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A framework for measuring coral species-specific contribution to reef functioning in the Caribbean

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ABSTRACT

Species morpho-functional traits provide general and predictable rules to understand the dynamics of ecological communities; therefore, considering species identity is crucial in understanding ecosystem functioning. Here, we propose a framework to estimate the species-specific functional contribution of Caribbean corals according to their capacity to create complex three-dimensional structures by means of calcium carbonate precipitation and their morphological complexity. We use a combination of field data and bibliographic information to integrate a Reef Functional Index (RFI) that considers the calcification rate, structural complexity and abundance (cover) of each coral species. As an example application of this tool, we evaluated various sites along the Mesoamerican Reef showing that the RFI can be used to compare reef sites or communities. The construction capacities of Caribbean coral species are highly variable, thus, different species configurations of a coral community result in a high level of functional variation. Most coral assemblages on the Mesoamerican Reef show non-framework species dominance (e.g. *Undaria* spp. and *Porites astreoides*), compromising reef functioning. However, sites with key reef-building species present showed considerably greater functioning despite those species not being dominant. The functional approximation for coral species proposed can be used by future studies considering changes in coral community composition, keystone species loss or to estimate reef function loss due to climate change or other stressors.

1. Introduction

Assessing ecosystem functioning based on species traits provides general and predictable rules to understand community dynamics, particularly in the context of climate change and biodiversity loss (Haddad et al., 2008; Hooper et al., 2005; McGill et al., 2006); and reveals community responses to natural or anthropogenic disturbances (Mouillot et al., 2013). This is possible as the nature and magnitude of species functional traits can vary considerably (Naeem et al., 1999), and also have variable response capacity, depending on the type and intensity of pressure to which the species are subjected (Darling et al., 2013; Hooper et al., 2005; Okazaki et al., 2017; Pakeman, 2011). Therefore, while species diversity or abundance cannot reliably serve to understand the response of communities to disturbances, a functional trait-based approach can quantify, predict, and better anticipate, the impacts of disturbances on ecological communities (Mouillot et al., 2013). This is particularly important since functional traits are strongly linked to ecosystems properties, such as the role of dominant species, keystone species, ecological engineers, and species interactions such as competition, facilitation, mutualism, disease, and predation (Hooper et al., 2005). In terrestrial ecology, patterns of ecological specialization have been reported in plants using species functional traits, as well as to explain mechanisms such as growth, survival, and reproduction (Díaz et al., 2015, 2004). In marine ecosystems, coral species functional traits have been utilized to examine global patterns of functional diversity and functional redundancy, in order to identify locations and functions where redundancy is critically lacking (McWilliam et al., 2018). This functional approach suggests that there are mechanisms of the species traits, which elucidate ecological and evolutionary processes, and the functioning of species and ecosystems.

Ecosystem structure and function are intrinsically linked to the identity of the species that create habitats (foundation species). In tropical coastal ecosystems, corals are primarily responsible for building the three-dimensional matrix that supports biodiversity and ecosystem services. In coral reefs, functioning depends, to a large extent, on coral life history strategies, which are strongly linked to species

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morphological and physiological attributes (Darling et al., 2013; Denis et al., 2017). In particular, growth rates and structural complexity define the processes of accretion and provision of habitat. Reefs dominated by species with high structural complexity and high growth rates not only maintain more diverse communities but also regulate the functional structure of ecological communities at different spatial scales (Graham and Nash, 2013; Richardson et al., 2017a,b). However, few studies recognize coral species identity and they are generally considered to be a functionally homogeneous group when assessing reef condition or conservation status (Alvarez-Filip et al., 2013; Mouillot et al., 2013; Perry et al., 2012).

The habitat-forming performance of different taxa can be approximated using a number of techniques, including the use of geometric shapes. This approach has been used for estimating phytoplankton biovolume and surface area in transitional water ecosystems (Vadrucci et al., 2013, 2007), in gorgonian and sponge ecology (Santavy et al., 2013), and in coral reef ecology and physiology (Babcock, 1991; Naumann et al., 2009; Szmant-Froelich, 1985). This approach offers important advantages as it is non-invasive and allows rapid data collection. Furthermore, geometric shapes and surface area are basic morphometric descriptors of diverse taxa communities, by which other morphometric and body–size related descriptors can be obtained (*i.e.* biomass, surface-to-volume ratio, length-to-width ratio, size spectra or categorization into morphological functional groups; Vadrucci et al., 2013, 2007). Recent studies propose the integration of information regarding morphology and bio-volume to estimate structural complexity and calcification rates of scleractinian coral species. Alvarez-Filip et al. (2013) estimated the calcification rate of four dominant Caribbean coral genera (*Acropora, Orbicella, Undaria,* and *Porites*) considering the morphology of each genus and assigning them to a geometric shape according to their growth form. Alvarez-Filip et al. (2013) found that calcification and structural complexity varied considerably among the four genera. *Acropora*, which forms branching structures, displayed the highest calcification rate and rugosity, while foliose *Undaria* had the lowest values. Bozec et al. (2015) used morphometric rules to describe the 3D growth of massive Caribbean corals. Santavy et al. (2013) proposed a method to quantify the ecosystem services provided by the physical structural of gorgonians and sponges of the Western Central Atlantic, based on colony morphology and measurements of colony height and diameter in the field and generation of 3D models.

Long-term changes in coral reef functioning have been most evident in the Caribbean (Gardner et al., 2003; Jackson et al., 2014). The rapid loss of coral cover has resulted in a considerable decrease in reef accretion and rugosity coral growth, calcium carbonate deposition and structural complexity (Alvarez-Filip et al., 2011, 2009; Perry et al., 2015), which seriously compromises the functional maintenance of reefs in the future (Alvarez-Filip et al., 2013; Perry et al., 2015). In addition to coral cover loss, Caribbean reefs are also experiencing a change in species composition. The few species responsible for the majority of the structural complexity have been replaced by opportunistic species (Alvarez-Filip et al., 2013, 2011; Green et al., 2008). For example, brooding reproduction species with high population turnover are generally more tolerant to environmental changes, but predominantly form small physical structures that contribute little to reef structural complexity (e.g. *Undaria* spp. and *Porites astreoides*). While branching and massive forms such as *Acropora* spp. and *Orbicella* spp., which contribute greatly to the accumulation of calcium carbonate and reef complexity, are notably less tolerant to environmental changes (Alvarez-Filip et al., 2013; Darling et al., 2013, 2012). The decline in reef structural complexity negatively affects many associated species and directly affects ecosystem processes and services essential to human well-being (Hughes et al., 2017; Jackson et al., 2014; Mumby et al., 2007; Newman et al., 2015; Richardson et al., 2017a,b).

Coral community functioning depends on three fundamental axes of each species present: (1) abundance, generally estimated as a percent cover; (2) capacity to accumulate calcium carbonate (calcification rates); and (3) morphological complexity (Fig. 1). Although some protocols already consider the inclusion of species-specific information to estimate ecosystem functioning (e.g. the Reef Budget; Perry et al., 2008, 2012), they are generally based on intensive fieldwork following specific protocols, making it difficult to estimate the functional potential of sites surveyed with other methods (*e.g.* historical data, simplified monitoring programs used by some MPAs). Here we propose a methodology to complement the efforts made to date, through a theoretical approach based on the morphology, skeletal density and extension (calcification rates), height and rugosity (structural complexity) of each species. We use field and bibliographic data to propose a quantitative coefficient to evaluate reef-building capacity and structural complexity of the most common coral species in the Caribbean Sea. This coefficient in combination with the abundance patterns of the species present in a coral assemblage can be integrated into an index to represent the site functional potential (Fig. 1); which can easily be incorporated in other methodologies. As an example application of this tool we evaluated various sites along the Mesoamerican Reef (MAR) showing that the Reef Functional Index (RFI) can be used to compare reef sites or communities, where, depending on the coral assemblage and dominant species present, site functioning will tend towards one extreme (high or low functioning) (see Fig. 1). We expect that these results will help to better understand the functional status and condition of reefs throughout the Caribbean, as well as being used by researchers, governmental and non-governmental institutions to perform rapid assessments of coral reef condition and explore how reef functional capacity has changed over time using historical data.

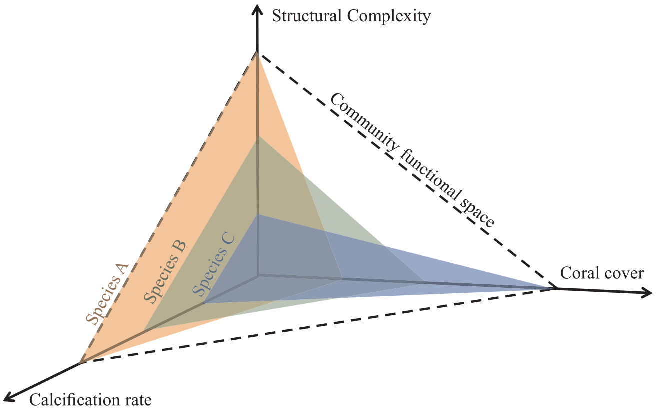

Fig. 1. Caribbean coral community functional space. Each species has three main characteristics represented by the different axes: 1) coral cover, 2) calcification rate (kg $CaCO_3$ m^{-2} yr^{-1}) and 3) structural complexity (given by size and rugosity). Species with different levels of functionality in the ecosystem are exemplified: Individual contributions can vary naturally according to environmental conditions and human pressure (trade-offs). The combination of these three variables represents the effect of each species on the ecosystem. Community functioning is given by the integration of the individual contributions of each species. In this way, the effect of the coral community on the reef-building processes and habitat generation depend not only on the quantity of corals present but also on the traits of each species.

2. Methods

Morphology and growth patterns were used to estimate structural complexity and calcification rates of the 47 most common scleractinian coral species reported in the Caribbean Sea. The species were selected using the ecological census databases of the Atlantic and Gulf Rapid Reef Assessment (AGRAA) (Lang et al., 2010) and Healthy Reefs Initiative (HRI) (McField and Kramer, 2007). To estimate calcification rate and structural complexity we used a combination of published