Title:

Structural complexity mediates functional structure of reef fish assemblages among coral habitats

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Abstract

Coral community composition varies considerably due to both environmental conditions and disturbance histories. However, the extent to which coral composition influences associated fish assemblages remains largely unknown. Here an ecological trait-based ordination analysis was used to compare functional richness (range of unique trait combinations), functional evenness (weighted distribution of fishes with shared traits), and functional divergence (proportion of total abundance supported by species with traits on the periphery of functional space) of fish assemblages among six distinct coral habitats. . Despite no significant variation in species richness among habitats, there were differences in the functional richness and functional divergence, but not functional evenness, of fish assemblages among habitats. Structural complexity of coral assemblages was the best predictor of the differences in functional richness and divergence among habitats. Functional richness of fish assemblages was highest in branching *Porites* habitats, lowest in *Pocillopora* and soft coral habitats, and intermediate in massive *Porites*, staghorn *Acropora*, and mixed coral habitats. Massive and branching *Porites* habitats displayed greater functional divergence in fish assemblages than the *Pocillopora* habitat, whilst the remaining habitats were intermediate. Differences in functional richness and divergence were largely driven by the presence of small schooling planktivores in the massive and branching *Porites* habitats. These results indicate that differential structural complexity among coral communities may act as an environmental filter, affecting the distribution and abundance of associated species traits, particularly those of small-bodied schooling fishes.

Keywords

coral composition; fish assemblage structure; functional diversity; traits; environmental filtering

Introduction

Scleractinian corals are foundation species on coral reefs, providing important microhabitats and food to a diverse range of reef fishes (reviewed in Coker et al. 2014). Most coral reef fish are associated with the physical structure created by live corals, evidenced by well-established positive correlations between local fish diversity, abundance, and biomass with reef-scale architectural complexity (Graham and Nash 2013). Broad scale loss of coral cover can cause concomitant declines in fish abundance and biomass (Wilson et al. 2006), diversity (Sano et al. 1984), shifts in body-size distributions (Rogers et al. 2014), trophic structure, and loss of specialist species (Bellwood et al. 2006a; Wilson et al. 2008; Pratchett et al. 2011; Alvarez-Filip et al. 2015). Such marked reductions in coral cover at both local and regional scales have been well documented (Gardner et al. 2003; Bruno and Selig 2007) as a result of anthropogenic stressors such as overfishing, pollution, and sedimentation, compounded by climate change. Despite concerns for comprehensive and widespread mortality of reef-building corals (Hoegh-Guldberg et al. 2007; Veron et al. 2009), it appears likely that many reefs will persist into the future, albeit with an altered composition (Riegl and Purkis 2009; Pandolfi et al. 2011). Increasing evidence suggests that differential vulnerability of coral species to a range of stressors, and variation in recovery potential is leading to shifts in species dominance towards taxa with stress-tolerant and/or weedy life-histories (Darling et al. 2013; Graham et al. 2014; Aronson et al. 2004; van Woesik et al. 2011; Bento et al. 2015). Whilst coral communities vary with natural biotic and abiotic factors (Hughes et al. 2012; Williams et al. 2013), predictions of further community shifts associated with anthropogenic disturbance suggest that understanding the role of community composition in structuring reef fish assemblages may be increasingly important in the future. However, evidence for impacts of coral composition on reef fishes is sparse (but see Berumen and Pratchett 2006; Alvarez-Filip et al. 2011b; Messmer et al. 2011)..

The level of dependence and preferential use of different coral species varies greatly among fish species (Coker et al. 2014) and ontogenetic stages (Jones et al. 2004). For example, many small-bodied species and juveniles of large-bodied species demonstrate preference for branching corals such as acroporids, pocilloporids, and branching poritids (Shulman 1984; Bonin 2012). Likewise, some larger-bodied fishes such as groupers and snappers have been shown to shelter preferentially under tabular acroporid corals (Kerry and Bellwood 2015). At a reef scale, structural complexity of Caribbean reefs has been shown to be determined by the identity and cover of corals present (Alvarez-Filip et al. 2011a), which in turn may influence the size-spectra and trophic structure of local fish assemblages (Alvarez-Filip et al. 2011b). On Indo-Pacific reefs, coral diversity has been shown to affect fish assemblage structure (Messmer et al. 2011; Komyakova et al. 2013), but these studies have been limited in their spatial extent ($\leq 4\text{m}^{-2}$) and not focused on specific configurations of corals *per se*. A detailed quantitative assessment of how fish assemblages vary among habitats with specific coral configurations is required to understand the likely impact of predicted directional shifts in coral composition.

Traditionally, studies that have investigated fish-habitat associations have focused on changes in the taxonomic composition of fish assemblages (Mouillot et al. 2013b). However, there is an emerging interest in investigating species assemblages in terms of their roles in ecosystem function as opposed to their taxonomic identity (Bellwood et al. 2004). In combination with community surveys, the distribution and abundance of ecological and morphological traits can be assessed, and by doing so provides some insight into the processes driving community assembly (Mouillot et al. 2013b). Ecological theory broadly predicts that two processes may determine community assembly: interactions among species with shared traits (i.e. competition), and interactions between species and their environment (i.e. environmental filtering) (Diamond 1975; Weiher and Keddy 2001). Locally, competition can limit the ecological similarity of species, thereby differentiating co-occurring species (Macarthur and Levins 1967). Environmental filtering reduces the spread of traits within a habitat, reflecting shared ecological tolerances and a reduction in the range of successful ecological strategies among co-occurring species, thereby reducing functional capacity of the community (Keddy 1992; Cornwell et al. 2006). Previous analyses have considered the functional structure of reef fish communities (captured by species traits) in relation to habitat disturbance (Pratchett et al. 2011), and ecosystem recovery potential (Graham et al. 2015), and have identified predictable outcomes for ecosystem function. These studies focus on the functional implications of catastrophic bleaching and widespread coral mortality, however the extent to which functional diversity varies among reef habitats that remain coral dominated is untested.

The objective of this study is to investigate the variation in functional structure of reef fish assemblages among six distinct coral habitats. Specifically, we use an ecological trait-based ordination analysis to quantify the functional diversity of fish assemblages in relation to benthic composition in order to address the following questions: (1) does the functional richness, functional evenness, and functional divergence of fish assemblages vary with changes in the taxonomic composition of coral habitats?; and (2) do particular benthic characteristics (benthic composition, benthic diversity, structural complexity, and depth) predict these differences?

Material and methods

Study location

Fish and coral assemblages were surveyed on reefs surrounding Lizard Island, in the northern Great Barrier Reef, Australia (14°41′S, 145°27′E) in October and November 2014. Sampling was conducted on shallow (< 6-m) reef slopes on the western (i.e. leeward) side of the island. Sites were selected to represent six distinct coral habitats characterised by: (i) branching *Porites,* (ii) massive *Porites*, (iii) *Pocillopora*, (iv) staghorn *Acropora*, (v) soft coral, and (vi) mixed coral assemblages. Two replicate sites of each habitat were sampled, except staghorn *Acropora* where only one suitable site was located. Sites were > 250-m long by > 5-m wide reef slopes; with adjacent sites separated by at least 500 m. All sites were in areas protected from fishing and the prevailing SE swells and currents, and had comparable water clarity and geomorphology. At each site, benthic composition, structural complexity, and associated fish assemblages were surveyed along four replicate 50 m transects positioned parallel to the reef edge, with a minimum of 5-m separating adjacent replicates.

Benthic composition and structural complexity

Benthic composition was quantified using the point intercept method, recording substratum types directly beneath 100 points spaced at 50 cm intervals along each transect line. Substratum types were hard (scleractinian) corals (identified to genus and growth form), soft (alcyonacean) corals, macroalgae, 'other benthos' (primarily sponges, giant clams, and ascidians), dead coral and pavement, rubble, and sand. The structural complexity of the reef was estimated visually at the start, middle and end of each transect using a 6-point scale, with a score of 0 indicating a flat surface, and a score of 5 an exceptionally complex reef with numerous caves and overhangs (following Wilson et al. 2007).

Fish functional structure

The abundance and body-length (total length (TL), to the nearest cm) of all diurnally active non-cryptic fishes were recorded along each transect using underwater visual census. Large, mobile fish (> 10 cm TL) were recorded within a 5-m wide belt while simultaneously deploying the transect tape (to minimise disturbance). Smaller, site-attached fish (< 10 cm TL) were then recorded within a 1-m wide belt during a return swim along the same transect (following Hoey et al. 2011). Care was taken to minimise the resurveying of individuals that left and subsequently re-entered the transect area. All fish surveys were conducted by a single observer (ASH) and the fish abundances standardised per 250 m^{-2}.

Two hundred and eighteen observed fish species from twenty-six families were assigned traits from six categories relating to their diet, mean observed species body-size, mobility, time of activity, social grouping, and position in the water column (Online Resource Tables S1 and S2; adapted from Mouillot et al. 2013a). These traits were chosen to represent implicit roles performed by reef fishes (following Mouillot et al. 2013a; Mouillot et al. 2013b), as well as having demonstrable relationships with benthic variation (e.g. Pratchett et al. 2011; Nash et al. 2013). Fish were classified into established trophic categories that cover the main feeding functions performed by fishes on coral reefs, including removal of algae, and trophic mediation via predation. Body-size, that captures variation in both the identity and magnitude of functions relating to feeding, movement, home range size and energetic requirements, was assigned into 10 cm size-class categories based on the mean observed body size of each species. Diet and body-size encompass a large proportion of the implicit functional roles of coral reef fishes (Bellwood et al. 2004, Lokrantz et al. 2008). However, mobility, time of activity, social grouping, and position in the water column provide additional information on the likely spatial and temporal scales at which the various functions are realised/exerted, and are therefore included to capture maximal estimations of functional diversity (Mouillot et al. 2013a).

Statistical analyses

Variation in benthic composition between coral habitats was visualised using principal component analysis (PCA) based on the covariance matrix of log (x+1) transformed data. The analysis was based on the percent cover of substratum types on transects in each habitat, including: branching *Porites*, massive *Porites*, *Pocillopora,* and staghorn *Acropora*, ‘other’ hard coral genera, soft coral, macroalgae, ‘other benthos’ (described above), dead coral and pavement, rubble, and sand. Analysis of benthic composition using a non-metric Multiple Dimension Scaling (nMDS) based on Bray-Curtis similarities showed comparable groupings among habitats and sites (Online Resource Fig. S1). Benthic composition was compared among habitats (fixed) and sites (random) using a two-way permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances of the log (x+1) transformed data (Primer V6, PERMANOVA + add on package, n = 999 permutations). Pairwise comparisons were carried out at the transect level based on unrestricted permutation of raw data to allow for a sufficient number of unique permutations (> 420) to be tested. Similarity Percentage analysis (SIMPER) was used post-hoc to identify benthic categories consistently contributing to average similarity within, and dissimilarity between habitats with a test ratio value of 1.5 or higher (Clarke and Warwick 2001).

To assess variation in fish assemblage functional structure among surveyed coral habitats, a trait-based ordination analysis was used to generate three complementary indices of functional diversity: functional richness, evenness, and divergence (Fig. 1). These independent indices measure all facets of functional diversity (Villéger et al. 2008): (1) functional richness (the number of unique trait value combinations in an assemblage calculated according to the minimum convex hull volume incorporating species present in functional space relative to the total pool of species); (2) functional evenness (the regularity of the distribution of abundance in this volume calculated as the sum of the minimum spanning tree branch length weighted by relative abundance); and (3) functional divergence (species deviance from the mean distance to the centre of the neutral functional space, weighted by relative abundance) (Mason et al. 2005). Based on pairwise Gower's distances between species, principal coordinates analysis (PCoA) was used to construct a synthetic multidimensional ordination from which functional diversity indices were computed by transect. The first four dimensions of the ordination were selected *a posteriori* (following Maire et al. 2015), and single score functional diversity indices were calculated according to species' position in this four-dimensional space. A square root correction for negative eigenvalues was applied for Euclidean representation of distance relationships among species and to avoid biased estimations of functional diversity (Legendre and Legendre 1998).

Variation in functional richness, evenness, and divergence, as well as species richness (total number of species) of fish assemblages among coral habitats was modelled using the lme function from the *nlme* package in R (R Development Core Team 2015), with habitat as a fixed effect, and *post hoc* Tukey multi-comparison tests. Models with and without site as a random effect were compared using the minimisation of corrected Akaike information criterion (AICc; Akaike 1974) to rank alternative models. Since exploratory graphical analysis suggested possible differences in variance among habitats, models which did and did not allow heterogeneity of variance among habitats were also compared. Multiple linear regression was then used to estimate relationships between functional richness, evenness, and divergence with six continuous benthic explanatory variables: benthic diversity (Shannon-Wiener H'), the first two axes of the benthic PCA as proxies of benthic composition, structural complexity, coral cover, and depth (Fig. 3; mean ± SE values detailed in Online Resource Table S3). Collinearity between explanatory variables was assessed using Spearman's correlation coefficients (for numerical values), and variance inflation factors (VIF). All variables had a correlation coefficient of < 0.7 and VIF values < 3 and so were retained for model selection. Information-theoretic model selection based on the AICc ranking was used to quantify model uncertainty (Burnham and Anderson 2002). The top models, based on ΔAICc values < 2 (Burnham and Anderson 2002) are presented and detail the changes in AICc and model weights to illustrate the strength of the optimum model. Parameter estimates and significance values are also presented for the top-ranked models for each functional diversity index. Analyses were performed in R using the packages *ape*, *ade4*, *cluster*, *geometry*, *MuMIn*, *nlme*, *polycor*, *rcdd*, *vegan*, as well as the function FDchange in the package *FD*, unless otherwise specified.

Results

Benthic composition and structural complexity

Dominant benthic components in each habitat were those coral taxa identified *a priori* in site selection, covering 22.6-51.6% of total benthos, and 38.5-89.7% of total live coral (Online Resource Table S3). Principal component analysis (PCA) revealed variation in benthic composition among habitats, with transects in each habitat generally grouping together (Fig. 2a). Branching *Porites* habitats were clearly separated from soft coral, *Pocillopora*, and staghorn *Acropora* habitats along the first axis (PC1), while soft coral habitats were differentiated from staghorn *Acropora* and *Pocillopora* along PC2. Groupings identified in the PCA were supported by the PERMANOVA with significant differences in benthic composition between habitats (Pseudo-$F = 3.37$, $P = 0.002$, 945 Permutations). Pairwise comparisons and SIMPER analysis indicated that all habitats differed in benthic composition (all $P \leq 0.05$, Online Resource Table S4).

Fish functional diversity

The first four dimensions of the PCoA cumulatively explained 55.5% of the projected inertia in the distribution of fish species traits (first two independent axes accounted for 38% of the variance and are illustrated in Figs 4 and 6). Generally, fish body-size and mobility increased from right to left along the first axis of the PCoA, and social grouping broadly changed along the second axis (Fig. 4). Grazers, scrapers, and excavators were positioned top-left in functional space, and sedentary farmers, and corallivores were in the top-right. Planktivores were positioned in the middle-right, and larger piscivores and mixed-diet feeders typically mobile within reefs were positioned in the bottom-left (Fig. 4).

Model comparisons using AICc indicated that neither inclusion of site as a random effect, nor allowing heterogeneity of variance among habitats, improved the model fit for estimations of functional diversity metrics, and were excluded from subsequent analyses. There were significant differences among coral habitats in the average functional richness of fish assemblages (ANOVA, $F(5,38) = 3.62$, $P = 0.008$), with branching *Porites* habitats supported functionally richer fish assemblages than both soft coral and *Pocillopora* habitats (Tukey pairwise comparisons, $P = 0.009$ and $P = 0.004$, respectively; Figs 5a and 6). Modelling of the individual-scale predictors of functional richness yielded 2 models within ΔAICc < 2 of the top model (Table 1). The most parsimonious model (wAICc = 0.7) contained structural complexity alone and was 2.33 times more plausible than the next model (wAICc = 0.3), which included structural complexity and the second axis of the benthic PCA. Structural complexity was the only variable present in both top models, and had a top relative importance of 1 (Table 1). The positive parameter estimate for structural complexity (± SE; 0.08 ± 0.02) indicates greater structural complexity to be associated with higher fish functional richness (full model, linear regression, $r^2 = 0.248$, $F(5,38) = 3.84$, $P = 0.01$; optimal model structural complexity ~ functional richness, $r^2 = 0.296$, $F(1,42) = 19.08$, $P < 0.001$; Fig. 7a). The effect size of PCA axis 2 was less substantial, reflected by its relative importance score (0.30). Total coral cover was a poor predictor of functional richness (and divergence; >2 ΔAICc of the top ranked multiple linear models). Pairwise comparisons revealed that non-overlap of mean convex hull volumes among habitats varied from 20.6 – 40.9% (Online Resource Table S5).

No difference in functional evenness was detected between habitats (ANOVA, $F(5,38) = 1.01$, $P = 0.43$; Fig. 5b). There was also no significant difference in the mean species richness of fish assemblages among coral habitats (best model fit: ANOVA, $F(5,5) = 1.21$, $P = 0.42$).

Functional divergence varied significantly between habitats (ANOVA, *F*(5,38) = 3.41, *P* = 0.01) with greater divergence in massive and branching *Porites* habitats than *Pocillopora* habitats (Tukey pairwise comparisons, *P* = 0.003 and *P* = 0.03, respectively; Figs 5c and 6). Sensitivity analysis of individual-scale benthic predictors (full model, linear regression, *r*2 = 0.077, *F*(5,38) = 1.72, *P* = 0.15) yielded 4 models within ΔAICc < 2 of the top model (Table 2). The top ranked model (wAICc = 0.43; *r*2 = 0.123, *F*(1,42) = 7.03, *P* = 0.01; Fig. 7b) contained structural complexity alone and was 2.05 times more likely than the next model that included structural complexity and the second axis of the benthic PCA (wAICc = 0.21). Structural complexity featured in all four top models, with a high relative importance score of 1.00. The positive parameter estimate for structural complexity (± SE; 0.01 ± 0.004) indicated higher fish functional divergence in coral habitats characterised by greater structural complexity.

Discussion

The composition and functions of coral reef fish assemblages are mediated by the availability of live coral habitat (reviewed in Pratchett et al. 2008). However, the role of coral community composition, specifically the dominance of different coral taxa, in shaping fish assemblages is not yet well understood. This study revealed variation in the functional diversity of fish assemblages among six surveyed coral habitats. These results suggest that coral composition may act as an environmental filter on the distribution and abundance of associated fish traits. Functional richness and functional divergence, but not functional evenness or taxonomic richness, of fish assemblages varied among coral-dominated habitats, with the structural complexity of the habitats being the best predictor of these measures. Functional richness was highest in branching *Porites* habitats, lowest in *Pocillopora* and soft coral habitats, and intermediate in massive *Porites*, staghorn *Acropora*, and mixed coral habitats. Functional divergence was greatest in branching *Porites* and massive *Porites* habitats, and lowest in *Pocillopora* habitats.

Functional richness reflects the range of unique trait combinations held by coexisting fish species, which for some groups (e.g. herbivores) may indicate the potential resilience of an ecosystem (Rasher et al. 2013; Nash et al. 2015a). Results of this study suggest that at a reef-scape scale, coral habitats dominated by complex coral growth forms (such as branching *Porites*) may accommodate a greater range of niches, or functional strategies, than corals that provide less structural complexity (such as *Pocillopora* and soft coral). Fish with particular shared functions were found across all habitats (e.g. solitary grazers, scrapers and excavators, small sedentary farmers, and pairing corallivores). However, others were largely restricted to branching *Porites* habitats, namely nocturnally active, schooling planktivores (i.e. planktivorous species of the Apogonidae and Holocentridae). Branching *Porites* tends to form large dome-shaped colonies that offer potential refugia for other organisms at multiple spatial scales, both between its narrow-spaced branches, between colonies, and under colony ledges. In this way, branching *Porites* contains structural similarities of both branching and massive morphologies, importantly providing structure for fishes across a range of scales (Nash et al. 2013). Nocturnal planktivorous cardinalfishes, in particular, can exhibit high levels of habitat specialisation with branching *Porites*, occupying colonies at diurnal resting sites on the reef (Gardiner and Jones 2005).

Experimental analysis of the effects of coral species richness on fish assemblage diversity shows that habitat specialists are vulnerable to shifting coral composition (Holbrook et al. 2015), in accordance with the specialisation-disturbance hypothesis (Vázquez and Simberloff 2002). Thus, where shifts in coral composition are characterised by the loss of structurally complex corals, reef fish assemblages may become less functionally diverse and dominated by habitat generalists that utilize a range of habitat types at the expense of habitat specialists (Bellwood et al. 2006a; Wilson et al. 2008). Nocturnally active planktivores, such as cardinalfishes, are typically fast growing and short-lived, and have been suggested to play an important role in recycling and concentrating energy on reefs through the provision of a trophic link between emergent (nocturnal) plankton and higher trophic levels (Marnane and Bellwood 2002). Although the functional importance of fish such as cardinalfish is not well understood, a loss of functional richness and ecological complementarity among fish can have important and unexpected consequences for ecosystem function (Bellwood et al. 2003, 2006b). For example, certain processes are maintained by just one or a few fish species, making ecosystem function highly vulnerable to the loss of those species (Hoey and Bellwood 2009; Mouillot et al. 2014).

Fish assemblages in massive and branching *Porites* habitats were more functionally divergent than those in *Pocillopora* habitats, driven by the dominance of small, schooling planktivorous fishes in the two *Porites* habitats. Higher functional divergence suggests greater niche specialisation among coral habitats due to higher abundances of species close to the volume borders of the functional space, i.e. specialist species (Mouillot et al. 2013). Massive *Porites* corals appear to provide little shelter from predation, water movement, or solar radiance for small-bodied fish across the relatively planar colony surface. However, some evidence suggests that small fishes may use massive corals when their primary branching coral microhabitat has been lost (Wellington and Victor 1985; Precht et al. 2010). Branching *Porites* habitats had similarly high functional divergence, and was differentiated from other habitats due to the abundance of schooling, nocturnal planktivores which were absent or in low abundance elsewhere. The branching *Porites* habitat also had the highest abundance of small, sedentary fish (e.g. damselfishes *Pomacentrus moluccensis*, *P. grammorhynchus*, and *Chromis viridis*). Branching *Porites* is somewhat morphologically similar to massive *Porites* in that they both form large mound-shaped colonies providing shelter between colonies or under ledges created by overhangs (Kerry and Bellwood 2015), with branching *Porites* also providing smaller refuges between its branches.

Differential structural complexity among coral habitats was the best predictor (of the five explanatory variables examined) of fish functional richness and divergence. The relationship between structural complexity and coral composition illustrated in this study is consistent with analyses from the Caribbean emphasising the variable morpho-functional characteristics of individual coral species (Alvarez-Filip et al. 2011a). Studies concerned with impacts of reef degradation demonstrate the importance of habitat structure for reef fish taxonomic diversity and abundance (Graham and Nash 2013), fish body-size distributions (Wilson et al. 2010), trophic structure (Alvarez-Filip et al. 2011b), and habitat selection of recruits and juvenile fishes (Jones et al. 2004). Despite little variation in fish species richness among habitats, the increasing functional richness across a structural complexity gradient in this study is consistent with the concept of environmental filtering, where species with certain ecological or morphological traits were excluded if unsuited to low complexity habitat (Cornwell et al. 2006). The positive correlation between functional divergence and structural complexity also suggests that the performance of particular groups of specialist species may be restricted on low complexity reefs due to limited available refugia from predation or environmental conditions such as water flow or solar radiance (sensu performance filter hypothesis) (Mouillot et al. 2013b). Species can exhibit a range of responses to environmental disturbance, such as increases in herbivores in response to coral loss (Wilson et al. 2006; Pratchett et al. 2011). Therefore, where functional diversity is greater in more structurally complex coral habitats, a broader range of processes may be supported that underpin ecosystem performance (Rasher et al. 2013).

Coral communities are known to vary with natural physical features (e.g. geomorphology, exposure, reef zonation and depth), biological processes (e.g. recruitment, predation, inter- and intra-specific competition for space), and local disturbance histories (Pandolfi et al. 2011; Hughes et al. 2012; Williams et al. 2013). How these communities will change, and the implications for the functional diversity of reef fish assemblages will be largely dependent on the nature, frequency and severity of future disturbances, and the capacity for different coral taxa to adapt to changing conditions (Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011). Inter- and intra-taxon variation in colony morphology and physiology influence both the susceptibility to various stressors and patterns of larval recruitment and growth, which promote particular corals as more or less competitive, stress-tolerant and/or quick to colonize post-disturbance (reviewed in Darling et al. 2012; Hughes et al. 2012). For example, structurally complex branching corals (e.g. *Acropora* and *Pocillopora*) are often the most susceptible taxa to a range of disturbances such as thermal bleaching (Marshall and Baird 2000), storms (Madin and Connolly 2006), and crown-of-thorns starfish (Baird et al. 2013), yet they are also fast-growing and in areas of sufficient larval supply can quickly dominate areas post-disturbance (e.g. Berumen and Pratchett 2006). Branching *Porites* is similarly fast growing and sensitive to thermal stress, though there is little evidence of long-term recovery potential following disturbance (e.g. van Woesik et al. 2011; Johns et al. 2014). Conversely, slow-growing coral genera with massive or encrusting life forms, such as massive *Porites*, typically exhibit less sensitivity to thermal stress or colony damage caused by large storms (e.g. Hughes 1994; van Woesik et al. 2011; but see Guest et al. 2012), and have been predicted to persist in a changing climate characterised by warmer temperatures and high disturbance frequency (Riegl and Purkis 2009; Bento et al. 2015). Soft corals are relatively stress tolerant and opportunistic (Darling et al. 2012), and have been documented to rapidly colonise and dominate benthic assemblages following the widespread mortality of hard corals (reviewed in Norström et al. 2009; Johns et al. 2014). Although the most likely scenarios facing coral reefs will be a shift away from structurally complex branching corals to less complex mound and massive growth forms, or toward benthic communities dominated by other non-coral taxa, the exact nature of these shifts remain uncertain and are likely to vary between locations.

This study provides some initial insights into the role of coral composition in structuring reef fish assemblages via the differential structural complexity provided by coral taxa. Despite being conducted at a single location (Lizard Island), with limited availability of habitats with *a priori* defined coral composition, significant differences in the functional diversity of fish assemblages were evident. Although our assessment of structural complexity captured differences in broad-scale habitat features and was an important predictor of fish functional diversity, more detailed quantification of multiple scales of complexity and across broader spatial scales are warranted to improve the understanding of how coral composition may structure ecosystems through differential habitat provision.

Corals do not provide equal resources to reef fishes, so predicted shifts in coral species composition (e.g. Graham et al. 2014) will likely to have important effects on the functional composition of reef fish assemblages. Recent work has shown substantially altered functional structure of fish assemblages on reefs that have shifted from coral to algal dominance (Hoey and Bellwood 2010; Wilson et al. 2010; Rasher et al. 2013; Chong-Seng et al. 2014; Graham et al. 2015). This study shows that functional diversity and structure of fish assemblages also varies in coral dominated habitats that differ in composition and structural complexity. These results suggest that despite little variation in taxonomic richness of fish assemblages among coral habitats, coral composition may mediate the distribution and abundance of fish traits, which is likely to influence the maintenance of populations, ecosystem processes to which they contribute, and therefore the resilience of that system (Larsen et al. 2005; Nash et al. 2015a). This study highlights the need to delve further into trait-based exploration of the functional implications of altered coral habitats across multiple locations as ecosystem performance may hinge upon it.

Compliance with Ethical Standards

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Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval: This study was purely observational. No animals were collected or handled in any way by any of the authors.

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Fig. 1 Assessing variation in the functional structure of ecological communities. (a) Species are plotted in multidimensional space according to shared trait values; (b) Functional richness, the proportion of the functional space filled by species, illustrated by the convex surface encompassing species present from the total species pool; (c) Functional evenness, the regularity of abundance distributions in functional space, where circle sizes are proportional to species relative abundances; (d) Functional divergence, the proportion of the total abundance characterised by species with functional traits positioned in towards the periphery of functional space, calculated as the distance from the grey to black cross (Villéger et al. 2008, Mouillot et al. 2013b). We use a four-dimensional space to assess functional diversity, however two axes are shown here for illustrative purposes

Fig. 2 Principal components analysis showing relationships among benthic assemblages across six coral habitats on Lizard Island (a) Spatial variation in benthic habitat on reefs at the transect level on natural log(x+1) transformed data. Data symbols represent transects within habitats: staghorn *Acropora* (filled square); branching *Porites* (filled circle), massive *Porites* (filled triangle); mixed assemblages (open circle), *Pocillopora* (open square); and soft coral (open triangle). (b) Relative contribution of 10 benthic habitat categories to the observed variation in reef benthic composition.

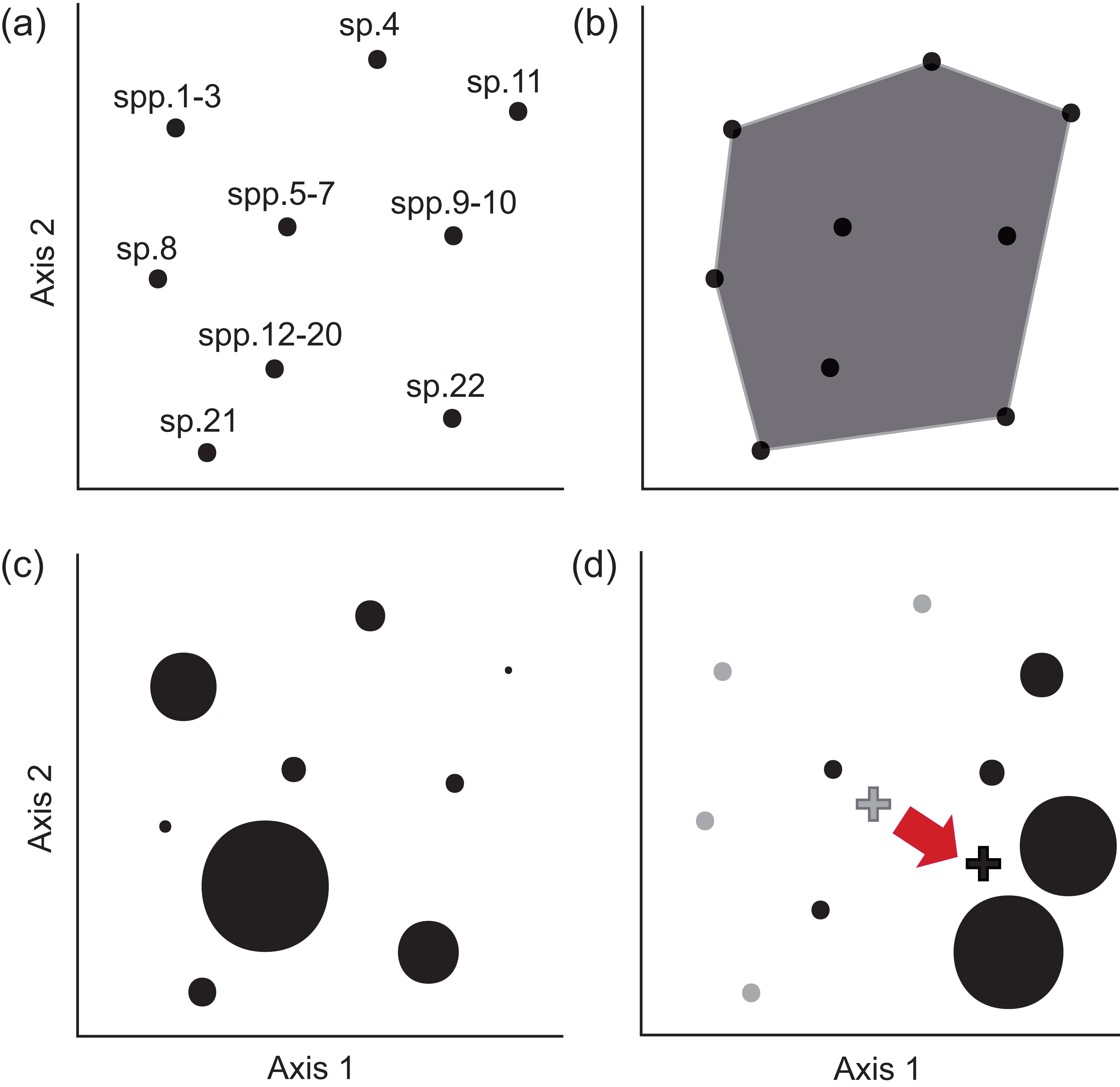
Fig. 3 Variation in structural complexity (a), and benthic diversity (b) among surveyed coral habitats (*n* = 4-8 per habitat). Significant differences between sites revealed by *post hoc* Tukey pair-wise comparisons are illustrated by the pairing of letters (A – C; Tukey, all $P < 0.04$)

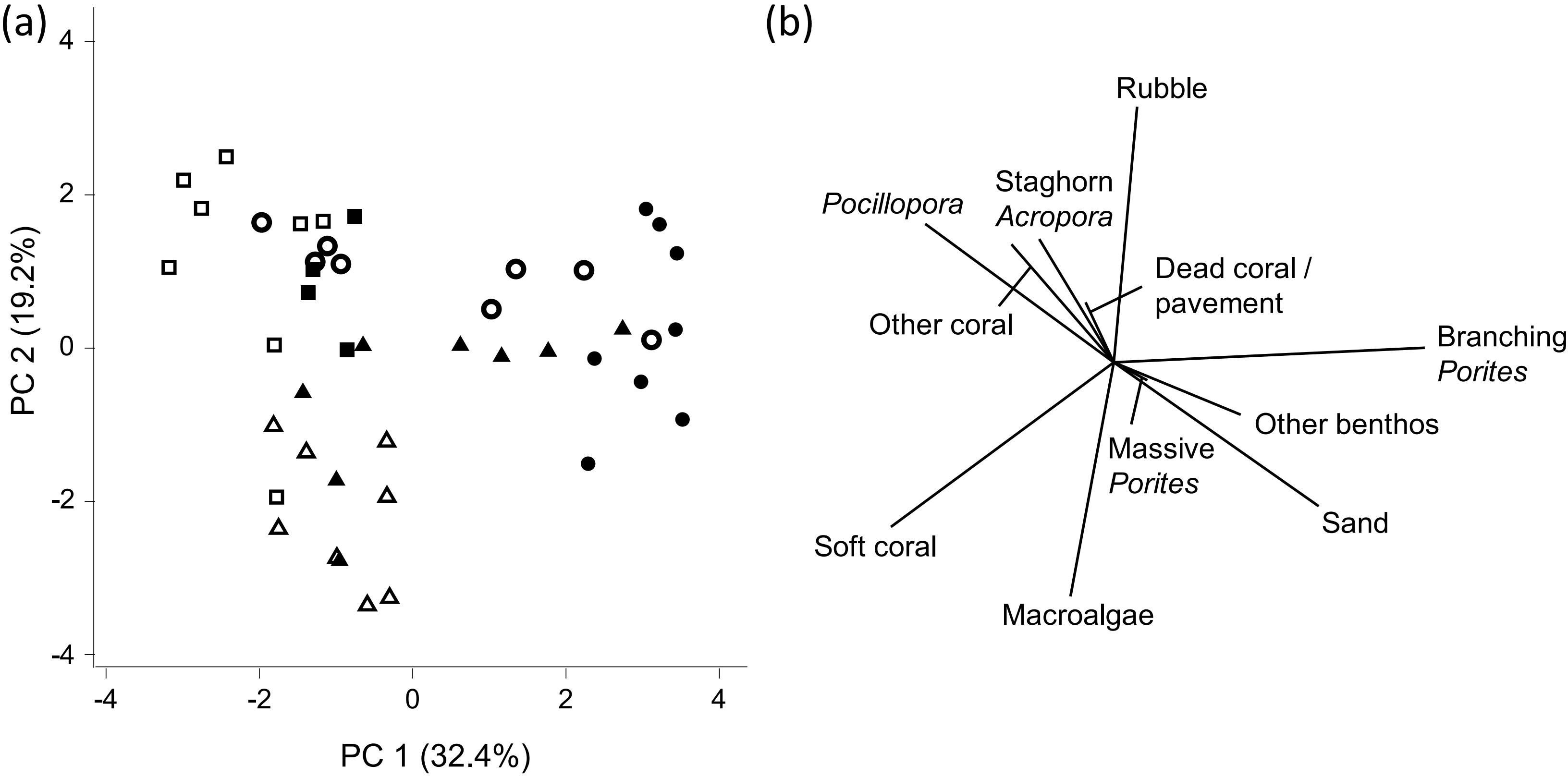
Fig. 4 Principal coordinates analysis of fish assemblage functional space. 218 recorded fish species (black dots) plotted in the first two dimensions (four total) of functional space defined by six traits: mean observed total body length (blue directional arrow indicating increasing size), diet (fish symbols); mobility (blue text); time of activity (sun and/or moon); social grouping (green text); and position in the water column (red text). Illustrations and text show the position of average trait levels in the functional space

Fig. 5 Variation in functional richness (a), evenness (b), and divergence (c) of fish assemblages among the six surveyed coral habitats (*n* = 4-8 per habitat). Significant differences between sites revealed by post hoc Tukey pair-wise comparisons are illustrated by the pairing of letters (A – B; Tukey, all $P \leq 0.05$)

Fig. 6 Variation in fish assemblage functional structure among coral habitats (a-f). Shaded convex surfaces illustrate the first two dimensions of functional space filled by species present from the total species pool (functional richness; FRic), and circle sizes are proportional to species mean relative abundances (illustrating patterns in functional divergence)

Fig. 7 Relationship between structural complexity and (a) fish functional richness, and (b) fish functional divergence (95% CIs). Symbols relate to transects in different coral habitats: Staghorn *Acropora* (filled square); branching *Porites* (filled circle); massive *Porites* (filled triangle); mixed (open circle); *Pocillopora* (open square); and soft coral (open triangle)


(a)
sp.4
spp.1-3
sp.11
spp.5-7
spp.9-10
sp.8
spp.12-20
sp.22
sp.21
Axis 2
(b)
(c)
Axis 2
Axis 1
(d)
Axis 1


(a)
4
2
0
-2
-4
-4
-2
0
2
4
PC 2 (19.2%)
PC 1 (32.4%)
(b)
Rubble
Staghorn
Acropora
Pocillopora
Dead coral /
pavement
Other coral
Branching
Porites
Other benthos
Massive
Porites
Sand
Soft coral
Macroalgae

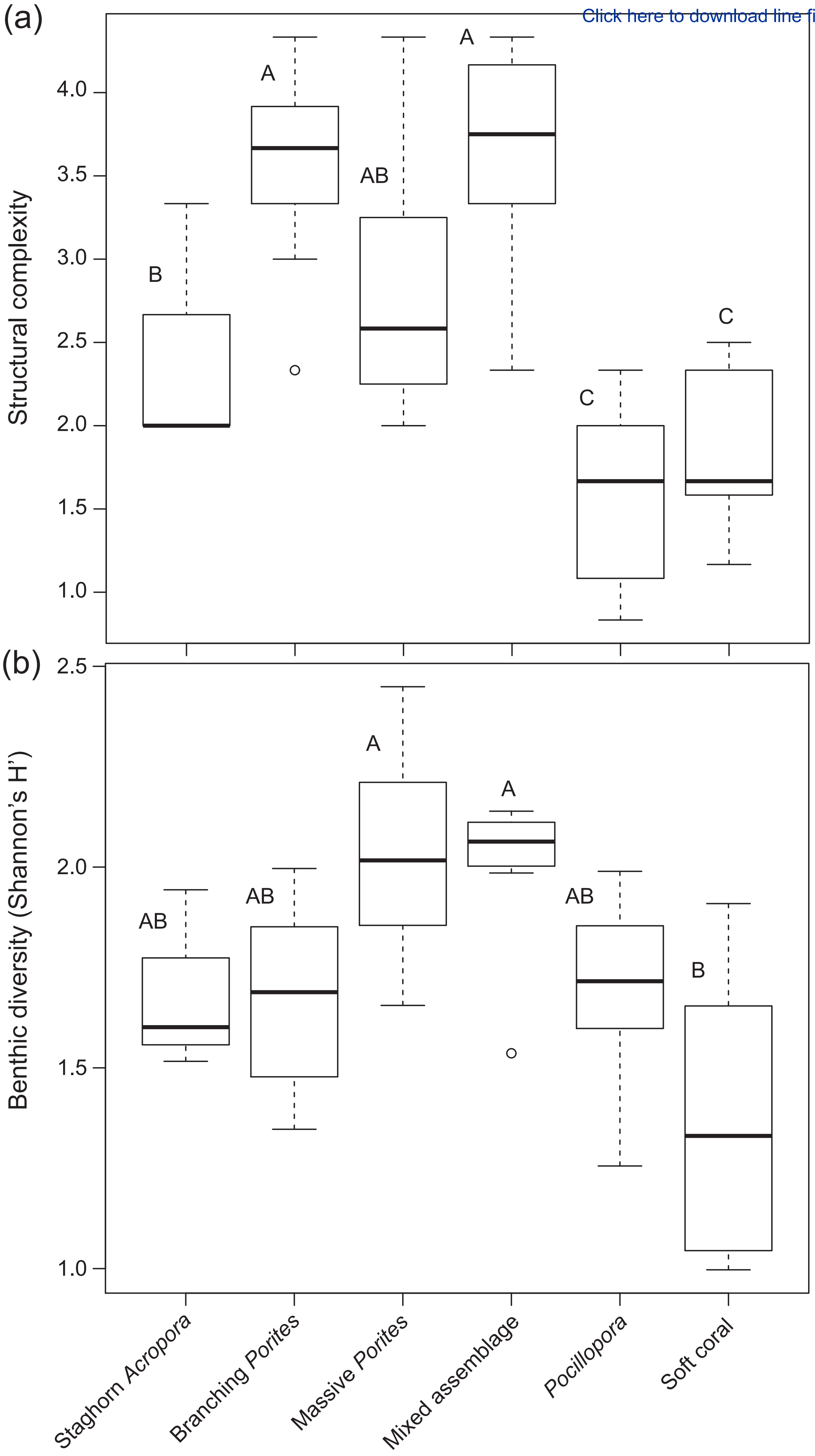

(a)
Structural complexity
4.0
3.5
3.0
2.5
2.0
1.5
1.0
B
A
AB
A
C
C
(b)
Benthic diversity (Shannon's H')
2.5
2.0
1.5
1.0
AB
AB
A
A
AB
B
Staghorn *Acropora*
Branching *Porites*
Massive *Porites*
Mixed assemblage
Pocillopora
Soft coral

Fig4

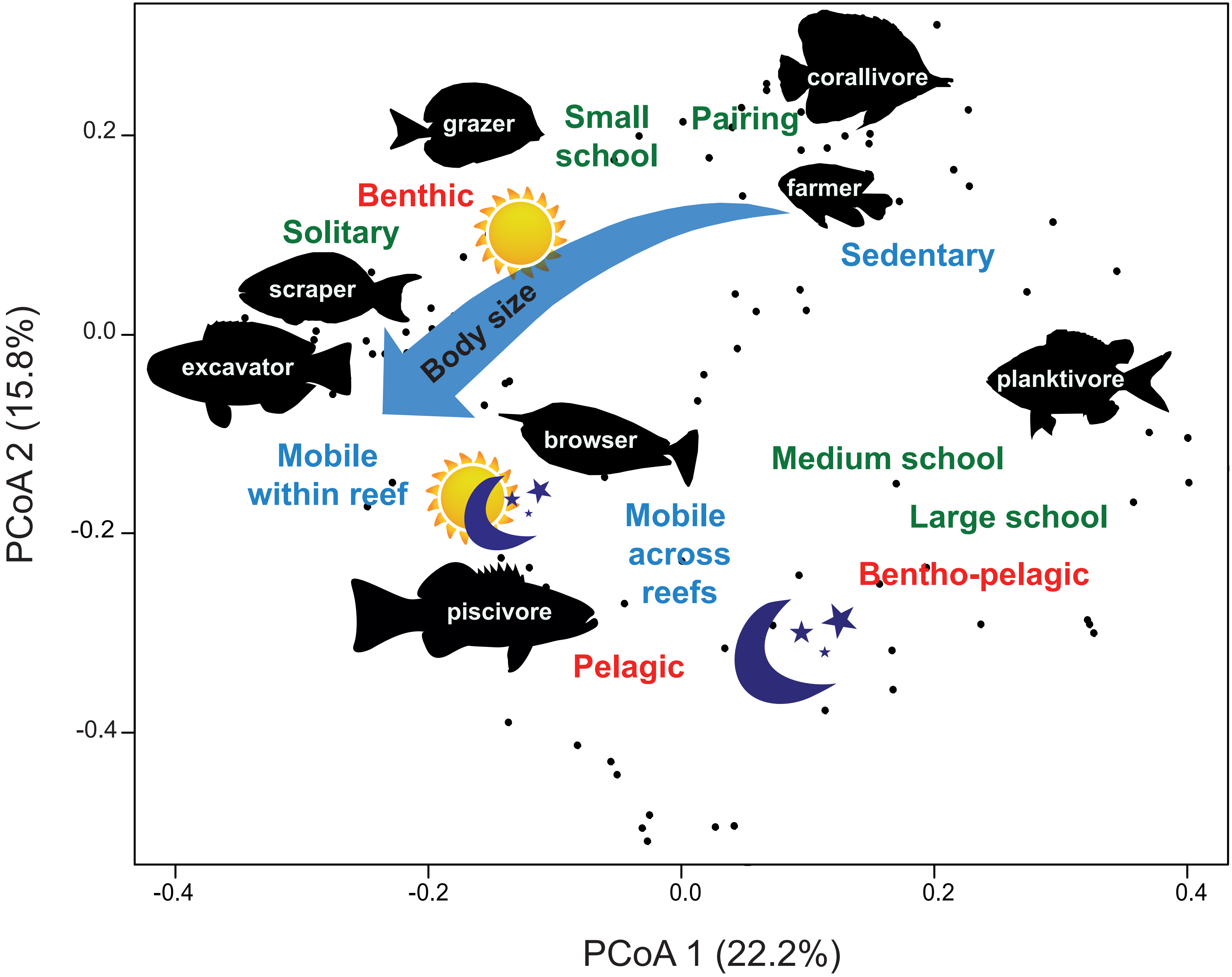
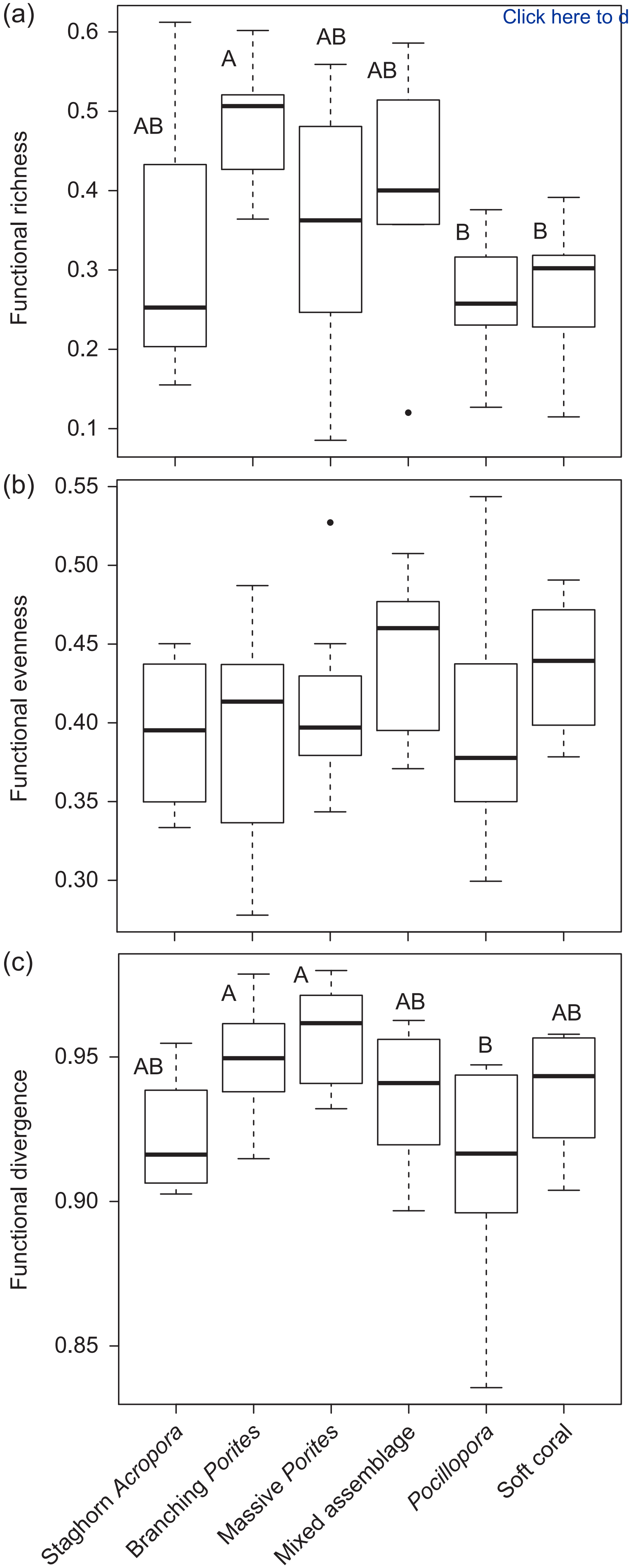
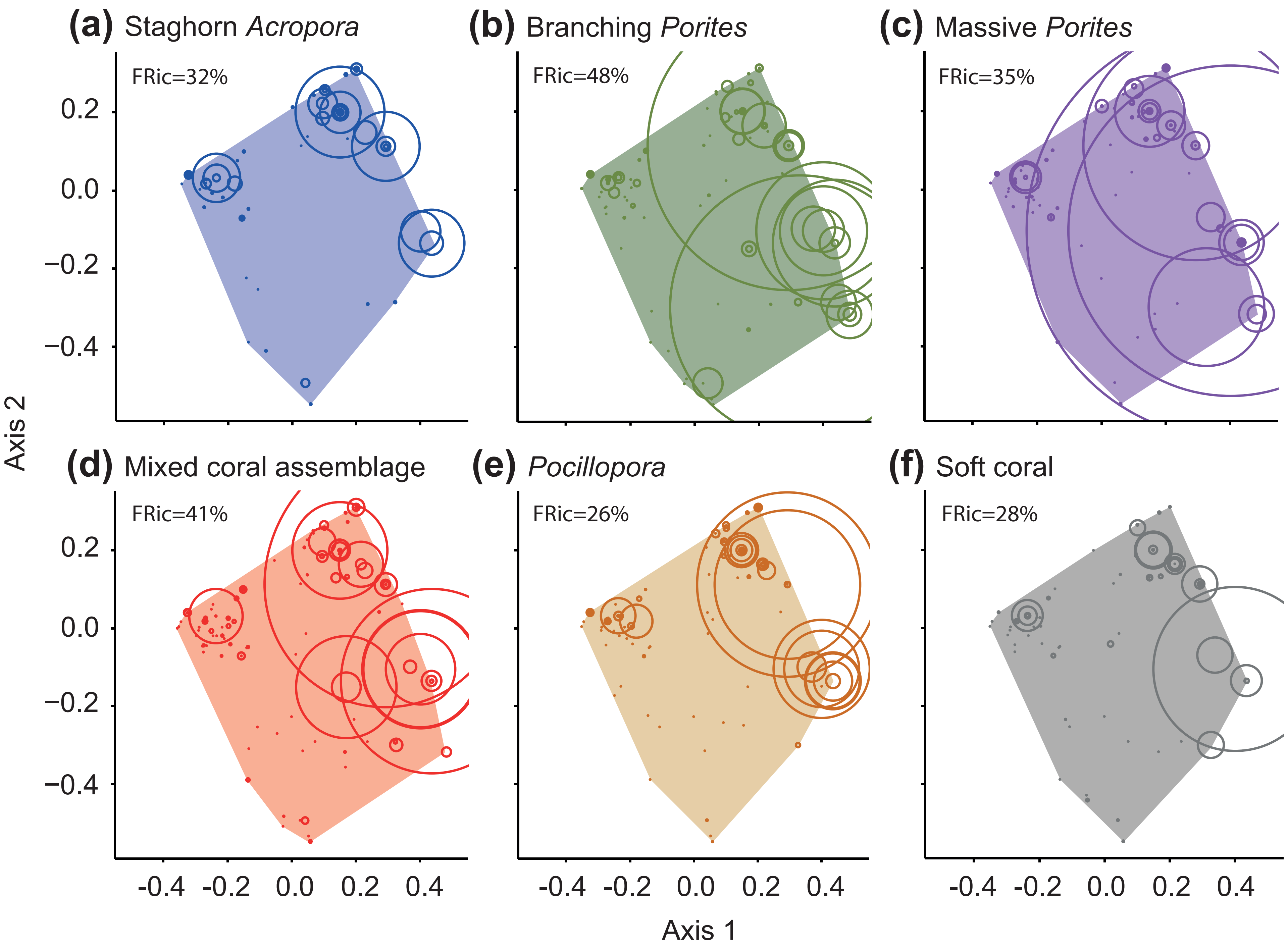

corallivore
grazer
Small school
Pairing
farmer
Benthic
Solitary
Sedentary
scraper
Body size
excavator
planktivore
browser
Mobile within reef
Medium school
Large school
Mobile across reefs
Bentho-pelagic
piscivore
Pelagic
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
PCoA 2 (15.8%)
PCoA 1 (22.2%)

Fig5


(a)
Functional richness
0.1
0.2
0.3
0.4
0.5
0.6
AB
A
AB
AB
B
B
(b)
Functional evenness
0.30
0.35
0.40
0.45
0.50
0.55
(c)
Functional divergence
0.85
0.90
0.95
AB
A
A
AB
B
AB
Staghorn *Acropora*
Branching *Porites*
Massive *Porites*
Mixed assemblage
Pocillopora
Soft coral


(a) Staghorn *Acropora*
FRic=32%
(b) Branching *Porites*
FRic=48%
(c) Massive *Porites*
FRic=35%
(d) Mixed coral assemblage
FRic=41%
(e) *Pocillopora*
FRic=26%
(f) Soft coral
FRic=28%
Axis 2
0.2
0.0
−0.2
−0.4
-0.4
-0.2
0.0
0.2
0.4
Axis 1

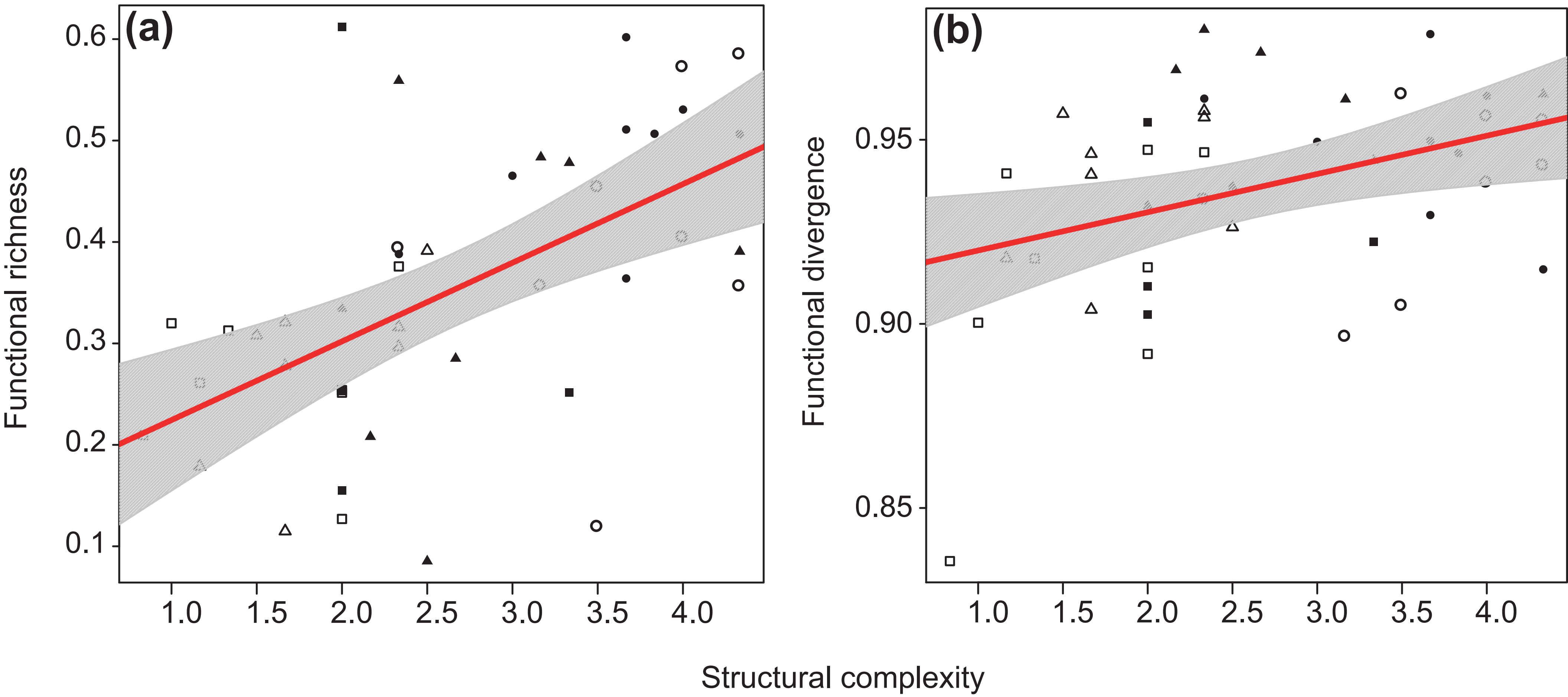

(a)
Functional richness
0.6
0.5
0.4
0.3
0.2
0.1
1.0
1.5
2.0
2.5
3.0
3.5
4.0
(b)
Functional divergence
0.95
0.90
0.85
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Structural complexity

Table 1 The two candidate models selected to describe the relationship between benthic characteristics and fish assemblage functional richness

Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Structural complexity	Benthos (PCA axis 2)	Benthos (PCA axis 1)	Benthic diversity (Shannon)	Depth (m)	Model output (lm)
1	-58.27	3	32.44	0.00	0.70	X					*F*1,42 = 19.08, ***P* < 0.001**
2	-56.61	4	32.82	1.67	0.30	X	X				*F*2,41 = 9.83, ***P* < 0.001**
Relative importance						1.00	0.30	N/A	N/A	N/A	
Model average						0.08 ± 0.02	0.003 ± 0.01	N/A	N/A	N/A	

Models are ranked by corrected Akaike's information criteria (AICc), with all models within ΔAICc < 2 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. The parameter estimates ± unconditional standard errors averaged over the 2 models are given along with the relative importance of each variable based on the sum of Akaike weights of the models in which the variable is present.

Table 2 The four candidate models selected to describe the relationship between benthic characteristics and fish assemblage functional divergence

Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Structural complexity	Benthos (PCA axis 2)	Benthos (PCA axis 1)	Benthic diversity (Shannon)	Depth (m)	Model output (lm)
1	-191.27	3	98.94	0.00	0.43	X					*F*1,42 = 7.03, ***P* = 0.01**
2	-189.88	4	99.45	1.39	0.21	X	X				*F*2,41 = 4.00, ***P* = 0.03**
3	-189.79	4	99.41	1.48	0.20	X				X	*F*2,41 = 3.95, ***P* = 0.03**
4	-189.28	4	99.15	1.99	0.16	X			X		*F*2,41 = 3.67, ***P* = 0.03**
Relative importance						1.00	0.21	N/A	0.16	0.20	
Model average						0.01 ± 0.004	-0.001 ± 0.002	N/A	0.001 ± 0.01	0.001 ± 0.002	

Models are ranked by Akaike's information criteria (AICc), with all models within ΔAICc < 2 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. The parameter estimates ± unconditional standard errors averaged over the 4 models are given along with the relative importance of each variable based on the sum of Akaike weights of the models in which the variable is present.