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1 **A trait-based approach to advance coral reef science**

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24

25 **Abstract**

26   Coral reefs are biologically diverse and ecologically complex ecosystems constructed

27 by stony corals. Despite decades of research, basic coral population biology and community

28 ecology questions remain unanswered. Quantifying trait variation among species can help

29 resolve these questions, but progress has been hampered by a paucity of trait data for the

30 many, often rare, species and by a reliance of non-quantitative approaches. Therefore, we

31 propose filling data gaps by prioritizing traits that are easy to measure, estimating key traits

32 for species with missing data, and identifying "super-traits" that capture a large amount of

33 variation for a range of biological and ecological processes. Such an approach can accelerate

34 our understanding of coral ecology, and our ability to protect critically threatened global

35 ecosystems.

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Main text

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 global ocean area [2], reefs are important to humankind for food, coastal protection and many other goods and services [3]. Indeed, the ecosystem value of non-tradable 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 highly 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]. Non-quantitative 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 macro-evolutionary patterns [14]. Consequently, we review recent examples of trait-based coral research, highlighting in particular how wider quantification of species traits could advance understanding across a

63   hierarchy of scales—ranging from organisms to populations, communities, and

64   biogeographical regions and macro-evolutionary time scales. We also proffer some insights

65   from other fields for resolving knowledge gaps in reef coral science. We conclude by

66   identifying data gaps and conceptual priorities, including a focus on "easy" traits, "trait

67   infilling" and identifying coral "super-traits" to rapidly advance our ability to understand the

68   drivers and consequences of changing coral species composition on reefs in an era of rapid

69   environmental change.

70

71   **Organism biology and population persistence**

72   Traits, and their differences amongst individuals, have strong effects on the

73   organismal and population biology of species. For instance, the energy and nutrients available

74   to an individual are limited, and the way energy and nutrients are distributed amongst various

75   processes such as growth, reproduction and maintenance shape life history strategies [15].

76   Advancing knowledge at these scales requires understanding the patterns of energy allocation

77   within individuals, and identifying the key demographic traits that regulate population size

78   and demography. There is no practical way to comprehensively measure demographic trait

79   values for a large proportion of assemblages in species-rich systems, like coral reefs. Instead,

80   trait infilling can be used to infer demographic trait values from other, more readily

81   measurable traits, like colony morphology, that constrain and influence demographic rates

82   (Box 1).

83   More generally, trade-offs among traits influence many aspects of organism biology,

84   such as generation times [16], and they influence responses to disturbance and stress [17]. In

85   many fields, progress in in identifying trait trade-offs has been limited because traits are

86   rarely measured in a common currency [18]. Attempts to overcome this measurement

87   inconsistency typically require the use of mathematical models that integrate traits with

88   different units into a common currency. For instance, Silvertown et al. [19] used matrix

89   models to recreate Grime's triangle using population growth factor as a common currency for

90   plant traits. Similarly, Madin et al. [20] used an integrated biomechanical and photosynthetic

91   model to convert coral species traits, including size and morphology, into the common

92   currency of lifetime reproductive output. A more pragmatic approach is to search for super-

93   traits that are relatively easy to measure, and that are reasonable proxies for the rates at which

94   important organismal, population and community processes occur. We here posit that colony

95   mass per unit tissue surface area is one such super-trait, serving as a surrogate for

96   demographic rates like growth (Box 2). Other super-traits might capture important

97   information about other aspects of coral biology, such as competition and dispersal (Table 1).

98   Intra-specific trait plasticity is another aspect of organism biology that can greatly

99   influence population ecology, and the capacity of species to acclimatize or adapt to changing

100   environmental conditions [22], a key concern for reef corals today. However, trait plasticity

101   data are rare and measured for few species. Instead, species-level characteristics are

102   commonly used as proxies for plasticity (Table 1, "Plasticity"), because across taxonomic

103   groups, species with greater capacity for physiological plasticity generally occupy a greater

104   range of local habitats and have broader geographical ranges because they are able to cope

105   with a wider range of conditions [21]. However, direct tests of these proxies are rare for

106   corals because we lack the necessary data to allow multispecies comparisons of the

107   magnitude of trait plasticity. Indeed, in a recent example, physiological plasticity of

108   photosynthetic traits was not correlated with depth range in four *Acropora* species [23],

109   whereas the ability to up-regulate heterotrophic feeding allowed colonies to better survive

110   bleaching than colonies of species with less dietary plasticity [24]. A full understanding of

111   the relationship between trait plasticity and population persistence requires data to be

112   compiled that enables interspecific comparison of the magnitude of plasticity of physiological

113 traits that control energy acquisition and allocation. To be pragmatic, a subset of common or

114 functionally important species should be selected for intensive intraspecific trait measurement

115 to allow for characterizations of trait plasticity, and the potential for adaptation or acclimation

116 to global change. To ensure consistency, we recommend that a handbook of standardised trait

117 measurement protocols and conditions is compiled [52].

118

119 **Community structure and response to disturbance**

120 An increasingly important goal of modern ecology is to identify general rules of

121 community assembly, disassembly and recovery under global change. Community assembly

122 represents the filtering of a regional species pool by local environmental conditions and

123 ecological interactions, based on the organismal and population traits exhibited by those

124 species [26]. Thus, approaches to characterizing communities that incorporate the trait values

125 exhibited by species can improve our understanding of how local communities are assembled

126 [18]. Increasing evidence that non-neutral community structure is widespread also indicates

127 that species traits will need to be actively incorporated into biodiversity theory to explain

128 patterns in the commonness and rarity of species [27-30]. Therefore, to advance reef coral

129 research, a publically-accessible resource is required with sufficient trait data for an adequate

130 number of species to allow generalizable, global associations among traits to be identified

131 [31]. The authors and others are working towards such a compilation [32], which

132 concentrates on capturing historical data and legacy datasets initially, followed by submission

133 of newly collected data. This collective effort has already highlighted significant data gaps

134 (Figure 1) and we hope to draw the scientific community together to fill these gaps.

135 In addition to prioritizing collection of new data, inferring unmeasured trait values via

136 trait infilling will lead to compilations that are potentially useful for predicting the responses

137 of species and assemblages to multiple stressors. For example, novel trait-based metrics of

138   functional diversity in fishes can identify assemblages susceptible to disturbance [33]. For

139   reef corals, structural complexity (a measure of the relative abundance of colonies with

140   different morphologies) is a good predictor of recovery from catastrophic bleaching

141   disturbances [34]. Similarly, coral morphology can predict size specific mortality better than

142   species identity [35], and life-history strategies that captured morphology predicted the

143   response of reef coral assemblages to disturbance [36]. Therefore, knowledge of the

144   frequencies of different morphological groups present within an assemblage provides a tool

145   for predicting the impacts of environmental change. Given the importance of colony

146   morphology for coral demographic and life-history traits, and the fact that this trait is well

147   described for all coral species, we propose that colony morphology can provide a basis for

148   inferring unmeasured growth rates (Box 1), and thus be a key component of a coral super-

149   trait (Box 2).

150

151   **Macroecology and macroevolution**

152   A trait-based approach that focuses on filling in data gaps at the organismal,

153   population and community level can provide insight into the underlying drivers of larger-

154   scale patterns, such as geographical range distributions and species diversity patterns. In

155   particular, we can test whether the observed distribution of traits through space and time fits

156   with different macroecological hypotheses which, in turn, allows the relative importance for

157   different processes to be disentangled. For example, the Metabolic Theory of Ecology

158   proposes that body size and temperature explain the variation in ecological patterns over

159   space and time [37], such that metabolism should constrain small animals to grow and

160   reproduce rapidly [38]. These predictions can be tested with trait data: traits of amphibian

161   populations indeed show that species at higher altitudes and latitudes have shorter breeding

162   seasons and longer larval periods as well as larger size as adults and produce fewer and larger

163   clutches of larger eggs [39].

164   Traits are particularly powerful for revealing the drivers of macroecological patterns

165   when they are combined with abundance distributions. For instance, the relative role for

166   dispersal versus establishment in determining successful colonization across biogeographic

167   borders has been difficult to resolve. However, recent work using coral traits has shown that

168   assemblages on isolated high-latitude reefs include a relatively high proportion of species that

169   brood larvae, a trait that is hypothesised to enhance capacity to consolidate range expansions

170   due to rapid settlement [40]. Trait-based analyses therefore reveal that establishment success

171   is a dominant process in this system. Traits can also mediate the impact of environmental

172   filtering at biogeographic transition zones between tropical and temperate corals, where

173   generalist and stress-tolerant species dominate assemblages [41]. At very large spatial and

174   temporal scales, trait analyses provided support to the mechanism of selective colonization

175   mediated by plate tectonic movement as an explanation for the generation of coral

176   biogeographic provinces throughout the Indo-Pacific [42].

177   Answers to many macroevolutionary questions also might be illuminated by

178   consideration of traits, because traits are often strongly correlated with speciation and

179   extinction probabilities. For instance, the extinctions of marine taxa during the Permian mass

180   extinction event was related to physiological traits associated with hypercapnia and

181   calcification [43]. For Caribbean coral taxa, the probability of going extinct during the late

182   Miocene was associated with numerous traits, including colony morphology [44,45], tissue

183   thickness and endo-symbiont type [44], larval development strategy [46] and maximum

184   colony size [45]. Despite the challenges of isolating key explanatory traits among a suite of

185   potential traits, such approaches can inform decisions on the trait state of fossil taxa. For

186   example, identifying traits associated with the capacity to form symbiotic relationships in the

187   modern scleractinian fauna, could inform predictions about whether or not fossil taxa were

188   symbiotic [47,48].

189   Traits also have the potential to provide important insights into phylogenetic

190   relatedness because those that have a clear role to play in an individual's fitness are under the

191   strongest selection pressure and, therefore, might be highly conserved [14]. With such

192   information, we could begin to resolve the directionality of trait evolution and the

193   mechanisms by which trait transitions are constrained or correlated. Indeed, understanding

194   the interaction amongst traits over evolutionary timescales can help explain correlated

195   variation of these traits within and among species today [49]. The importance of traits for

196   understanding macroevolutionary processes is further exemplified by the recognition that

197   construction of the scleractinian phylogeny can be improved by incorporation of traits beyond

198   simple colony morphology, such as reproductive mode.

199

200   **Challenges**

201   We have outlined numerous ways that quantification of species traits can advance

202   knowledge in coral population, community, ecosystem, macro- and evolutionary ecology.

203   However, several challenges exist in applying trait-based approaches to coral reef research.

204   First, there is a lack of data coverage for many traits in many species (Figure 1), particularly

205   traits relating to physiological and demographic rates that relate organismal performance to

206   environmental conditions [11,12] and for deeper dwelling, slow growing and rare taxa. For

207   example, in a global survey of reef traits, Darling et al. [50] collected trait information for

208   847 species, but only 143 species had enough information to be included in the analysis.

209   Clearly, more comprehensive trait information would facilitate addressing key research

210   questions relating to resource acquisition and allocation, including rates of photosynthetic and

211   heterotrophic energy acquisition, proportional energy allocation to growth, fecundity and

212   survival, and how such traits scale with colony size and change along environmental

213   gradients. In lieu of comprehensive trait information, further development of statistical

214   approaches for trait infilling is needed (Box 1).

215   Second, traits are often used as proxies for the rates at which particular life history

216   processes occur that are hypothesized to be linked to those traits. For example, polyp size is

217   considered a proxy for heterotrophic feeding despite the fact that species that up-regulate

218   feeding during bleaching events have among the smallest polyp sizes of all corals. Therefore,

219   a major challenge is to test the relationship between trait distributions and the rates at which

220   processes occur that are hypothesized to be linked to those traits. Moreover, corals are further

221   complicated because they are colonial. It is critically important to quantify how traits of

222   individuals (i.e., polyps) scale with colony size, and how multiple traits combine to influence

223   individual and population-level fitness. Scaling-up from the individuals to biogeographical

224   patterns has been attempted in other fields using theoretical frameworks such as metabolic

225   scaling relationships [37] and dynamic energy budget theory [51], but it remains to be

226   explored how well such theory will fit modular, mixotrophic and symbiotic organisms [52].

227   Third, a major knowledge gap relates to how trait expression varies through space,

228   and how rapidly it can change through ecological and evolutionary time. Context-dependency

229   of trait expression is increasingly a challenge for macroecological analyses that attempt to

230   find generalizable explanations, often over a large biogeographic extent, as it becomes

231   increasingly evident that traits collected at one reef might not represent the traits expressed by

232   individuals of the same species elsewhere. A similar challenge exists with macroevolutionary

233   questions that are concerned with large temporal extents. Slow growing organisms, like

234   corals, experience longer time scales than other faster-growing organisms, introducing the

235   challenge of non-stationary environments into trait responses [53]. Understanding corals'

236   capacity 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. Recognising such limitations, plant scientists have

focused on trait proxies in order to rank life history processes and rates for the greater than

30,000 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 super-traits (Box 3). As ocean

warming, acidification, sea level rise and a myriad of human pressures continue to push reef

corals to their limit, adopting a global effort for trait-based science is necessary—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.

Supplementary Data associated with this article can be found at doi:XXXXXXX

Figure Caption

262

263   **Figure 1.** Coverage of data for 78 coral species traits in the Coral Trait Database

264   (https://coraltraits.org) mapped onto the current molecular phylogeny to illustrate gaps at

265   different scales (see Online Supplementary Material Method S3). The presence of trait values

266   for species is shown with points radiating from the phylogeny, with colours representing level

267   of organisation. Basal clades are labelled at the centre and families at the periphery.

268

269

270 **Glossary**

271

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 potentially be used as proxies for individual-level traits.
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.
Super-trait	A trait or combination of traits that capture a large amount of variation for a broad range of biological, ecological and evolutionary processes.
Easy trait	A proxy for a process that is easy to measure for lots of species.
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).

272

273

Table 1. The common challenges faced by corals and some suggested traits relevant to research to understand these challenges (adapted from [55]). The easy traits listed are available from the Coral Trait Database, but species coverage is highly variable. Relationships among difficult traits and easy traits, and the challenges they are hypothesised to represent, need to be tested. ~ is related to or equivalent to.

Challenge	Difficult trait	Easy trait
1. Dispersal		
Dispersal in space	• Dispersal distance • Barrier-crossing	• Larval development strategy • Egg or larvae size (small~more chances, large~greater reserves) • *Symbiodinium* 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)
2. Establishment		
Juvenile growth	• Settlement size • Growth rate	• Larval size • Sexual system • *Symbiodinium* spp. in larvae • Colony mass per area (CMA) • *Symbiodinium* per area (~energy acquistion) • RNA:DNA ratio
3. 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 • *Symbiodinium* makeup • Mechanical integrity	• CMA • Colony shape factor • Symbiodinium 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)

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