Running Title: Herbivore cross-scale redundancy

Herbivore cross-scale redundancy supports response diversity and coral reef resilience

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Abstract

1. Where a group of similar species exhibit a range of responses to disturbance (response diversity) ongoing maintenance of important ecosystem processes is anticipated. The cross-scale resilience model proposed that the scale at which an individual provides its function will influence its response to scale-specific disturbances. Thus, the presence of species operating at different scales within a community (cross-scale redundancy), should promote response diversity and thus be a useful indicator of resilience.
2. Coral reefs are diverse systems that provide key ecosystem services, and are subject to increasing anthropogenic disturbance. Herbivorous reef fish are critical for maintaining reefs within coral-dominated states, through the grazing and removal of algae, which competes with coral for space. To date, there has been no evaluation of the traits driving response diversity in reef fishes.
3. We assessed the effectiveness of cross-scale redundancy in herbivores as an indicator of response diversity and benthic recovery on reefs monitored through a major climatic disturbance event (coral bleaching) that caused widespread coral mortality.
4. The distribution (redundancy) of herbivorous species operating across a broader range of spatial scales prior to the coral bleaching corresponded with increased reef recovery post-disturbance. Analysis of the change in biomass across size classes indicated that response diversity, whereby a decline in small bodied biomass was compensated for by increases in biomass of large herbivores, drove an increase in the overall herbivore biomass at recovering sites. These compensatory mechanisms were not found at sites with herbivores operating over a narrower range of spatial scales.
5. *Synthesis and applications:* This study highlights the need to manage herbivores, and the function they provide on reefs by supporting the delivery of herbivory across

spatial scales. The importance of large individuals for controlling algae and providing compensation for the loss of smaller size classes emphasizes the necessity for effective fisheries management of reef herbivores. Importantly, cross-scale redundancy provides managers with a measurable indicator of resilience and an avenue to support the ongoing delivery of herbivore function.

Key words: body size; coral reef management; cross-scale resilience model; ecosystem processes; effect trait; fisheries; functional diversity; herbivory; resilience; response trait.

Introduction

The resilience of an ecosystem can be defined as its capacity to absorb disturbances whilst maintaining structure and function (Holling 1973; Carpenter *et al.* 2001). It has proved challenging to predict ecosystem resilience because reduced resilience is often only apparent when thresholds are reached and the system moves to an alternate state (Bellwood *et al.* 2004). Nonetheless, reversing or mitigating unwanted ecosystem shifts may be expensive or unfeasible so it is critical for managers to seek out methods to anticipate and, if possible, prevent unwanted shifts (Scheffer *et al.* 2001). One such set of methods search for ‘early warning signals’ in time-series data to anticipate shifts (Scheffer *et al.* 2009; Dakos *et al.* 2011). However, these techniques require large datasets, which may not be available (Biggs, Carpenter & Brock 2009). A second set of methods seek indicators of ecosystem state or function as proxies of resilience, but there have been few empirical tests of indicator performance to date (Thrush *et al.* 2009).

Species provide a variety of functions driving key ecosystem processes, thus, functional diversity within a community ensures the delivery of a range of processes that underpin ecosystem performance and support resilience (Walker, Kinzig & Langridge 1999;

Hooper *et al.* 2005). Such diversity may be explored by assessing the presence and distribution of effect traits among species, i.e. those life history and ecological traits that support specific ecosystem functions. However, ecosystems are dynamic, experiencing a range of natural and anthropogenic impacts; to allow system recovery, ecosystem processes need to be buffered to ensure their maintenance in the face of disturbance. Multiple species performing a similar functional role should give a degree of redundancy, because the decline of one species and its function in response to a disturbance may be compensated for by other species increasing their contribution to that function (Nyström 2006). However, redundancy only supports the maintenance of ecosystem function if different species performing the same function respond to a disturbance in distinct ways (response diversity; Elmqvist *et al.* 2003). This response diversity will ensure the continued delivery of the function, promoting recovery of a habitat post-disturbance (Mori, Furukawa & Sasaki 2012).

Response diversity may be explored by assessing the presence and distribution of response traits among species, i.e. those life history and ecological traits that are likely to support different responses to environmental change (Laliberté *et al.* 2010). Peterson, Allen & Holling (1998) proposed the cross-scale resilience model, suggesting that if members of a functional group operate at different spatial scales (termed cross-scale redundancy), they are likely to respond differently to scale-specific disturbances. Consequently, variance in the range of spatial scales over which species perform a particular function should be proportional to ecosystem resilience and the potential for a site to recover after a perturbation (Fig. 1; Peterson, Allen & Holling 1998).

To date, the cross-scale resilience model has undergone little testing (but see Fischer *et al.* 2007; Sundstrom, Allen & Barichievy 2012). To our knowledge, no studies have empirically assessed whether cross-scale redundancy within important functional groups supports the recovery of a system through a major disturbance event. Coral reefs are high diversity systems that provide key ecosystem services such as fisheries and coastal protection (Duffy 2002; Hughes *et al.* 2010). Human impacts are causing significant and ongoing reef degradation (Gardner *et al.* 2003), with increasing evidence of phase-shifts from coral to algal-dominated reefs in response to pressures such as bleaching events and overfishing (e.g. Hughes 1994; Hoegh-Guldberg *et al.* 2007). Nevertheless, reefs do not all respond to disturbance in the same way (e.g. Wilson *et al.* 2012).

Herbivorous fishes mediate competition between corals and macroalgae and are thus expected to affect the response of reefs to disturbances (Mumby *et al.* 2006); generating an extensive literature examining functional diversity and effect traits within these species. Herbivorous fishes may be characterised as grazers/detritivores, scrapers/excavators, and browsers (Bellwood *et al.* 2004). Grazers/detritivores and scrapers/excavators reduce the colonisation rates of macroalgae and potentially promote coral recruitment (Wilson & Bellwood 1997; Mumby 2009), with the latter group also contributing to bioerosion (Green & Bellwood 2009). In contrast, browsers feed on mature macroalgae and can help reverse shifts from coral to macroalgal dominance (Bellwood et al. 2006).

There has been considerably less work focused on response diversity within herbivorous fishes, with no exploration of the traits that support a range of responses to environmental change. The cross-scale resilience model provides a means of evaluating the importance of the spatial scales over which reef herbivores provide their functions as a driver of response diversity. Furthermore, given the functional role of herbivorous fishes in controlling algae, the cross-scale resilience model predicts that the variance in the range of spatial scales at which grazers/detritivores, scrapers/excavators and browsers perform their function would influence the capacity of a reef to recover following a disturbance event.

Seychelles' reefs were substantially disturbed in 1998 when the interaction of an El Nino and the Indian Ocean dipole led to elevated water temperature, coral bleaching and a resultant loss of >90% live coral cover (Wilkinson 2000). Subsequently, some reefs have shown signs of recovery, whereas other areas are shifting to an algal-dominated state (Chong-Seng *et al.* 2012). Benthic community composition and the size and species composition of herbivorous fishes have been monitored over 17 years from 1994, spanning the disturbance event. Here, we use the long-term data from Seychelles to test the cross-scale resilience model.

Methods

Field Methods

Fish and benthic communities were surveyed at twenty one reef sites in the inner Seychelles in 1994, 2005 and 2011. Fish abundance and individual body length (to the nearest cm) of diurnally active non-cryptic herbivorous species (37 species from 4 families) were estimated in 8 to 16 replicate survey areas (7m radius measured with a precut length of rope) at each site using instantaneous underwater visual census (UVC). Larger, mobile species were recorded before smaller, more site attached species to minimize bias caused by diver effects. The accuracy of fish body length estimations were assessed daily using sections of PVC pipe, prior to the start of data collection, and length estimates were consistently within 5% of actual lengths. On completion of each UVC replicate, the percent cover of different benthic components (macroalgae, hard coral, soft coral and non-living substrata) and the structural complexity of the reef (six point visual scale) were estimated. This method provided rapid estimates of percent cover and complexity in the replicate survey areas and gives comparable results to methods such as line intercept transects of benthic cover and the linear versus contour rugosity measure (Wilson, Graham & Polunin 2007). In 1994 and 2005, 16 replicate areas were surveyed at each site, whereas in 2011, 8 replicates were surveyed as statistical power analyses indicated that surveying 16 replicates did not significantly alter the percentage change detectable among years in either coral cover or fish biomass (Table S1). Individual body mass was estimated from body length using published length-mass relationships (Froese & Pauly 2012). Further details of survey methods and data processing are provided by Jennings, Grandcourt & Polunin (1995), Graham *et al.* (2006), and Wilson *et al.* (2012).

Data Analysis

Benthic condition

Variation in the benthic composition among sites and time periods was assessed using principal component analysis (PCA) in the statistical software PRIMER (Clarke 1993). PCA axis 1 values (hereafter PCA1), which separated sites with high coral cover and complexity (positive values) from those with high macroalgal cover (negative values), were extracted for each site as an index of benthic condition.

Redundancy metrics

The herbivorous fishes were assigned to one of three functional groups: browser, grazer/detritivore and scraper/excavator (Green & Bellwood 2009). Two sets of redundancy metrics were calculated for each site and year. The first set solely incorporated the categorical trait ‘functional group’ (browser, grazer/detritivore, scraper/excavator) and consisted of the two complementary metrics: functional dispersion and functional evenness, to indicate the distribution of function in trait space (see Villéger, Mason & Mouillot 2008 for further details; Laliberté & Legendre 2010). Functional dispersion is the mean distance of each species to the mean functional group value weighted by biomass. Higher values indicate biomass is more dispersed among the functional groups (Table S2Ai). Functional evenness describes the distribution of biomass across functional groups. Higher values indicate biomass is more evenly distributed among functional groups (Table S2Aii). Together these metrics indicate the functional group diversity and redundancy within groups (Fig. S1). To calculate the metrics, two data matrices were developed: sites*species, populated with biomass data, and species*trait, populated with trait attributes (Table S3). Calculation of functional dispersion and evenness were performed in the FD package in R (Laliberté & Legendre 2010).

The second set of metrics once again consisted of the complementary metrics functional dispersion and functional evenness, but they incorporated both the categorical trait 'functional group' and the continuous trait 'size'. The cross-scale resilience model is based on the assumption that size is a good proxy for the scale at which a species operates and provides its function, i.e. larger species operate at larger scales than smaller species (Calder 1984). Recent work exploring the relationship between body length and the scale of functional movements made by herbivorous reef fishes support this assumption (Nash, Graham & Bellwood 2013). Thus, higher values of functional dispersion indicate biomass is more dispersed among functional groups and size classes (Table S2Bi), whilst higher values of functional evenness indicate biomass is more evenly distributed among functional groups and size classes (Table S2Bii). Together these metrics indicate the degree of functional group diversity and cross-scale redundancy for a community (Fig. S1). Intraspecific variability in body length is thought to be important for size structured aquatic communities (Shurin, Gruner & Hillebrand 2006), and for examining interactions between habitat and reef fishes (Nash *et al.* 2014). To incorporate intraspecific size variability into the metrics, each species was split into 5cm size classes (hereafter referred to as species-size categories) and we developed two data matrices based on these species-size categories: sites*species-size categories, populated with biomass data, and species-size categories* traits populated with trait attributes (Table S4).

Redundancy as an indicator of reef resilience

To evaluate if redundancy metrics predict resilience, we assessed the extent to which the above metrics calculated for data from 1994 predicted post disturbance benthic trajectories. To achieve this, change in benthic condition (position on the PCA1) post-disturbance (2005-2011) was modelled as a function of the two sets of redundancy metrics: functional dispersion 1994 + functional evenness 1994, function & size dispersion 1994 + function & size evenness 1994, and the null model. Models were compared with the Akaike Information Criteria adjusted for small sample sizes (AICc, AICcmodavg package in R; Mazerolle 2013). To understand the relative importance of the two explanatory variables in the optimal model, a second model selection step evaluated the relative performance of all possible models within the global model (function & size dispersion 1994 + function & size evenness 1994). Prior to model fitting, the explanatory variables were checked for collinearity. The residuals were checked to ensure they met the assumptions of the models. The explanatory variables in the optimal model were used in subsequent analyses.

Herbivorous reef fish are targets of small-scale artisanal fisheries in Seychelles. Some of the sites were located in no-take marine reserves (n=9), whereas others were located in fished areas (n=12). To evaluate the effects of any differences in fishing pressure on the results, the analysis was repeated, incorporating the level of protection (no-take vs. fished) into the models.

Redundancy as an indicator of response diversity

For those metrics that successfully predicted benthic trajectories, we evaluated their link to herbivore biomass through time. Changes in herbivore biomass were assumed to reflect changes in the delivery of herbivory through time (before and following the disturbance event). Thus, herbivore biomass (square root transformed to meet model assumptions) in 1994, 2005 and 2011 was modelled as a function of function & size dispersion and evenness in 1994. For those redundancy metrics related to the maintenance of herbivore function (biomass), we investigated patterns of response diversity among size classes. Sites were grouped according to low, mid and high redundancy in 1994 (equal groupings with 7 sites in each category), and we calculated mean change in herbivore biomass within size classes, through the disturbance event (1994-2005) and post-disturbance (2005-2011). Bootstrapped 95% confidence intervals were calculated for each mean biomass change.

Redundancy over time

For those metrics that successfully predicted benthic trajectories, we evaluated the stability of the metrics, and hence redundancy, through the disturbance event. This would allow us to understand whether recovery of the benthos after the disturbance event was reflective of consistent redundancy within the herbivore community, or masked fluctuations in redundancy. To achieve this, values of the function & size metrics in each sampling year were compared with their values in other years (2005 vs. 1994, 2011 vs. 2005, 2011 vs. 1994).

RESULTS

Benthic community change

The sites showed differential resilience to the bleaching event as reflected in the different trajectories of benthic community change (Fig. 2). The first principle component axis (PCA1) explained 35.9% of the variation among sites and time periods, and differentiated between high coral cover and complexity at positive PCA1 scores, and high macroalgal cover at negative PCA1 scores. The second axis (PCA2) explained 24.4% of the variation among sites and time periods, and differentiated between high rubble and sand at negative PCA2 scores and high rock cover at positive PCA2 scores. In 1994, sites were located at positive values on PCA1 (high coral cover and complexity and low algal cover, mean of 0.35 ±0.14SE). In 2005, following bleaching in 1998, sites had moved varying distances in a negative direction along PCA1 (mean of -0.43 ±0.31SE). By 2011, sites were even more dispersed along PCA1, with some returning to locations on PCA1 that were close to those in 1994, whereas other sites moved further towards the negative end of PCA1 with high macroalgal cover and low coral cover and complexity (mean of -0.57 ±0.45SE) .

Redundancy as an indicator of reef resilience

Change in benthic condition post-disturbance was best explained by a model incorporating the function & size metrics (Table 1A). There was more support for the function & size model incorporating dispersion and evenness than for one solely including dispersion (Table 1B; AICc weight of 0.60). The optimal model explained 26% of the variation in changing benthic condition, with sites with greater dispersion and evenness in 1994 showing greater recovery post-disturbance (larger positive change on benthic PCA1 between 2005 and 2011; Fig. 3).

The outcome of the analyses incorporating fishing pressure was qualitatively similar to those ignoring fishing pressure. Specifically, change in benthic condition post-disturbance was still explained by a model incorporating the function and size metrics (Table S5A), and this model performed less well with the inclusion of fishing pressure (Table S5B). Therefore, fishing pressure was not included in the remaining analyses.

Redundancy as an indicator of response diversity

The evaluation of the maintenance of herbivore function over time, in relation to the best performing redundancy metrics, showed a positive relationship between function & size dispersion in 1994 and herbivore biomass in 1994, 2005 and 2011, suggesting ecosystem function was enhanced (Table 2A; Fig. 4). Sites with low dispersion in 1994 exhibited little change in biomass over time, whereas sites with high dispersion in 1994 exhibited an increase in biomass over time (Fig. 4). In contrast, there was no relationship between function & size evenness in 1994 and herbivore biomass in 1994, 2005 and 2011 (Table 2B).

Patterns of response diversity among size classes indicated a decline in biomass in the smallest size classes following the disturbance, for sites with low, mid and high function & size dispersion in 1994 (Fig. 5). There were concurrent increases in biomass at mid-large size classes for those sites with mid and high dispersion in 1994. This increase was only replicated in some of the mid-size classes at sites with low function & size dispersion in 1994. Post-disturbance (2005-2011) there was considerable variability in biomass trends among sites, however, there were some consistent increases in biomass at small-mid size classes across all sites.

Redundancy over time

There was no evidence of predictable patterns in the redundancy metrics over time. Specifically, there was no relationship between function & size dispersion in 1994 and 2005, 2005 and 2011 or 1994 and 2011 (Table S6A). Similarly, no relationships were found for function & size evenness between the same year combinations (Table S6B).

Discussion

Consistent with the predictions of the cross-scale resilience model (Peterson, Allen & Holling 1998), metrics incorporating the distribution of herbivore biomass across functional groups and size classes (and therefore spatial scales; Nash, Graham & Bellwood 2013), were better predictors of reef recovery than those solely describing the distribution of species' biomass across functional groups. Greater dispersion and evenness of herbivores across size classes and functional groups supported coral recovery after disturbance, whereas sites with low dispersion and evenness were more likely to shift to a macroalgal dominated state. Response diversity was size-based, with small individuals more negatively impacted by the bleaching event. Loss of the function provided by these individuals appears to have been compensated for through increases in the biomass of large individuals. Patterns of cross-scale redundancy were not retained through the disturbance event and had not recovered to pre-disturbance levels by 2011, suggesting fish community regeneration may take several decades or may follow new trajectories.

Redundancy as an indicator of response diversity and reef resilience

Conservation of the herbivore function through time was a consequence of the breadth of responses by different sized individuals to the bleaching. The proximate driver of decline in small individuals is likely to be habitat loss, in particular the collapse of coral skeletons following coral mortality (Bellwood *et al.* 2006; Graham *et al.* 2006). An increase in large bodied herbivores may result from the subsequent proliferation of algae, leading to more feeding opportunities and reduced competition (Pratchett *et al.* 2008). Similar declines in small herbivores, coincident with stable or increased abundance of large herbivore following bleaching events, were recorded at Scott Reef in the eastern Indian Ocean (Halford & Caley 2009) and in Fiji (Wilson *et al.* 2008; Wilson *et al.* 2010). Such coherence suggests this is a general response of herbivore communities following extensive coral mortality. Critically, reorganisation of the benthos and coral recovery was reliant on the presence of large herbivores. In contrast, on reefs where recovery was not seen, similar increases in the biomass of large individuals were lacking, presumably due to the scarcity of large herbivores pre-disturbance. The importance of large individuals in recovery is not limited to reefs; in tropical forests large trees that remain after a disturbance may play a central role in renewal (Elmqvist *et al.* 2002).

Large herbivores may also provide greater functional impact, with studies showing that larger individuals remove exponentially more algae (Bonaldo & Bellwood 2008; Lokrantz *et al.* 2008), and have greater functional breadth (Green & Bellwood 2009) than small bodied counterparts. As a consequence, body size of reef fish appears to act as both an effect (prior work) and a response trait (this study). The greater functional impact by large individuals implies that cross-scale redundancy may not prove as effective an indicator of resilience in instances where large rather than small individuals respond negatively to a disturbance. However, Adam *et al.* (2011) provided evidence that very high densities of small herbivores are capable of controlling algal growth and opening space for coral recruitment and recovery. Nevertheless, this uncertainty highlights that cross-scale response diversity needs to be explored among different herbivore species following a wider range of natural and anthropogenic disturbances (Winfree 2013).

Redundancy over time

We found no relationship between redundancy metrics over time. At recovering sites the compensatory increases in herbivore biomass in large size classes maintained the functional impact of this group, but masked the variability in dispersion and evenness at these sites. However, further disturbances that occur either before cross-scale patterns of function return to pre-disturbance levels or where patterns of cross-scale function follow a new trajectory may have different effects to the 1998 bleaching event because: (1) small individuals from large species were depleted and thus the mortality of existing large individuals is unlikely to be fully compensated for by recruits, compromising the long-term viability of populations (Graham *et al.* 2007); and (2) other types of disturbance occurring in the future e.g. cyclones or coastal development, may result in different response capabilities among fish size classes (Graham, Nash & Kool 2011; Winfree 2013).

Work on other isolated Indian Ocean reefs showed recovery of coral cover after twelve years (Chagos Reef; Sheppard *et al.* 2012; Scott Reef; Gilmour *et al.* 2013) following the 1998 bleaching event, but community composition differed to starting conditions. A study on the Great Barrier Reef found that fish communities have not returned to pre-bleaching composition more than 16 years after the 1998 bleaching (Bellwood *et al.* 2012). Thus, it is perhaps not surprising that whilst the Seychelles reefs were showing signs of recovery 11 years after the 1998 bleaching event (Wilson *et al.* 2012), both coral and fish communities were not approaching pre-disturbance composition or cross-scale redundancy across all sites, and indeed may be establishing different long-term configurations. Thus reefs that were resilient to past disturbances may not exhibit the same degree of resilience to future disturbances. Indeed, where cross-scale redundancy of herbivores has declined there is a need for careful management to help sustain the herbivore function into the future.

Management Implications

Our findings indicate that sustaining robust and functional herbivore communities through the maintenance or rebuilding of cross-scale redundancy provides an avenue to support reef resilience and prevent shifts to macro-algal dominated states. Non-random loss of herbivores, following bleaching suggests it is not enough for management actions to support redundancy, they must also conserve the response diversity underpinning this redundancy. This could be achieved by moving beyond strategies aimed at protecting specific species, to management actions that sustain broad size spectra within species.

Protecting large individuals may be difficult as fishing efforts are typically directed at larger-bodied fish (Bellwood, Hoey & Choat 2003; Hawkins & Roberts 2004). A multi-pronged management strategy may best address the impacts of fishing on herbivorous fish communities, blending management approaches such as controls on fishing effort, the types of gears used by fisherman and access rights (Hilborn 2007). Balanced harvesting which distributes fishing effort across size classes and species has been presented as one way of achieving goals aimed at promoting both biodiversity conservation and fishery yields (García *et al.* 2012). Such an approach would assist in supporting specific size classes within species, helping to maintain robust levels of cross-scale herbivore redundancy. However, herbivore redundancy cannot be considered in isolation, other factors related to reef structural complexity, juvenile coral density, nutrient regimes and coral community composition have been shown to influence the resilience of coral-dominated reefs both in the Seychelles and elsewhere (Graham et al. in review; McClanahan *et al.* 2012). Consequently, managers need to employ a suite of strategies to enhance reef resilience, along with controls on fishing.

Despite the apparent importance of cross-scale redundancy as an indicator of reef resilience, we are not advocating specific thresholds for function and size dispersion in herbivore communities for two reasons: (1) There is a need to be cautious about basing management actions on response diversity with respect to a single disturbance type, due to the range of pressures acting on coral reefs and the likely variability in response diversity to different disturbances (Mori, Furukawa & Sasaki 2012); and (2) Cross-scale redundancy needs to be considered in relation to reef context. For example low levels of cross-scale redundancy within specific functional groups may arise due to the evolutionary history of a region, such as relatively low variation in abiotic drivers over time (Walker, Kinzig & Langridge 1999; Bellwood *et al.* 2004), rather than be the result of recent recurrent impacts. Thus setting targets for cross-scale redundancy globally, would not signify baseline conditions in different regions, and are likely to present unattainable objectives in many locations. Nevertheless, our results provide clear evidence that a wide distribution of herbivore biomass among functional groups and size classes increases the resilience of reefs to disturbance, and the cross-scale resilience model provides a promising avenue for coral reef managers developing frameworks for predicting reef resilience..

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Table 1. Model selection comparing the performance of the different redundancy metrics in 1994 as predictors of reef benthic trajectories from 2005 to 2011. A) Step 1 evaluated the performance of the metrics from the functional group and the functional & size approaches, and B) Step 2 evaluated the performance of models combining different metrics arising from the functional & size approach.

Model	K	AICc	Δ AICc	AICc Wt
A				
Functional group & size dispersion + Functional group & size evenness	4	62.2	0.00	0.75
Null	2	64.9	2.70	0.20
Functional group dispersion + Functional group evenness	4	67.7	5.42	0.05
B				
Functional group & size dispersion + Functional group & size evenness	4	62.2	0.00	0.60
Null	2	64.9	2.70	0.17
Functional group & size dispersion	3	65.2	2.96	0.14
Functional group & size evenness	3	65.6	3.42	0.11

Table 2: Models of relationships between herbivore biomass in different years and A) functional & size dispersion, and B) functional & size evenness. Significant relationships are shown in bold. Herbivore biomass was square root transformed to meet model assumptions.

Model	**F**	**P value**	**Adj R_2**
A			
Sqrt Herbivore Biomass 94 ~ Functional group & size dispersion 94	**12.06**	**<0.01**	**0.36**
Sqrt Herbivore Biomass 05 ~ Functional group & size dispersion 94	**8.83**	**<0.01**	**0.28**
Sqrt Herbivore Biomass 11 ~ Functional group & size dispersion 94	**7.96**	**0.01**	**0.26**
B			
Sqrt Herbivore Biomass 94 ~ Functional group & size evenness 94	3.89	0.06	0.17
Sqrt Herbivore Biomass 05 ~ Functional group & size evenness 94	2.48	0.13	0.07
Sqrt Herbivore Biomass 11 ~ Functional group & size evenness 94	1.44	0.24	0.02

Figure 1. Responses to a disturbance event predicted by the cross-scale resilience model, showing the proposed influence of A) high herbivore functional redundancy (multiple species providing the same role) and B) high herbivore functional and cross-scale redundancy (multiple species providing the same role but at different spatial scales as indicated by variable body sizes) on community response diversity, leading to either reef recovery or decline. Both communities have the same total herbivore biomass and functional diversity prior to disturbance. Red arrows indicate a disturbance event (e.g. coral bleaching) and black arrows indicate reef trends post-disturbance.

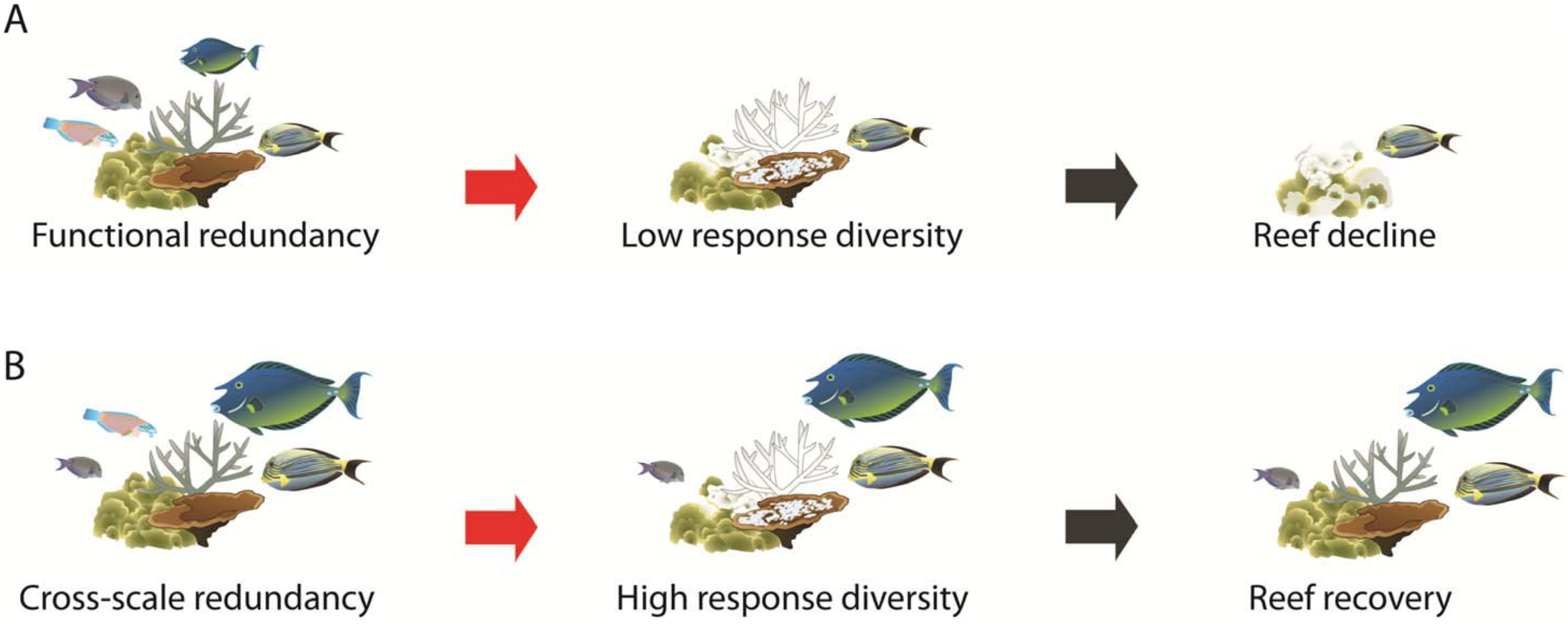
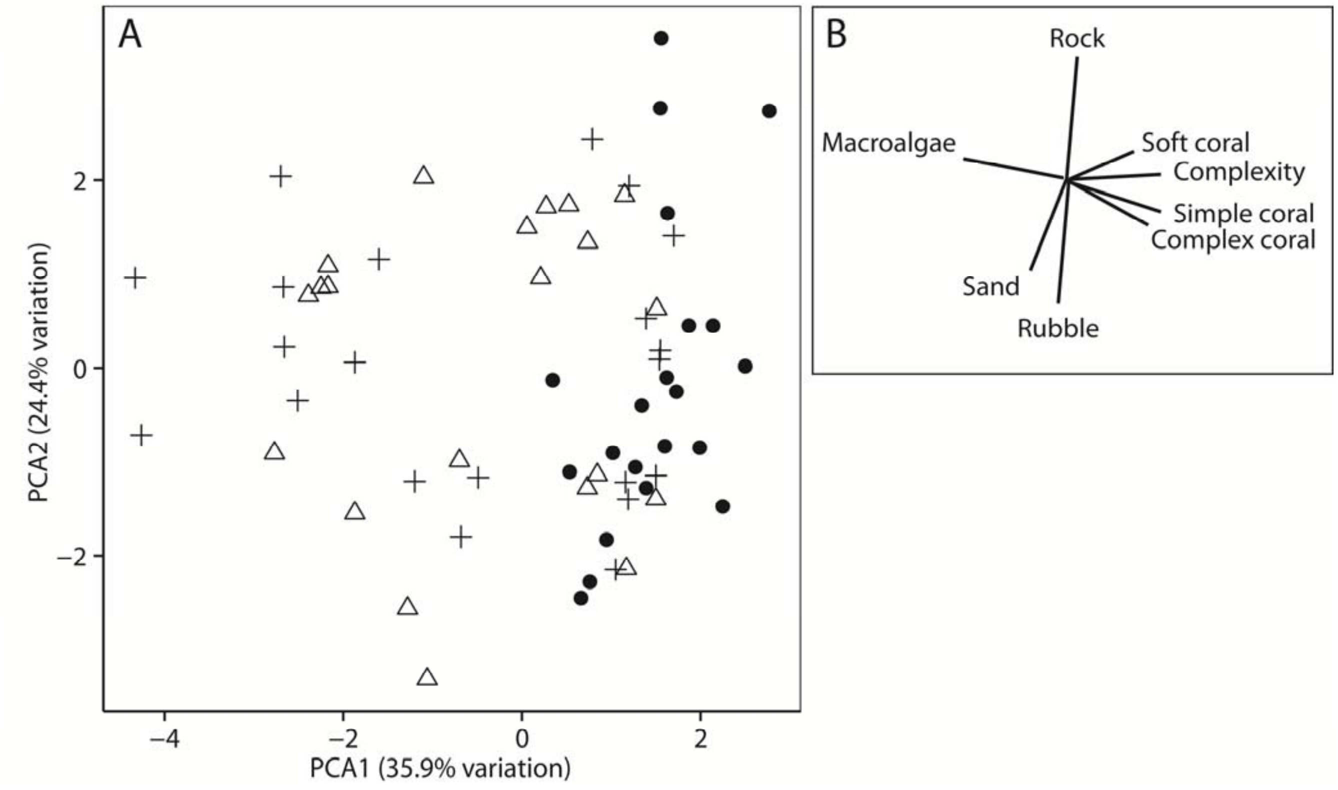


Figure 2. Principal component analysis of benthic habitat variables in 1994 (circles), 2005 (triangles) and 2011 (crosses). A) Variation in the benthic habitat among sites shown for the first two axes of a principal component analysis. B) Relative contribution of the benthic variables to the variation in benthic condition.



615 **Figure 3.** The relationship (±SE) between change in benthic condition (position on PCA1) from 2005 to 2011 and A) function & size dispersion

616 and B) function & size evenness. $F_{2,18} = 4.51$; p=0.03; Adj. $R^2 = 0.26$.

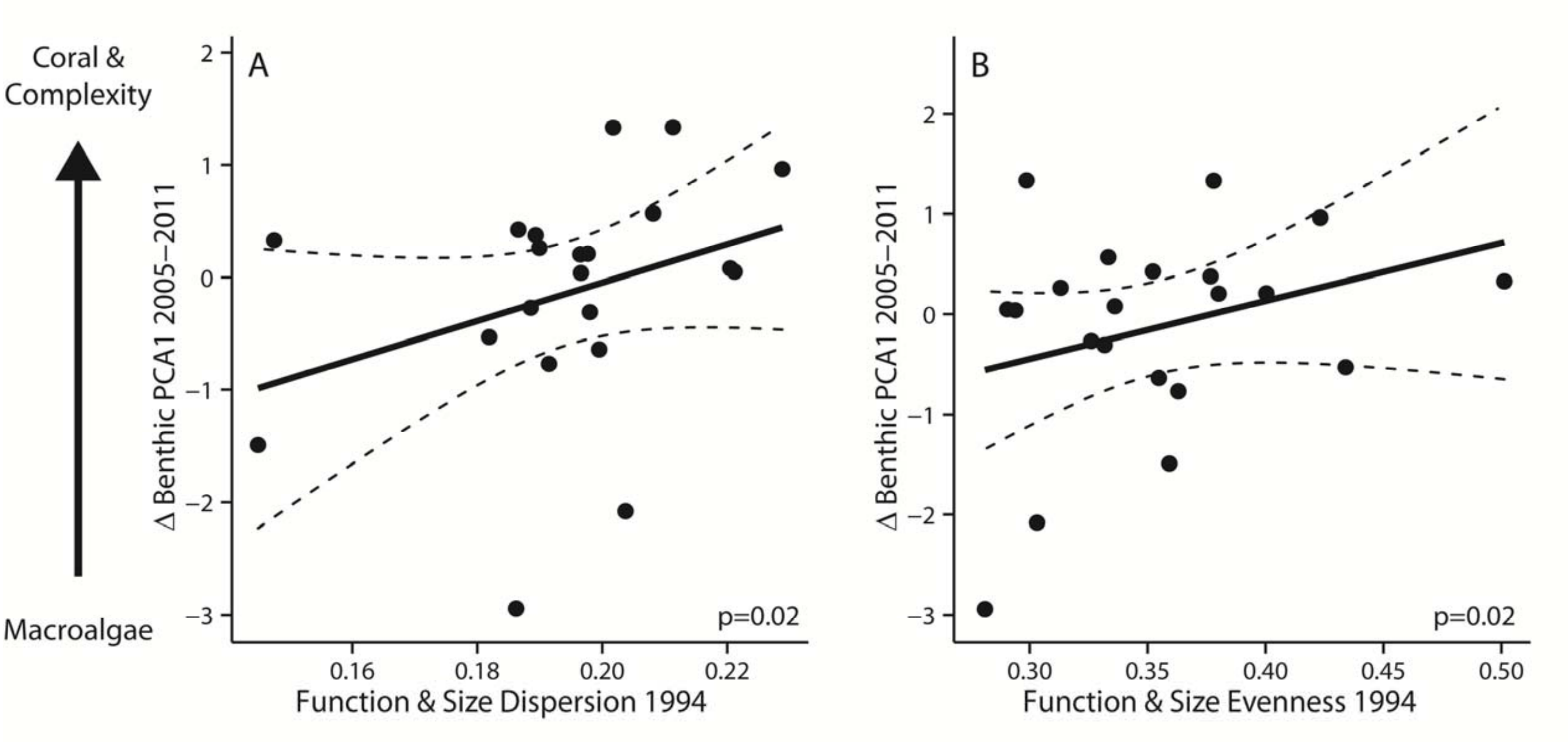


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Figure 4. Relationships between log herbivore biomass in 1994 (circles, solid line), 2005 (triangles, dashed line) and 2011 (crosses, dotted line) and function & size dispersion in 1994.

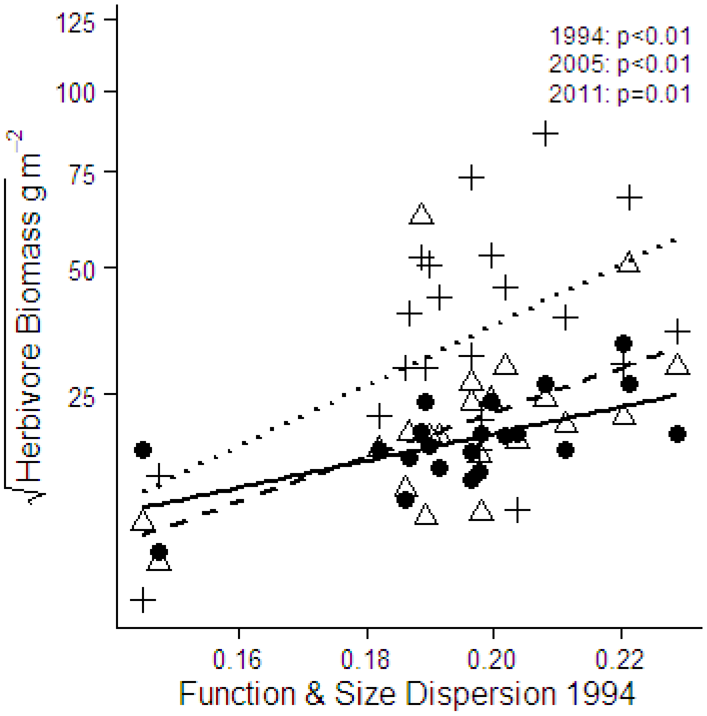

Figure 5. Mean change (±95% CI) in herbivore biomass within size classes between 1994-2005 and 2005-2011 for sites with low, mid or high functional & size dispersion in 1994. Red crosses represent confidence intervals that are significantly different from zero. Note, change in biomass for large size classes may be driven by few individuals due to their large mass, e.g. non-significant decline of individuals >65cm between 1994 and 2005 at sites with high function & size dispersion is driven by loss of 1 large individual.