

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.

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,

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.

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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.

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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

interspecific comparisons of the magnitude of plasticity of physiological traits that control energy acquisition and allocation. To be pragmatic, a subset of common or functionally important species should be selected for intensive intraspecific trait measurement to allow for characterizations of genotype by environment interactions, trait plasticity, and the potential for adaptation or acclimation to global change. To ensure consistency, we recommend that a handbook of standardized trait measurement protocols and conditions is compiled [25].

Community Structure and Response to Disturbance

An increasingly important goal of modern ecology is to identify general rules of community assembly, disassembly, and recovery under global change. Community assembly represents the filtering of a regional species pool by local environmental conditions and ecological interactions, based on the organismal and population traits exhibited by those species [26]. Thus, approaches to characterizing communities that incorporate the trait values exhibited by species can improve our understanding of how local communities are assembled [18]. Increasing evidence that non-neutral community structure is widespread also indicates that species traits will need to be actively incorporated into biodiversity theory to explain patterns in the commonness and rarity of species [27–30]. Therefore, to advance reef coral research, a publically accessible resource is required with sufficient trait data for an adequate number of species to allow generalizable, global associations among traits to be identified [31]. The authors and others are working towards such a compilation [32], which is concentrating initially on capturing historical data and legacy data sets, followed by the submission of newly collected data. This collective effort has already highlighted significant data gaps (Figure 1) and we hope to draw the scientific community together to fill those gaps.

In addition to prioritizing the collection of new data, inferring unmeasured trait values via trait infilling will lead to compilations that are potentially useful for predicting the responses of species and assemblages to multiple stressors. For example, novel trait-based metrics of functional diversity in fish can identify assemblages that are susceptible to disturbance [33]. For reef corals, structural complexity (a measure of the relative abundance of colonies with different morphologies) is a good predictor of recovery from catastrophic bleaching disturbances [34]. Similarly, coral morphology predicted size-specific mortality better than species identity [35], and life-history strategies that captured morphology predicted the response of reef coral assemblages to disturbance [36]. Therefore, knowledge of the frequencies of different morphological groups present within an assemblage provides a tool for predicting the impacts of environmental change. Given the importance of colony morphology for coral demographic and life-history traits, and the fact that this trait is well described for all coral species, we propose that colony morphology can provide a basis for inferring unmeasured growth rates (Box 1) and, thus, be a key component of a coral supertrait (Box 2).

Macroecology and Macroevolution

A trait-based approach that focuses on filling in data gaps at the organismal, population, and community level can provide insight into the underlying drivers of larger-scale patterns, such as geographical range distributions and species diversity patterns. In particular, we can test whether the observed distribution of traits through space and time fits with different macroecological hypotheses, which, in turn, allows the relative importance of different processes to be disentangled. For example, the metabolic theory of ecology proposes that body size and temperature explain the variation in ecological patterns over space and time [37], such that metabolism should constrain small animals to grow and reproduce rapidly [38]. These predictions can be tested with trait data: traits of amphibian populations indeed show that species at higher altitudes and latitudes have shorter breeding seasons and longer larval periods, as well as larger sizes as adults and produce fewer, larger clutches of larger eggs [39].

Glossary

Easy trait: a proxy for a process that is easy to measure for lots of species.

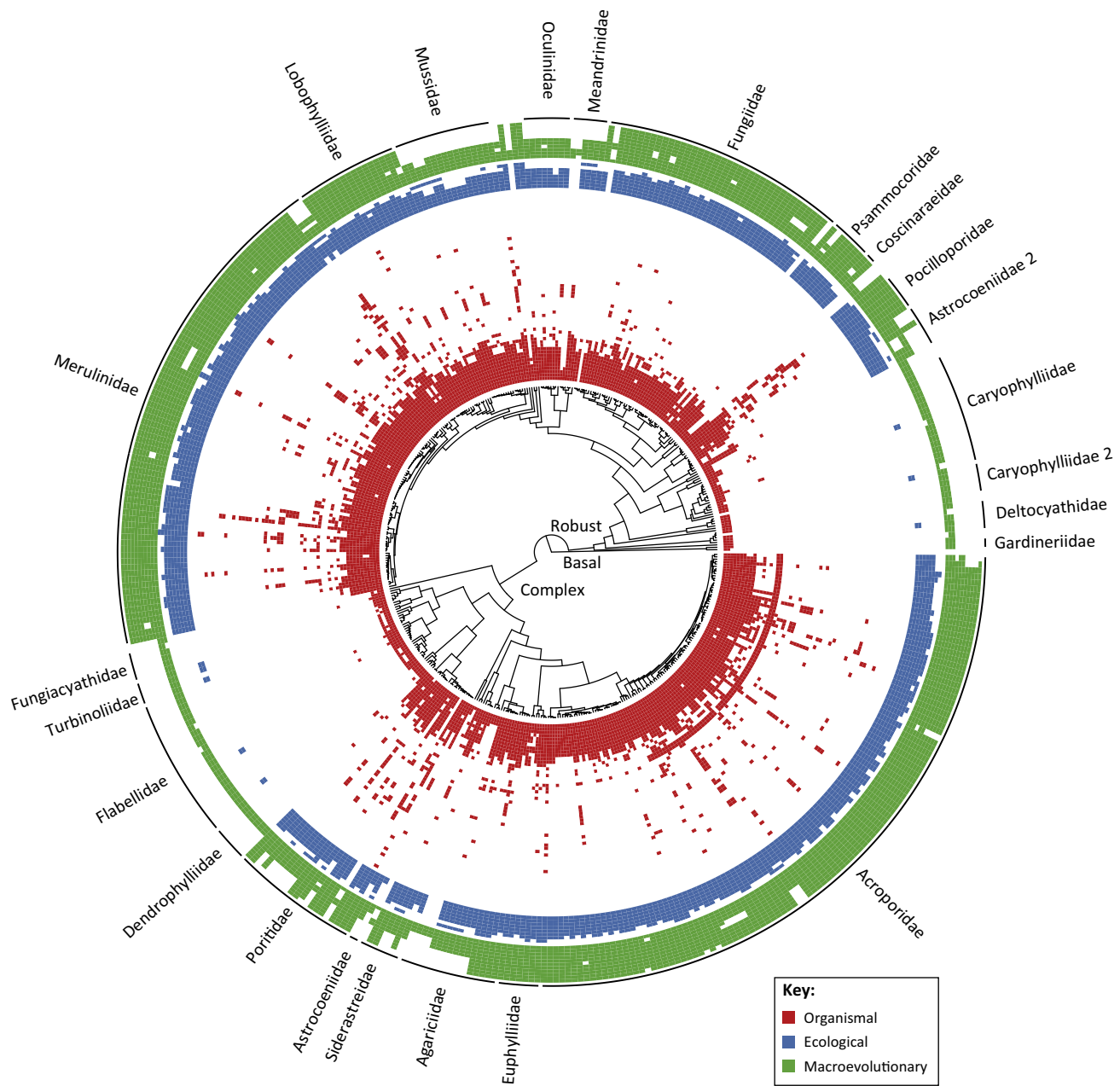
Expert opinion: assigning a species trait based on knowledge and anecdotal experience rather than measuring the trait directly.

Proxy: a trait that provides an estimate for a biological or ecological process based on hypothesis or experience. Proxies are used when more appropriate traits are not available.

Supertrait: a trait or combination of traits that capture a large amount of variation for a broad range of biological, ecological, and evolutionary processes.

Trait infilling: estimating probable values (with uncertainty bounds) for a missing trait based on evolutionary relatedness and other traits that improve accuracy (e.g., geometry).

Trait: broadly refers to both individual-level traits (i.e., potentially heritable quality of an organism) and species-level characteristics (i.e., characteristics of species as entities). We include both, because species-level characteristics can be used as proxies for individual-level traits.



Trends in Ecology & Evolution

Figure 1. Coverage of Data for 78 Coral Species Traits in the Coral Trait Database (<https://coraltraits.org>) Mapped onto the Current Molecular Phylogeny to Illustrate Gaps at Different Scales. The presence of trait values for species is shown with points radiating from the phylogeny, with colors representing the level of organization. Major clades are labeled at the center and families at the periphery. For further details, see Method S3 in the supplemental information online.

Traits are particularly powerful for revealing the drivers of macroecological patterns when they are combined with abundance distributions. For instance, the relative role for dispersal versus establishment in determining successful colonization across biogeographic borders has been difficult to resolve. However, recent work using coral traits has shown that assemblages on

Box 1. How Do We Deal with So Many Species?

In diverse ecosystems, such as coral reefs, it is not plausible to measure the traits of all species, especially in all environmental settings across space [55]. For corals, most traits have been measured only for a subset of the extant species; for example, growth rates have been measured for 105 coral species [32]. One way to cope with missing trait measurements in species-rich systems is to develop suitable methods for estimating probable trait values for unmeasured species. For instance, some categorical traits can be assigned confidently based on phylogeny (e.g., sexuality [56]), but a new method is required to estimate trait values for continuous variables [57]. Given that growth rates are phylogenetically conserved (see Method S1 in the supplemental information online), we used multiple regression to predict growth rates for coral species with missing data based on two traits that are known for almost all species: colony growth form (a geometric constraint) and phylogeny (Figure I). These two variables explained 57% of variation in growth rates (blue symbols). Our method enables estimation of the mean and 95% confidence interval of growth rates for species with missing data (red symbols). Care must be taken with interpreting subsequent analysis, but this approach allows important research questions to be addressed immediately as opposed to waiting for further empirical data.

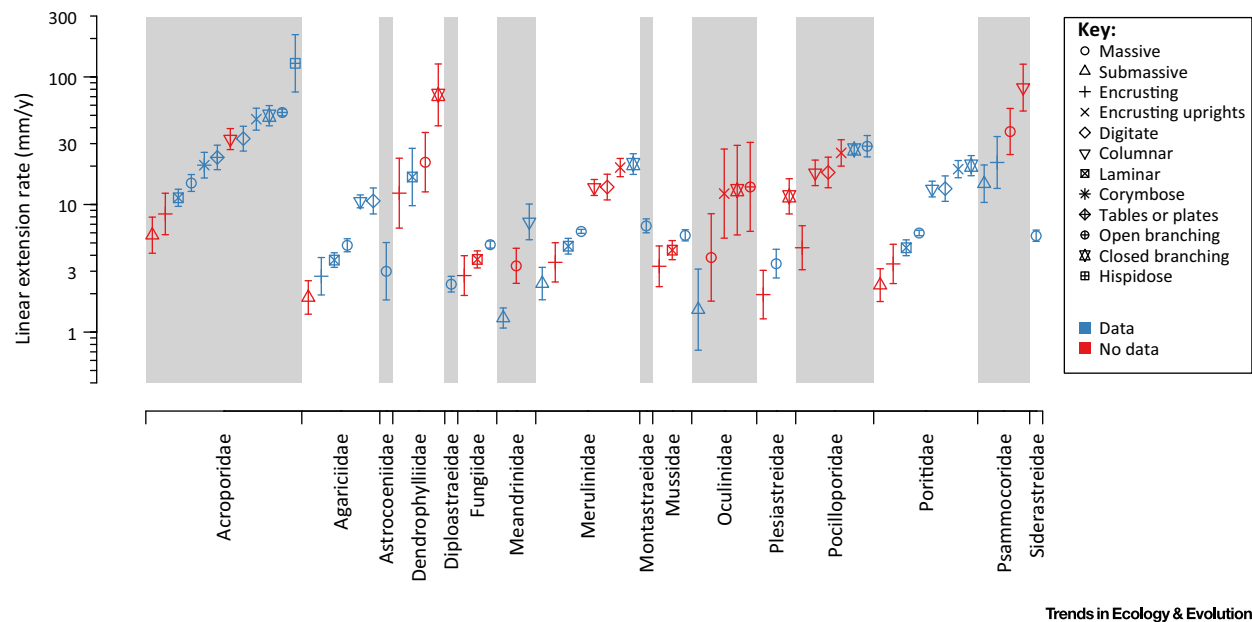


Figure I. Estimated Growth Rates (Linear Extension) and 95% Confidence Intervals for Corals as a Function of Growth Form (Symbols) and Family (Delineated by Vertical Bands).

isolated high-latitude reefs include a relatively high proportion of species that brood larvae, a trait that is hypothesized to enhance capacity to consolidate range expansions due to rapid settlement [40]. Therefore, trait-based analyses reveal that establishment success is a dominant process in this system. Traits can also mediate the impact of environmental filtering at biogeographic transition zones between tropical and temperate corals, where generalist and stress-tolerant species dominate assemblages [41]. At large spatial and temporal scales, trait analyses provided support for the mechanism of selective colonization mediated by plate tectonic movement as an explanation for the generation of coral biogeographic provinces throughout the Indo-Pacific [42].

Answers to many macroevolutionary questions might also be illuminated by consideration of traits, because traits are often strongly correlated with speciation and extinction probabilities. For instance, the extinctions of marine taxa during the Permian mass extinction event were related to physiological traits associated with hypercapnia and calcification [43]. For Caribbean coral taxa, the probability of going extinct during the late Miocene was associated with numerous traits, including colony morphology [44,45], tissue thickness and endosymbiont type [44], larval development strategy [46], and maximum colony size [45]. Despite the challenges of isolating key explanatory traits among a suite of potential traits, such approaches can inform decisions on

Box 2. A Supertrait for Corals?

Decades ago, plant ecologists and ecophysicists identified a ‘supertrait’ known as leaf mass per area (LMA, leaf photosynthesizing surface area per unit leaf dry mass). This easy-to-measure trait summarizes the energy-acquiring part of the plant, which is tightly correlated with a broad array of biological and ecological processes, including relative growth rate (weight increment per unit weight present per unit of time), mass-based leaf nitrogen, and leaf longevity [31,58]. Here, we propose that colony mass per unit tissue surface area is a comparable supertrait for corals. For corals, traits such as tissue biomass and symbiont density are variable, plastic, and unlikely to be good candidates for capturing levels of long-term colony investment. However, the weight of the skeleton reflects the investment and growth of colonies integrated over their lifetime. New technologies are making it easier to measure surface area and volume of corals in the field [59] and skeletal density is an easily measured trait [60] that already exists for numerous species. Colony mass per area (CMA) can be estimated using Equation 1:

$$CMA = \frac{mass}{A} = \frac{V\rho_{skel}}{SA} \quad [1]$$

To demonstrate the potential of this metric, we used geometric formulae to estimate surface area to volume (SA:V) ratios for ten typical coral colony growth forms, ranging from 0.5 (e.g., massive and columnar) to 1 (e.g., encrusting and laminar) up to 4 (e.g., corymbose and open branching) (see Method S2 in the supplemental information online). Skeletal density and growth rate data were available for 28 species in the Coral Trait Database. Using Equation 1, we calculated CMA and correlated it against growth rate, finding a highly significant relation with slope of -1.015 ± 0.25 95% confidence intervals. CMA explained more variation in (78%), and was a better predictor of, growth rate than the reciprocal of SA:V alone (AICc 11.7 and 13.8, respectively) suggesting that investment in skeletal supporting structure is a strong determinant of an important coral demographic rate (Figure 1).

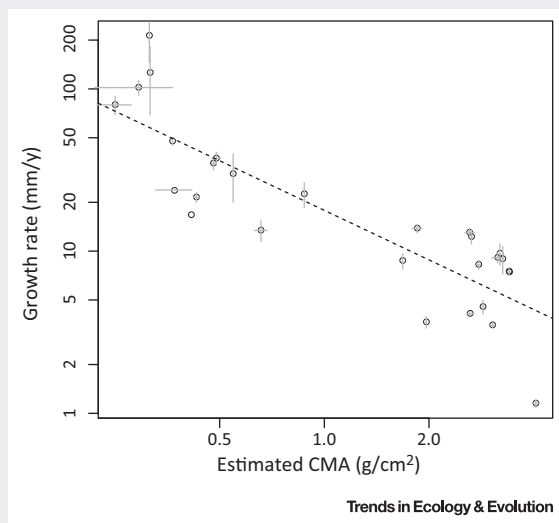


Figure 1. The Relation between Colony Mass Per Area and Growth Rate for 28 Coral Species. Standard errors (gray lines) given where available.

the trait state of fossil taxa. For example, identifying traits associated with the capacity to form symbiotic relations in the modern scleractinian fauna could inform predictions about whether fossil taxa were symbiotic [47,48].

Traits also have the potential to provide important insights into phylogenetic relatedness, because those that have a clear role in the fitness of an individual are under the strongest selection pressure and, therefore, might be highly conserved [14]. With such information, we could begin to resolve the directionality of trait evolution and the mechanisms by which trait transitions are constrained or correlated. Indeed, understanding the interaction among traits over evolutionary timescales can help explain correlated variation of these traits within and among species today [49]. The importance of traits for understanding macroevolutionary processes is further exemplified by the recognition that construction of the scleractinian

Table 1. The Common Challenges Faced by Corals and Suggested Traits Relevant to Research to Understand Those Challenges^{a,b}

| Challenge | Difficult Trait | Easy Trait |
|---|--|--|
| Dispersal | | |
| Dispersal in space | Dispersal distance; barrier crossing | Larval development strategy; egg or larval size (small ~more chances; large ~greater reserves); <i>Symbiodinium</i> spp. in larvae (autotrophic); larval lifespan (~pelagic larval duration); also see 'Acquiring space' below |
| Dispersal in time | Larval longevity; recruit longevity | Larval survivorship; recruit survivorship in conditions not conducive to positive growth (~seed bank) |
| Establishment | | |
| Juvenile growth | Settlement size; growth rate | Larval size; sexual system; <i>Symbiodinium</i> spp. in larvae; colony mass per area (CMA); <i>Symbiodinium</i> per area (~energy acquisition); RNA:DNA ratio |
| Persistence | | |
| Gamete production | Fecundity | Eggs per polyp; polyps per area; CMA |
| Competitive ability | Competitive effect and response | Adult size (~resistance to partial mortality); growth form (~capacity to overtop neighbor); attachment (~escape from neighbor); clonality or solitary (~capacity to overgrowth or overtop); polyp size (~neighbor digestion) |
| Plasticity | Reaction norm | Depth range; geographic range; habitat breadth (exposure, turbidity) |
| Space holding and longevity | Life span | Life-history strategy; skeletal density (~investment in structure); CMA |
| Acquiring space | Vegetative spread | Growth form; probability of fragment reattachment; attachment strength; clonality or solitary |
| Response to local disturbance; stress and disturbance avoidance | Phenology; palatability; <i>Symbiodinium</i> composition; mechanical integrity | CMA; colony shape factor; <i>Symbiodinium</i> clade and subclade; lipid content; protein biomass |
| Response to global disturbance; mass extinction events | Heterotrophy; range size | Calcification; tissue thickness; growth form; depth range; range size |
| Origin | Fossil age | Phylogenetic age; fossil age (for certain species) |

^aAdapted from [61].^bThe easy traits listed are available from the Coral Trait Database, but species coverage is highly variable. Relations among difficult traits and easy traits, and the challenges they are hypothesized to represent, need to be tested. '~' indicates is related, or equivalent, to.

phylogeny can be improved by incorporation of traits beyond simple colony morphology, such as reproductive mode.

Challenges

Here, we have outlined numerous ways in which the quantification of species traits can advance knowledge of coral population, community, ecosystem, and macro- and evolutionary ecology. However, several challenges exist in applying trait-based approaches to coral reef research. First, there is a lack of data coverage for many traits in many species (Figure 1), particularly those pertaining to physiological and demographic rates that relate organismal performance to environmental conditions [11,12] and for deeper-dwelling, slow-growing, and/or rare taxa.

For example, in a global survey of reef traits, Darling *et al.* [50] collected trait information for 847 species, but only 143 species had enough information to be included in the analysis. Clearly, more comprehensive trait information would facilitate the addressing of key research questions relating to resource acquisition and allocation, including rates of photosynthetic and heterotrophic energy acquisition, proportional energy allocation to growth, fecundity, and survival, and how such traits scale with colony size and change along environmental gradients. In lieu of comprehensive trait information, further development of statistical approaches for trait infilling is needed (Box 1).

Second, traits are often used as proxies for the rates at which particular life-history processes occur that are hypothesized to be linked to those traits. For example, polyp size is considered a proxy for heterotrophic feeding despite the fact that species that upregulate feeding during bleaching events have among the smallest polyp sizes of all corals. Therefore, a major challenge is to test the relation between trait distributions and the rates at which processes occur that are hypothesized to be linked to those traits. Moreover, corals are further complicated because they are colonial. It is important to quantify how traits of individuals (i.e., polyps) scale with colony size, and how multiple traits combine to influence individual and population-level fitness. Scaling-up from individual to biogeographical patterns has been attempted in other fields using theoretical frameworks, such as metabolic scaling relations [37] and dynamic energy budget theory [51], but it remains to be explored how well such theories fit modular, mixotrophic, and symbiotic organisms [52].

Third, a major knowledge gap relates to how trait expression varies through space, and how rapidly it can change through ecological and evolutionary time. Context dependency of trait expression is increasingly a challenge for macroecological analyses that attempt to find generalizable explanations, often over a large biogeographic extent, given that it is becoming increasingly evident that traits collected at one reef might not represent the traits expressed by individuals of the same species elsewhere. A similar challenge exists with macroevolutionary questions that are concerned with large temporal extents. Slow-growing organisms, such as corals, experience longer timescales than other faster-growing organisms, introducing the challenge of nonstationary environments into trait responses [53]. Understanding the capacity of corals to sense and respond to environmental conditions via trait expression over space and time, and how this is affected by the dynamism of symbiotic switching and shuffling, and host epigenetics, are critical areas of research necessary to anticipate rates of acclimatization and adaptation under rapid environmental change. Trait probability distributions are more informative of trait expression than measures of central tendency, but there is a trade-off in the difficulty of obtaining sufficient data. Recognizing such limitations, plant scientists have focused on trait proxies to rank life-history processes and rates for >30 000 known species of plants [54]. Despite dealing with an order of magnitude fewer coral species, many are rare and difficult to access at deeper depths. Therefore, we must work collaboratively to find solutions to these challenges and move forward with trait-based approaches.

Concluding Remarks

To advance coral reef science, we need concerted and coordinated efforts to curate trait information (statistically and empirically) that can improve and validate proxies for key biological and ecological processes and identify potential supertraits (see Outstanding Questions). As ocean warming, acidification, sea-level rise, and myriad human pressures continue to push reef corals to their limit, adopting a global effort for trait-based science is necessary, both for reefs and the societies that depend on them. We call for a rigorous and quantitative focus on species differences, rather than opinion and speculation, to understand the unique biology of reef builders, and to predict and protect reef ecosystem function into the future.

Outstanding Questions

Which traits are not only relatively easy to measure, but also reliable proxies for organismal, population, and community processes?

How can key traits and demographic rates be estimated based on other more easily measurable traits and by using our rapidly improving understanding of the tree of life?

Are there supertraits to be discovered that are tightly correlated with a broad array of biological and ecological challenges?

Which common or ecologically important species should we target for intensive intraspecific trait measurement to allow for characterizations of trait plasticity?

How can we best consolidate and standardize trait measurement protocols and conditions?

Can trait, or supertraits, be used to identify broad functional groups or adaptive strategies among corals? Are functional groups useful for understanding or predicting organism or assemblage response to stress or disturbance?

How do we generate and maintain a community resource with sufficient trait data for an adequate number of species to allow general, larger-scale and higher organizational-level associations among traits to be resolved?

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2016.02.012>.

References

- Fisher, R. *et al.* (2015) Species richness on coral reefs and the pursuit of convergent global estimates. *Curr. Biol.* 25, 500–505
- Spalding, M.D. and Grenfell, A.M. (1997) New estimates of global and regional coral reef areas. *Coral Reefs* 16, 225–230
- Moberg, F. and Folke, C. (1999) Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* 29, 215–233
- de Groot, R. *et al.* (2012) Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* 1, 50–61
- Jackson, J.B.C. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637
- Pandolfi, J. *et al.* (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301, 955–958
- Hughes, T.P. *et al.* (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301, 929–933
- Pandolfi, J.M. *et al.* (2011) Projecting coral reef futures under global warming and ocean acidification. *Science* 333, 418–422
- Carpenter, K.E. *et al.* (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321, 560–563
- McClanahan, T.R. *et al.* (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE* 7, e42884
- Edmunds, P.J. *et al.* (2011) Benchmarks in organism performance and their use in comparative analyses. *Oecologia* 167, 379–390
- Edmunds, P.J. *et al.* (2014) Evaluating the causal basis of ecological success within the scleractinia: an integral projection model approach. *Mar. Biol.* 161, 2719–2734
- Huang, D. (2012) Threatened reef corals of the world. *PLoS ONE* 7, e34459
- Kerr, A.M. *et al.* (2011) Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). *Proc. R. Soc. Lond. B* 278, 75–81
- Stearns, S.C. (1992) *The Evolution of Life Histories*, Oxford University Press
- Martin, A.P. and Palumbi, S.R. (1993) Body size, metabolic-rate, generation time, and the molecular clock. *Proc. Nat. Acad. Sci. U.S.A.* 90, 4087–4091
- Grime, J.P. and Pierce, S. (2012) *The Evolutionary Strategies that Shape Ecosystems*, Wiley-Blackwell
- McGill, B. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185
- Silvertown, J. *et al.* (1992) A demographic interpretation of Grime's triangle. *Funct. Ecol.* 6, 130–136
- Madin, J.S. *et al.* (2012) Integrating physiological and biomechanical drivers of population growth over environmental gradients on coral reefs. *J. Exp. Biol.* 215, 968–976
- Tomanek, L. (2010) Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. *J. Exp. Biol.* 213, 971–979
- Stevens, G.C. (1989) The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *Am. Nat.* 133, 240–256
- Langlois, L.A. and Hoogenboom, M.O. (2014) Capacity for short-term physiological acclimation to light does not control the lower depth distributions of branching corals. *Mar. Ecol. Prog. Ser.* 508, 149–162
- Grottolli, A.G. *et al.* (2006) Heterotrophic plasticity and resilience in bleached corals. *Nature* 440, 1186–1189
- Cornelissen, J.H.C. *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380
- Poff, N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* 16, 391–409
- Cadotte, M.W. *et al.* (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087
- Bode, M. *et al.* (2012) Species differences drive nonneutral structure in Pleistocene coral communities. *Am. Nat.* 180, 577–588
- Connolly, S.R. *et al.* (2014) Commonness and rarity in the marine biosphere. *Proc. Nat. Acad. Sci. U.S.A.* 111, 8524–8529
- Falster, D. *et al.* (2015) Multi-trait eco-evolutionary dynamics explain niche diversity and evolved neutrality in forests. *BioRxiv* Published online January 30, 2015. <http://dx.doi.org/10.1101/014605>
- Wright, I. *et al.* (2004) The worldwide leaf economics spectrum. *Nature* 428, 821–827
- Madin, J.S. *et al.* (2016) The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Nat. Sci. Data* 3, 160012
- Mouillot, D. *et al.* (2013) functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177
- Graham, N.A.J. *et al.* (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518, 94–97
- Madin, J.S. *et al.* (2014) Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol. Lett.* 17, 1008–1015
- Darling, E.S. *et al.* (2013) Life histories predict coral community disassembly under multiple stressors. *Global Change Biol.* 19, 1930–1940
- Brown, J. *et al.* (2004) Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789
- Savage, V.M. *et al.* (2004) Effects of body size and temperature on population growth. *Am. Nat.* 163, 429–441
- Morrison, C. and Hero, J.M. (2003) Geographic variation in life-history characteristics of amphibians: a review. *J. Anim. Ecol.* 72, 270–279
- Keith, S.A. *et al.* (2015) Differential establishment potential of species drives a shift in coral assemblage structure across a biogeographic barrier. *Ecography* 38, 1–10
- Sommer, B. *et al.* (2014) Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* 95, 1000–1009
- Keith, S.A. *et al.* (2013) Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. *Proc. Roy. Soc. B* 280, 20130818
- Knoll, A.H. *et al.* (2007) Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* 256, 295–313
- van Woesik, R. *et al.* (2012) Hosts of the Plio-Pleistocene past reflect modern-day coral vulnerability. *Proc. Roy. Soc. B* 279, 2448–2456
- Johnson, K.G. *et al.* (1995) Extinction selectivity and ecology of neogene Caribbean reef corals. *Paleobiology* 21, 52–73
- Edinger, E.N. and Risk, M.J. (1995) Preferential survivorship of brooding corals in a regional extinction. *Paleobiology* 21, 200–219
- Stanley, G.D. and van de Schootbrugge, B. (2009) The evolution of the coral-algal symbiosis. *Coral Bleaching* 205, 7–19
- Simpson, C. (2013) Species selection and the macroevolution of coral coloniality and photosymbiosis. *Evolution* 67, 1607–1621
- Felsenstein, J. (1985) Phylogenies and the comparative method. *Am. Nat.* 125, 1–15
- Darling, E.S. *et al.* (2012) Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* 15, 1378–1386
- Nisbet, R. *et al.* (2000) From molecules to ecosystems through dynamic energy budget models. *J. Anim. Ecol.* 69, 913–926

52. Muller, E. *et al.* (2009) Dynamic energy budgets in syntrophic symbiotic relationships between heterotrophic hosts and photoautotrophic symbionts. *J. Theor. Biol.* 259, 44–57
53. Wolkovich, E.M. *et al.* (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature* 485, 494–497
54. Kattge, J. *et al.* (2010) A generic structure for plant trait databases. *Methods Ecol. Evol.* 2, 202–213
55. Laughlin, D.C. and Messier, J. (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends Ecol. Evol.* 30, 487–496
56. Baird, A.H. *et al.* (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Ann. Rev. Ecol. Syst.* 40, 551–571
57. Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. B* 255, 37–45
58. Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227
59. Johnson-Roberson, M. *et al.* (2010) Generation and visualization of large-scale three-dimensional reconstructions from underwater robotic surveys. *J. Field Robot.* 27, 21–51
60. Hughes, T. (1987) Skeletal density and growth form of corals. *Mar. Ecol. Prog. Ser.* 35, 259–266
61. Weiher, E. *et al.* (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.* 10, 609–620