesi	Pineapple coral
Diploria clivosa	Knobby brain coral
Eusmilia fastigiata	Smooth flower coral
Favia fragum	Golfball coral
Isophyllastrea rigida	Polygonal coral
Isophyllia sinuosa	Sinuous cactus coral
Leptoseris cucullata	Fragile lettuce coral
Madracis auretenra	Yellow pencil coral
Madracis carmabi	
Madracis decactis	Ten-ray star coral
Madracis pharensis	
Madracis senaria	
Meandrina brasiliensis	
Meandrina meandrites	Maze coral
Meandrina memorialis	
Millepora alcicornis	Branching fire coral
Millepora complanata	Blade fire coral
Millepora squarrosa	Box fire coral
Montastraea cavernosa	Great star coral
Mussa angulosa	Spiny flower coral
Mycetophyllia danaana	Lowridge cactus coral
Mycetophyllia ferox	Rough cactus coral
Mycetophyllia lamarckiana	Ridged cactus coral
Orbicella annularis	Boulder star coral
Orbicella faveolata	
Orbicella franksi	
Porites astreoides	Mustard coral
Porites branneri	hump coral
Porites colonensis	
Porites divaricata	Thin finger coral
Porites furcata	Thin finger coral
Porites porites	Finger coral
Pseudodiploria labyrinthiformis	Grooved brain coral
Pseudodiploria strigosa	Symmetrical brain coral
Scolymia cubensis	Artichoke coral
Siderastrea radians	Lesser starlet coral
Siderastrea siderea	Massive starlet coral
Siderastrea stellata	
Stephanocoenia intersepta	Blushing star coral
Tubastraea coccinea	Orange cup coral

Echinoderm species list

Species	Common Name
Davidaster rubiginosa	Golden crinoids
Diadema antillarum	Black-spined sea urchin
Echinometra lucunter	Rock-boring sea urchin
Echinometra viridis	Green rock-boring sea urchin
Eucidaris spp.	Pencil sea urchin
Holothuria mexicana	Donkey dung sea cucumber
Holothuria thomasi	Tiger tail sea cucumber
Isostichopus badionotus	Chocolate chip sea urchin
Lytechinus williamsi	Jewel sea urchin
Tripneustes ventricosus	West Indian sea egg
Astrophyton muricatum	Basket seastar

Flatworm species list

Species	Common Name
Black and white flatworm	Black and white flatworm
Pseudoceros pardalis	Leopard Flatworm

Octocoral species list

Species	Species
Briareum asbestinum	*Muriceopsis bayeriana*
Ellisella barbadensis	*Muriceopsis flavida*
Erythropodium caribaeorum	*Plexaura homomalla*
Eunicea asperula	*Plexaura kukenthali*
Eunicea calyculata	*Plexaura kuna*
Eunicea colombiana	*Plexaura slimy spp.*
Eunicea flexuosa	*Plexaurella dichotoma*
Eunicea fusca	*Plexaurella fusifera*
Eunicea lacinata	*Plexaurella grisea*
Eunicea mammosa	*Plexaurella nutans*
Eunicea pallida	*Pseudoplexaura flagellosa wagenaari*
Eunicea pinta	*Pseudoplexaura purosa*
Eunicea spp.	*Pseudopterogorgia acerosa*
Eunicea succinea	*Pseudopterogorgia americana*
Eunicea tourneforti	*Pseudopterogorgia bipinnata*
Gorgonia ventalina	*Pseudopterogorgia elisabethae*
Iciligorgia schrammi	*Pseudopterogorgia kallos*
Muricea atlantica	*Pseudopterogorgia rigida*
Muricea muricata	*Pterogorgia citrina*
Muricea pinnata	*Pterogorgia guadalupensis*

Sponge species list

Species	Species
Agelas clathrodes	*Ectyoplasia ferox*
Agelas conifera	*Erylus bahamensis*
Agelas dispar	*Haliclona walentina*
Agelas sceptrum	*Halisarca caerulea*
Agelas schmidti	*Hyrtios caracasensis*
Agelas sventres	*Hyrtios violaceus*
Aiolochroia crassa	*Igernella notabilis*
Aka coralliphaga	*Iotrochota arenosa*
Aka xamaycaensis	*Iotrochota birotulata*
Amphimedon compressa	*Ircinia campana*
Amphimedon viridis	*Ircinia felix*
Aplysina archeri	*Ircinia strobilina*
Aplysina cauliformis	*Leucetta floridana*
Aplysina fistularis	*Merlia normani*
Aplysina fulva	*Monanchora arbuscula*
Aplysina insularis	*Mycale laevis*
Aplysina lacunosa	*Myrmekioderma gyroderma*
Artemisina melana	*Myrmekioderma rea*
Batzella rubra	*Neofibularia nolitangere*
Biemna sp.	*Neopetrosia proxima*
Callyspongia armigera	*Neopetrosia rosariensis*
Callyspongia fallax	*Niphates caycedoi*
Callyspongia plicifera	*Niphates erecta*
Callyspongia tenerrima	*Pachataxa lutea*
Callyspongia vaginalis	*Pandaros acanthifolium*
Chalinula zeae	*Petrosia pellasarca*
Chelonaplysilla erecta	*Petrosia weinbergi*
Chondrilla caribensis	*Phorbas amaranthus*
Cinachyrella kuekenthali	*Plakinastrella onkodes*
Clathria venosa	*Plaktoris angulospiculatus*
Clathria faviformis	*Plaktoris halicondrioides*
Clathria spinosa	*Polymastia tenax*
Clathria virgultosa	*Prosuberites laughlini*
Cliona aprica	*Ptilocaulis walpersi*
Cliona caribbaea	*Scopalina ruetzleri*
Cliona delitrix	*Smenospongia aurea*
Cliona laticavicola	*Smenospongia conulosa*
Cliona tenuis	*Spirastrella coccinea*
Cliona varians	*Spirastrella hartmani*
Cribrochalina vasculum	*Svenzea flava*
Desmapsamma anchorata	*Svenzea zeai*
Dictyonellidae funicularis	*Tectitethya crypta*
Diplastrella micraster	*Topsentia ophiraphidites*
Dragmacidon explicatum	*Verongula reiswigi*
Dysidea janiae	*Verongula rigida*

Ectyoplasia ferox	*Xestospongia muta*
Erylus bahamensis	

Fish species list

Species	Common Name
Abudefduf saxatilis	Sergeant major
Acanthemblemaria aspera	Roughhead blenny
Acanthemblemaria maria	Secretary blenny
Acanthostracion polygonia	Honeycomb cowfish
Acanthurus bahianus	Ocean surgeonfish
Acanthurus coeruleus	Blue tang
Aluterus scriptus	Scrawled filefish
Amblycirrhitus pinos	Redspotted hawkfish
Anisotremus surinamensis	Black margate
Anisotremus virginicus	Porkfish
Apogon binotatus	Barred cardinalfish
Apogon lachneri	Whitestar cardinalfish
Apogon maculatus	Flamefish
Apogon townsendi	Belted cardinalfish
Aulostomus maculataus	Trumpetfish
Balistes vetula	Queen triggerfish
Bodianus rufus	Spanish hogfish
Bothus lunatus	Peacock flounder
Cantherhines macrocerus	Whitespotted filefish
Cantherhines pulles	Orangespotted filefish
Canthidermis sufflamen	Ocean triggerfish
Canthigaster rostrata	Sharpnose puffer
Caranx bartholomaei	Yellow Jack
Caranx crysos	Blue runner
Caranx ruber	Bar jack
Centropyge argi	Cherubfish
Cephalopholis cruentatus	Graysby
Cephalopholis fulvus	Coney
Chaetodon aculeatus	Longsnout butterflyfish
Chaetodon capistratus	Foureye butterflyfish
Chaetodon ocellatus	Spotfin butterflyfish
Chaetodon striatus	Banded butterflyfish
Chilomycterus antennatus	Bridled burrfish
Chromis cyanea	Blue chromis
Chromis multilineata	Brown chromis
Clepticus parrae	Creole wrasse
Coryphopterus dicrus	Colon goby
Coryphopterus eidolon	Pallid goby
Coryphopterus glaucofraenum	Bridled goby
Coryphopterus hyalinus	Glass goby

Coryphopterus lipernes	Peppermint goby
Diodon holocanthus	Balloonfish
Diodon hystrix	Porcupinefish
Echidna catenata	Chain moray
Emblemariopsis spp.	Darkheaded blenny
Enchelycore carychroa	Chestnut moray
Enneanectes boehlkei	Roughhead triplefin
Epinephelus guttatus	Red Hind
Equetus punctatus	Spotted drum
Ginglymostoma cirratum	Nurse shark
Gnatholepis thompsoni	Goldspot goby
Gobiosoma chancei	Shortstripe goby
Gobiosoma dilepis	Orangesided goby
Gobiosoma evelynae	Sharknose goby
Gobiosoma horsti	Yellowline goby
Gobiosoma randalli	Yellownose goby
Gobiosoma sp.	Linesnout goby
Gobiosoma xanthiprora	Yellowprow goby
Gramma loreto	Fairy basslet
Gymnothorax miliaris	Goldentail moray
Gymnothorax moringa	Spotted moray
Haemulon carbonarium	Caesar grunt
Haemulon chrysargyreum	Smallmouth grunt
Haemulon flavolineatum	French grunt
Haemulon macrostomum	Spanish grunt
Haemulon parra	Sailor's choice
Haemulon plumieri	White grunt
Haemulon sciurus	Bluestriped grunt
Halichoeres bivitattus	Slippery dick
Halichoeres cyanocephalus	Yellowcheek wrasse
Halichoeres garnoti	Yellowhead wrasse
Halichoeres maculipinna	Clown wrasse
Halichoeres pictus	Rainbow wrasse
Halichoeres poeyi	Blackear wrasse
Halichoeres radiatus	Puddingwife
Heteropriacanthus cruentatus	Glasseye snapper
Holacanthus ciliaris	Queen angelfish
Holacanthus tricolor	Rock beauty
Holocentrus adscensionis	Squirrelfish
Holocentrus rufus	Longspine squirrelfish
Hypoplectrus chlorurus	Yellowtail hamlet
Hypoplectrus guttavarius	Shy hamlet
Hypoplectrus indigo	Indigo hamlet
Hypoplectrus puella	Barred hamlet
Hypoplectrus sp.	Tan hamlet
Hypoplectrus unicolor	Butter hamlet

Inermia vittata	Boga
Kyphosus sectatrix	Bermudan chub
Labrisomus gobio	Palehead blenny
Lachnolaimus maximus	Hogfish
Lactophrys bicaudalis	Spotted trunkfish
Lactophrys triqueter	Smooth trunkfish
Liopropoma rubre	Peppermint basslet
Lutjanus apodus	Schoolmaster snapper
Lutjanus griseus	Grey snapper
Lutjanus mahogoni	Mahogany snapper
Malacanthus plumieri	Sand tilefish
Malacoctenus boehlkei	Diamond blenny
Malacoctenus triangulatus	Saddled blenny
Melichthys niger	Black durgon
Micrognathus ensenadae	Harlequin pipefish
Microspathodon chrysurus	Yellowtail damselfish
Mulloidichthys martinicus	Yellow goatfish
Myrichthys breviceps	Sharptail eel
Myripristis jacobus	Blackbar soldierfish
Neoiphon marianus	Longjaw squirrelfish
Nes longus	Orangespotted goby
Nicholsina usta	Emerald parrotfish
Ocyurus chrysurus	Yellowtail snapper
Odontoscion dentex	Reef croaker
Opistognathus aurifrons	Yellowhead jawfish
Paranthias furcifer	Creolefish
Pempheris schomburgki	Glassy sweeper
Plectrypops retrospinis	Cardinal soldierfish
Pomacanthus arcuatus	Grey angelfish
Pomacanthus paru	French angelfish
Priolepis hipoliti	Rusty goby
Pseudopeneus maculatus	Spotted goatfish
Pterois volitans	Lionfish
Sargocentron vexillarium	Dusky squirrelfish
Scarus iserti	Striped parrotfish
Scarus taeniopterus	Princess parrotfish
Scarus vetula	Queen parrotfish
Scomberomorus regalis	Cero
Scorpaena plumieri	Spotted scorpionfish
Scorpaenodes caribbaeus	Reef scorpionfish
Serranus baldwini	Lantern bass
Serranus tobacarius	Tobaccofish
Sparisoma atomarium	Greenblotch parrotfish
Sparisoma aurofrenatum	Redband parrotfish
Sparisoma radians	Bucktooth parrotfish
Sparisoma rubripinne	Yellowtail parrotfish

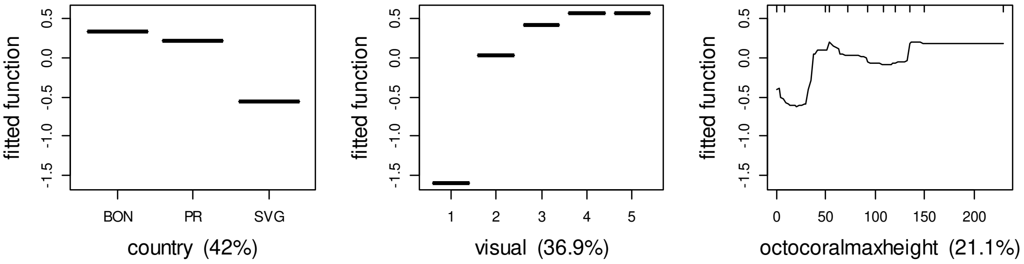
Sparisoma viride	Stoplight parrotfish
Sphyraena barracuda	Great barracuda
Stegastes adustus	Dusky damselfish
Stegastes diencaeus	Longfin damselfish
Stegastes leucostictus	Beaugregory
Stegastes partitus	Bicolor damselfish
Stegastes planifrons	Threespot damsel
Stegastes variabilis	Cocoa damselfish
Synodus intermedius	Sand diver
Synodus saurus	Bluestriped lizardfish
Thalassoma bifasciatum	Blue headed wrasse

Table S1. Predictive performance of boosted regression tree (BRT) models relating coral species presence to reef complexity and location. Table variables indicate the frequency of occurrence (percentage of 300 plots a species was present in), model learning rate, optimum number of trees fitted with all models with a learning rate of 3 (allowing for interactions), the mean residual deviance of the model, the mean deviance using 10-fold cross validation (CV), and the total deviance explained by each model. AUC scores (area under receiver operator character curve) provide a discrimination of probabilities between presence and absence samples, with values >0.8 considered here very good and >0.9 excellent.

Species	**Freq of occurrence**	**Learning rate**	**No. of trees**	**Model residual deviance**	**CV residual deviance ± SE**	**% Total Deviance**	**AUC score**	**CV AUC score (SE)**
Agaricia agaricites	90.67	0.003	700	0.34	0.40 (0.05)	45.98	0.92	0.85 (0.05)
Agaricia fragilis	16.67	0.003	800	0.63	0.76 (0.06)	30.29	0.90	0.77 (0.04)
Agaricia lamarcki	35.33	0.003	1250	0.77	0.99 (0.04)	40.81	0.92	0.82 (0.02)
Colpophyllia natans	46.33	0.003	1250	0.81	1.03 (0.05)	41.36	0.91	0.82 (0.02)
Eusmilia fastigiata	38.00	0.003	1400	0.53	0.68 (0.07)	60.41	0.96	0.89 (0.02)
Leptoseris cucullata	15.33	0.003	650	0.59	0.75 (0.04)	30.68	0.92	0.78 (0.03)
Madracis auretenra	14.33	0.003	1250	0.35	0.50 (0.06)	57.91	0.95	0.87 (0.04)
Madracis decactis	49.33	0.003	1450	0.43	0.58 (0.04)	68.97	0.98	0.95 (0.01)
Madracis pharensis	29.00	0.003	1300	0.40	0.58 (0.09)	66.79	0.97	0.93 (0.02)
Meandrina memorialis	50.00	0.003	1300	0.46	0.63 (0.05)	66.65	0.98	0.94 (0.01)
Montastraea cavernosa	74.67	0.003	1550	0.50	0.75 (0.04)	55.76	0.96	0.88 (0.02)
Orbicella annularis	65.00	0.003	1400	0.68	0.85 (0.06)	47.65	0.93	0.87 (0.02)
Orbicella faveolata	70.67	0.003	1400	0.61	0.82 (0.06)	49.27	0.94	0.85 (0.03)
Orbicella franksi	36.00	0.003	1300	0.75	0.96 (0.06)	42.92	0.91	0.82 (0.02)
Porites divaricata	32.33	0.003	1400	0.63	0.81 (0.04)	49.75	0.95	0.88 (0.02)
Porites furcata	46.33	0.003	1700	0.62	0.83 (0.07)	55.23	0.94	0.88 (0.02)
Porites porites	63.33	0.003	1000	0.91	1.08 (0.04)	30.46	0.86	0.77 (0.02)
Psuedodiploria labyrinthiformis	35.33	0.003	2100	0.77	1.02 (0.08)	40.67	0.90	0.81 (0.04)
Psuedodiploria strigosa	51.67	0.003	1800	0.74	1.02 (0.07)	46.38	0.93	0.83 (0.02)
Scolymia cubensis	10.33	0.003	2350	0.18	0.37 (0.03)	73.38	1.00	0.93 (0.01)
Siderastrea siderea	88.67	0.003	1050	0.40	0.56 (0.05)	43.73	0.94	0.83 (0.07)
Stephanocoenia intersepta	58.33	0.003	1350	0.60	0.77 (0.08)	56.05	0.95	0.90 (0.02)

Figure 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). Plots are presented for models with a percentage total explained deviance >40 %. Less than four plots for a species is due to non-significant variables dropped from the model. Note predictor names are as Table 1, "visual" stands for visually estimated 'reef complexity'.

Agaricia
agaricites



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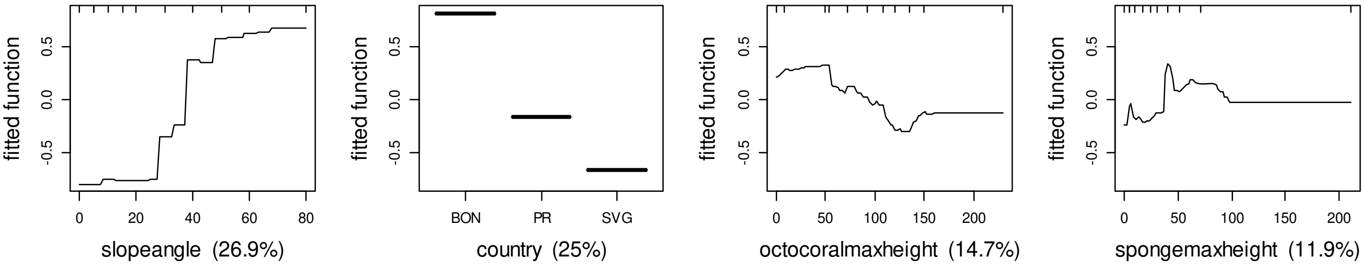
lamarcki



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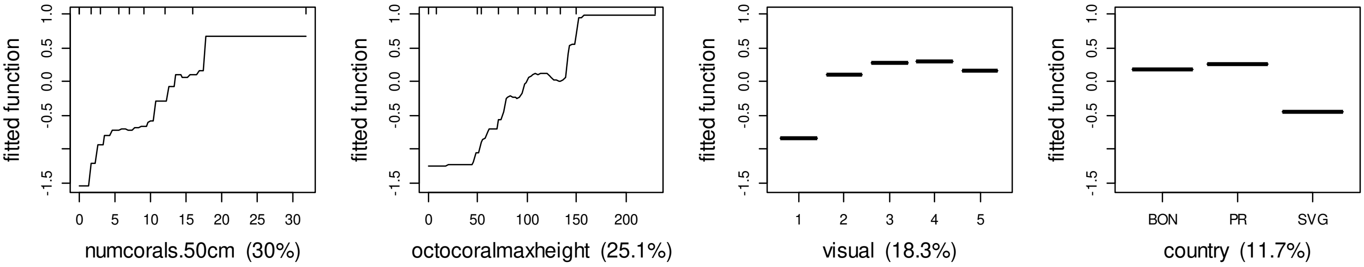

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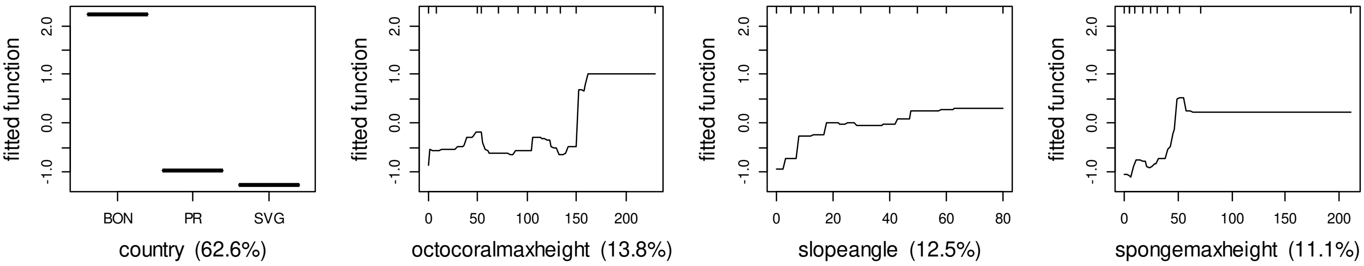
fastigiata



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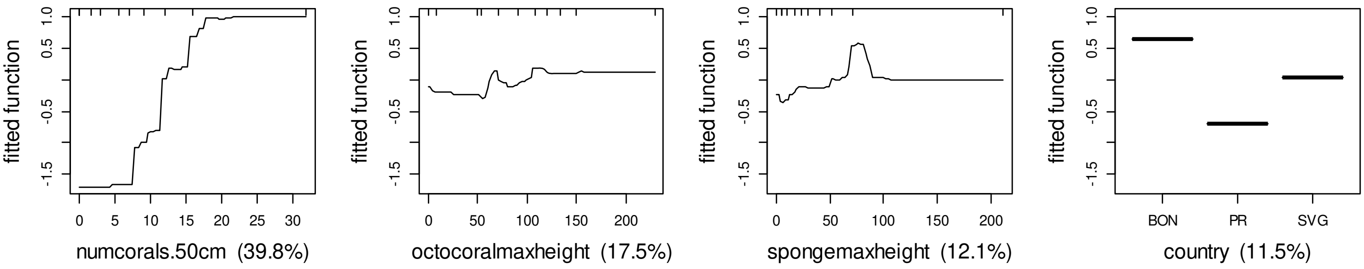
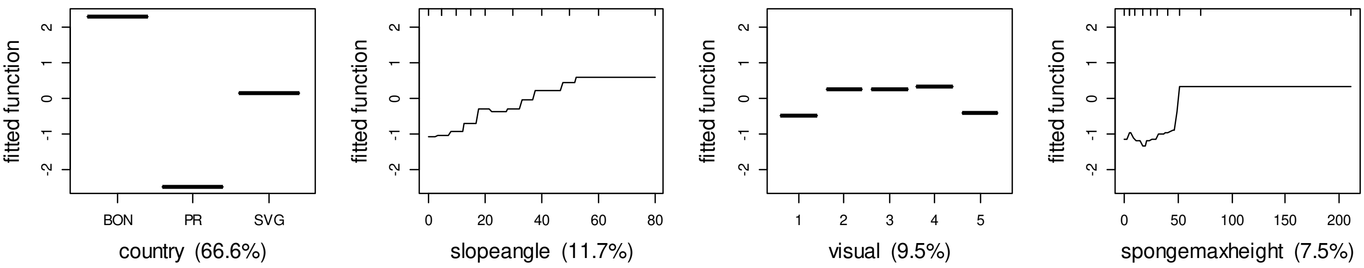
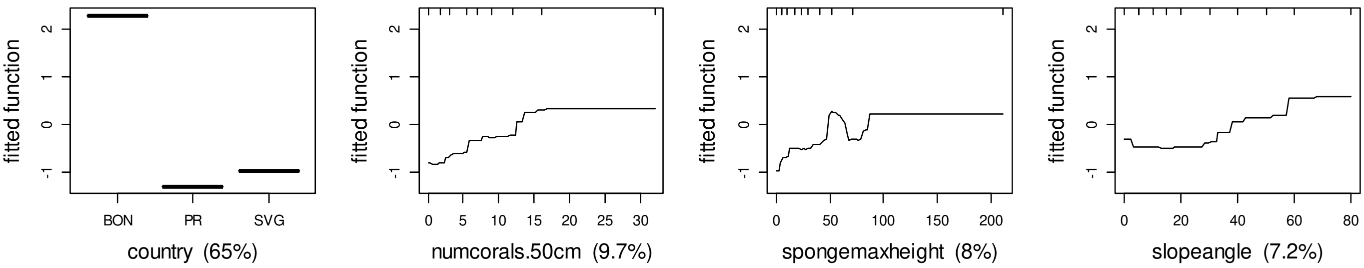
auretenra



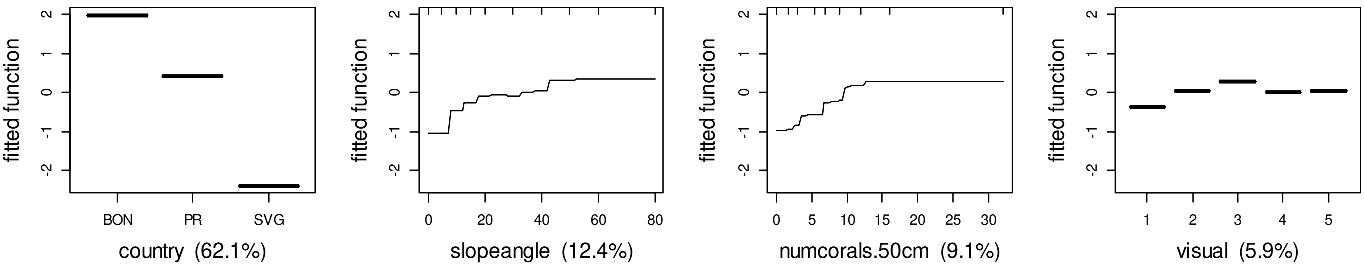
Madracis
decactis



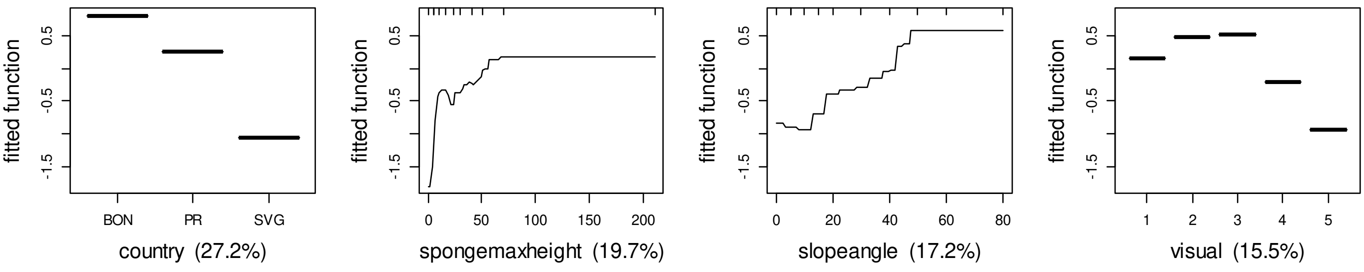
Madracis
pharensis



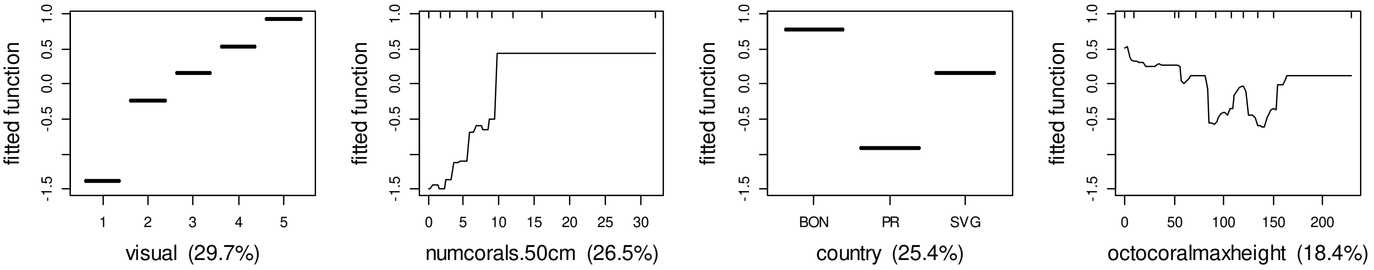
Meandrina
memorialis



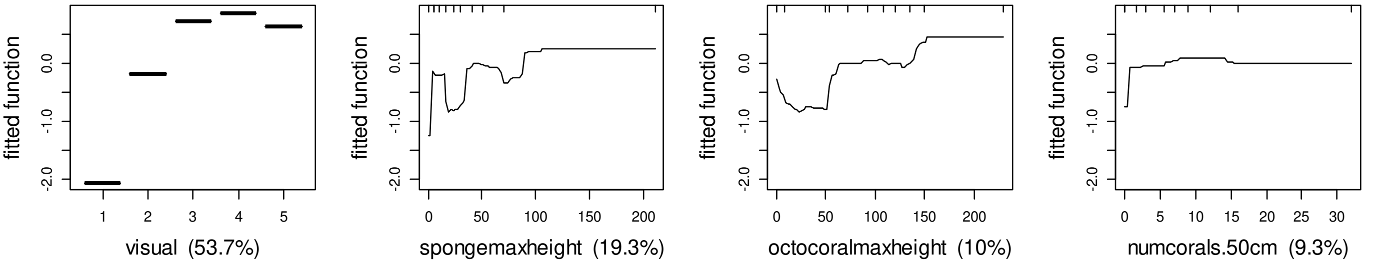
Montastraea cavernosa



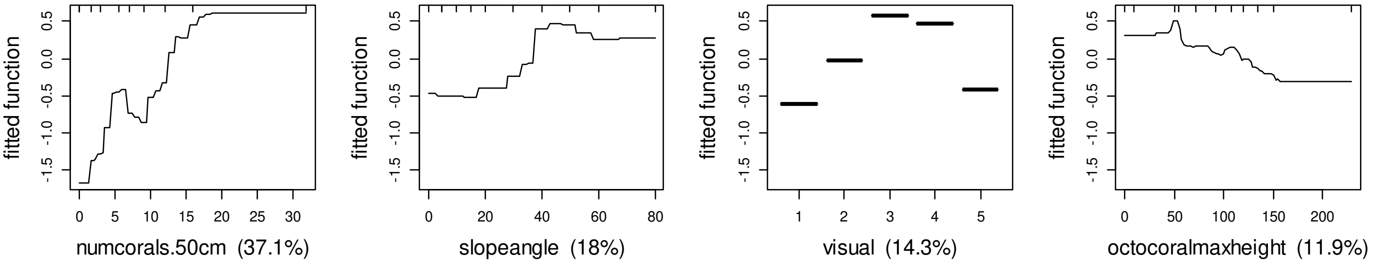
Orbicella
annularis



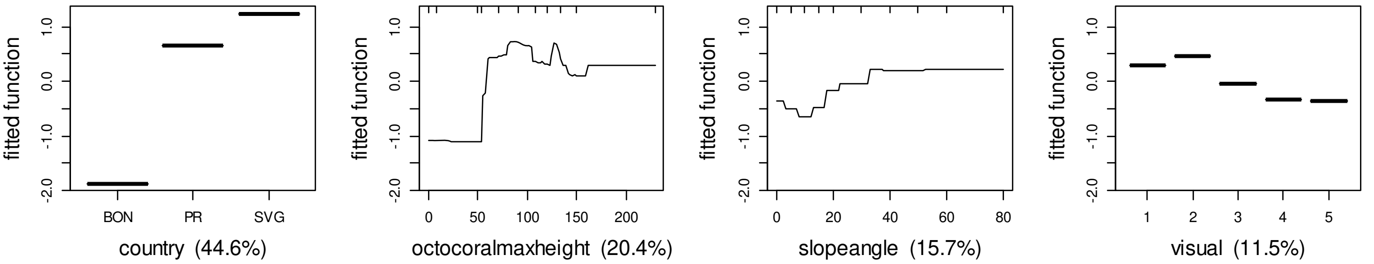
Orbicella faveolata



Orbicella franksi



Porites divaricata



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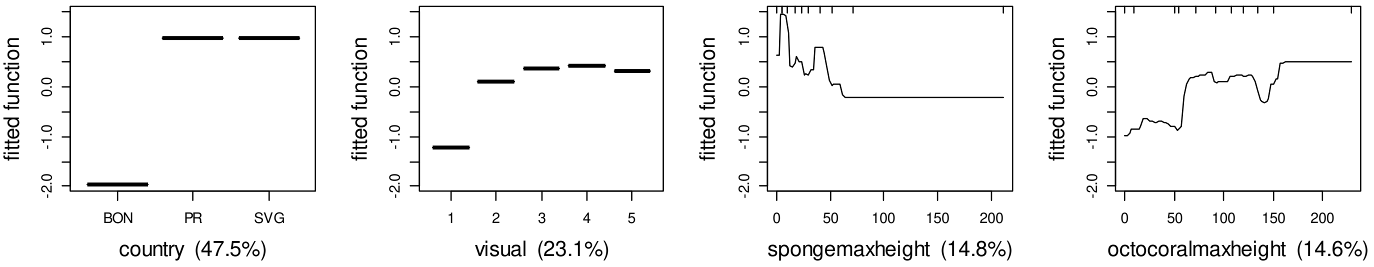
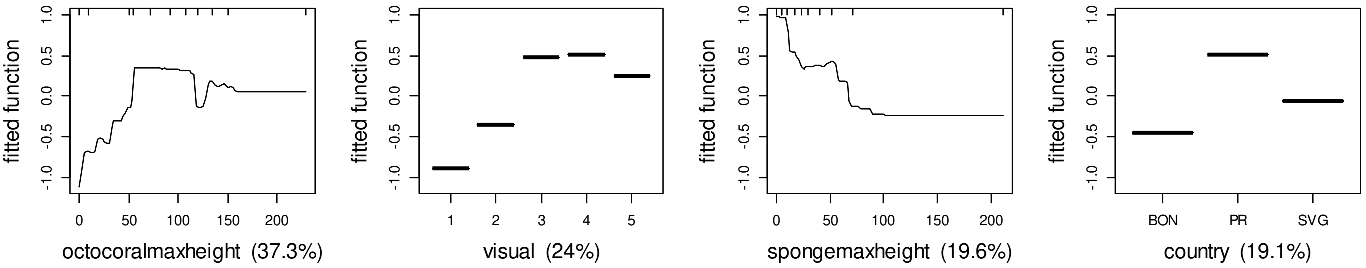
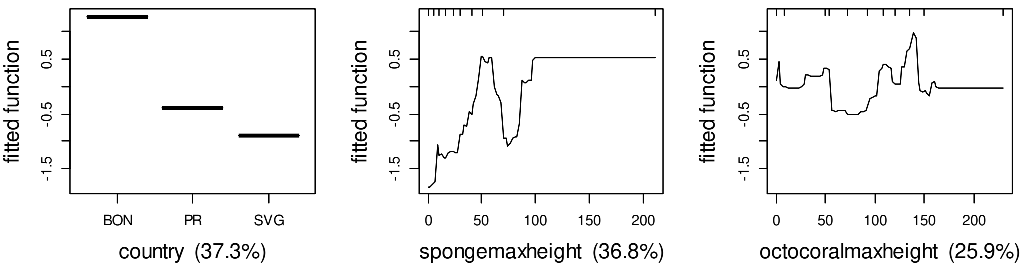


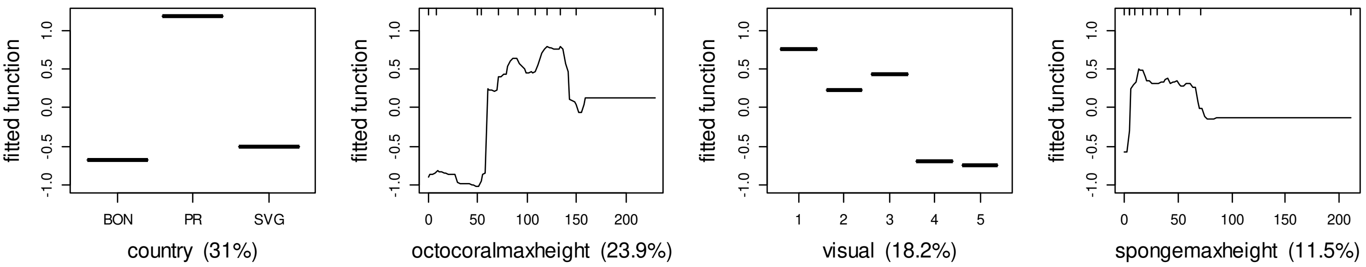
Porites porites



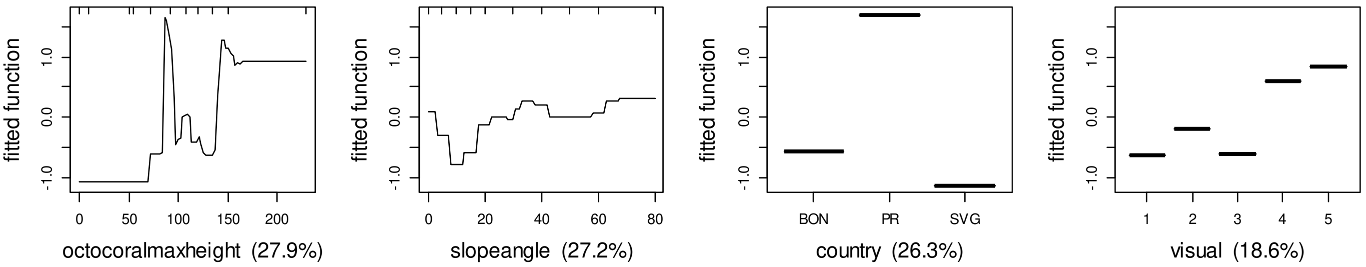
Pseudodiploria labyrinthiformis



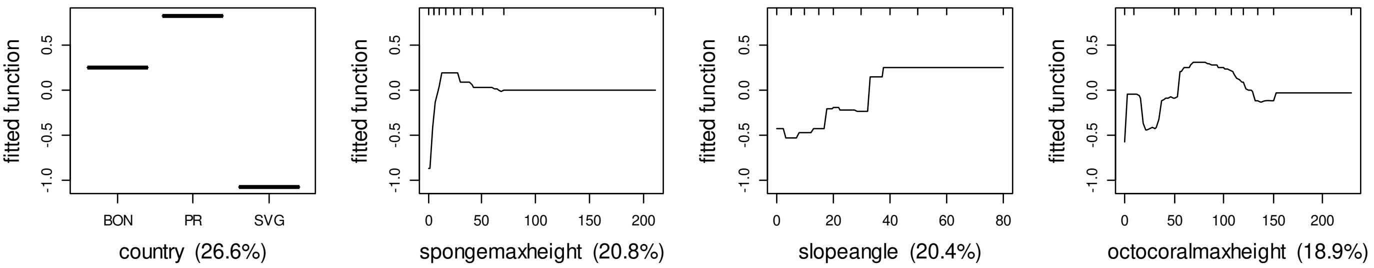
Psuedodiploria strigosa



Scolymia cubensis



Siderastrea siderea



Stephanocoenia intersepta

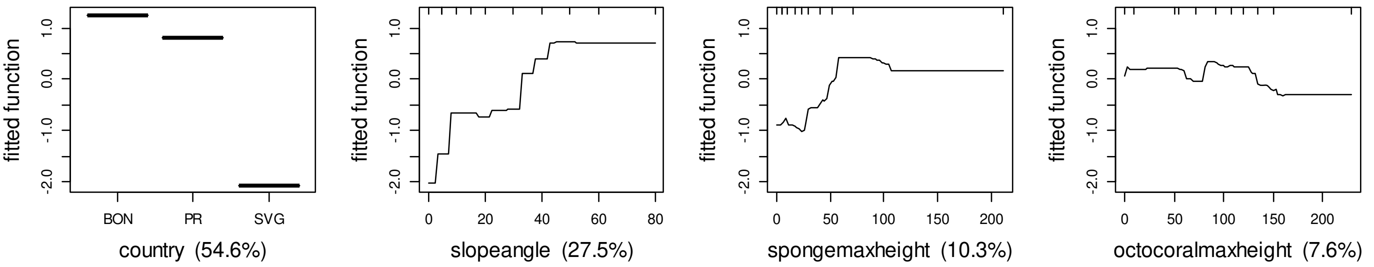


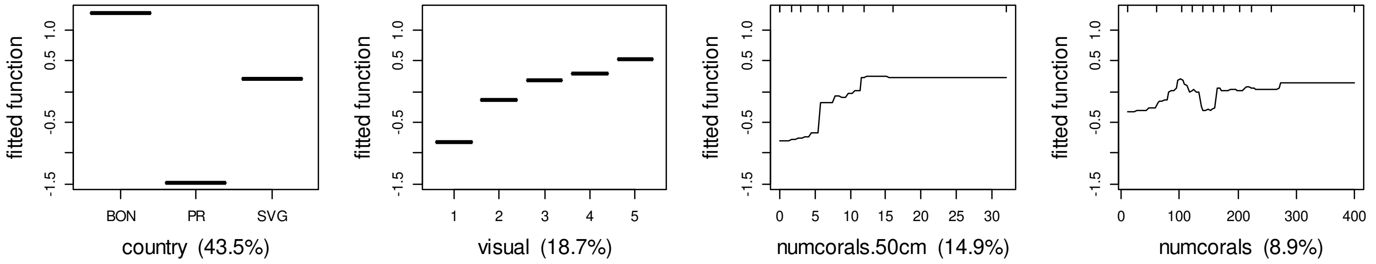
Table S2. Predictive performance of boosted regression tree (BRT) models relating coral fish species presence to reef complexity and location. Table variables indicate the frequency of occurrence (percentage of 300 plots a species was present in), model learning rate, optimum number of trees fitted with all models with a learning rate of 3 (allowing for interactions), the mean residual deviance of the model, training data correlation, the mean deviance using 10-fold cross validation (CV), and the total deviance explained by each model. AUC scores (area under receiver operator character curve) provide a discrimination of probabilities between presence and absence samples, with values >0.8 considered here very good and >0.9 excellent.

Species	**Freq of occurrence**	**Learning rate**	**No. of Trees**	**Model residual deviance**	**CV residual deviance**	**% Total Deviance**	**AUC score**	**CV AUC score (SE)**
Abudefduf saxatilis	14.33	0.003	650	0.53	0.66 (0.04)	35.94	0.91	0.81 (0.04)
Acanthemblemaria aspera	10.67	0.003	1100	0.45	0.55 (0.04)	34.39	0.91	0.83 (0.03)
Acanthemblemaria maria	60.00	0.003	1500	0.84	1.09 (0.04)	37.58	0.91	0.78 (0.02)
Acanthurus bahianus	21.33	0.003	400	0.89	1.01(0.02)	14.30	0.82	0.64 (0.04)
Acanthurus coeruleus	31.33	0.003	950	0.91	1.11 (0.02)	26.65	0.87	0.73 (0.01)
Bodianus rufus	8.00	0.003	400	0.39	0.49 (0.02)	30.18	0.93	0.80 (0.03)
Canthigaster rostrata	72.00	0.003	1000	0.73	0.92 (0.04)	38.48	0.91	0.81 (0.02)
Cephalopholis cruentatus	50.00	0.003	1350	0.68	0.91 (0.06)	50.89	0.94	0.87 (0.02)
Chaetodon capistratus	20.00	0.003	350	0.85	0.94 (0.02)	15.04	0.83	0.68 (0.03)
Chromis cyanea	28.33	0.003	1450	0.51	0.74 (0.09)	57.08	0.96	0.88 (0.04)
Chromis multilineata	46.67	0.003	1600	0.73	1.01 (0.06)	46.95	0.93	0.82 (0.03)
Clepticus parrae	17.67	0.003	1200	0.52	0.73 (0.05)	43.97	0.94	0.81 (0.03)
Coryphopterus dicrus	62.00	0.003	1350	0.70	0.87 (0.05)	47.12	0.93	0.87 (0.02)
Coryphopterus eidolon	34.67	0.003	1550	0.39	0.58 (0.05)	69.85	0.97	0.93 (0.01)
Coryphopterus glaucofraenum	46.33	0.003	850	0.95	1.09 (0.05)	31.01	0.87	0.80 (0.03)
Coryphopterus hyalinus	46.33	0.003	1300	0.57	0.76 (0.05)	58.37	0.96	0.92 (0.01)
Coryphopterus lipernes	25.67	0.003	1400	0.40	0.59 (0.08)	64.70	0.97	0.92 (0.02)
Equetus punctatus	7.00	0.003	250	0.44	0.49 (0.02)	14.22	0.86	0.70 (0.06)
Gnatholepis thompsoni	42.67	0.003	1350	0.72	0.95 (0.05)	47.05	0.93	0.84 (0.02)
Gobiosoma dilepis	12.67	0.003	850	0.53	0.65 (0.03)	29.91	0.89	0.76 (0.05)
Gobiosoma evelynae	48.33	0.003	850	1.02	1.21 (0.06)	26.24	0.86	0.73 (0.04)
Gobiosoma horsti	10.33	0.003	650	0.30	0.43 (0.03)	54.25	0.97	0.92 (0.02)

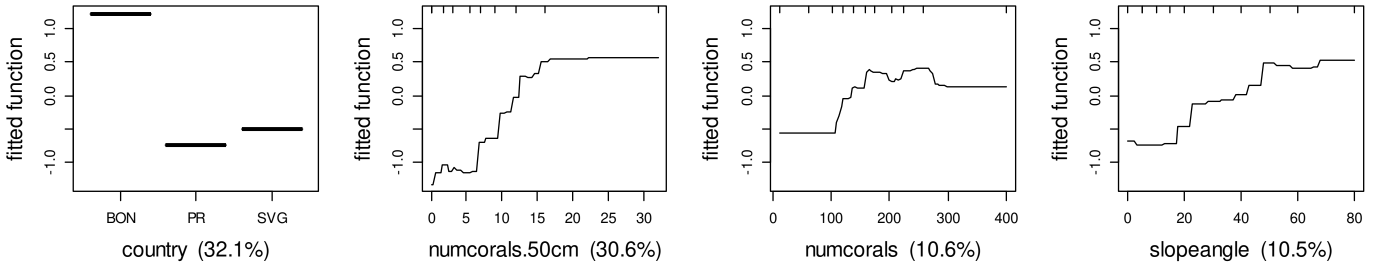
Gramma loreto	34.33	0.003	1600	0.43	0.65 (0.07)	66.34	0.98	0.93 (0.01)
Gymnothorax moringa	9.00	0.003	500	0.46	0.58 (0.03)	24.55	0.90	0.70 (0.03)
Haemulon flavolineatum	29.67	0.003	700	0.94	1.10 (0.03)	22.79	0.85	0.72 (0.03)
Halichoeres bivitattus	13.00	0.003	1050	0.24	0.38 (0.06)	69.53	0.98	0.95 (0.03)
Halichoeres garnoti	66.67	0.003	950	0.63	0.72 (0.05)	50.74	0.94	0.90 (0.01)
Halichoeres maculipinna	24.33	0.003	1200	0.56	0.69 (0.04)	49.71	0.94	0.90 (0.02)
Halichoeres pictus	21.00	0.003	1400	0.46	0.68 (0.04)	55.24	0.96	0.89 (0.02)
Heteropriacanthus cruentatus	12.33	0.003	800	0.50	0.67 (0.03)	32.81	0.93	0.73 (0.04)
Holocentrus rufus	24.33	0.003	1050	0.74	0.95 (0.04)	33.03	0.90	0.76 (0.03)
Hypoplectrus puella	8.00	0.003	500	0.41	0.53 (0.03)	26.08	0.92	0.65 (0.05)
Lactophrys triqueter	10.00	0.003	400	0.52	0.62 (0.02)	19.58	0.86	0.72 (0.05)
Lutjanus apodus	8.33	0.003	450	0.44	0.53 (0.04)	23.96	0.87	0.71 (0.07)
Malacoctenus boehlkei	11.00	0.003	1200	0.39	0.53 (0.04)	43.94	0.95	0.86 (0.03)
Malacoctenus triangulatus	10.00	0.003	1100	0.30	0.48 (0.04)	53.96	0.97	0.87 (0.03)
Microspathodon chrysurus	33.00	0.003	1100	0.83	1.01 (0.05)	34.33	0.89	0.81 (0.03)
Mulloidichthys martinicus	12.33	0.003	2200	0.31	0.60 (0.05)	58.84	0.98	0.84 (0.03)
Myripristis jacobus	26.67	0.003	950	0.61	0.84 (0.06)	47.15	0.94	0.87 (0.02)
Neoiphon marianus	13.00	0.003	950	0.35	0.48 (0.05)	54.48	0.96	0.87 (0.03)
Ocyurus chrysurus	7.00	0.003	400	0.37	0.46 (0.02)	28.01	0.93	0.75 (0.03)
Scarus iserti	56.33	0.003	1050	0.87	1.07 (0.06)	36.59	0.90	0.81 (0.03)
Scarus taeniopterus	63.67	0.003	1350	0.65	0.85 (0.05)	50.37	0.94	0.87 (0.02)
Scarus vetula	10.33	0.003	250	0.56	0.64 (0.02)	16.23	0.89	0.71 (0.04)
Sparisoma atomarium	10.33	0.003	900	0.33	0.48 (0.04)	50.92	0.96	0.85 (0.05)
Sparisoma aurofrenatum	73.67	0.003	750	0.79	0.91 (0.04)	31.83	0.89	0.82 (0.03)
Sparisoma viride	74.00	0.003	1500	0.65	0.86 (0.07)	43.28	0.92	0.83 (0.03)
Stegastes adustus	18.33	0.003	2000	0.44	0.74 (0.05)	53.91	0.97	0.83 (0.02)
Stegastes diencaeus	32.67	0.003	1750	0.69	0.90 (0.04)	45.20	0.93	0.84 (0.02)
Stegastes leucostictus	17.33	0.003	500	0.74	0.81 (0.03)	19.81	0.84	0.75 (0.03)
Stegastes partitus	82.00	0.003	1700	0.38	0.62 (0.06)	59.20	0.98	0.89 (0.02)
Stegastes planifrons	51.67	0.003	1750	0.45	0.68 (0.04)	67.25	0.98	0.93 (0.01)
Thalassoma bifasciatum	74.00	0.003	1050	0.67	0.86 (0.04)	41.53	0.92	0.83 (0.03)

Figure 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). Plots are presented for models with a percentage total deviance explained >40 %. Less than four plots for a species is due to non-significant variables dropped from the model. Note predictor names are as Table 1, "visual" stands for visually estimated 'reef complexity'.

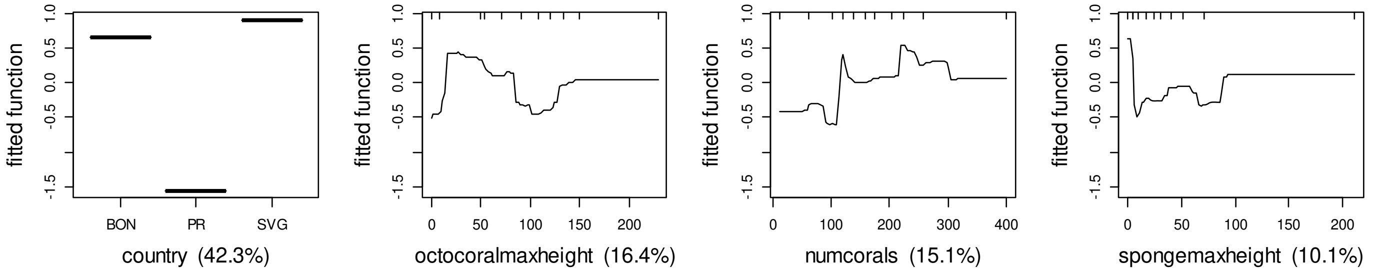
Cephalopholis cruentatus



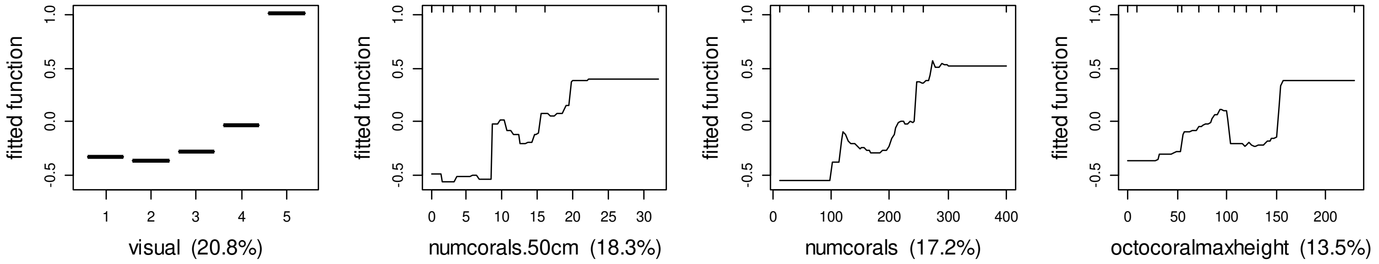
Chromis cyanea



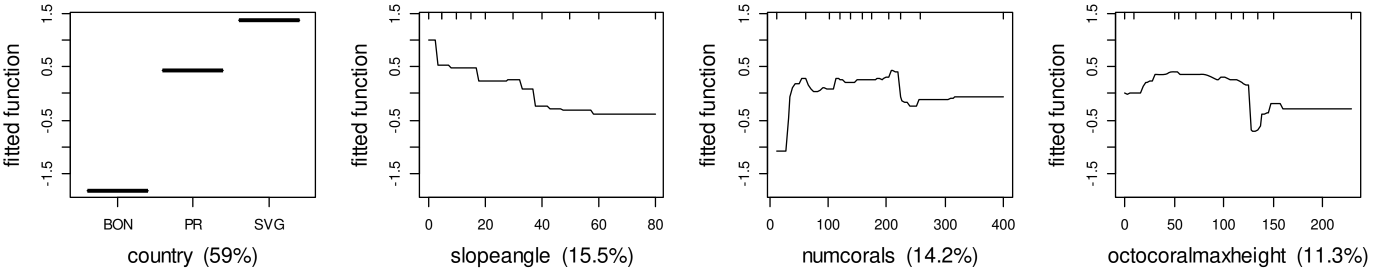
Chromis multilineata



Clepticus parrae



Coryphopterus
dicrus



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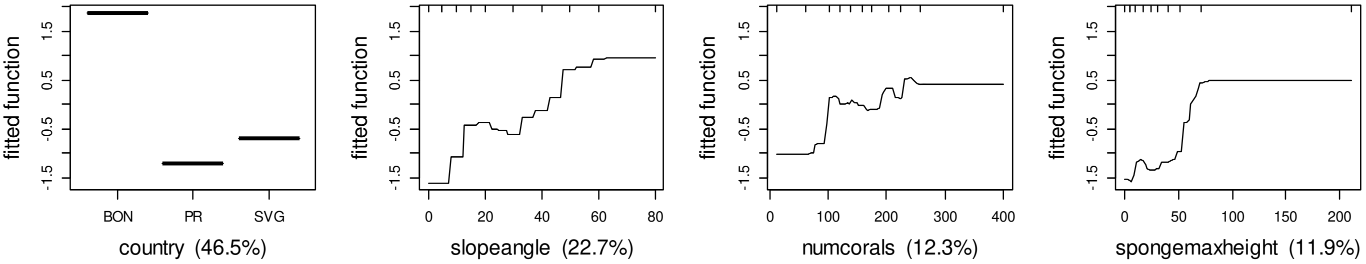
eidolon



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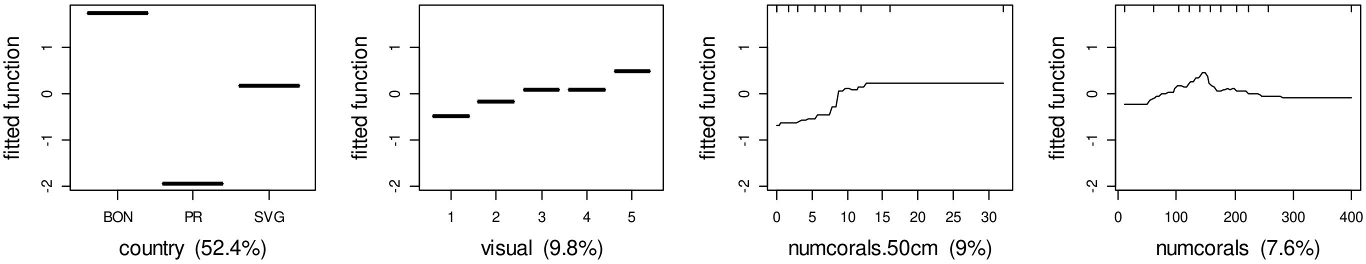
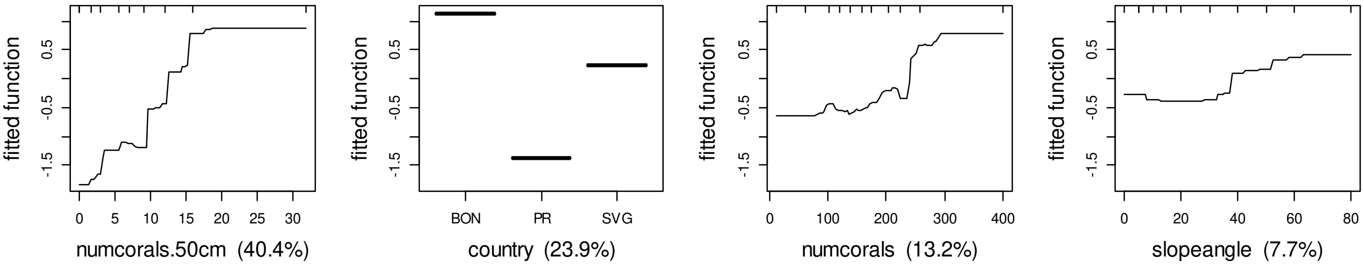
hyalinus

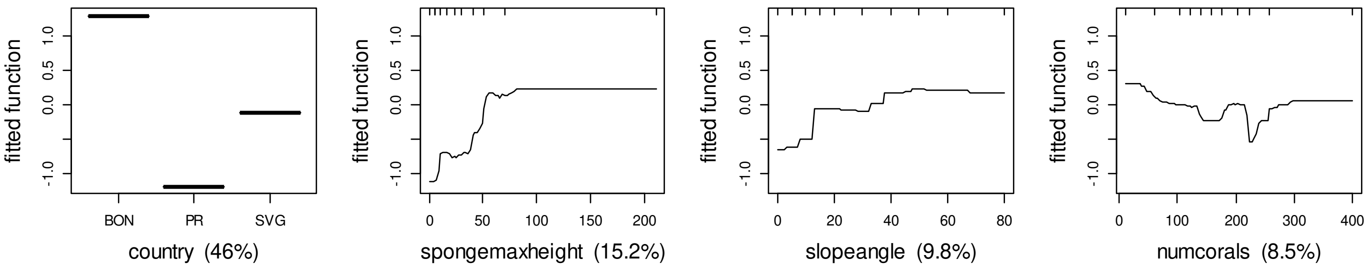


Coryphopterus
lipernes



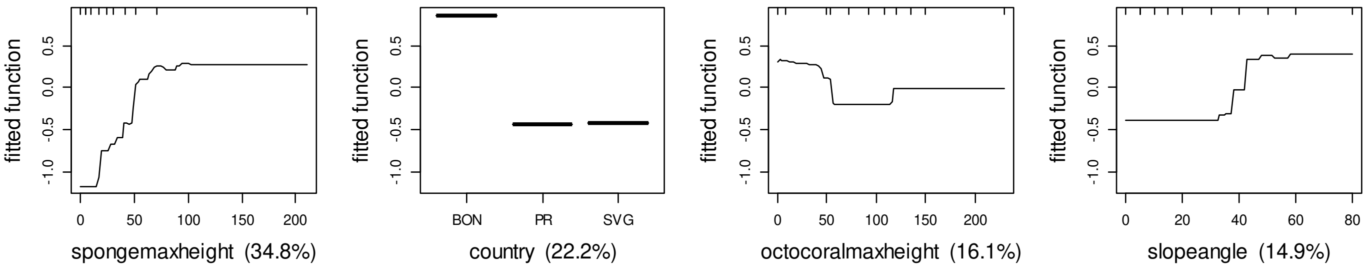
Gnatholepis

thompsoni



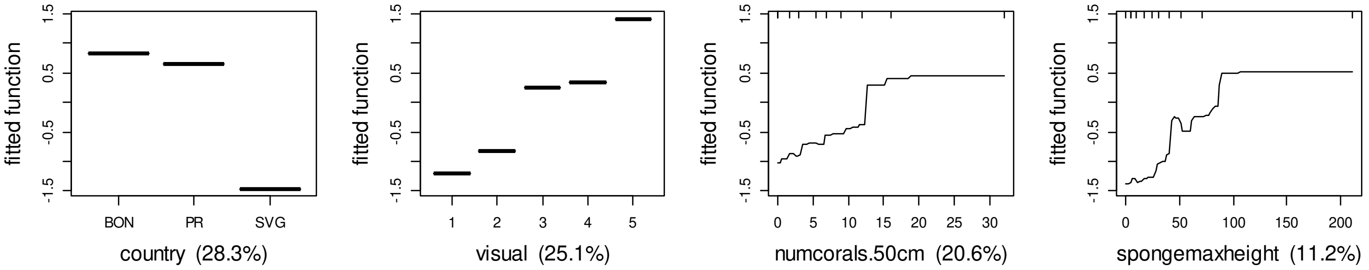
Gobiosoma

horsti



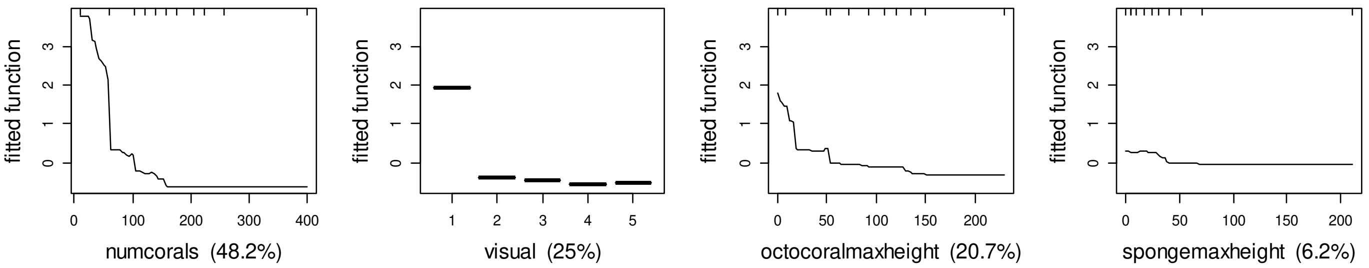
Gramma

loreto



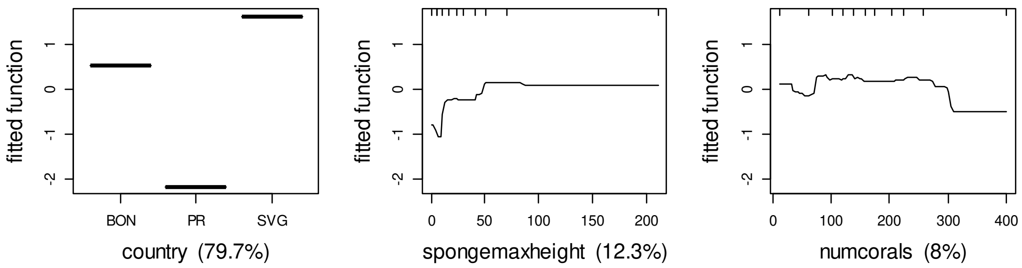
Halichoeres

bivitattus

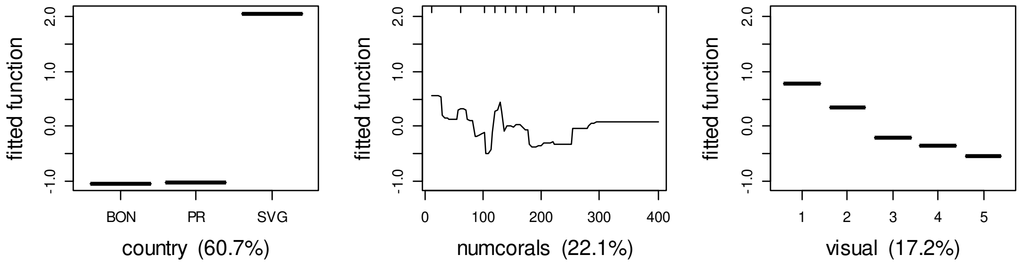


Halichoeres

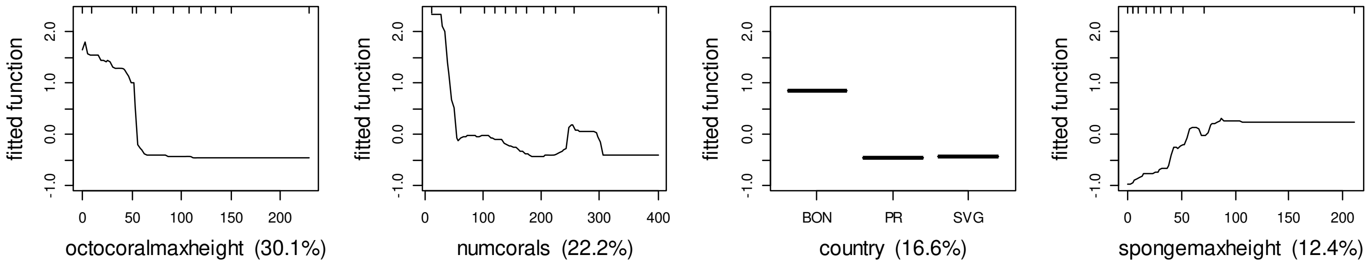
garnoti



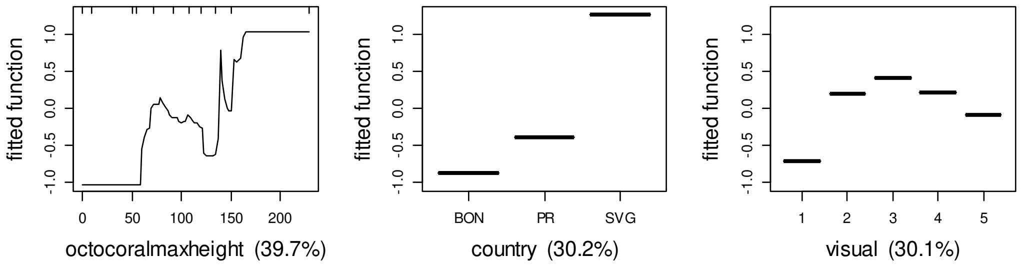
Halichoeres maculipinna



Halichoeres pictus

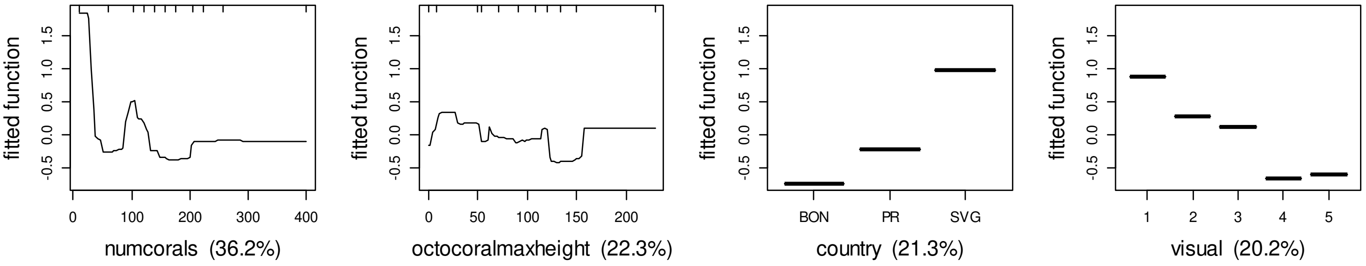


Malacoctenus boehlkei

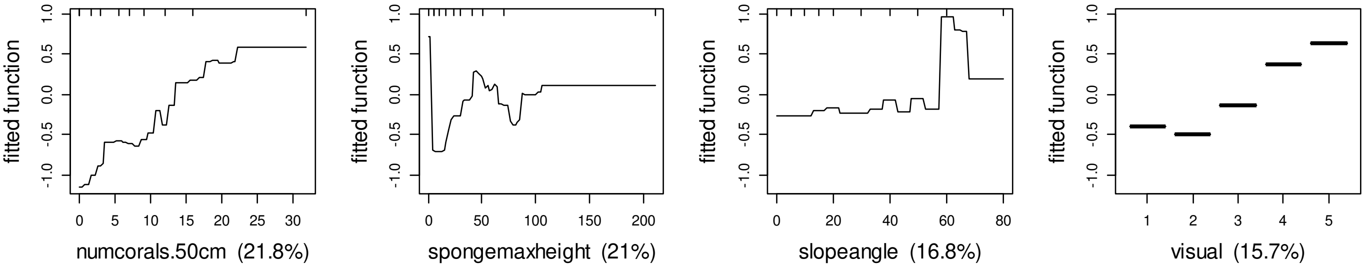


Malacoctenus

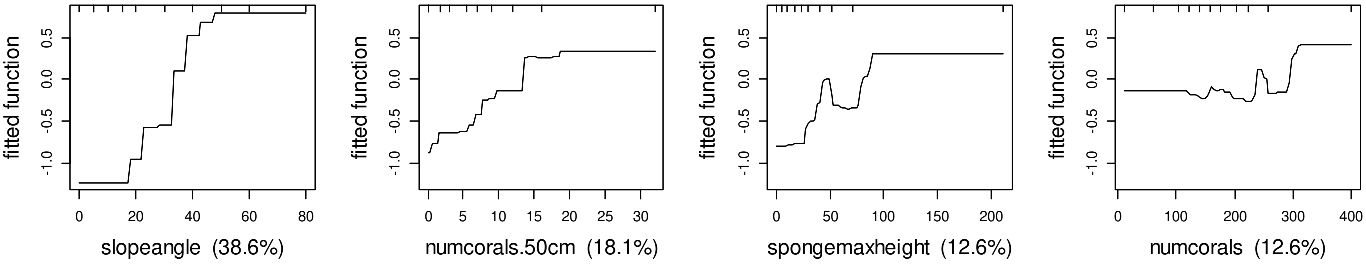
triangulatus



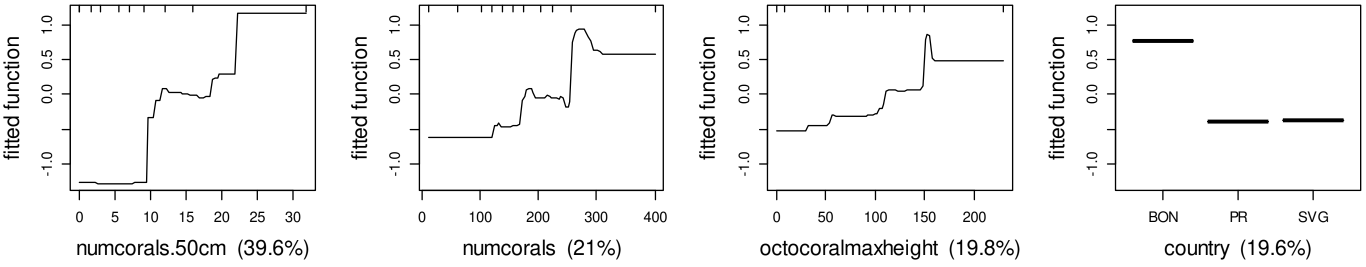
Mulloidichthys martinicus



Myripristis jacobus

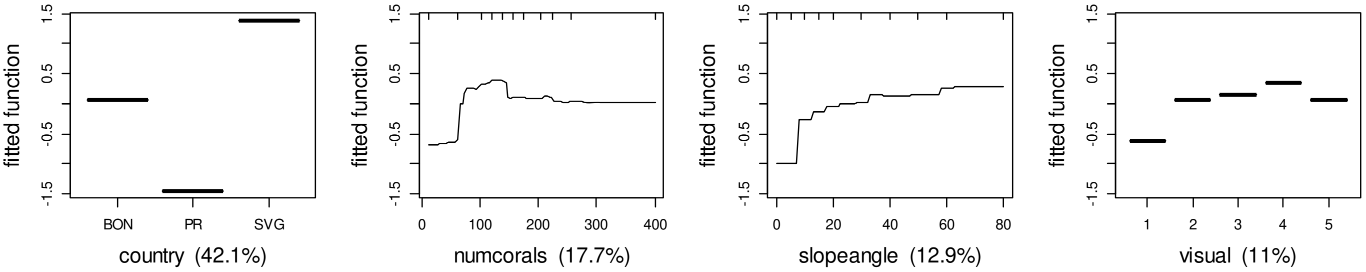


Neoiphon
marianus

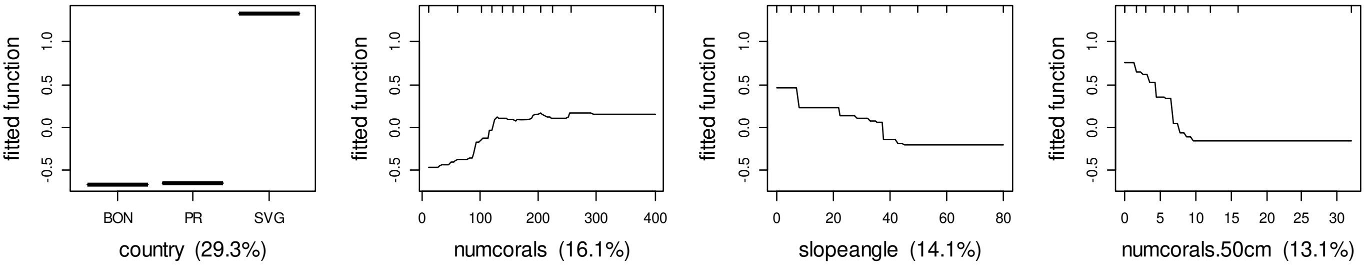


Scarus

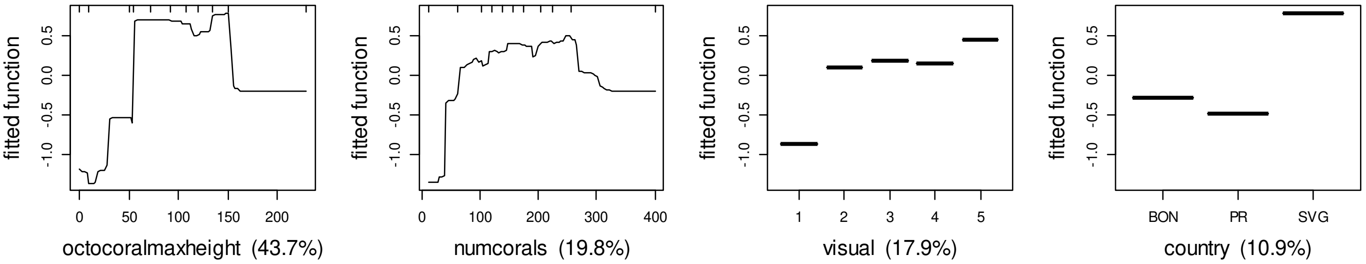
taeniopterus



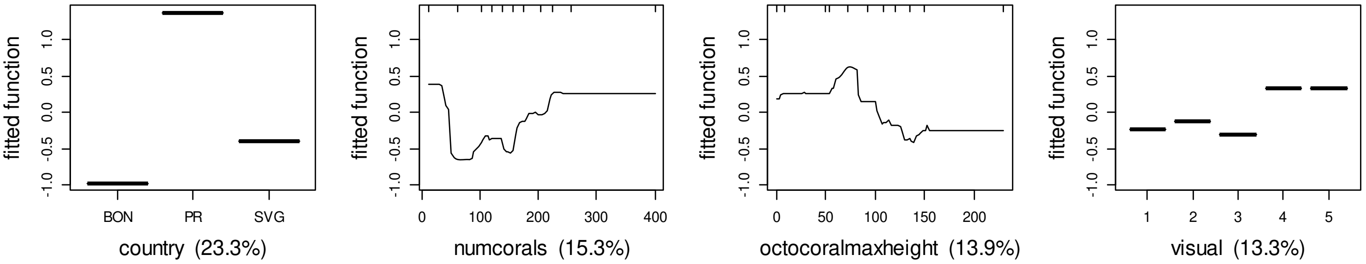
Sparisoma atomarium



Sparisoma viride

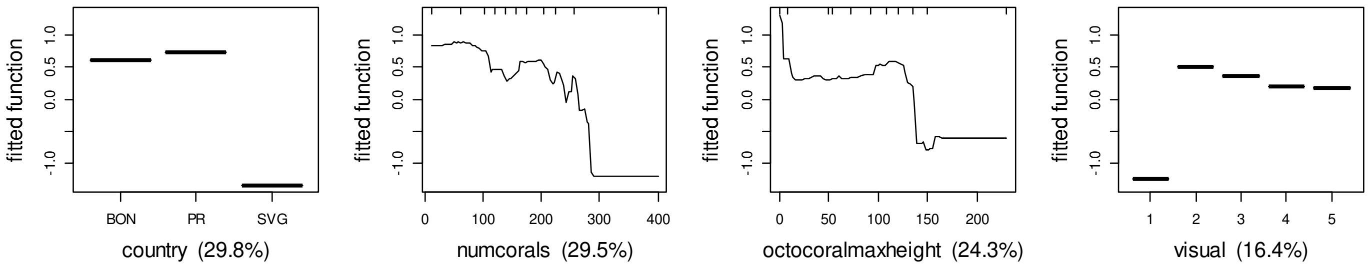


Stegastes adustus

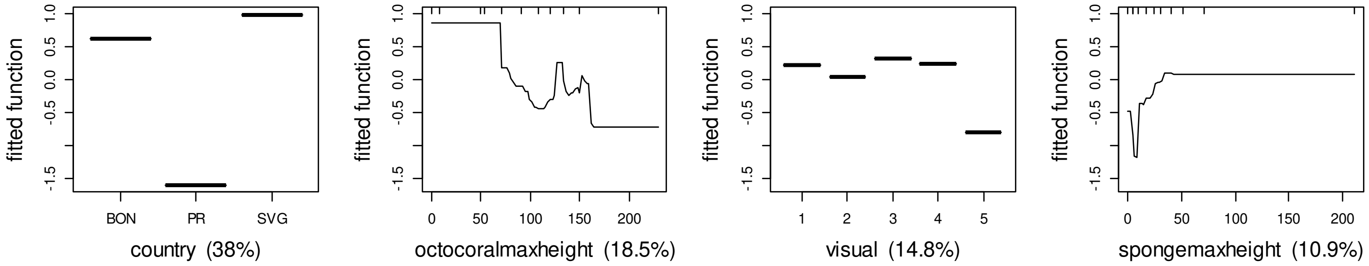


Stegastes

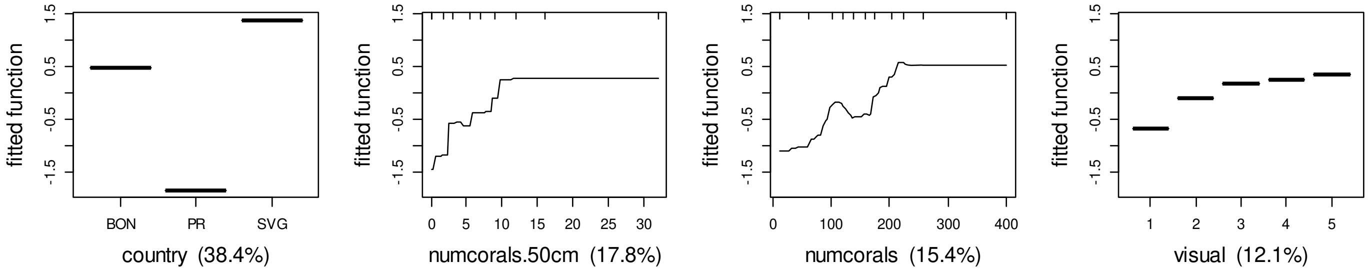
diencaeus



Stegastes partitus



Stegastes planifrons



Thalassoma bifasciatum