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Opinion

A Trait-Based Approach to Advance Coral Reef Science

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Coral reefs are biologically diverse and ecologically complex ecosystems constructed by stony corals. Despite decades of research, basic coral population biology and community ecology questions remain. Quantifying trait variation among species can help resolve these questions, but progress has been hampered by a paucity of trait data for the many, often rare, species and by a reliance on nonquantitative approaches. Therefore, we propose filling data gaps by prioritizing traits that are easy to measure, estimating key traits for species with missing data, and identifying 'supertraits' that capture a large amount of variation for a range of biological and ecological processes. Such an approach can accelerate our understanding of coral ecology and our ability to protect critically threatened global ecosystems.

Trends

Characterizing trait variation between species helps quantify fundamental biological, ecological, and evolutionary processes.

Hampered by a paucity of trait data, novel approaches are needed to fill data gaps by prioritizing traits that are easy to measure.

'Supertraits' capture a large amount of process variation. Their discovery will accelerate understanding of coral ecology and our ability to protect a critically threatened global ecosystem.

Trait Data: A Rarity in Coral Reef Science

Coral reefs are ecologically complex ecosystems engineered primarily by stony corals (Scleractinia) that support hundreds of thousands of species [1]. Despite covering less than 0.1% of the global ocean area [2], reefs are important to humans for food, coastal protection, and many other goods and services [3]. Indeed, the ecosystem value of nontradable public benefits per unit area of coral reef is larger than for any other ecosystem [4]. Despite their economic, cultural, and aesthetic value, coral reefs in most regions have been degraded due to human pressures [5,6]. Moreover, reefs are threatened by continuing global exploitation and intensifying climate change [7,8]. However, projections of future coral reef assemblage structure and ecosystem function remain speculative due to a lack of basic biological data at the individual, colony, and population level (Figure 1). For example, a widely cited estimate of the proportion of coral species under threat from climate change was based entirely on **expert opinion** (see Glossary) of organism **traits** and anecdotal accounts of population declines [9]. Nonquantitative approaches can provide initial insight and highlight fruitful avenues to pursue [10], but should yield swiftly to quantitative approaches that reduce uncertainty.

Understanding the evolution of species, as well as the dynamics of populations and communities in a changing world, depends critically upon robust quantification of differences among species. We argue that progress in coral reef research has been hindered by the limited number of species for which trait data are available [11,12]. Similarly, progress was previously hindered by a poor understanding of scleractinian evolutionary relationships, although substantial ongoing revision of scleractinian taxonomy has now yielded a reliable phylogeny [13] that is transforming our understanding of coral macroevolutionary patterns [14]. Thus, here we review recent examples of trait-based coral research, highlighting in particular how wider quantification of species traits could advance understanding across a hierarchy of scales, from organisms,

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populations, and communities to biogeographical regions and macroevolutionary timescales. We also proffer insights from other fields for resolving knowledge gaps in reef coral science. We conclude by identifying data gaps and conceptual priorities, including a focus on **easy traits**, **trait infilling**, and identifying coral **supertraits** to rapidly advance our ability to understand the drivers and consequences of changing coral species composition on reefs in an era of rapid environmental change.

Organism Biology and Population Persistence

Traits, and their differences among individuals, have strong effects on the organismal and population biology of species. For instance, the energy and nutrients available to an individual are limited, and the way in which energy and nutrients are distributed among various processes, such as growth, reproduction, and maintenance, shape life-history strategies [15]. Advancing knowledge at these scales requires understanding the patterns of energy allocation within individuals, and identifying the key demographic traits that regulate population size and demography. There is no practical way to comprehensively measure demographic trait values for a large proportion of assemblages in species-rich systems, such as coral reefs. Instead, trait infilling can be used to infer demographic trait values from other, more readily measurable traits, such as colony morphology, that constrain and influence demographic rates (Box 1).

More generally, trade-offs among traits influence not only many aspects of organism biology, such as generation times [16], but also responses to disturbance and stress [17]. In many fields, progress in identifying trait trade-offs has been limited because traits are rarely measured in a common currency [18]. Attempts to overcome this measurement inconsistency typically require the use of mathematical models that integrate traits with different units into a common currency. For instance, Silvertown *et al.* [19] used matrix models to recreate Grime's triangle using population growth factor as a common currency for plant traits. Similarly, Madin *et al.* [20] used an integrated biomechanical and photosynthetic model to convert coral species traits, including size and morphology, into the common currency of lifetime reproductive output. A more pragmatic approach is to search for supertraits that are both relatively easy to measure and reasonable **proxies** for the rates at which important organismal, population, and community processes occur. Here, we posit that colony mass per unit tissue surface area is one such supertrait, serving as a surrogate for demographic rates, such as growth (Box 2). Other supertraits might capture important information about other aspects of coral biology, such as competition and dispersal (Table 1).

Intraspecific trait plasticity is another aspect of organism biology that can greatly influence population ecology and the capacity of species to acclimatize or adapt to changing environmental conditions [21], a key concern for reef corals today. However, trait plasticity data are rare and species-level characteristics, which do not account for interindividual variation in responses to environmental gradients, are commonly used as proxies for plasticity (Table 1, 'Plasticity'). This approach is based on comparisons across taxonomic groups that indicate that species with greater capacity for physiological plasticity generally occupy a greater range of local habitats and have broader geographical ranges because they are able to cope with a wider range of conditions [22]. However, a species with a wide niche breadth may include individuals with consistently high plasticity or individuals with low plasticity that are specialized on different conditions along environmental gradients. However, direct tests of these alternative mechanisms that increase niche breadth are rare for corals. Recent examples focusing on species-level plasticity show conflicting patterns; physiological plasticity of photosynthetic traits was not correlated with depth range in four *Acropora* species [23], whereas the ability to upregulate heterotrophic feeding allowed colonies to better survive bleaching compared with colonies of species with less dietary plasticity [24]. A full understanding of the relation between trait plasticity and population persistence requires data to be compiled that enable both interindividual and