

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

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19 **Running headline:** Coral reef complexity and species richness

20

21 **Summary**

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

26 2. This study reveals the importance of reef habitat complexity and structural components
27 to different taxa of macro-fauna, total species richness, and individual coral and fish
28 species in the Caribbean.

29 3. Species presence and richness of different taxa were visually quantified in one-hundred
30 25m² plots in three marine reserves in the Caribbean. Sampling was evenly distributed
31 across five levels of visually estimated reef complexity, with five structural components
32 also recorded: the number of corals, number of large corals, slope angle, maximum
33 sponge and maximum octocoral height. Taking advantage of natural heterogeneity in
34 structural complexity within a particular coral reef habitat (*Orbicella* reefs) and discrete
35 environmental envelope, thus minimising other sources of variability, the relative
36 importance of reef complexity and structural components was quantified for different
37 taxa and individual fish and coral species on Caribbean coral reefs using Boosted
38 Regression Trees (BRTs).

39 4. BRT models performed very well when explaining variability in total (82.3 %), coral
40 (80.6 %) and fish species richness (77.3 %), for which the greatest declines in richness
41 occurred below intermediate reef complexity levels. Complexity accounted for very
42 little of the variability in octocorals, sponges, arthropods, annelids or anemones. BRTs
43 revealed species-specific variability and importance for reef complexity and structural
44 components. Coral and fish species occupancy generally declined at low complexity

45 levels, with the exception of two coral species (*Pseudodiploria strigosa* and *Porites*
46 *divaricata*) and four fish species (*Halichoeres bivittatus*, *H maculipinna*, *Malacoctenus*
47 *triangulatus* and *Stegastes partitus*) more common at lower reef complexity levels. A
48 significant interaction between country and reef complexity revealed a non-additive
49 decline in species richness in areas of low complexity and the reserve in Puerto Rico.

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

55 **Keywords** biodiversity, conservation, relief, topography, degradation

56

57

58 **Introduction**

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

69

70 Corals and fishes are the most studied coral reef organisms. Akin to birds in terrestrial
71 systems (Stattersfield et al. 1998), fishes are often used as a focal group to investigate trends
72 in species richness because they are speciose, widely distributed and easily observed (Allen
73 2008; Mumby et al. 2008). However, they may not always be a good proxy for other taxa
74 (e.g. Sutcliffe et al. 2012) and may not contribute greatly to overall diversity (Fisher et al.
75 2015). The pool of available species on reefs is determined by a combination of large-scale
76 processes such as latitude, temperature, habitat area or environmental stability (Fraser and
77 Currie 1996; Bellwood & Hughes 2001; Mora et al. 2003; Parravicini et al. 2013) as well as
78 small-scale variations in the local environment. Stochastic processes such as recruitment
79 (Sale 1991) may drive local fish species richness and abundance, but habitat structure appears
80 to mediate much of the post-settlement patterns (Syms & Jones 2000) through species-
81 specific habitat preferences or modification of competition and predation (Hixon & Menge

82 1991; Hixon & Beets 1993; Beukers & Jones 1997; Almany 2004; Grabowski, Hughes &
83 Kimbro 2008). Habitat structure has been shown repeatedly to be important to coral reef fish
84 and has received increasing attention (Graham & Nash 2013). This has largely been driven by
85 the threat ongoing loss of structural complexity on Caribbean coral reefs (Alvarez-Filip et al.
86 2009) poses to biodiversity and reef habitats (e.g. Chong-Seng et al. 2012). However, there is
87 a paucity of studies on other taxa or the response of individual species or families to changes
88 in reef structural complexity (Graham & Nash 2013; Pratchett et al. 2014).

89
90 Measures of habitat structure on coral reefs are often reduced to a single aggregate measure
91 such as chain and tape measures of rugosity (Risk 1972), visually estimated complexity (e.g.
92 Polunin & Roberts 1993), compound habitat (e.g. Gratwicke & Speight 2005b) and PCA
93 scores (e.g. Chong-Seng et al. 2012), or recently digital terrain models (e.g. Pittman et al.
94 2007, Pittman et al. 2009, Costa et al. 2014). However, a single measure is unlikely to capture
95 all the variability in complexity; habitat complexity has been defined as incorporating both
96 complexity and the abundance of individual structural components (McCoy & Bell, 1991),
97 and they can have separate effects on assemblages (Beck 2000). Thus a range of individual
98 structural components have been investigated on reefs including vertical relief, frequency of
99 tall corals, coral morphology and the amount of holes/refuge (McCormick 1994; Friedlander
100 & Parrish 1998; Gratwicke & Speight 2005a, b; Wilson, Graham & Polunin 2007; Harborne,
101 Mumby & Ferrari 2012; Graham & Nash 2013). Multiple measures of topographic
102 complexity and structural components may be required to elucidate individual species
103 relationships (e.g. Beck 2000; Harborne, Mumby & Ferrari 2012).

104
105 Reef complexity acts on fish species richness in concert with other covariates such as wave
106 exposure or depth, and the effects of complexity may be difficult to separate (Jennings,

107 Boullé & Polunin 1996; Graham et al. 2009; Chong-Seng et al. 2012; Wilson et al. 2012;
108 Graham & Nash 2013). The present study takes advantage of natural spatial heterogeneity in
109 structural complexity within small geographic areas within a discrete environmental envelope
110 (Chollett et al. 2012) and a particular habitat type (*Orbicella* reefs) to reduce spatio-temporal
111 confounding. This facilitates the elucidation of the relative importance of reef complexity
112 (within 25 m² plots) and five structural components (the number of corals, number of large
113 corals, slope angle, maximum sponge and maximum octocoral height) to 1) total richness on
114 coral reefs, 2) richness of different macrofauna taxa, and 3) individual coral and fish species
115 occupancy.

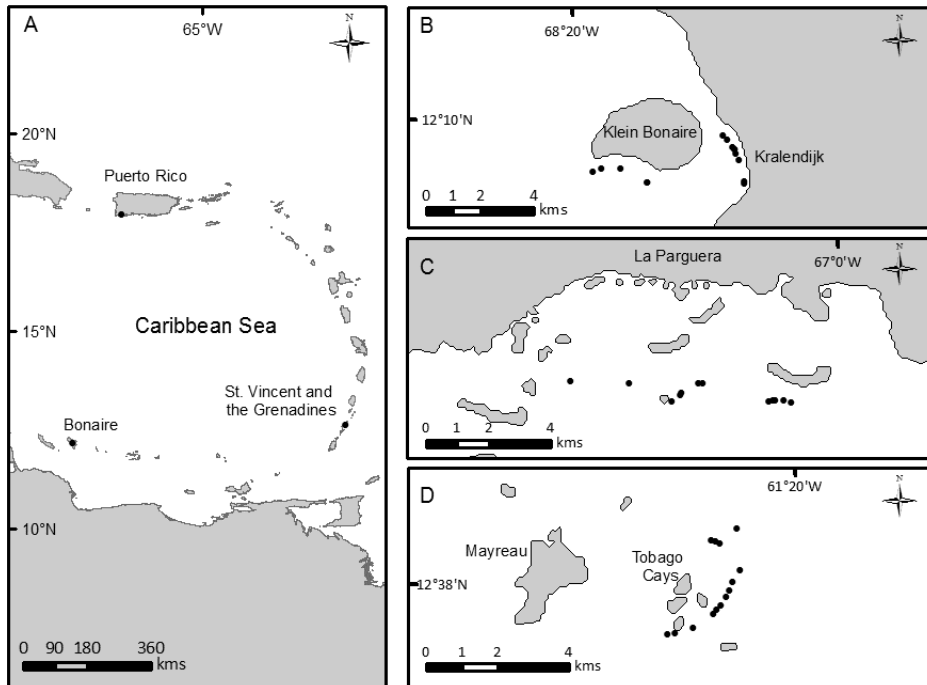
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117 **Methods**

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

127 Species presence was quantified in twenty 25 m² plots at each of five levels of reefscape
128 complexity in each country (100 plots total per country). Surveys were conducted in the same
129 reef system within each country in order to minimise other sources of variability (e.g.
130 physical conditions, fishing pressure etc.), in the same reef habitat in sheltered areas

131 (prevailing wind direction from the East in all cases, with all reefs sheltered either by land or
132 windward reefs).



133
134 **Figure 1** Survey locations: A) in eastern Caribbean, B) west coast of Bonaire, C) La
135 Parguera, south-west Puerto Rico and D) Tobago Cays in St. Vincent and the Grenadines.

136
137 The maximum distance between surveys was 5.5 km in Bonaire, 6.9 km in Puerto Rico, and
138 3.6 km in SVG. Plots were haphazardly situated in areas of uniform complexity at least 10 m
139 from a boundary between different complexity levels or from other plots, on coral fore-reefs
140 at depths of 5-15 m (mean 10.15 ± 0.14 S.E. $n = 300$).

141
142 Reefscape complexity was visually estimated on a scale of 1 (flat, little relief) to 5 (highly
143 complex with high vertical relief and overhangs) following Polunin & Roberts (1993). A
144 single complexity value was assigned by two experienced surveyors (SPN and CSD) to avoid

145 observer bias, and each plot was photographed to ensure continuity of complexity estimates
146 by enabling post-survey standardisation based on the range of reefscape complexity from all
147 plots surveyed (see Supporting Information Appendix S1 for examples of each complexity
148 level). Visual estimates of complexity have been widely employed (e.g. Polunin & Roberts
149 1993; Jennings, Boullé & Polunin 1996; Wilson, Graham & Polunin 2007), are strongly
150 correlated with coral reef fish richness (Wilson, Graham & Polunin 2007), and incorporate
151 aspects of complexity such as caves and overhangs (Polunin & Roberts 1993) that chain and
152 tape surface rugosity estimates (e.g. Risk 1972) may fail to accurately reflect. Visually
153 estimating complexity also allowed plots to be rapidly categorised and selected prior to
154 disturbing motile faunal communities. Three divers characterised the faunal communities and
155 one recorded structural complexity components.

156

157 Plots were delineated with tape measures in a 'T' shape, after first recording larger, more
158 mobile fish species (SPN) 2.5 m either side of the first 5 m tape as it was deployed following
159 the depth contour. Each plot half was then carefully searched for fish (by S Newman and C
160 Dryden) and arthropods (by C Dryden), emergent annelids, anemones, molluscs and
161 flatworms (by S Newman), and then corals, echinoderms, sponges, octocorals, zoanthids,
162 antipatharians and corallimorphs (by S Williams). Unknown species were photographed for
163 later identification. Survey time was greater in more complex plots due to greater surface area
164 and the necessity to thoroughly search for cryptic species, with total plot survey times
165 varying between 10 and 20 minutes.

166

167 In addition to visual assessment of reefscape complexity (hereafter referred to as just 'reef
168 complexity', while 'complexity' refers to the overall ecological concept), five structural
169 components (Table 1) were recorded (by C Sanchez) to characterise aspects of complexity

170 (*sensu* McCoy & Bell 1990) which can have separate effects on assemblages (Beck 2000).
 171 Numbers of live corals larger than 4 cm in diameter (*'no. corals'*) and of large corals (>50 cm
 172 height, *'no. large corals'*) provided metrics independent of the reef complexity scale
 173 representing different aspects of coral density that may be important predictors of fishes (e.g.
 174 Harborne, Mumby, & Ferrari 2012). Maximum octocoral height (*'octocoral max height'*) has
 175 been used to describe octocoral communities (Lasker & Coffroth 1983) and was recorded in
 176 each plot because soft corals may contribute to structural complexity (Dustan et al. 2013).
 177 Maximum sponge height in the plot (*'sponge max height'*) was included because sponges can
 178 also act as ecosystem engineers and provide biogenic structures in otherwise low relief
 179 habitats (e.g. McClintock et al. 2005) and may enhance fish species richness. *'Slope angle'*
 180 was visually estimated in degrees from the horizontal plane at each plot edge perpendicular to
 181 the reef slope and averaged, and was included as a predictor due to flatter reef areas typically
 182 having less coral development (e.g. Jones & Chase 1975). The requirements of a fish species
 183 for different aspects of architectural complexity was expected to remain the same regardless
 184 of location, and thus *'Country'* was included as a fixed effect in the analysis to account for
 185 any covariates that were not included in these models, despite best efforts to minimise other
 186 sources of variability by surveying within a discrete coral habitat and environmental
 187 envelope.

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

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

190

191 *Modelling approach*

192 Relationships between species richness of different taxonomic-groups and reef complexity
193 and structural components, and the relative importance of each complexity variable, were
194 examined using boosted regression trees (BRTs). This technique can accommodate
195 continuous, categorical or missing variables, can model non-linear and complex relationships,
196 and may outperform GLM and GAM approaches in terrestrial (Elith et al. 2006) and marine
197 systems (Leathwick et al. 2006). Separate BRT models were fitted predicting the total
198 number of species present (including all taxonomic groups; see Supporting Information
199 Appendix 2), for separate taxonomic groups (corals, fishes, arthropods, octocorals, annelids,
200 echinoderms and anemones) and the presence of each coral and fish species, in R (v2.15.3,
201 www.R-project.org; R Development Core Team 2013), using the ‘gbm’ package (Ridgeway
202 2004) and functions from Elith, Leathwick & Hastie (2008). Individual species were only
203 modelled if they were present in more than 20 plots (of 300 sampled) to avoid modelled
204 relationships based on sparse presence data. All models were fitted to allow interactions using
205 a tree complexity of 5, a bag fraction of 0.6, and a learning rate of 0.003 or 0.001 to minimise
206 predictive deviance and maximise performance. Interaction values indicate the relative
207 departure from a purely additive effect, with zero indicating no interaction. The predictor
208 variables ‘*sponge height*’, ‘*octocoral height*’ and ‘*number of corals*’ were excluded from
209 models of sponge, octocoral and coral richness respectively due to the direct relationship
210 between predictor and response. The ‘*number of large corals*’ was included as a predictor
211 because it was more independent of coral species richness as coral size distributions tend to
212 be right skewed (Bak & Meesters, 1999). Predictor variables that increased variance and
213 reduced model performance were dropped using the ‘gbm.step’ function from Elith,
214 Leathwick & Hastie (2008).

215

216 Ten-fold cross-validation (CV) was used to identify the optimum number of trees (1000 to
217 2650 for taxonomic group models and 250 to 2350 for individual species models) and to test
218 the model on randomly withheld portions of data (Hastie, Tibshirani & Friedman 2001), with
219 all data used to fit each model. BRTs tend to over-fit training data (Elith, Leathwick & Hastie
220 2008; Leathwick et al 2008) so model performance was based on predictions of data withheld
221 during cross-validation, and predictive deviance expressed as a percentage of the null
222 deviance for each group. For models predicting individual species occurrence, an additional
223 measure of performance was the area under the receiver operator characteristic curve (AUC;
224 Hanley & McNeil 1982). AUC values estimate how well fitted values discriminate between
225 observed presences and absences, with values ranging from 0.5 (no better than random) to 1.0
226 (perfect discrimination). Here, models with AUC scores >0.8 are considered very good and
227 >0.9 excellent (following Hosmer and Lemeshow 2000). The relative importance of each
228 predictor variable was estimated using formulae developed by Friedman (2001) and script
229 within the R package 'gbm', based on the number of times a variable was selected for splits
230 and weighted by the squared improvement of the model and averaged over all trees
231 (Friedman & Meulman 2003). This was then scaled to 100, with higher numbers indicating
232 stronger influence on the response variable. Here, partial dependence plots (where all other
233 predictors are kept at their mean) are presented for the four most important predictors in
234 models where complexity predictors explain at least 40 % of the total variability in a taxon's
235 species richness or a species occurrence. Plots include 95 % confidence intervals for each
236 predictor determined from 100 bootstrap replicates using a function written by the authors.

237

238 **Results**

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

241 species (80 genera, 41 families) were recorded, with 104 fish species in Bonaire (60 genera,
 242 33 families), 86 fish species in Puerto Rico (51 genera, 28 families) and 105 fish species in
 243 SVG (64 genera, 37 families). Due to their low occurrence and diversity, flatworms (2
 244 species), antipatharians (1 species), and corallimorphs (2 species) were excluded from further
 245 individual analysis, while molluscs were excluded from analysis due to absence of some
 246 species-level data.

247

248 **Table 2** Number of identified species in each taxonomic group in rank order of abundance in
 249 total and in each country with percentage of grand total in parentheses. Total richness
 250 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)

251

252 *Importance of complexity to different taxa*

253 BRT predictive deviance was greatest for total richness (82.3 %), octocoral (81.7 %), coral
 254 (80.6 %), fish (77.3 %) and anemone species richness (57.9 %, Table 3). BRTs explained
 255 very little variability in annelid, arthropod or sponge richness (Table 3), and complexity
 256 predictors accounted for little of the variability in octocoral and anemone richness (Fig. 2).
 257 Reef complexity and number of large corals were in the top four predictors for fish, corals

258 and total richness (Fig. 3), but their relative importance varied (Fig. 2) and fitted functions
 259 were mostly non-linear and complex (Fig. 3).

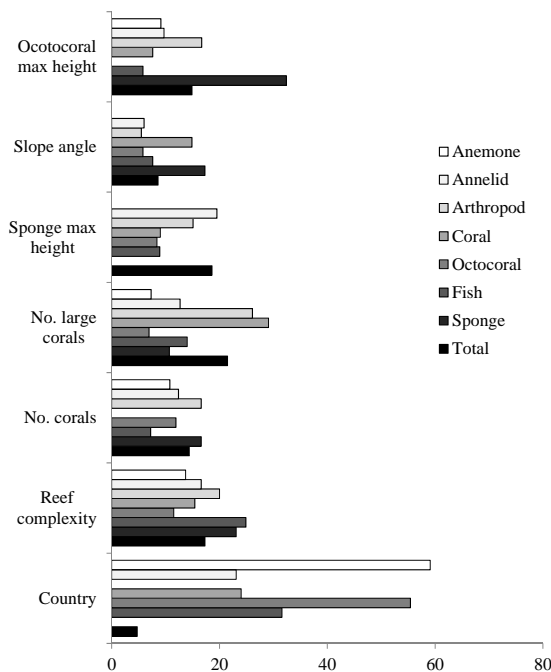


Figure 2 Relative influence (%) of complexity variables predicting richness of different taxa on Caribbean reefs. Total richness includes all listed taxa plus anemones, flatworms, antipatharians and corallimorphs (see Appendix S2 for full species list). Note ocotocoral and sponge height, and number of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

270 model.

271

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

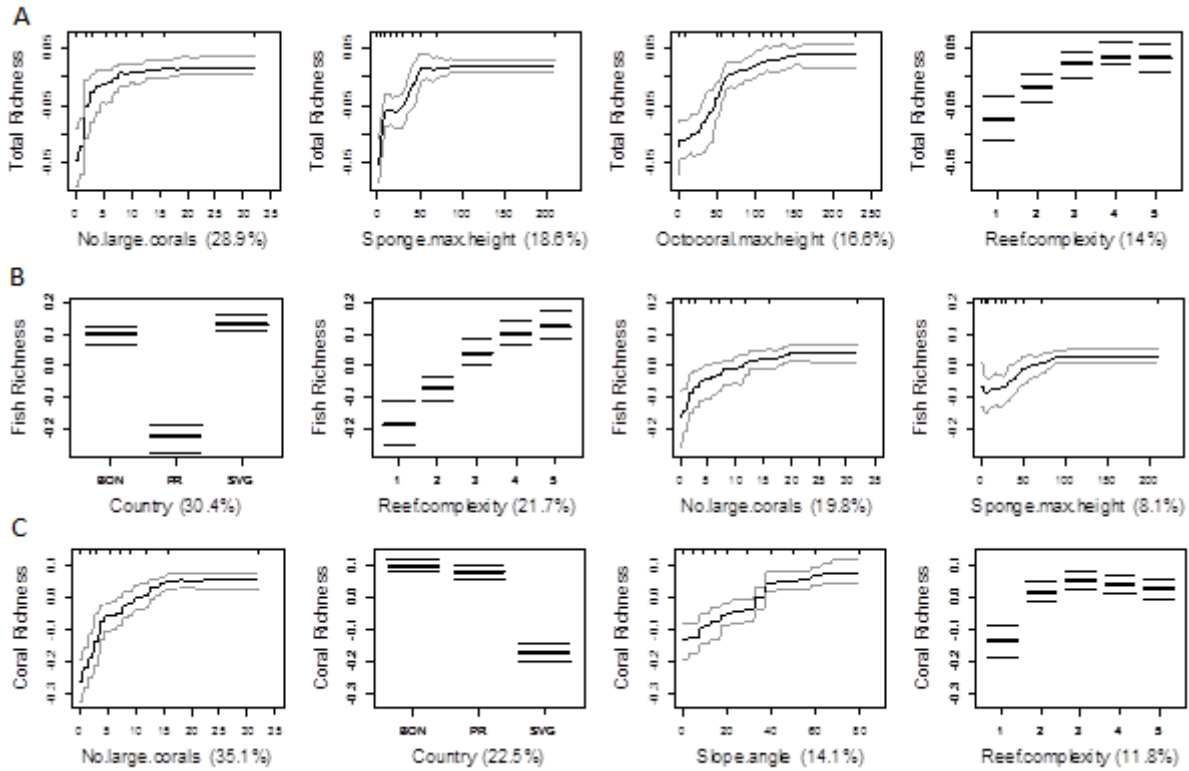
Taxonomic group	Learning rate	No. of trees	Model residual deviance	CV residual deviance (SE)	Total deviance (%)
Anemone	0.005	1000	0.35	0.43 (0.05)	57.9
Annelid	0.001	2150	0.49	0.58 (0.06)	29.6
Arthropod	0.001	1250	0.83	0.99 (0.06)	21.3
Coral	0.005	1450	0.27	0.43 (0.04)	80.6
Ocotocoral	0.005	2550	3.18	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

277

278

279



280

281

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

291

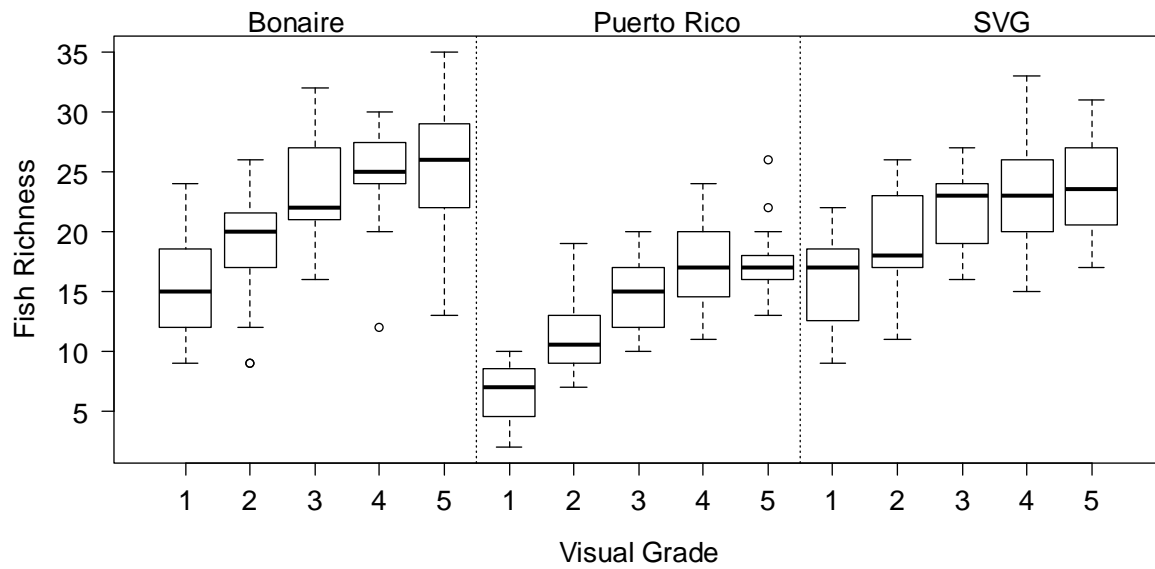
292 The model predicting total species richness explained the greatest variability (82.3 %) revealing the importance of habitat structural complexity to the total species richness of coral reef ecosystems in the Caribbean (Table 3). The fitted functions (Fig. 3a) reveal total species richness was greatest in plots with more than 10 large corals (per 25 m²) 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.

301

302 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).

316

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



320

321

322 *Species relationships*

323 *Coral species presence*

324 Presence of 23 of 51 coral species were modelled (45 %, see Table S1 for all species models),
325 with two species not modelled due to presence in over 95 % of surveyed plots (*Millepora*
326 *alcicornis* and *Porites asteroides*) while other non-modelled species were in less than 20 % of
327 plots. Models explained over 40 % of the total deviance in 19 coral species (Table 4) with
328 excellent performance (area under receiver operator characteristic curve, AUC score > 0.90;
329 Table S1). As a single predictor, country had the greatest relative importance across all coral
330 species (mean 35.6 %, range 7.0 – 66.6 %), but combined reef complexity and structural

331 components accounted for on average 64.4 % of the explained variance across all coral
 332 species (range: 33.4 – 93.0 %, Table 4).

333 **Table 4** Total deviance and percentage relative importance of reef complexity and structural
 334 components to coral species presence calculated using Boosted Regression Tree models (see
 335 Table S1 for model details). Only species modelled with total explained deviance >40% are
 336 reported. See Figure S1 for functions for all coral species modelled. Empty cells indicate non-
 337 significant variable dropped from model.

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

338

339 Reef complexity was retained as a significant predictor for 17 coral species (Table 4) and had
 340 the greatest relative importance of all the complexity predictors across all species modelled

341 (average 17.7 %). The importance of reef complexity varied with coral species, and was the
342 most important complexity predictor for the presence of *Orbicella faveolata* (53.7 %),
343 *Agaricia agaricites* (36.9 %), *Orbicella annularis* (29.7 %), and *Porites furcata* (23.1 %),
344 which contribute greatly to complexity on Caribbean coral reefs. Relationships between coral
345 species presence and reef complexity were highly variable in shape, and were frequently non-
346 linear (see Fig. S1 for the four most important functions for each coral species). Many coral
347 species showed dramatic declines in occurrence at low reef complexity levels (complexity
348 level one or two), with only two species showing greater occupancy at low complexities
349 (*Pseudodiploria strigosa* and *Porites divaricata*). Five coral species showed a peak in
350 occurrence at high complexity (*Agaricia lamarcki*, *Madracis auretenra*, *O. annularis*, *O.*
351 *faveolata*, *Scolymia cubensis*) although this only accounted for large amounts of predicted
352 deviance for *Orbicella* corals. Four coral species showed peaks at intermediate reef
353 complexity level three (*Colpophyllia natans*, *Montastraea cavernosa*, *O. franksi* and *P.*
354 *porites*; Fig. S1).

355

356 The number of large corals was the second most important complexity predictor averaged
357 across all modelled species (17.3 %), but was retained in models for only 11 of the 19 species
358 (Table 4). The number of large corals was the most important predictor of *Madracis*
359 *auretenra* (39.8 %), *Orbicella franksi* (37.2 %) and *O. annularis* (26.5 %, Table 4). Octocoral
360 maximum height was the only complexity predictor retained in all coral species models,
361 although on average the relative influence (15.7 %) was lower than that of reef complexity
362 and the number of large corals. The relationship between coral occurrence and octocoral
363 maximum height varied with species, with occurrence of seven species showing a clear
364 increase (*A. agaricites*, *C. natans*, *Eusimilia fastigiata*, *O. faveolata*, *P. divaricata*, *P. furcata*,

365 *P. strigosa*) and three species decreasing with increasing maximum octocoral height (*A.*
366 *lamarcki*, *O. annularis*, *O. franksii*; see Fig. S1).

367

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

373

374 *Fish species presence*

375 Presence of 54 of the 143 fish species identified were modelled with respect to reef
376 complexity (38 %, see Table S2), with all other species not modelled due to low occurrence
377 (observed in less than 20 % of plots). Models explained over 40 % of the total deviance for
378 28 fish species (Table 5), and performance was generally excellent with no species model
379 AUC score < 0.80 and AUC scores > 0.90 for 40 fish species (74 % of modelled fish species,
380 Table S2). As a single predictor, country had the greatest relative importance across all coral
381 species (mean 31.8 %, range 0 – 79.7 %), but combined reef complexity and structural
382 components accounted for on average 68.2 % of the explained variance across all coral
383 species (range: 20.3 – 100 %, Table 5). Variability in fish species richness with complexity
384 may be driven by identity effects, revealed by individual species relationships.

385

386 The number of corals, maximum octocoral height and reef complexity were the most
387 commonly retained complexity predictors of individual fish species presence, with the
388 number of corals and number of large corals having on average the greatest relative influence
389 across all species (17.1 % each; Table 5). The number of corals had the greatest relative

390 influence on the occurrence of the wrasses *Halichoeres bivittatus* (slippery dick), *H.*
391 *maculipinna* (clown wrasse), *H. pictus* (rainbow wrasse) and *T. bifasciatum* (blueheaded
392 wrasse), the saddled blenny *Malacoctenus triangulatus* and the longfin damsel *Stegastes*
393 *diencaeus* (Table 5), with all species exhibiting negative relationships with increasing number
394 of corals (see Fig. S2 for the four most important functions for all modelled fish species).

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

Species	Total Deviance	Reef complexity	No. large corals	No. of corals	Sponge max height	Octocoral max height
<i>Cephalopholis cruentatus</i>	50.89	18.67	14.89	8.92	8.62	5.44
<i>Chromis cyanea</i>	57.08	4.88	30.58	10.60	6.86	4.45
<i>Chromis multilineata</i>	46.95		7.88	15.14	10.14	16.41
<i>Clepticus parrae</i>	43.97	20.81	18.33	17.22	11.56	13.48
<i>Coryphopterus dicrus</i>	47.12			14.21		11.29
<i>Coryphopterus eidolon</i>	69.85		6.63	12.26	11.88	
<i>Coryphopterus hyalinus</i>	58.37	9.75	9.02	7.58	7.01	6.74
<i>Coryphopterus lipernes</i>	64.70	3.03	40.44	13.17	7.64	4.15
<i>Gnatholepis thompsoni</i>	47.05	7.40	5.53	8.52	15.18	7.51
<i>Gobiosoma horsti</i>	54.25	12.02			34.82	16.07
<i>Gramma loreto</i>	66.34	25.14	20.63	7.25	11.16	
<i>Halichoeres bivittatus</i>	69.53	24.96		48.16	6.22	20.65
<i>Halichoeres garnoti</i>	50.74			7.97	12.34	
<i>Halichoeres maculipinna</i>	49.71	17.20		22.11		
<i>Halichoeres pictus</i>	55.24	3.75	9.88	22.22	12.38	30.05
<i>Malacoctenus boehlkei</i>	43.94	30.10				39.73
<i>Malacoctenus triangulatus</i>	53.96	20.16		36.22		22.33
<i>Mulloidichthys martinicus</i>	58.84	15.68	21.84		20.98	13.40
<i>Myripristis jacobus</i>	47.15	5.91	18.14	12.57	12.63	7.84
<i>Neoiphon marianus</i>	54.48		39.64	20.95		19.77
<i>Scarus taeniopterus</i>	50.37	11.00	9.64	17.75		6.57
<i>Sparisoma atomarium</i>	50.92	10.30	13.08	16.05	6.60	10.56
<i>Sparisoma viride</i>	43.28	17.86		19.77	7.78	43.71
<i>Stegastes adustus</i>	53.91	13.32	8.89	15.32	12.44	13.92
<i>Stegastes diencaeus</i>	45.20	16.41		29.47		24.35
<i>Stegastes partitus</i>	59.20	14.82		10.82	10.89	18.50
<i>Stegastes planifrons</i>	67.25	12.06	17.79	15.38	4.98	5.95
<i>Thalassoma bifasciatum</i>	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 *Pseudodiploria 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.

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Data Accessibility

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

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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

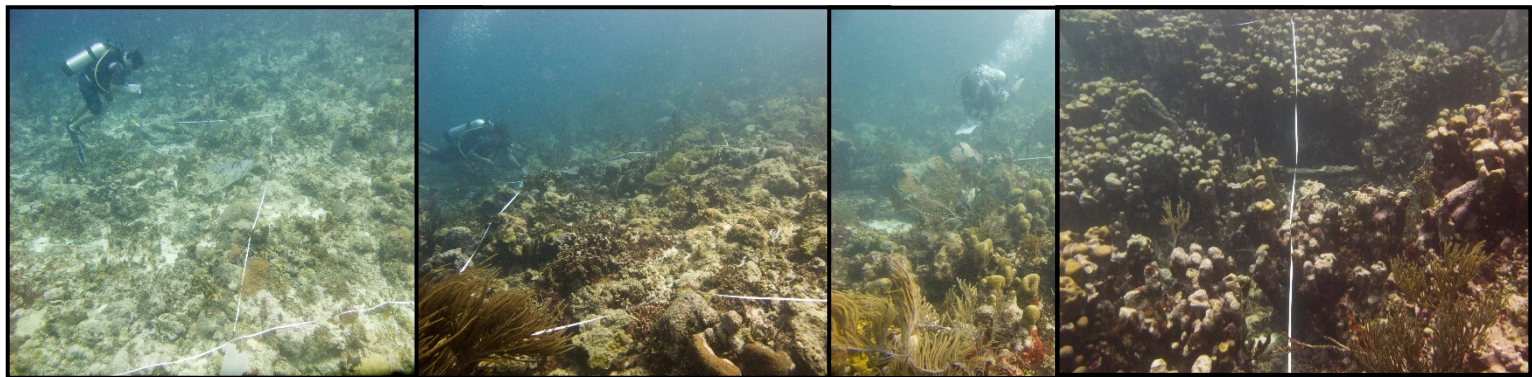
operator character curve) provide a discrimination of probabilities between presence and absence samples, with values >0.8 considered here very good and >0.9 excellent.

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 complex with numerous fine-scale features

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

Anemone species list

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

Annelid species list

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

Arthropod species list

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

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

Coral species list

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

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

Echinoderm species list

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

Flatworm species list

Species	Common Name
Black and white flatworm	Black and white flatworm
<i>Pseudoceros pardalis</i>	Leopard Flatworm

Octocoral species list

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

Sponge species list

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

<i>Ectyoplasia ferox</i>	<i>Xestospongia muta</i>
<i>Erylus bahamensis</i>	

Fish species list

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

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

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

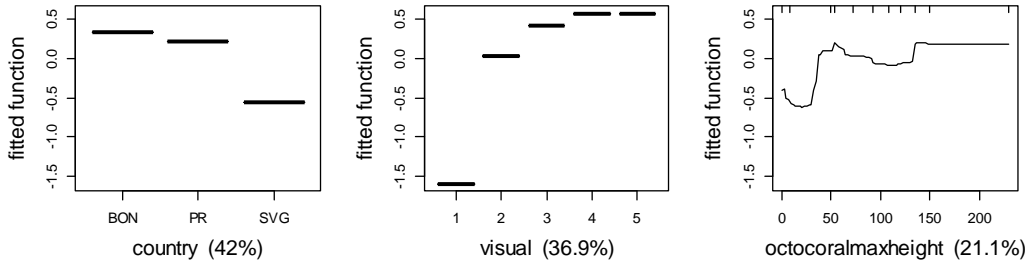
<i>Sparisoma viride</i>	Stoplight parrotfish
<i>Sphyraena barracuda</i>	Great barracuda
<i>Stegastes adustus</i>	Dusky damselfish
<i>Stegastes diencaeus</i>	Longfin damselfish
<i>Stegastes leucostictus</i>	Beaugregory
<i>Stegastes partitus</i>	Bicolor damselfish
<i>Stegastes planifrons</i>	Threespot damsel
<i>Stegastes variabilis</i>	Cocoa damselfish
<i>Synodus intermedius</i>	Sand diver
<i>Synodus saurus</i>	Bluestriped lizardfish
<i>Thalassoma bifasciatum</i>	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.

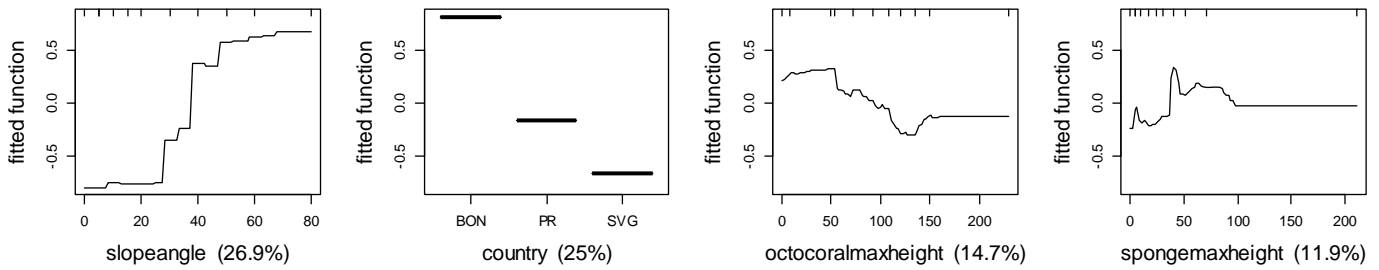
Species	Freq of occurrence	Learning rate	No. of trees	Model				
				residual deviance	CV residual deviance \pm SE	% Total Deviance	AUC score	CV AUC score (SE)
<i>Agaricia agaricites</i>	90.67	0.003	700	0.34	0.40 (0.05)	45.98	0.92	0.85 (0.05)
<i>Agaricia fragilis</i>	16.67	0.003	800	0.63	0.76 (0.06)	30.29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

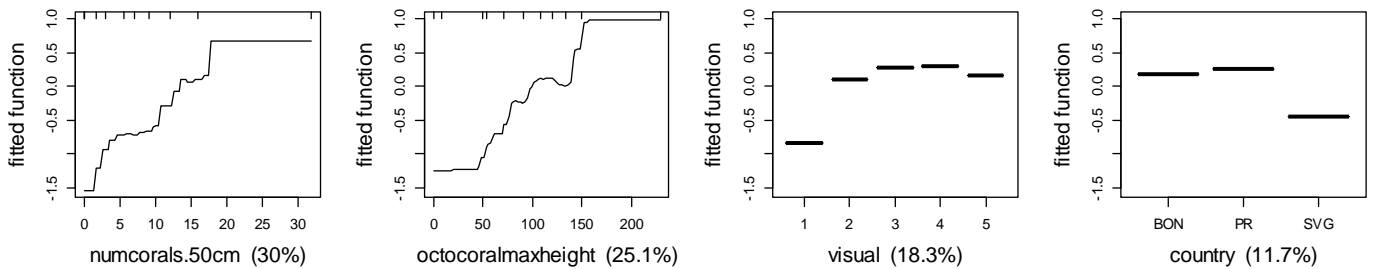
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agaricites*



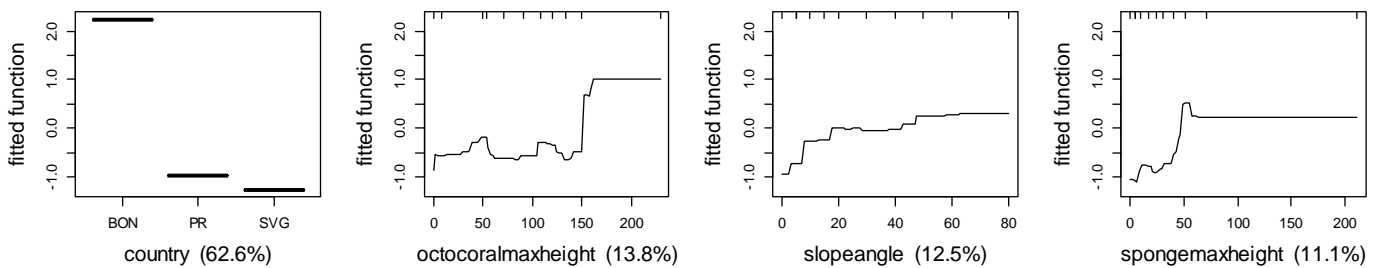
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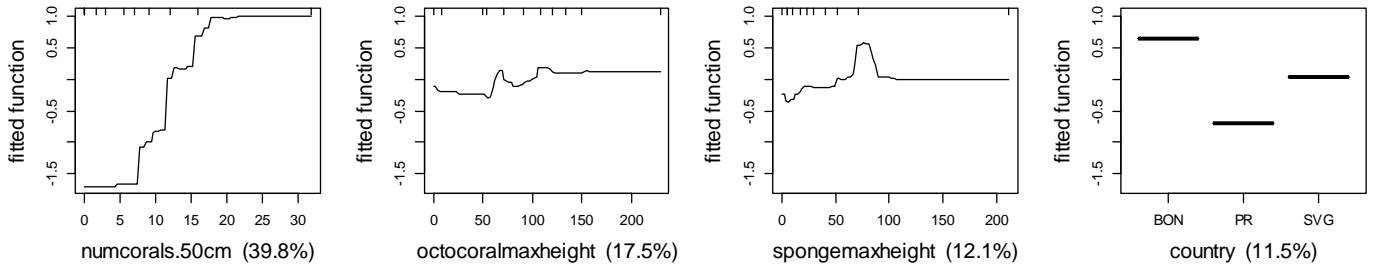
*Colpophyllia
natans*



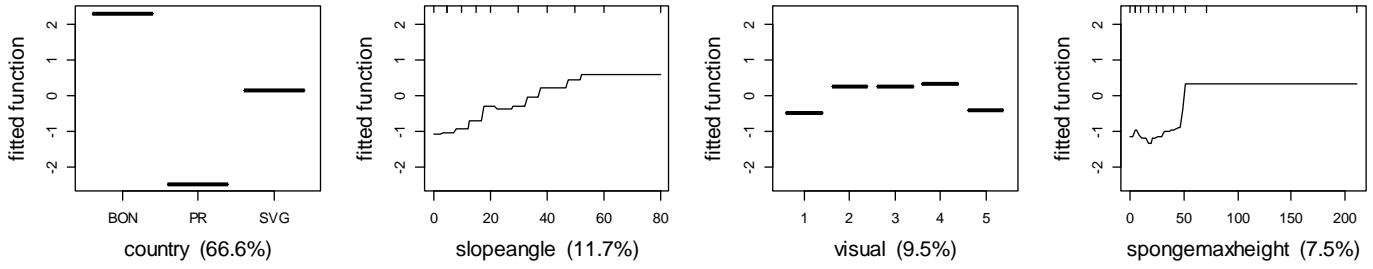
*Eusmilia
fastigiata*



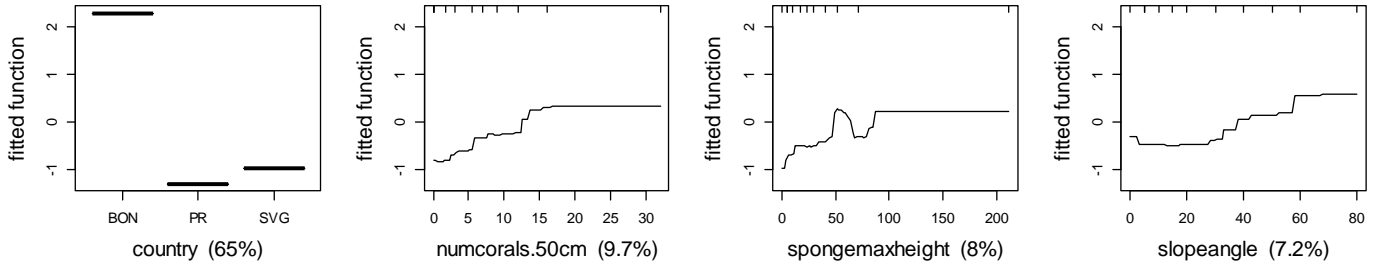
*Madracis
auretenra*



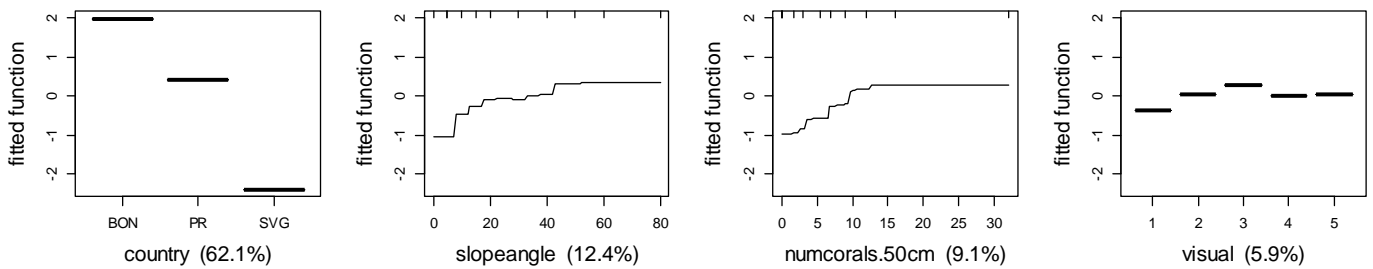
Madracis decactis



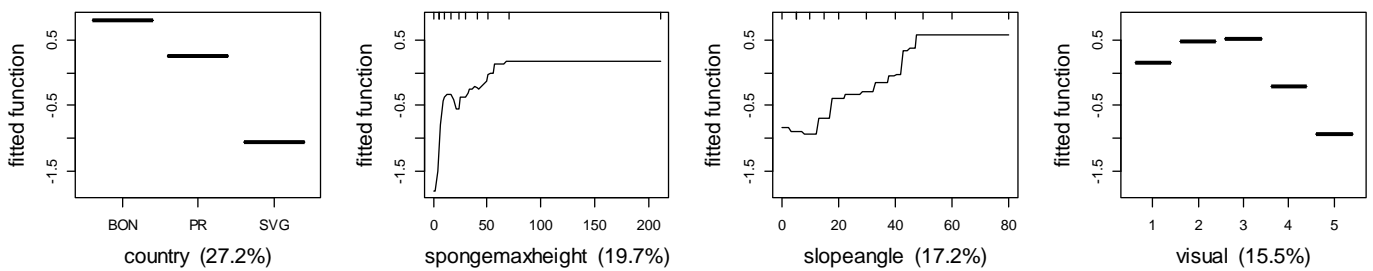
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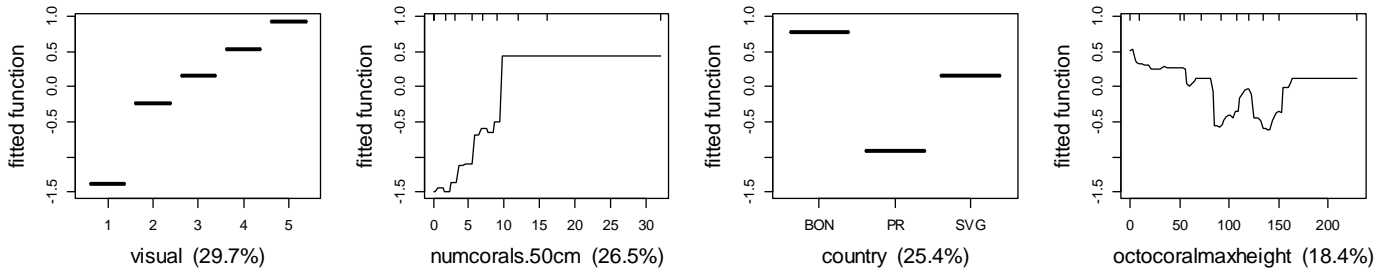
Meandrina memorialis



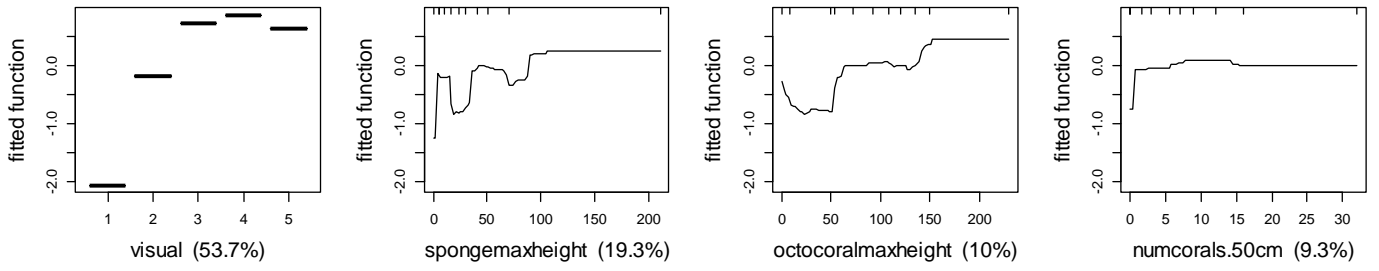
Montastraea cavernosa



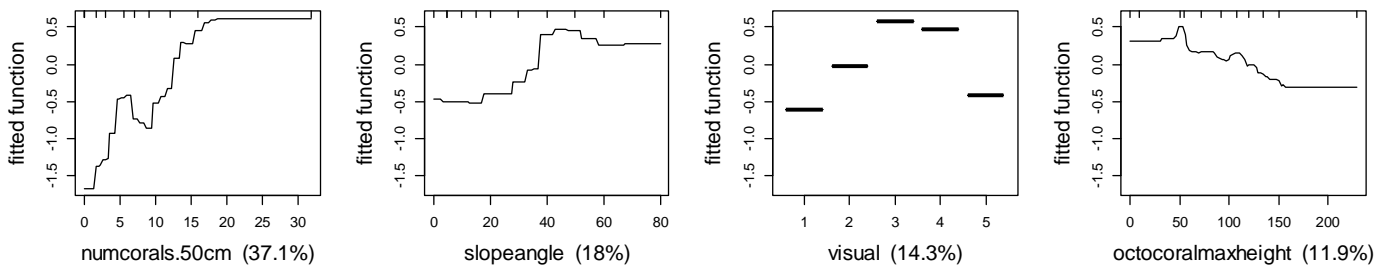
Orbicella annularis



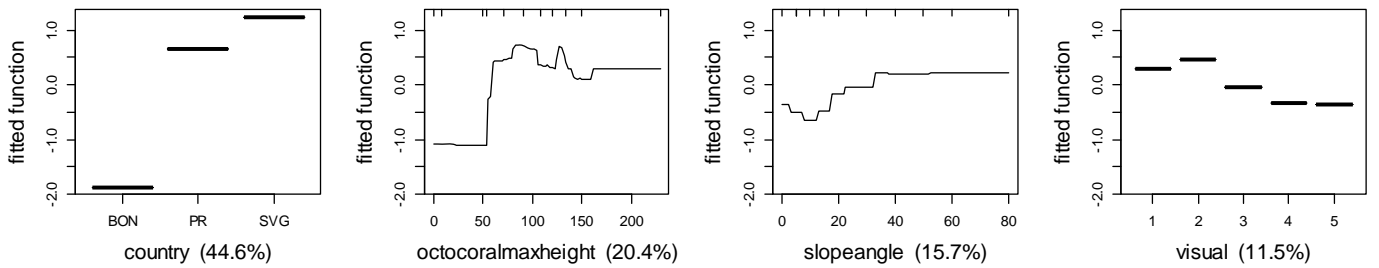
Orbicella faveolata



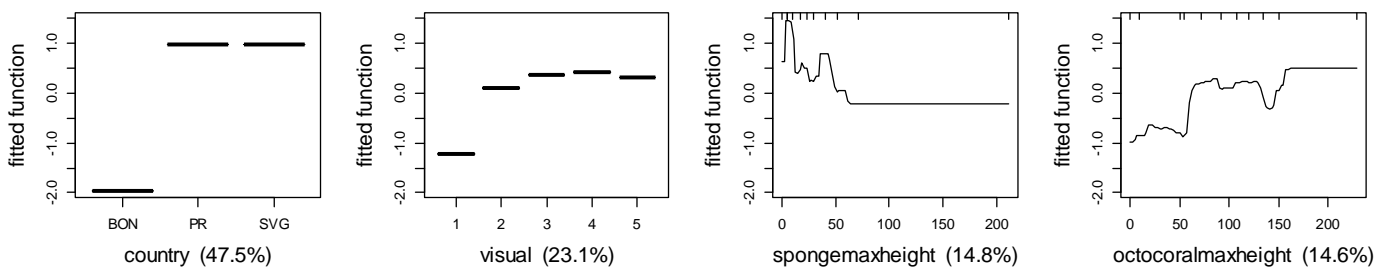
Orbicella franksi



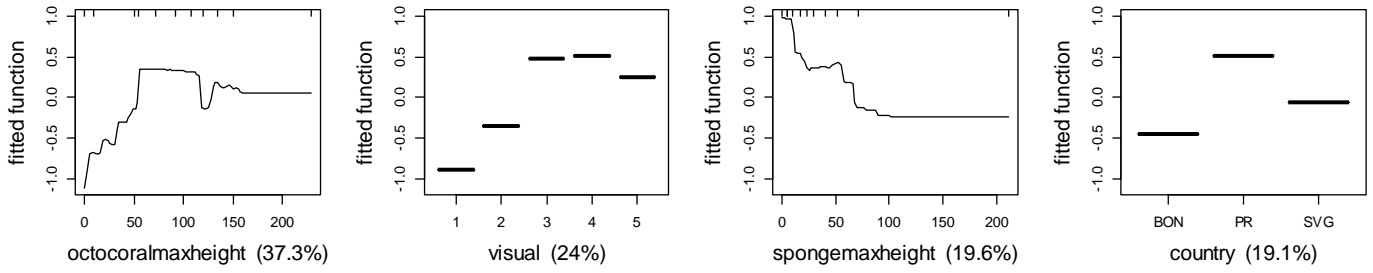
Porites divaricata



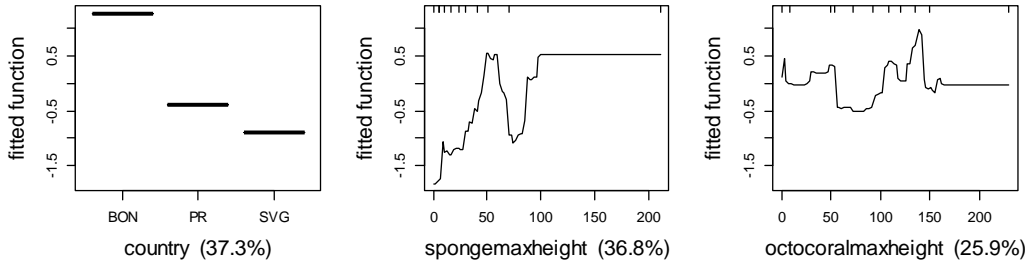
Porites furcata



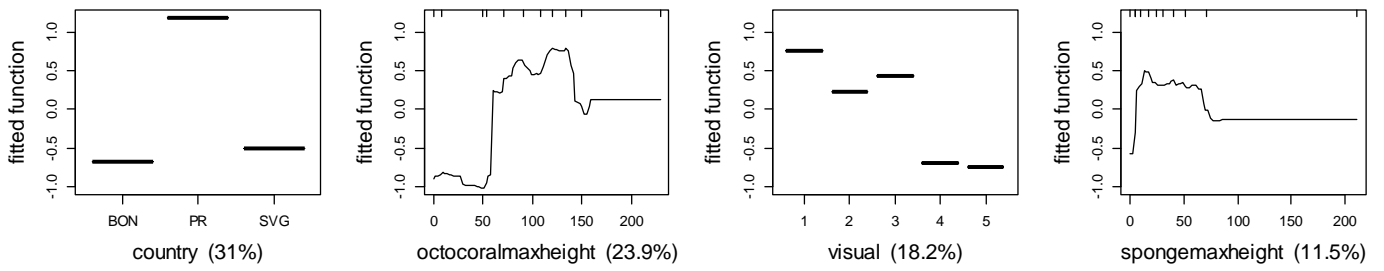
Porites porites



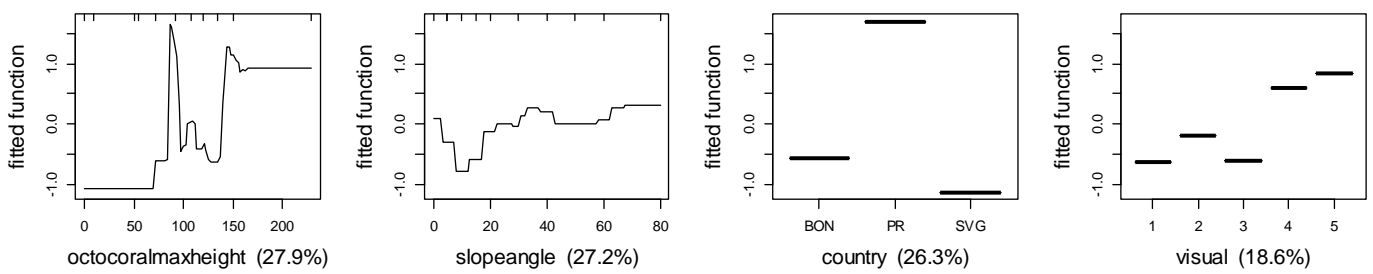
Pseudodiploria labyrinthiformis



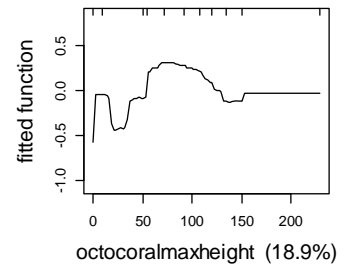
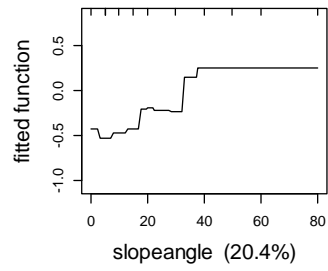
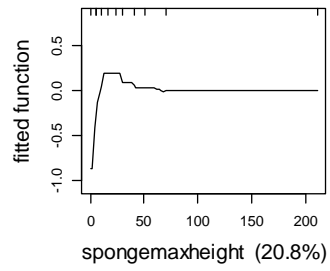
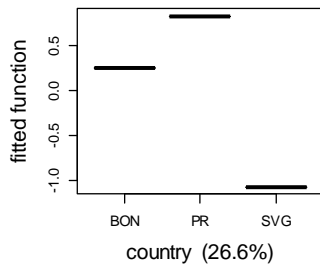
Pseudodiploria strigosa



Scolymia cubensis



Siderastrea siderea



Stephanocoenia intersepta

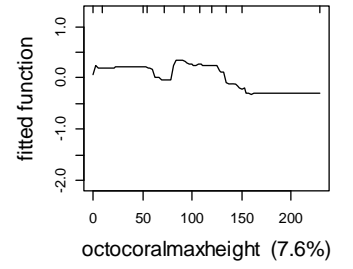
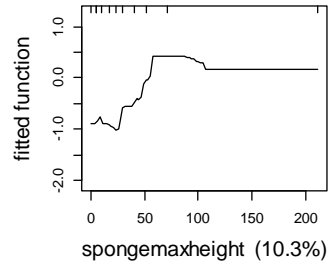
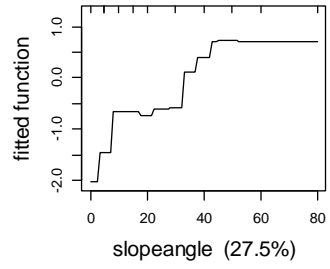
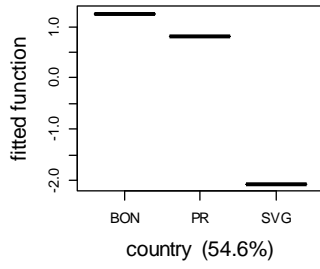


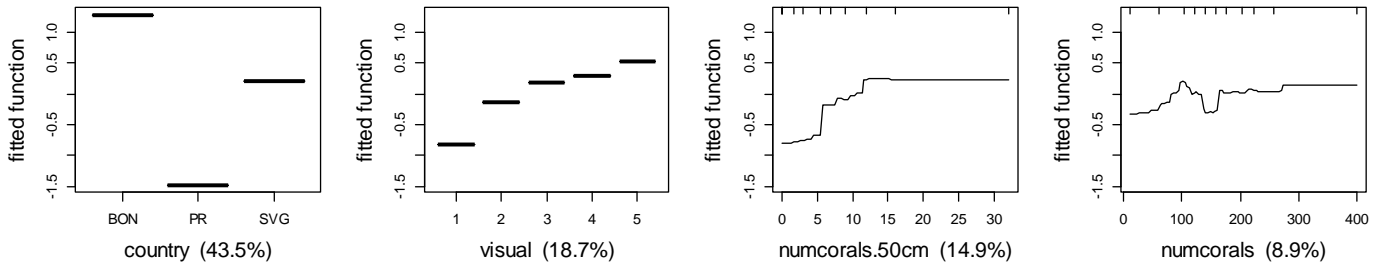
Table S2. Predictive performance of boosted regression tree (BRT) models relating coral fish species presence to reef complexity and location. Table variables indicate the frequency of occurrence (percentage of 300 plots a species was present in), model learning rate, optimum number of trees fitted with 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)
<i>Abudefduf saxatilis</i>	14.33	0.003	650	0.53	0.66 (0.04)	35.94	0.91	0.81 (0.04)
<i>Acanthemblemaria aspera</i>	10.67	0.003	1100	0.45	0.55 (0.04)	34.39	0.91	0.83 (0.03)
<i>Acanthemblemaria maria</i>	60.00	0.003	1500	0.84	1.09 (0.04)	37.58	0.91	0.78 (0.02)
<i>Acanthurus bahianus</i>	21.33	0.003	400	0.89	1.01(0.02)	14.30	0.82	0.64 (0.04)
<i>Acanthurus coeruleus</i>	31.33	0.003	950	0.91	1.11 (0.02)	26.65	0.87	0.73 (0.01)
<i>Bodianus rufus</i>	8.00	0.003	400	0.39	0.49 (0.02)	30.18	0.93	0.80 (0.03)
<i>Canthigaster rostrata</i>	72.00	0.003	1000	0.73	0.92 (0.04)	38.48	0.91	0.81 (0.02)
<i>Cephalopholis cruentatus</i>	50.00	0.003	1350	0.68	0.91 (0.06)	50.89	0.94	0.87 (0.02)
<i>Chaetodon capistratus</i>	20.00	0.003	350	0.85	0.94 (0.02)	15.04	0.83	0.68 (0.03)
<i>Chromis cyanea</i>	28.33	0.003	1450	0.51	0.74 (0.09)	57.08	0.96	0.88 (0.04)
<i>Chromis multilineata</i>	46.67	0.003	1600	0.73	1.01 (0.06)	46.95	0.93	0.82 (0.03)
<i>Clepticus parrae</i>	17.67	0.003	1200	0.52	0.73 (0.05)	43.97	0.94	0.81 (0.03)
<i>Coryphopterus dicrus</i>	62.00	0.003	1350	0.70	0.87 (0.05)	47.12	0.93	0.87 (0.02)
<i>Coryphopterus eidolon</i>	34.67	0.003	1550	0.39	0.58 (0.05)	69.85	0.97	0.93 (0.01)
<i>Coryphopterus glaucofraenum</i>	46.33	0.003	850	0.95	1.09 (0.05)	31.01	0.87	0.80 (0.03)
<i>Coryphopterus hyalinus</i>	46.33	0.003	1300	0.57	0.76 (0.05)	58.37	0.96	0.92 (0.01)
<i>Coryphopterus lipernes</i>	25.67	0.003	1400	0.40	0.59 (0.08)	64.70	0.97	0.92 (0.02)
<i>Equetus punctatus</i>	7.00	0.003	250	0.44	0.49 (0.02)	14.22	0.86	0.70 (0.06)
<i>Gnatholepis thompsoni</i>	42.67	0.003	1350	0.72	0.95 (0.05)	47.05	0.93	0.84 (0.02)
<i>Gobiosoma dilepis</i>	12.67	0.003	850	0.53	0.65 (0.03)	29.91	0.89	0.76 (0.05)
<i>Gobiosoma evelynae</i>	48.33	0.003	850	1.02	1.21 (0.06)	26.24	0.86	0.73 (0.04)
<i>Gobiosoma horsti</i>	10.33	0.003	650	0.30	0.43 (0.03)	54.25	0.97	0.92 (0.02)

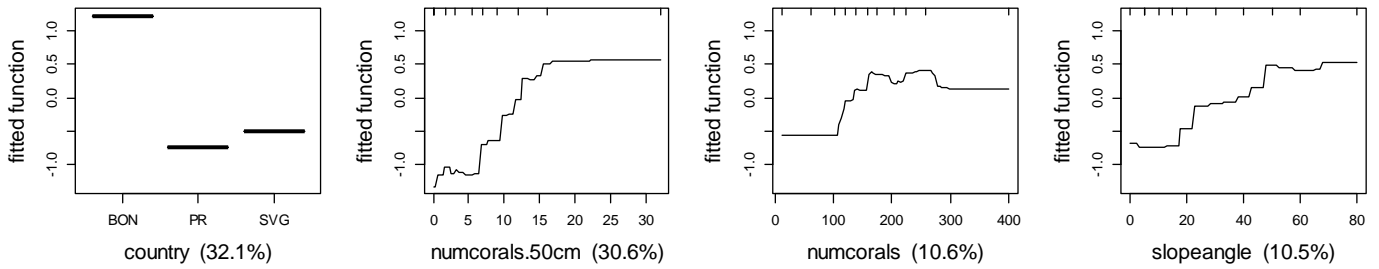
<i>Gramma loreto</i>	34.33	0.003	1600	0.43	0.65 (0.07)	66.34	0.98	0.93 (0.01)
<i>Gymnothorax moringa</i>	9.00	0.003	500	0.46	0.58 (0.03)	24.55	0.90	0.70 (0.03)
<i>Haemulon flavolineatum</i>	29.67	0.003	700	0.94	1.10 (0.03)	22.79	0.85	0.72 (0.03)
<i>Halichoeres bivittatus</i>	13.00	0.003	1050	0.24	0.38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

1 Figure S2. Fitted functions for the four most important predictor variables relating presence of fish
 2 species to complexity and location calculated using Boosted Regression Tree models (see Tables S3
 3 and S4 for model details). Plots are presented for models with a percentage total deviance explained
 4 >40 %. Less than four plots for a species is due to non-significant variables dropped from the model.
 5 Note predictor names are as Table 1, “visual” stands for visually estimated ‘reef complexity’.

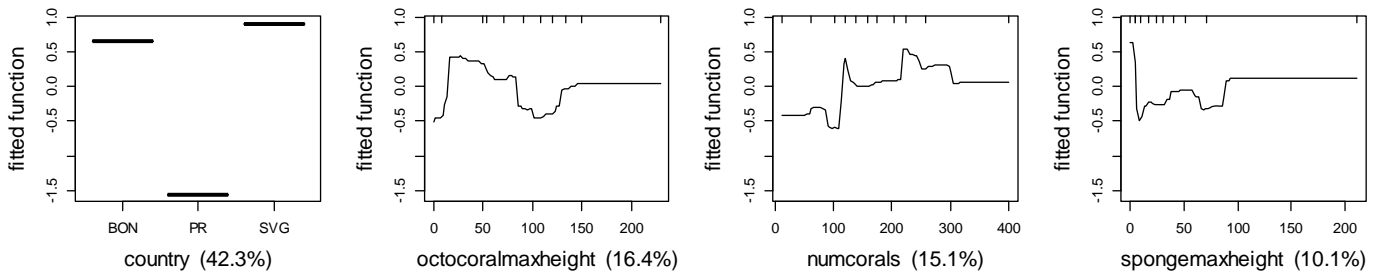
6 *Cephalopholis*
 7 *cruentatus*



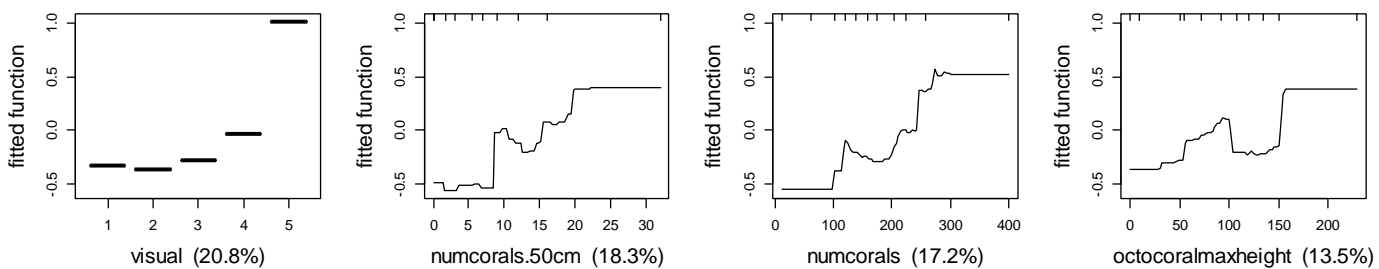
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 9 *Chromis*
 10 *cyanea*



11
 12 *Chromis*
 13 *multilineata*



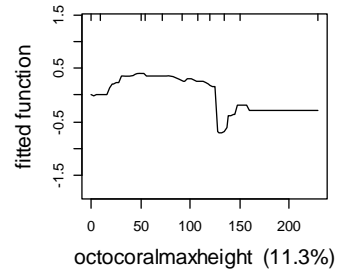
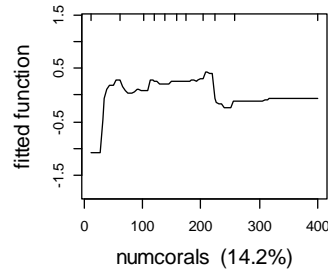
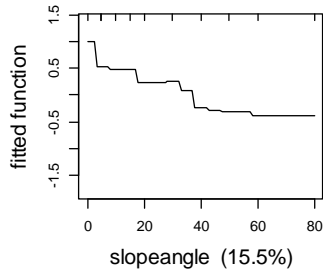
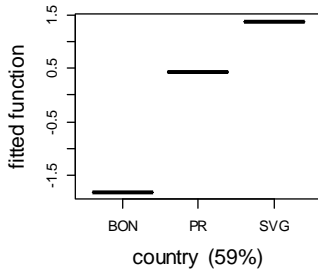
14
 15 *Clepticus*
 16 *parrae*



17

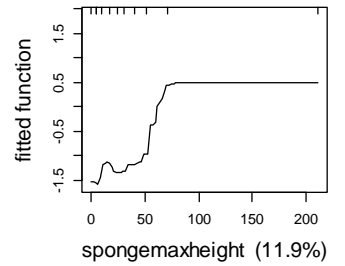
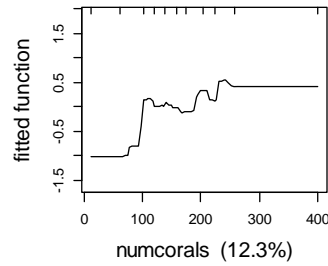
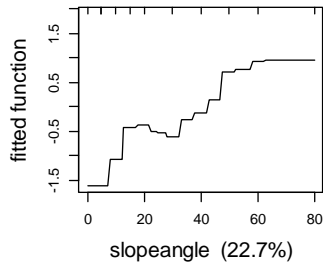
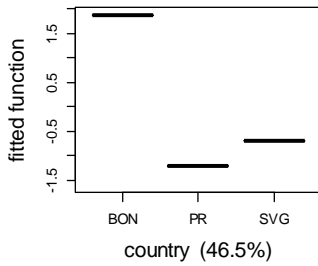
18 *Coryphopterus*

19 *dicrus*



20 *Coryphopterus*

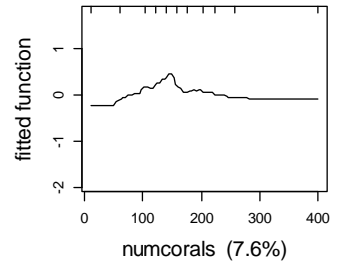
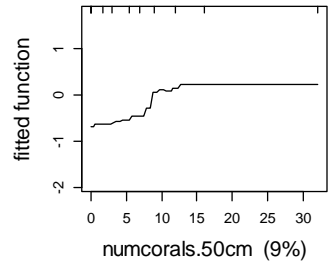
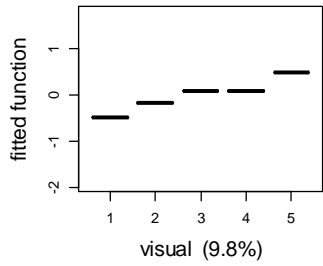
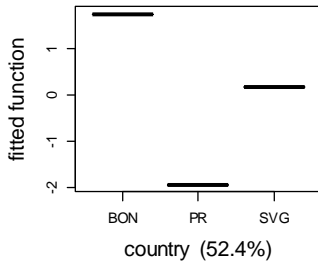
21 *eidolon*



23

24 *Coryphopterus*

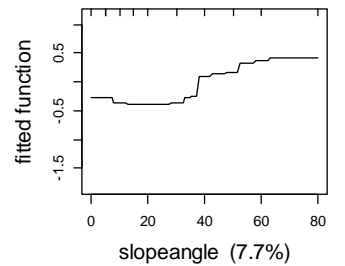
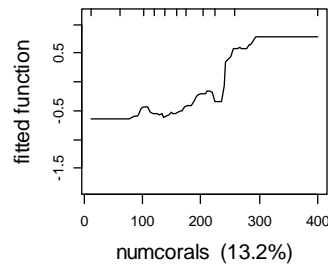
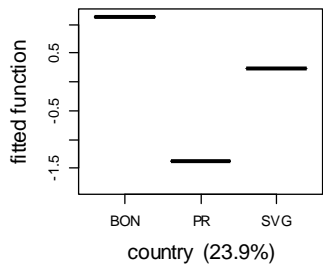
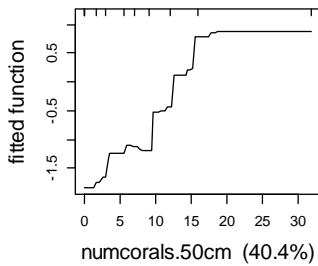
25 *hyalinus*



26 *Coryphopterus*

27 *lipernes*

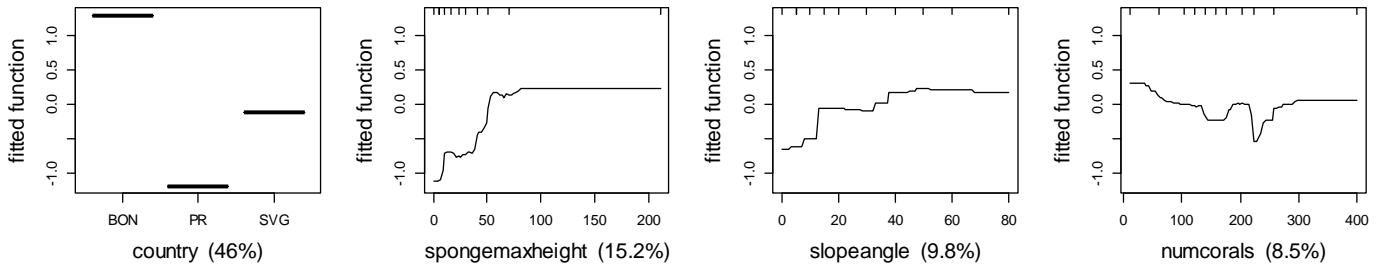
28 *lipernes*



29 *Gnatholepis*

30 *Gnatholepis*

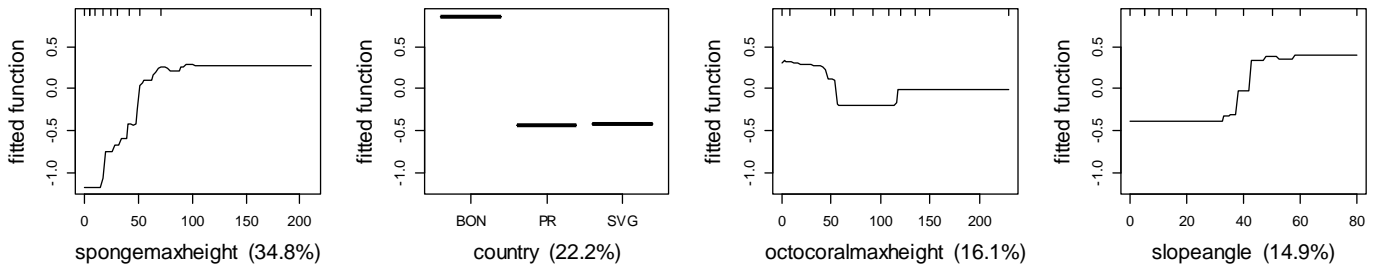
31 *thompsoni*



32

33 *Gobiosoma*

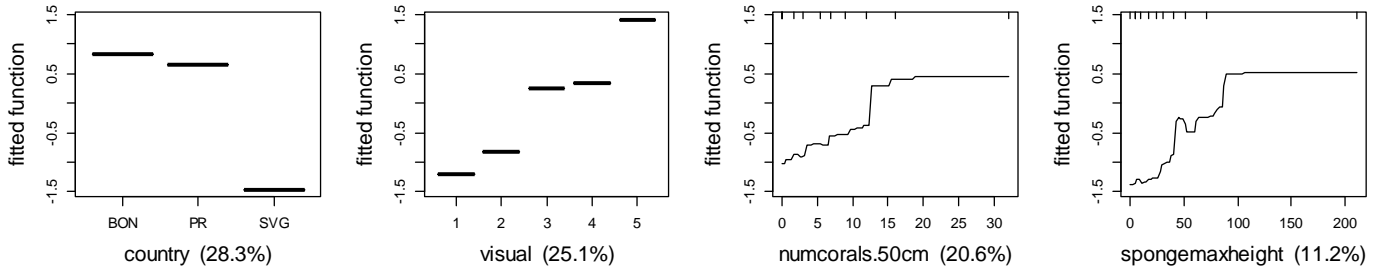
34 *horsti*



35

36 *Gramma*

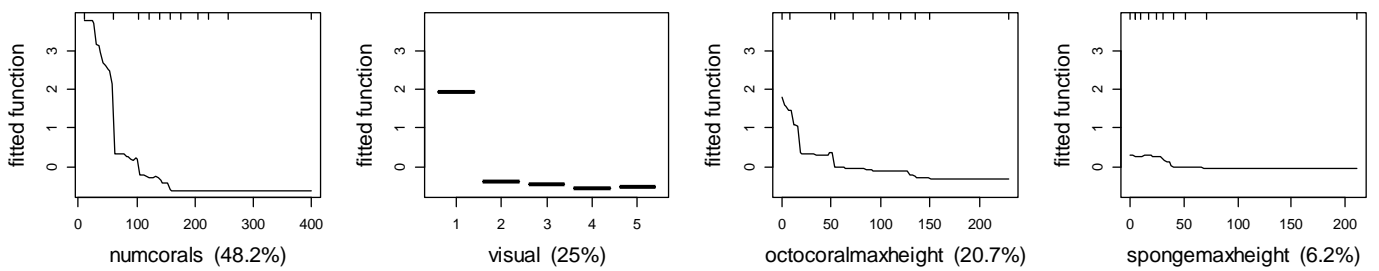
37 *loreto*



38

39 *Halichoeres*

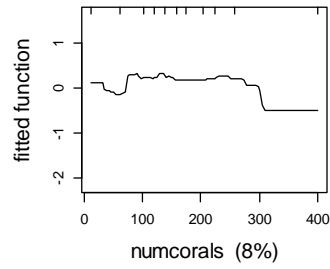
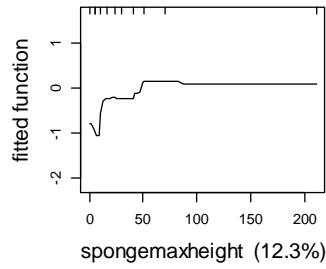
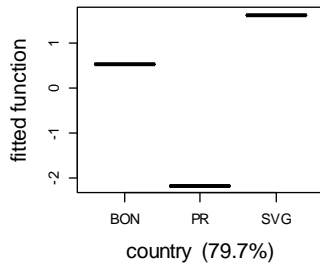
40 *bivitattus*



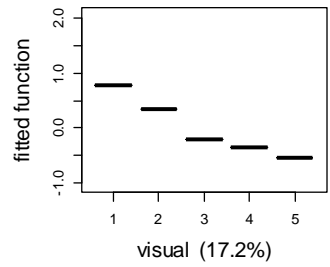
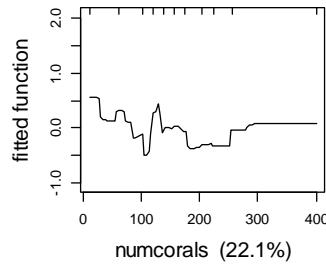
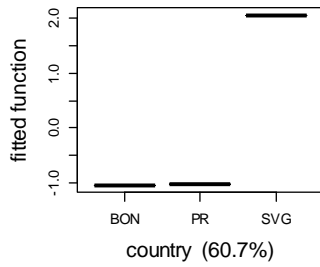
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42 *Halichoeres*

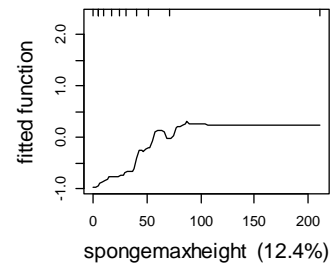
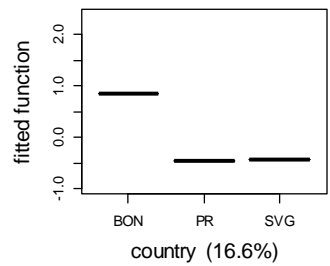
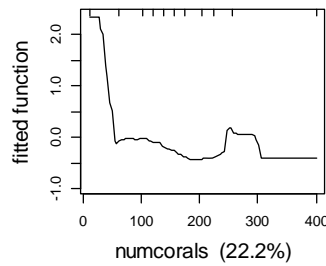
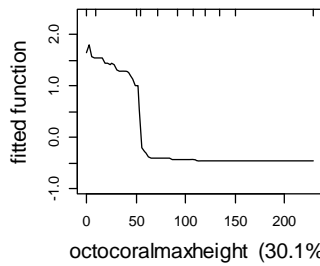
43 *garnoti*



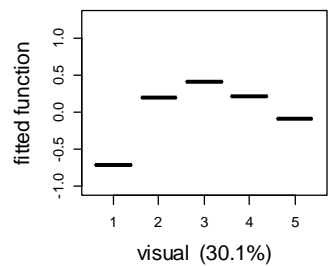
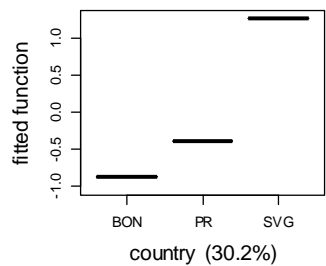
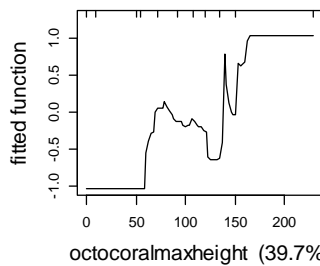
44
45 *Halichoeres*
46 *maculipinna*



47
48 *Halichoeres*
49 *pictus*

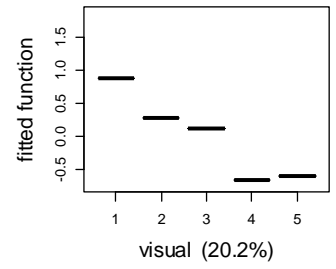
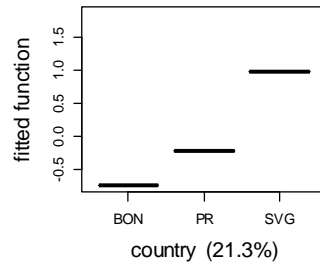
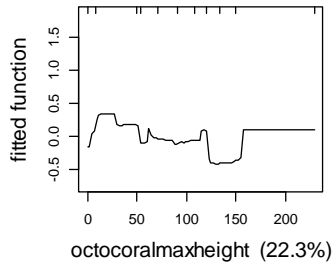
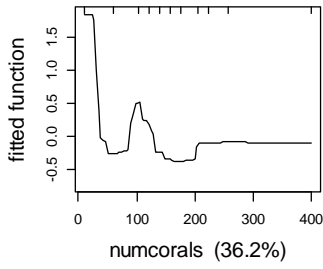


50
51 *Malacoctenus*
52 *boehlkei*



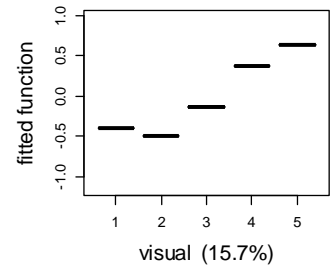
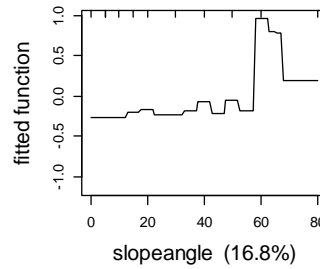
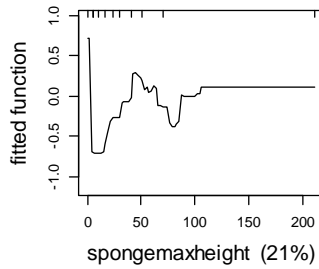
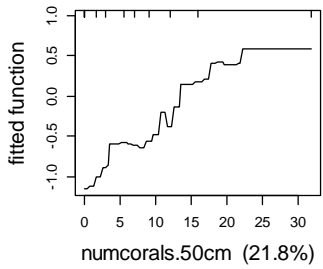
53
54 *Malacoctenus*

55 *triangulatus*



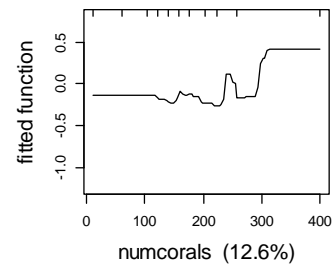
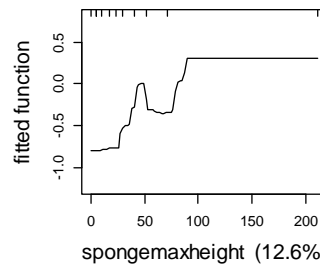
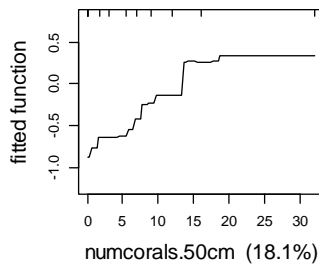
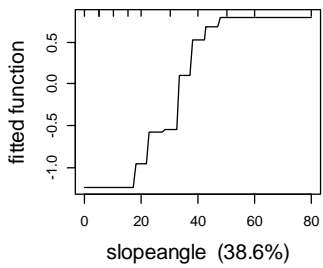
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57 *Mulloidichthys martinicus*



58

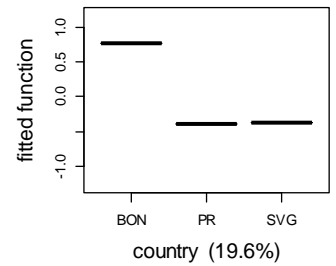
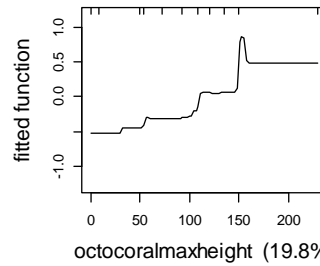
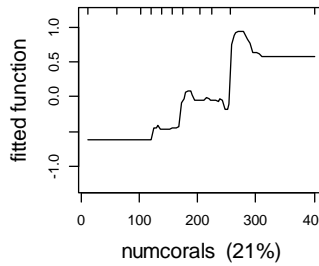
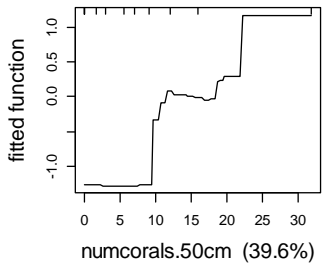
59 *Myripristis jacobus*



60

61 *Neoiphon*

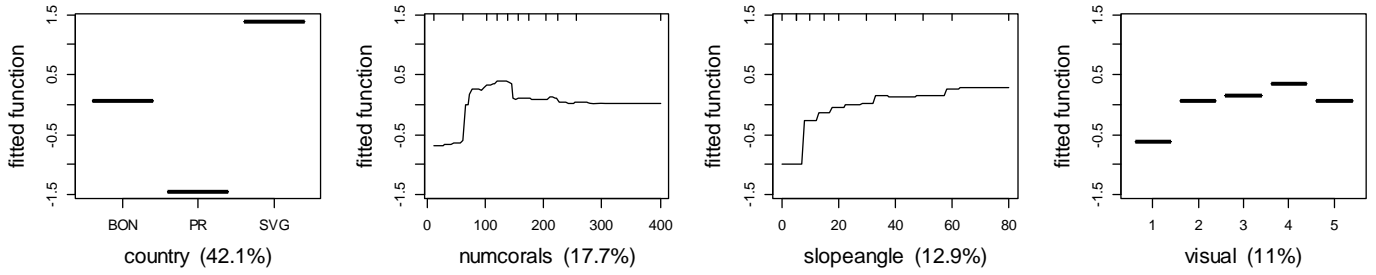
62 *marianus*



63

64 *Scarus*

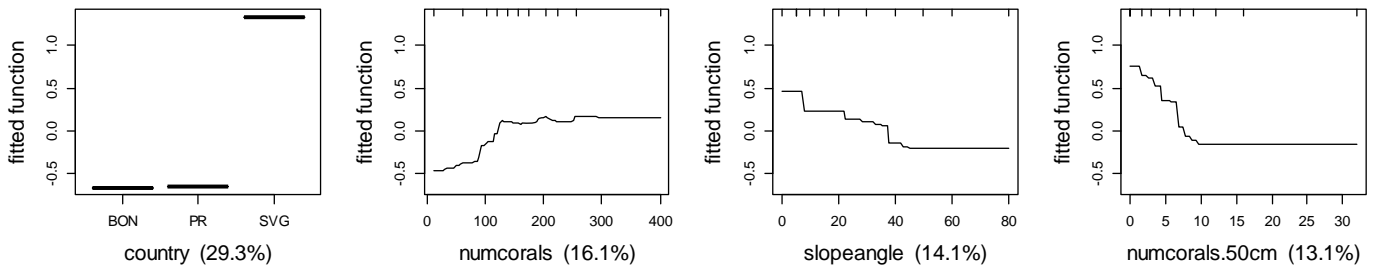
65 *taeniopterus*



66

67 *Sparisoma*

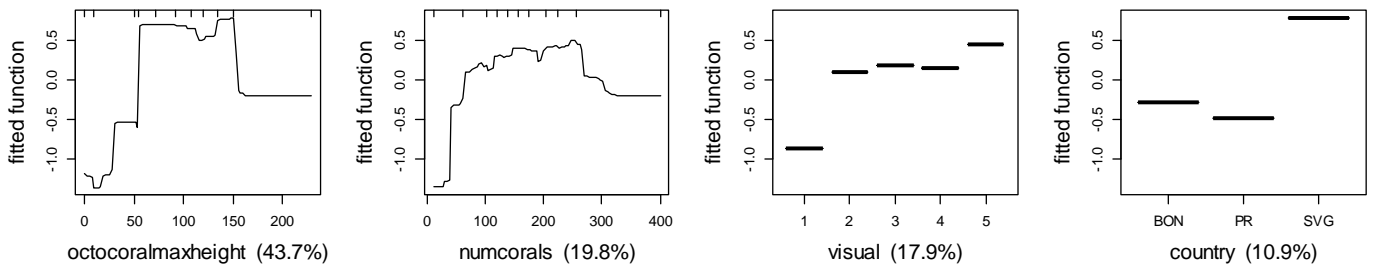
68 *atomarium*



69

70 *Sparisoma*

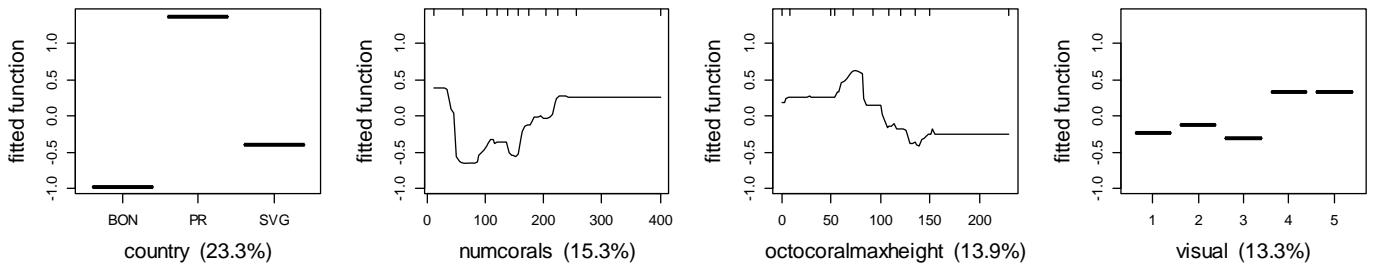
71 *viride*



72

73 *Stegastes*

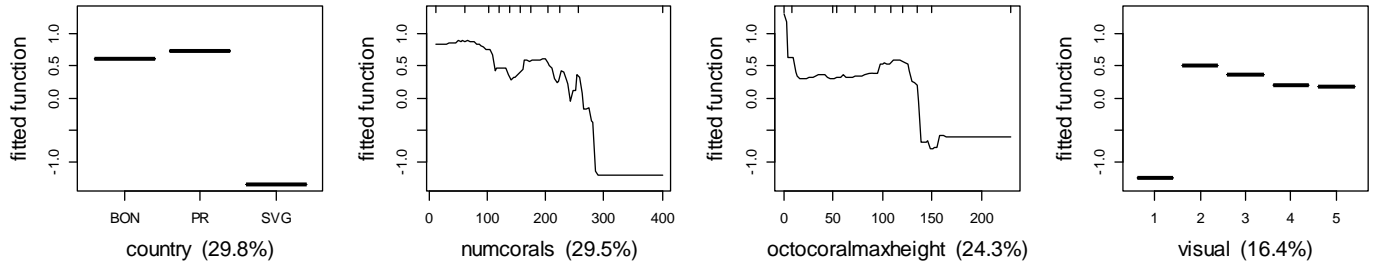
74 *adustus*



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76 *Stegastes*

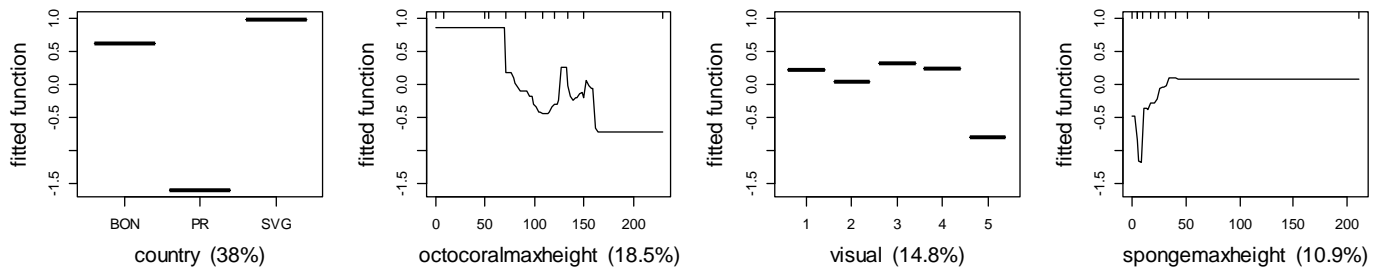
77 *diencaeus*



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79 *Stegastes*

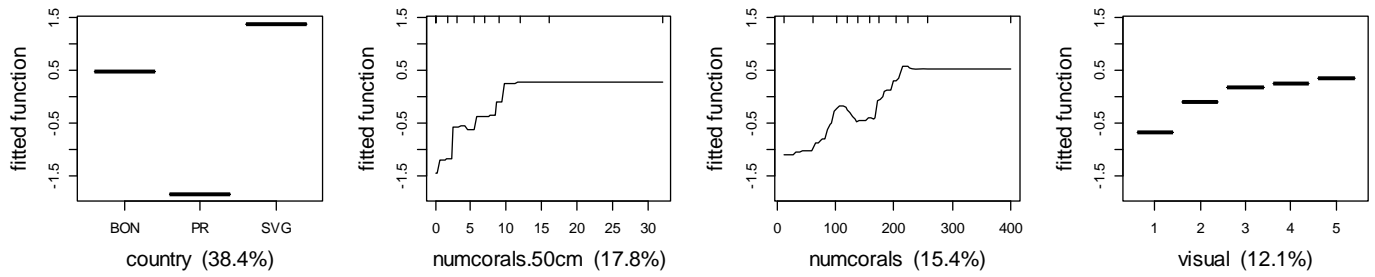
80 *partitus*



81

82 *Stegastes*

83 *planifrons*



84

85 *Thalassoma bifasciatum*

86