LETTER

Low functional redundancy in coastal marine assemblages

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Abstract

The relationship between species and functional diversity remains poorly understood for nearly all ecosystem types, yet determining this relationship is critically important for developing both a mechanistic understanding of community assembly and appropriate expectations and approaches to protecting and restoring biological communities. Here we use two distinct data sets, one from kelp forests in the Channel Islands, California, and one from a global synthesis of marine reserves, to directly test how variation in species diversity translates into changes in functional diversity. We find strong positive relationships between species and functional diversity, and increased functional diversity of fish assemblages coinciding with recovery of species diversity in marine reserves, independent of the method used for classifying species in functional groups. These results indicate that low levels of redundancy in functional species traits exist across a suite of marine systems, and that fishing tends to remove whole functional groups from coastal marine ecosystems.

INTRODUCTION

Human impacts on the marine environment are causing widespread local and regional extirpation of species (Dulvy *et al.* 2003) and dramatic shifts in the relative abundances of remaining species (Jackson *et al.* 2001; Myers & Worm 2003; Pandolfi *et al.* 2003). These alterations of the diversity and structure of marine communities can disrupt the ecological functions that species assemblages perform (Hughes *et al.* 2003). For example, reduced abundances of herbivorous fishes through fishing, followed by mass mortality of the herbivorous sea urchin *Diadema antillarum* in the early 1980s most likely caused the switch from coral to algal-dominated reefs documented in Jamaica (Hughes 1994). The sequential near-elimination of species performing similar functions, in this case the control of macroalgal growth, reduced the resilience of these ecosystems to intervening disturbances. In particular, rapid algal growth and space pre-emption prevented coral recovery following hurricane disturbance (Hughes 1994).

Unexpected consequences of biodiversity loss for marine ecosystem functioning highlight the importance of under-standing how structural properties of marine communities, such as the number, identity, and relative abundance of species, are related to the ecological functions performed by individual species and species groups. However, to date, the degree to which taxonomic and functional diversity are correlated is unknown for most ecosystems (Naeem 2002).

The strength and the shape of the relationship between taxonomic and functional diversity depend on the extent of ecological redundancy within the assemblage, i.e. the number of taxonomically distinct species that exhibit similar ecological functions (Walker 1992, 1995; Lawton & Brown 1993; Naeem 1998). For example, some species of roving herbivorous parrotfishes (Scaridae) may be functionally equivalent, and therefore interchangeable, in their effects on algal productivity and standing crops on coral reefs. In contrast, only two of 27 species of parrotfish in the Great Barrier Reef are reef bioeroders, consuming algae, live corals, and structural reef carbonates (Bellwood *et al.* 2003). The loss of bioeroding parrotfishes may have dramatic effects on carbonate accumulation on reefs (Bellwood *et al.* 2003). Functional categorization of marine species can be a useful approach for comparing communities over large
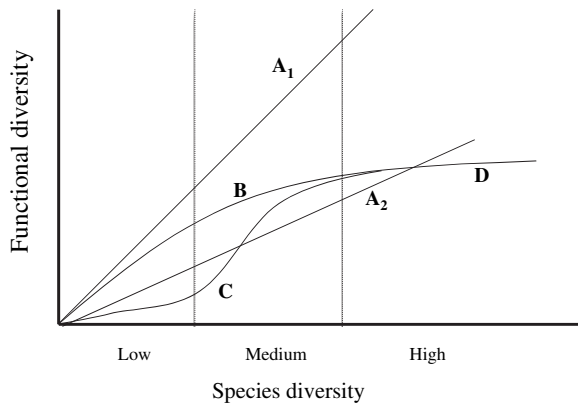
Figure 1 Schematic of possible relationships between functional and species diversity within three levels of diversity at which communities have been arbitrarily delimited: low, medium, and high diversity. In scenarios A, functional diversity increases linearly with increasing species diversity, regardless of diversity level (although it would likely reach a plateau at high diversity levels). In scenario A_1, each species plays a unique functional role (slope = 1), whereas multiple species have similar functional traits in A_2, (slope < 1). In scenario B, functional diversity increases at declining rates with increased species diversity, and reaches an asymptote at high diversity levels (D). Scenario C depicts high functional redundancy at low species diversity followed by rapid increase at intermediate species diversity, until functional diversity asymptotes at high diversity levels (D).

scales in a way that transcends taxonomic boundaries, and for linking changes in structure to effects on ecological function (e.g. Bellwood *et al.* 2003; Floeter *et al.* 2004).

Depending on the extent to which different species exhibit similar functional traits, we would expect different relationships between taxonomic and functional diversity (Fig. 1). At one extreme, each species performs a unique function, resulting in a linear, positive relationship between taxonomic and functional diversity with a slope of 1 (Fig. 1, curve A_1). If multiple species perform similar functions, the relationship between taxonomic and functional diversity will have a shallower slope (Fig. 1 curve A_2) or will be non-linear. In particular, functional diversity may increase rapidly at low diversity levels if new species have functional traits not already represented in the community and subsequently increase at declining rates (Fig. 1, curve B). Another biologically plausible scenario is depicted in curve C, where functional diversity remains low at low levels of species diversity. This might occur, for example, if disturbance leads to the persistence of a subset of species sharing a limited number of specific functional traits. When conditions change, species addition leads to the addition of unique functions represented only at higher diversity levels (Fig. 1, curve C). For this scenario to occur, addition or loss of species would occur in a particular order, depending on

species' traits, rather than randomly. Finally, at high diversity levels new species would be functionally similar to species already present, causing functional diversity to increase asymptotically with increasing species diversity (Fig. 1, curve D). At what level of diversity this asymptote may occur remains a critical question for both ecology and conservation.

Most ecological research has relied on trophic groups as a classification scheme for defining functional groups, although multivariate methods that allow for continuous rather than discrete functional classifications have recently been developed (e.g. Petchey & Gaston 2002; Petchey *et al.* 2004). Functional classifications of species are not without their limitations, regardless of the method used (Naeem & Wright 2003). The relationship between taxonomic and functional diversity, and the sensitivity of functional diversity to species losses, is dependent on the number of functional traits or groups considered (Fonseca & Ganade 2001; Petchey & Gaston 2002). Thus, all methods are sensitive to the identity and specificity of the traits or functions chosen – if every species is assigned a unique set of functional traits, then species and functional diversity will be perfectly correlated (Naeem & Wright 2003). Furthermore, some functions may be more important than others for regulating community and ecosystem dynamics, suggesting the need for a weighting system (Petchey & Gaston 2002). However, weighting functional groups according to their importance requires knowledge of the interaction strengths between all pairs of species in a community. Unfortunately, such knowledge is unavailable for most, if not all, natural assemblages. Thus, using a weighting system for functional groups may introduce additional subjectivity and arbitrariness to functional classifications. Because of the limitations inherent in functional classifications, research on the relationship between species and functional diversity must also evaluate the sensitivity of results to the classification scheme used for functional groups (or in the cases of continuous measures of functional diversity, functional traits).

Determining the strength and shape of the relationship between taxonomic and functional diversity has important implications for predicting the consequences of disturbances and management interventions on the functioning of marine ecosystems. Low ecological redundancy implies that functional traits are rapidly lost from a system as diversity declines (Fig. 1, curves A–C). In contrast, high redundancy would indicate that ecosystem functions are robust to changes in diversity, possibly along the trajectory of both degradation and recovery (Fig. 1, curve D).

In recent years, marine protected areas (MPAs) have received increasing attention as a means of conserving marine biodiversity and restoring degraded marine ecosystems (National Research Council 2001; Palumbi 2002).

Networks of MPAs are currently designed in a variety of marine settings (e.g. the Great Barrier Reef, Australia, the Channel Islands, California, and Baja California, Mexico; Sala *et al.* 2002; Airamé *et al.* 2003; GBRMPA 2004) based on the objective of maximizing representation of habitat and species within the network (Possingham *et al.* 2000). It is assumed that protection of representative components of the biodiversity of a region will maintain or restore the ecological functioning of the ecosystem as whole, including its productivity and resilience to disturbance (Hughes *et al.* 2003). Moreover, a recent synthesis of studies evaluating the effects of MPAs on species assemblages documented increased species richness within reserves (Halpern 2003). Thus, the metric of biodiversity most commonly used in the design and evaluation of MPAs is taxonomic diversity. However, unless taxonomic and functional diversity are strongly correlated, taxonomic diversity will not serve as a surrogate for functional diversity (e.g. Possingham *et al.* 2000; Naeem 2002).

Here we used data from ongoing monitoring of rocky reef communities at 16 sites within the Channel Islands, CA, USA, and data we compiled from studies of MPAs from 31 temperate and tropical locations to examine relationships between taxonomic and functional diversity. Specifically, we asked: (1) What is the relationship between species and functional diversity in coastal marine assemblages? and (2) How do changes in species diversity in response to natural variability or human intervention affect functional diversity?

METHODS

Temperate rocky reefs: Channel Islands, CA

From the database developed as part of the kelp forest monitoring program (KFM; Davis *et al.* 1997) at the Channel Islands, CA, USA, we extracted the densities of 49 species, including four algae, 30 invertebrates, and 15 fishes, that were measured via permanent band-transects or randomly placed quadrates along a transect at 16 different rocky reef sites around the five Channel Islands that are part of the National Park (see Davis *et al.* 1997 for details on survey methods). Data from 1986 to 2003 were used to calculate species and functional richness and diversity.

Species were classified into functional groups as listed in Table 1. Algal species were classified as either the giant kelp *Macrocystis pyrifera* or the other fleshy algae. *Macrocystis pyrifera* was treated as its own functional group because of the dominant and unique role it plays in creating and structuring kelp forest communities. Invertebrates were classified as herbivorous, predatory, omnivorous/scavenger, or planktivorous, and fish were classified as planktivorous, herbivorous, fish that eat large invertebrates (e.g. sea urchins), two groups of fish that eat small invertebrates

Table 1 List of species and functional groups from the kelp forest monitoring program (KFM) in the Channel Islands, CA, USA

Autotrophs

Fleshy algae
  Eisenia arborea, Pterygophora californica, Laminaria farlowii
Giant kelp
  Macrocystis pyrifera

Invertebrates

Herbivorous invertebrates
  Strongylocentrotus purpuratus, Strongylocentrotus franciscanus, Lytechinus anamesus, Haliotis corrugata, Haliotis rufescens, Haliotis fulgens, Lithopoma undosum, Megathura crenulata, Aplysia californica
Omnivorous/scavenger invertebrates
  Parastichopus parvimensis, Asterina miniata, Cypraea spadicea
Sessile planktivorous invertebrates
  Crassedoma giganteum, Stylaster californica, Urticina lofotensis, Corynactis californica, Balanophyllia elegans, Serpulorbis squamigerus, Astrangia lajollaensis, Lophogorgio chilensis, Muricea fruticosa, Tethya aurantia, Diaperoecia californica, Phragmatopoma californica, Dioptra ornata, Styela montereyensis
Predatory invertebrates
  Pisaster giganteus, Pycnopodia helianthoides, Kelletia kelletti, Panulirus interruptus

Fishes

Herbivorous fish
  Girella nigricans
Planktivorous fish
  Chromis punctipinnis, Sebastes mystinus
Mobile small-invertebrate-eating fish
  Embiotoca jacksoni, Embiotoca lateralis, Oxyjulis californica, Damalichthys vacca, Hypsypops rubicundus, Alloclinus holderi,
Territorial small-invertebrate-eating fish
  Rhinogobiops nicholsii, Lythrypnus dalli
Large-invertebrate-eating fish
  Semicossyphus pulcher
Invertebrate-eating fish/piscivores
  Sebastes serranoides, Sebastes atrovirens, Paralabrax clathratus

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(e.g. small molluscs), and invertebrate feeders/piscivores (preying upon both fish and invertebrates). There were no strict piscivores in the data set. The mobility of species (see Species and functional diversity in MPAs) was incorporated as a functional trait implicitly for the invertebrates (all planktivores are sessile while all other invertebrates are mobile) and explicitly for the fishes by dividing the fish that eat small invertebrates into territorial and mobile groups. Fishes in the other trophic groups are all of similar mobility. The size of a species was not included as a functional trait since results from the MPA data set indicate the trophic group and mobility are a sufficient set of traits for capturing true functional groups (see Results and Recovery of species and functional diversity in MPAs).

Species and functional diversity in MPAs

We searched the literature for field studies that examined responses of multi-species assemblages to protection within no-take marine reserves. We included studies where abundances or biomass within no-take reserves were reported at the species level and had been compared with reference conditions, determined from spatial reference sites or measurements before the reserve establishment. Data from 20 studies, conducted at 31 different locations, were included in these analyses. Only three studies compared fish assemblages before and after reserve establishment. In a majority of studies, fish assemblages within no-take reserves were compared with assemblages at fished reference sites. Between 10 and 134 fish species were counted in each study. The final data set comprised a total of 376 fish species, belonging to 62 families (see summary table in Supplementary materials, and Micheli *et al.* (2004), for a full description of this data set).

We selected three different functional traits of species based on biological knowledge of species characteristics that are key to determining their role within coastal marine assemblages, as well as their responses to disturbance. These included trophic group, size, and adult mobility. A species' trophic group, in combination with its size, is a determinant of that species' role in energy transfer within a food web and in controlling other species within the assemblage. A species' mobility is likely correlated with species' responses to local disturbances, such as habitat destruction from storms or trawling, and a species' ability to recolonize a depleted site from distant sources.

Each species was assigned to one of seven trophic groups (herbivores, detritivores, omnivores, planktivores, invertebrate feeders, invertebrate feeders/piscivores, and piscivores), one of four size classes (≤ 25, 25–50, 50–100, and > 100 cm, based on maximum standard lengths), and one of three mobility categories (sedentary or territorial, roving, and highly mobile or migratory). Information about the diets, trophic levels, reported lengths, and habitat use and mobility of individual species were obtained from *FishBase* (Froese & Pauly 2003).

Assignment of species to combinations of these three functional traits resulted in a large number of functional groups represented in each assemblage (up to 23 in temperate rocky-reef studies, and up to 27 in coral reefs). System-specific knowledge of the functional role of species in ecosystem processes would allow pooling some of our functional groups into broader categories – for example Bellwood *et al.* (2004) identified 14 functional groups in coral reef fish assemblages. In this study, we used combinations of functional traits to allow for comparisons across a suite of different ecosystem types. To determine whether results were robust across a range of different functional categorizations of species, we examined relationships between responses of taxonomic and functional diversity to protection in MPAs for functional groups resulting from different combinations of the three functional traits considered (see Data analyses).

Data analyses

For each site-time combination (16 sites, 18 years) in the KFM database and for each study in the MPA data set, we calculated species richness and species diversity (as the Shannon–Wiener diversity index) and functional richness (i.e. the number of functional groups) and functional diversity (i.e. the Shannon–Wiener diversity calculated on species abundances pooled by functional group). Previous studies have quantified functional diversity as functional richness and Shannon–Wiener diversity. In particular, Stevens *et al.* (2003) found that these diversity measures were correlated but captured unique aspects of variation in diversity. For the KFM database, we averaged all temporal values of richness and diversity per site to evaluate the relationship between species and functional diversity across space, but used each site-time measure to evaluate how functional diversity changes as species diversity changes. For the former analyses, we could then examine the relationships between species and functional richness or diversity using regression models. Models were compared (e.g. linear vs. logarithmic vs. exponential) using the associated R^2 values. For the latter analyses, we calculated the natural log of the ratio of richness and diversity values from year t over year t-1 (response ratios, ln R; Gurevitch & Hedges 1993; Osenberg *et al.* 1997; Hedges *et al.* 1999).

Response ratios were also used to compare richness and diversity values within marine reserves to reference conditions in the MPA data set. Positive response ratios indicate that the assemblage had greater diversity the next year (KFM data set) or within reserves (MPA data set), whereas negative values are indicative of greater diversity the previous year (KFM data set) or in reference conditions (MPA data set). In some cases in the MPA data set, separate comparisons had been conducted within different habitat types and depth strata within each study. Comparisons between reserves and reference conditions conducted in different habitat types or depth strata were kept separate in this meta-analysis because sampling had targeted different assemblages. Thus, separate response ratios were calculated for each comparison, resulting in 40 separate comparisons of richness or diversity between no-take reserves and reference conditions.

For the MPA data set, we repeated all analyses for different combinations of three functional traits considered to evaluate whether our results were robust to the criteria used for assigning species to different functional groups.

Combinations tested included: trophic group × size class × mobility category (up to 27 different functional groups per study, each including 1–18 species, *average* = 1.8); trophic group × size class (up to 17 functional groups, with 1–25 species per group, *average* = 2.4); trophic group × mobility category (up to 15 functional groups, with 1–28 species per group, *average* = 2.8); and trophic group (up to seven functional groups, with 1–42 species per group, *average* = 5.1). We did not examine whether results were robust to different functional group assignments in the KFM data set. This data set focused on a single ecosystem type (kelp forests) at a single location, and extensive natural history information from expert opinion and literature searches allowed for robust functional group assignment.

To determine which functional groups are more strongly impacted by fishing, and therefore which groups may recover within no-take reserves, we examined variation in species numbers across functional groups in the studies in the MPA data set. We focused on studies that were conducted in reef ecosystems because sample size for other ecosystems was too small to allow cross-study comparisons. Average numbers of species were calculated for each functional group from studies conducted in coral ($n = 18$ comparisons) and temperate rocky reefs ($n = 19$ comparisons) separately to remove potential latitudinal biases.

RESULTS

Spatial and temporal patterns in species and functional diversity in rocky reef assemblages

There was a significant and positive relationship between species and functional richness ($F = 11.01$, d.f. $= 14$, $P = 0.005$, linear $R^2 = 0.44$, slope $= 0.16$; Fig. 2a) and species and functional diversity ($F = 33.8$, d.f. $= 14$, $P < 0.0001$, linear $R^2 = 0.71$, slope $= 0.97$; Fig. 2b). In both cases, linear, log linear, and exponential models explained similar amounts of variation in the data (richness: log linear model, $R^2 = 0.43$, exponential model, $R^2 = 0.44$; diversity: log linear model, $R^2 = 0.71$, exponential model, $R^2 = 0.72$). The relationship between changes in species and functional richness, calculated as the change from 1 year to the next at each site, was also positive and significant ($F = 79.08$, d.f. $= 270$, $P < 0.0001$, $R^2 = 0.23$, slope $= 0.42$; Fig. 3a). Similarly, year-to-year changes in species and functional diversity were also significantly related, but there was very low explanatory power in the relationship ($F = 7.39$, d.f. $= 270$, $P = 0.007$, $R^2 = 0.03$, slope $= 0.44$; Fig. 3). Changes in richness were due to the presence/absence of only a subset of species (approximately half); the other species were present in almost every site-year combination. In some cases, decreases in species richness or diversity led to increased functional richness/diversity, and vice-versa
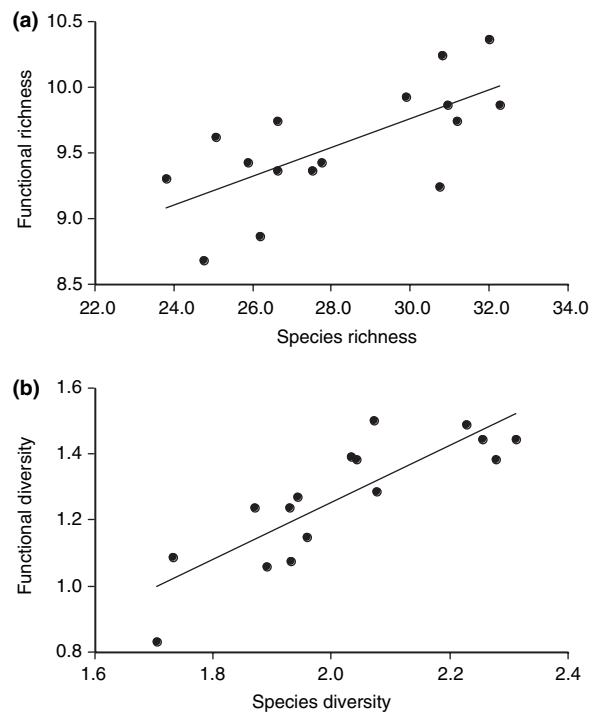

Figure 2 Relationship between functional and species richness (a), and functional and species diversity (b) across 16 rocky-reef locations sampled throughout the Channel Islands, CA. Each data point is the average richness or diversity over the 18 years of monitoring, at each of 16 rocky-reef locations.

(Fig. 3). These responses result from changes in community composition, i.e. from the simultaneous addition and loss of species from different functional groups. For example, the loss of two species from a functional group, without loss of the whole group, accompanied by the addition of one species to a different functional group would result in the overall loss of one species but the overall gain of a functional group. However, the positive and significant relationships between year-to-year fluctuations in taxonomic and functional diversity indicate that most commonly the addition (or loss) of species coincided with net increases (or decreases) of functional diversity.

Recovery of species and functional diversity in MPAs

There was a significant, positive relationship between responses of species and functional richness to protection in no-take marine reserves (quantified as *ln R*), indicating that enhanced species richness in reserves (e.g. Halpern 2003) results in greater functional richness across this diverse set of ecosystems ($F = 88.6$, d.f. $= 39$, $P < 0.001$, $R^2 = 0.70$, slope $= 0.83$; Fig. 4a). These results were robust to using different criteria for assigning species to functional groups. The amount of variation explained by the
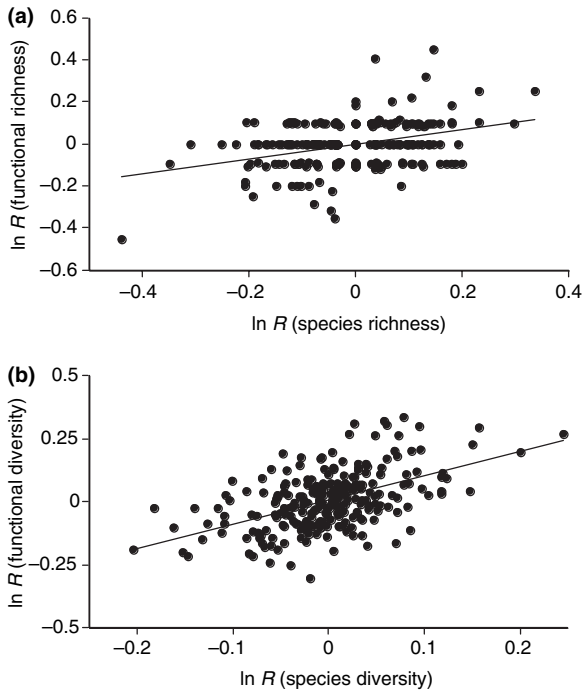
Figure 3 Relationship between year-to-year fluctuations in functional and species richness (a) and diversity (b) across 16 rocky-reef locations sampled throughout the Channel Islands, CA. Year-to-year changes in richness and diversity are quantified as the natural log of the ratio between richness or diversity in a given year vs. the previous year (*ln R*).

Figure 4 Relationship between responses of functional and species richness (a) and diversity (b) to protection in no-take marine reserves. Responses to protection are quantified as the natural log of the ratio between richness or diversity within no-take reserves and in reference conditions (*ln R*), for different sets of functional groups: trophic groups (*n* = 7 groups), and combinations of trophic groups with mobility (*n* = 15), size (*n* = 17), and mobility and size categories (*n* = 27).

relationship increased with increasing numbers of functional groups, but relationships were significant and positive in all cases, with nearly identical slopes in all cases except for trophic groups (trophic groups: $R^2 = 0.35$, slope = 0.55, $P < 0.001$; trophic group × mobility: $R^2 = 0.49$, slope = 0.83, $P < 0.001$; trophic group × size: $R^2 = 0.63$, slope = 0.78, $P < 0.001$; Fig. 4a). Significant, positive relationships were also observed between responses of species and functional diversity, quantified as the Shannon–Wiener diversity index ($F = 175.6$, d.f. = 39, $P < 0.001$, $R^2 = 0.82$, slope = 1.1, $P < 0.001$; Fig. 4b), and were robust across different sets of functional groups (trophic groups: $R^2 = 0.32$, slope = 0.77, $P < 0.001$; trophic group × mobility: $R^2 = 0.59$, slope = 0.98, $P < 0.001$; trophic group × size: $R^2 = 0.80$, slope = 1.1, $P < 0.001$; Fig. 4b). In some cases, simultaneous loss and addition of species resulted in decreases in species richness or diversity coinciding with increased functional richness or diversity, and conversely increases in species richness or diversity being accompanied by decreases in functional richness or diversity (Fig. 4). However, these compositional changes did not influence the overall positive relationships between response ratios, indicating that net increases (or
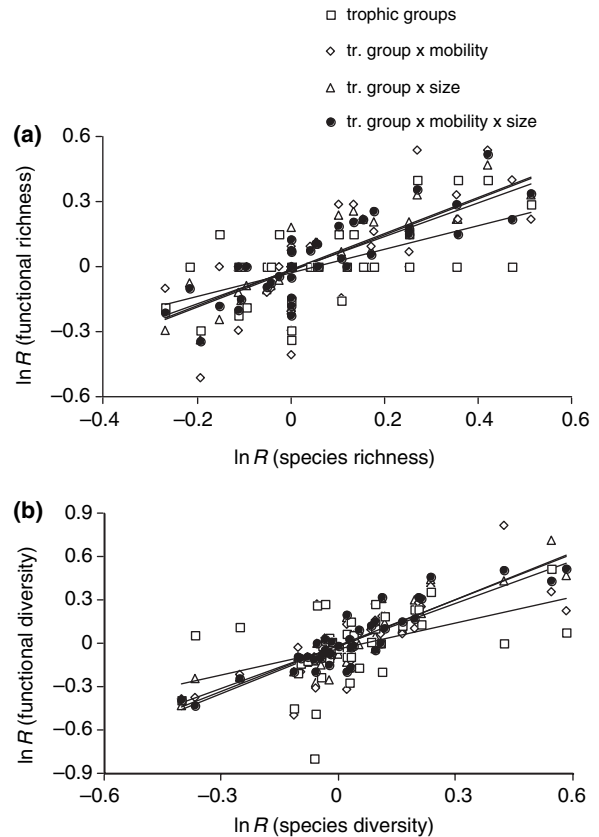
decreases) in both species and functional richness and diversity tended to be prevalent.

When species were assigned to functional groups based on their trophic group, size, and mobility, the highest redundancy was observed among territorial and roving herbivores, and territorial planktivores and invertebrate feeders on coral reefs, and in roving invertebrate feeders on temperate rocky reefs, in all cases smaller than 50 cm in maximum reported length (Fig. 5). Over half of the functional groups were comprised, on average, of one species or less, particularly among herbivores and detritivores in rocky reefs and invertebrate feeders/piscivores and piscivores in both rocky and coral reefs (Fig. 5). Average numbers of species within functional groups were greater in no-take reserves compared with fished areas for 23 of a total of 41 functional groups across all coral reef studies (reserve: average = 2.3 + 2.5 SD; fished areas: average =

Figure 5 Average numbers of species within functional groups from MPA studies of coral reefs (a) and temperate rocky reefs (b). Functional groups are combinations of seven trophic groups: HB, herbivores; DT, detritivores; OM, omnivores; PK, planktivores; IV, invertebrate feeders; IP, feeding both on invertebrates and fishes; PI, piscivores; three mobility classes: sedentary or territorial (1, 3, 6, 9, 15, 17, 19, 20, 23, 26, 29, 32, 34, 36, 37, 39, 42, 45–46, 48, 51); roving (2, 4, 7, 8, 10–12, 14, 16, 18, 21, 24, 27, 30, 33, 35, 38, 40, 43, 47, 49, 52); highly mobile or migratory (5, 13, 22, 25, 28, 31, 41, 44, 50, 53); and four size classes: ≤ 25 cm (1, 2, 9, 10, 15, 16, 20–22, 26–28, 36, 45); 25–50 cm (3–5, 11, 17–18, 23–24, 29–31, 37, 38, 46, 47), 50–100 cm (6, 7, 12, 13, 19, 32, 33, 40, 41, 48–50), and > 100 cm (8, 14, 34, 35, 42–44, 51–53) in maximum reported length.
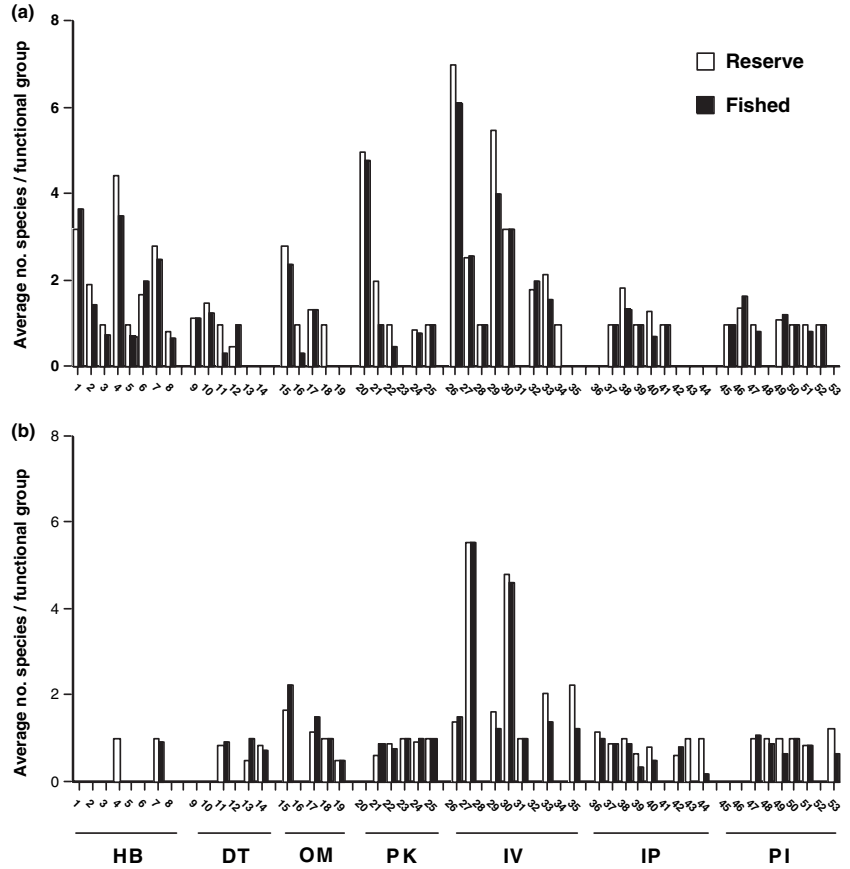
2.0 + 2.2 SD, $n = 18$ comparisons) and 17 of 33 functional groups in temperate rocky reefs (reserve: *average* = 1.6 + 1.6 SD; fished areas: *average* = 1.5 + 1.7 SD, $n = 19$ comparisons) (Fig. 5).

Species recovery in reserves resulted in the addition of whole functional groups across different studies (Figs 4 and 5). In particular, a suite of functional groups were represented within no-take reserves but not in fished areas in multiple studies. On coral reefs, these included some of the herbivores, detritivores, omnivores, planktivores and invertebrate feeders smaller than 50 cm in maximum length, and large (> 50 cm in maximum length) sedentary invertebrate feeders and piscivores. On temperate reefs, functional groups that were present in reserves but not in fished areas across multiple studies included roving or territorial invertebrate feeders/piscivores smaller than 50 cm, and roving or highly mobile invertebrate feeders, invertebrate feeders/piscivores, and piscivores larger than 50 cm in maximum length.

DISCUSSION

It is commonly assumed that changes in species diversity lead to changes in functional diversity, but the relationship between these two community properties remains largely unknown for most ecological systems (Naeem 2002). Here we show that functional richness and diversity are positively related to species richness and diversity in a temperate reef assemblage, and that year-to-year fluctuations in species richness and diversity in this system led to significant, although smaller changes in functional richness and diversity. Moreover, recovery of fish species richness and diversity in marine reserves coincided with increased functional richness and diversity with slopes approaching 1, indicating that low levels of redundancy in functional species traits exist across a suite of different marine systems, and that fishing tends to remove whole functional groups from marine ecosystems.

Responses of species and functional diversity to protection exhibited similar relationships for different functional group categorizations, across a range (15–27) in the number of functional groups used. Only when species were assigned to functional groups based on trophic mode (seven groups) were the slopes of the relationship shallower, indicative of greater functional redundancy within the trophic categories (i.e. smaller changes in functional diversity associated with changes in species diversity) when compared with all other methods of functional categorization. For trophic groups,

many of the response ratios for functional richness and to a lesser extent diversity are 0 along a range of responses in species richness and diversity (Fig. 4).

While the result that functional redundancy decreases with increasing numbers of functional groups or traits considered is not surprising (e.g. Fonseca & Ganade 2001; Petchey & Gaston 2002), it is interesting that adding only an additional trait known to be directly related to functional roles of reef fishes, such as size or mobility, results in relationships that are similar to those obtained with an even finer categorization. Thus, even a relatively parsimonious approach to functional categorization results in patterns consistent with low redundancy of reef fish communities. In contrast, grouping species by trophic group overlooks well known variation in the functional roles of species within a trophic guild, such as the diverse and complementary roles the herbivorous coral reef fishes play in controlling algal standing stocks and reef bioerosion (Bellwood et al. 2004).

These results provide predictions about potential gains and losses in functional diversity associated with marine community assembly (through conservation or succession) and disassembly (through anthropogenic and natural disturbance). Our analyses suggest that small changes in species diversity can have significant impacts on functional diversity, and possibly ecosystem functioning within a community. Results were similar for the KFM and MPA data sets, despite that half of the functional groups in the KFM data set were relatively speciose (3–14 species per group, Table 1), suggesting that changes in functional richness and diversity with species loss may be common even in ecosystems with multiple species (redundancy) within several functional groups.

Strong coupling between species and functional diversity indicates that reef communities may be shaped by competition on ecological and evolutionary scales, resulting in partitioning of resources among component species and relatively low overlap in their functional traits. Resource partitioning among functional groups, combined with fisheries selectivity for species in functional groups that are frequently not the most species-rich (e.g. Bellwood et al. 2004), may explain the significant, positive increase in functional diversity in marine reserves. A suite of functional groups were under-represented at fished locations compared with no-take reserves, particularly large carnivores in both tropical and temperate reefs, and some of the small herbivores, detritivores, omnivores, planktivores and invertebrate feeders on coral reefs. Thus, protection in reserves tended to result in increased representation across different functional categories, including functional groups that have been reported to play key roles in ecosystem processes on reefs, such as top carnivores and herbivores (e.g. Bellwood et al. 2003, 2004; Mumby & Dytham 2005).

These results arise from two distinct data sets, each with its own strengths and limitations. The MPA data set evaluates only responses of fish communities to protection, but comes from both temperate and tropical coastal marine ecosystems from around the world and includes studies where abundances of up to 134 species were quantified. In addition, each study compared no-take reserves with adjacent fished areas, allowing for an examination of the effects of fishing on the taxonomic and functional composition of each assemblage. Thus, the MPA are large-scale 'experiments', examining responses of multi-species communities to protection from extractive uses. By examining changes in taxonomic and functional diversity in response to manipulation of human use, these studies complement existing small-scale manipulations investigating links between diversity and function in marine systems (Stachowitcz et al. 1999; Duffy et al. 2001), and comparative studies of variation in functional diversity conducted over regional scales (Bellwood et al. 2004; Floeter et al. 2004).

In contrast with the MPA data set, the KFM data set focuses on one region and a smaller number of species, but those species include invertebrates and algae, in addition to fish, and sampling methods were standardized across all sites and times. The fact that analyses of these two distinctly different data sets across a breadth of community types gave similar results of significant and positive responses of functional richness and diversity to variation in species richness and diversity suggests our results may be highly general. Interestingly, the slopes for year-to-year variation in richness and diversity in the KFM data set were smaller than for changes associated with protection in MPAs, suggesting that human impacts on reef fish functional diversity are greater than background natural variation.

In the KFM and MPA studies, communities were allowed to naturally assemble, removing many of the potential biases that can be introduced through experimental manipulation. To date, most studies evaluating how changes in species richness and diversity affect functional diversity have used removal experiments that target particular species thought to provide a key function, or simulation experiments that artificially (and usually randomly) assemble communities (Diaz et al. 2003). Although these studies provide critical insights into the functional role of particular species, they are necessarily artificial. It is important to complement experimental analyses with studies that address the relationship between species and functional diversity in naturally assembling communities, such as the one presented here.

Both data sets quantified abundances of a subset of species, thereby preventing an examination of relationships and responses of functional and species diversity over the full range of diversity in these ecosystems. In addition, some species may not be present in the data sets because they

exist only at low abundances, and none of the studies had conducted exhaustive biodiversity surveys. Thus, the species included in the KFM and MPA data sets represent low levels of diversity for these assemblages, across a narrow range of possible species diversity (Fig. 1). Within this limited range, linear and nonlinear models explained similar amounts of variation in the KFM data set and we were not able to distinguish between different types of relationships. Examination of trends in taxonomic and functional diversity over a broader range of diversity is needed to discriminate between linear and nonlinear relationships.

Surprisingly, we found limited functional redundancy even in coral reef ecosystems, which are characterized by relatively high species diversity. This suggests that even ecosystems that have similar functional richness but vary greatly in the amount of species redundancy within those functional groups (e.g. Great Barrier Reef vs. Caribbean; Bellwood *et al.* 2004) may be similarly vulnerable to the loss of key ecosystem processes with small changes in species diversity (Bellwood *et al.* 2003). At even higher levels of diversity, the relationship between species and functional diversity may become flat once all functional roles are represented (Fig. 1). However, even at high diversity levels, variance in the numbers of species performing similar ecological roles may remain high, with some functions exhibiting low redundancy (e.g. Bellwood *et al.* 2003). These alternative predictions can be tested only by studying relatively pristine, highly diverse systems.

Predictions regarding the relationship between species and functional diversity in species-poor ecosystems (Fig. 1, low diversity) are less obvious. If species loss causes equivalent loss across different functional groups, as our results here suggest, then ultimately the relationship between species and functional diversity will have a slope of 1 (each species is a functional group; Fig. 1, line A_1). If instead certain functional groups are more resistant to disturbance than others, low-diversity communities may have few functional groups with many species in each group (the scenario presented in Fig. 1, curve C). Distinguishing between different scenarios is critical to predicting alterations of ecological functions following species losses in degraded systems, and will require combining experimental and comparative approaches with investigations of the consequences of species losses for ecological functions in large-scale 'experiments' associated with natural events or management interventions, particularly studies of how taxonomic and functional diversity are disassembled and re-assembled along trajectories of degradation and recovery of marine ecosystems. Determining which of these relationships holds for different communities remains a fundamentally important question to address, as human disturbance to ecosystems continues to alter diversity patterns.

Management and conservation of marine ecosystems will require a better understanding of how ecological functions are linked to the diversity and identities of species. Such relationships must be examined at both local and regional scales, and across a range of diversity levels and intensities of human impacts. Increased understanding of relationships between species and functional diversity, and between functional diversity and ecosystem functioning will provide guidance for conservation and restoration of marine communities, particularly by identifying vulnerable functional groups, understanding their roles in maintaining ecosystem functioning, and highlighting what species and levels of diversity are needed to maintain functions in different marine ecosystems. Our results offer an important first glimpse at what these relationships may look like, and suggest that these relationships may be general across different types of marine communities.

SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE731/ELE731sm.htm

Table S1 Summary table of MPA studies from which data on responses of species and functional diversity to protection were extracted.

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