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High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs

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A B S T R A C T

Determining how ecosystem function and services are related to diversity is necessary for predicting the consequences of diversity loss and for setting goals and priorities for marine conservation. The consequences of biodiversity loss for ecosystem functions and services depend on the level of functional redundancy – the number of species with similar ecological functional traits. Using field data on fish assemblages from 199 coral reef and lagoon sites from six islands, and on local fisheries from four islands in The Bahamas, we examined levels of functional diversity and redundancy within these assemblages and determined how fish biomass and local fisheries catches vary with local diversity. A majority of functional groups contain few species, suggesting that these assemblages have limited functional redundancy. Most also include species targeted by local fisheries, thus fishing has the potential to broadly impact food webs. Comparisons between a large marine reserve and fished reefs confirm that fishing significantly reduces functional redundancy and removes whole functional groups. Positive exponential relationships of fish biomass and fisheries catches with species and functional diversity highlight that even small declines in biodiversity may result in large reductions in secondary production and seafood provision. Taken together, these results indicate that Caribbean fish assemblages have low functional redundancy and high vulnerability of ecosystem functions and services to diversity loss, and that protection of multi-species assemblages is needed to maintain functions and services.

1. Introduction

The impacts of human activities on marine biodiversity are nearly ubiquitous (Halpern et al., 2008) – causing declines in ecosystem functions, such as productivity and resilience, and the loss of key services (Millennium Ecosystem Assessment, 2005; Worm et al., 2006). However, the generality of a relationship between diversity, functions, and services is still debated (Hooper et al., 2005; Stachowicz et al., 2007; Reich et al., 2012). In particular, the extent of diversity loss that can occur before functions and services are lost (e.g., Loreau et al., 2001; Micheli and Halpern, 2005; Danovaro et al., 2008) is unknown for most marine ecosystems. Determining how ecosystem function and services are related to diversity is necessary for predicting the consequences of diversity loss and for setting goals and priorities for marine conservation.

Functional redundancy within a community (defined as the number of taxonomically distinct species that exhibit similar ecological functions; Walker, 1992; Naeem, 1998) mediates the consequences of diversity loss because the loss of one species, and of its functional role, may be compensated by the persistence of other species with similar functional roles. Thus, a first step for linking

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diversity and function is to examine the relationship between measures of diversity, such as species diversity, functional diversity and redundancy, and measures of ecosystem function and services.

The consequences of diversity loss for ecosystem functions and services are likely dependent on the shape of diversity-function or diversity-service relationships and on the range of diversity over which species are lost or added (Fig. 1). This relationship is expected to be linear with a slope of 1 if each species has a unique functional role (Fig. 1b), or greater if a subset of species can each perform multiple functions. In contrast, multiple species performing similar functions will result in a linear relationship with a shallower slope. Alternatively, measures of ecosystem functions or services may increase rapidly at low diversity levels if new species perform functions not already represented in the community while at higher diversity levels new species may be functionally redundant and the rate of addition slows down (Fig. 1a). Another biologically plausible scenario is where functions or services remain low at low levels of species diversity (Fig. 1c). This might occur, for example, if disturbance leads to the persistence of a subset of species sharing a limited number of functional traits. When conditions change, species addition leads to the addition of functions represented, but only at higher diversity levels. As in Fig. 1a, a plateau is eventually reached in 1c as it becomes increasingly likely that additional species at higher diversity levels are functionally similar to species already present in the community. Under all the scenarios above, species loss will ultimately result in decreasing ecosystem function but the rate and extent of this decrease is greatest for exponential relationships (Fig. 1c), least for saturating relationships (Fig. 1a), and intermediate in the linear case (Fig. 1b).

Few studies have addressed biodiversity-function relationships in marine ecosystems, and even fewer studies have addressed relationships between diversity and services (Raffaelli, 2007).

Experimental manipulations rigorously testing effects of diversity on ecosystem function (e.g., Worm et al., 2006; Stachowicz et al., 2007) are limited because of logistical constraints, and therefore the consequences of diversity loss in high-diversity assemblages are generally unknown (e.g., Micheli and Halpern, 2005; Guillemot et al., 2011). Correlative analyses from natural ecosystems have highlighted both linear and non-linear saturating relationships between marine species and functional diversity (Micheli and Halpern, 2005; Halpern and Floeter, 2008). Exponential relationships between species diversity and ecosystem functions, including biomass, secondary production, and decomposition rates, were reported in the deep sea (Danovaro et al., 2008), and non-saturating relationships between fish biomass and functional diversity were found in a global analysis of coral reef fish assemblages (Mora et al., 2011). Furthermore, linear relationships between taxonomic diversity and variables describing the magnitude and variability of fisheries catches were found in a global analysis conducted at the scale of large marine regions (Worm et al., 2006).

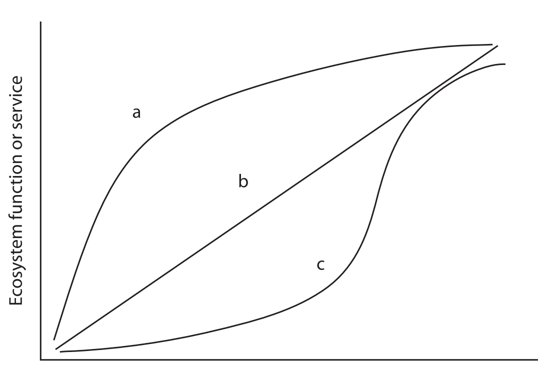

Fig. 1. Possible relationships of functional diversity, ecosystem function and/or services with species diversity (modified from Micheli and Halpern 2005). Depending on levels of functional redundancy within assemblages, functional diversity, ecosystem function or ecosystem services may increase linearly with increasing species diversity (b), or at declining (a), or increasing rates (c). These ecosystem properties are expected to reach a plateau at high diversity levels (a,c).

It is particularly important to examine the shape of diversity-function and diversity-service relationships in coral reefs because they are the most diverse and among the most threatened marine ecosystems (Bellwood et al., 2004; Hoegh-Guldberg et al., 2007; Halpern et al., 2008). Coral reef ecosystems worldwide have undergone significant decline and degradation due to combinations of anthropogenic and natural disturbances, including increases in water temperature and consequent coral bleaching, hurricanes, disease and direct impacts of fishing and coastal development on reef, mangrove, and seagrass habitats (Gardner et al., 2003; Pandolfi et al., 2005; Mora et al., 2011; De'ath et al., 2012). Such impacts have been particularly severe in the Caribbean (Gardner et al., 2003). Lower species diversity and limited functional redundancy of Caribbean reef assemblages, compared to Indo-Pacific reefs, may underlie low resilience in the face of increasing disturbance (Bellwood et al., 2004; Roff and Mumby, 2012). For example, mass mortality of a single sea urchin species, *Diadema antillarum*, and two coral species, the staghorn and elkhorn corals (*Acropora cervicornis* and *A. palmata*) from disease in the 1980s virtually eliminated entire ecological functions, namely the control of macroalgae by invertebrate grazers and the provision of complex three-dimensional habitat by live branching corals (Roff and Mumby, 2012). Under currently low sea urchin abundance, parrotfishes are the key remaining grazers that control macroalgae and allow for coral recovery (Mumby et al., 2006a, 2007), though functional effects of parrotfishes do not completely replace those of urchins across the range of environmental conditions (Mumby et al., 2006b; Korzen et al., 2011).

In this study, we examine levels of functional redundancy and relationships between total biomass, fisheries catches and diversity in fish assemblages of the Bahamian archipelago. Fish species perform critical ecosystem functions on coral reefs and provide key resources to local human communities (Moberg and Folke, 1999; Harborne et al., 2006; Broad and Sanchirico, 2008; Mumby et al., 2008). Because fishing and seafood provisioning are marine ecosystem services of primary interest to many people, and fish diversity, abundance, and biomass are relatively well understood ecological metrics, we utilize these variables as a first step in exploring the empirical relationships among diversity, function, and services in coral reef ecosystems. Specifically, we use data from field surveys of fish assemblages across a suite of habitats to examine (1) the distribution of species across different functional groups and the levels of functional redundancy within these assemblages, (2) the impacts of local extractive activities (i.e., small-scale food and ornamental fisheries) on functional diversity and redundancy, and (3) the significance and shape of the relationship between diversity and fish biomass or fisheries catches in these assemblages.

2. Materials and methods

2.1. Survey methods

We surveyed 199 sites, comprising a total of 12 different habitat types, within island regions of the Bahamian archipelago (Appendix Table A1). Nine to 15 habitat types (e.g., forereef, patch reef, gorgonian plains, seagrass, algal beds, mangrove stands; Table A1) were surveyed within the island systems of Abaco, Andros, Bimini, and San Salvador in The Bahamas and South Caicos in the Turks and