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Editorial: Variance matters: Individual differences and their consequences for natural selection within and among coral holobionts

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Editorial on the Research Topic
Variance Matters: Individual Differences and Their Consequences for Natural Selection Within and Among Coral Holobionts

The coral reef crisis has entered a critical stage. Ongoing political efforts to reduce greenhouse gas emissions have been ineffective at slowing the global decline of reef habitats and associated biodiversity. Restoration practitioners have been forced to focus on stop-gap measures to ensure that at least some coral species persist into the future (National Academies of Sciences Engineering and Medicine, 2018). Key examples include establishing nurseries wherein corals can be grown and later outplanted onto reefs (Young et al., 2012), identifying heat-tolerant individuals for nursery propagation (Cunning et al., 2021), and facilitating the natural ability of corals to adapt through interventions like assisted gene flow (Baums et al., 2019).

Corals may uniquely benefit from such interventions because they feature high adaptive capacity owing to their diverse symbiotic microbial associations (Voolstra et al., 2021). The coral host produces a suitable micro-habitat for intracellular populations of dinoflagellate photosymbionts (Symbiodiniaceae; LaJeunesse et al., 2018), as well as intra- and extra-cellular bacteria, archaea, fungi, algae, and viruses. Taken together, the entire biological unit is termed the coral holobiont. Each member includes its own genetic and physiological diversity, and can contribute to the plasticity of the whole. In such a system, natural selection can play out at multiple levels, such as through changes in partnerships (Torda et al., 2017). Different pairings of host and symbiont genotypes may contribute to intraspecific variation in important coral holobiont phenotypes, which may ultimately scale up to affect associated reef organisms (Parkinson and Baums, 2014). For example, coral holobiont heat tolerance can be impacted by host species identity (Loya et al., 2001), the identity of individual host colonies within a species (Parkinson et al., 2015), the Symbiodiniaceae species identity

(Sampayo et al., 2008), the bacterial consortium (Rosado et al., 2019), as well as interactions between any of these players (*e.g.*, Kavousi et al., 2020).

Projections of reef decline that fail to account for the coral holobiont's evolutionary response to climate change are unrealistic (Hughes et al., 2003). Similarly, projections based on the average ecophysiological responses of coral colonies to environmental shifts might be inappropriate because only a subset of existing partnerships survive stress events and repopulate reefs (Kubicek et al., 2019). To better predict the future trajectory of reef ecosystems and to stage effective interventions, it will be critical to (1) monitor changes in coral holobiont partnerships due to heat stress; (2) identify high-performing outlier colonies; and (3) estimate the breadth of intraspecific variation among colonies, as this variability forms the foundation for natural selection (Violle et al., 2012). Inferences must also come from the wide array of "coral" holobionts, including soft corals, black corals, leather corals, blue corals, fire corals, and other sessile cnidarians.

Observations such as the divergent bleaching outcomes of two adjacent *Porites astreoides* colonies depicted in Figure 1 provide a sense of hope. Clearly, there is a high degree of variability within populations of reef-building corals. The question now is: to what extent can coral holobiont evolution keep pace with climate change? The goal of this Research Topic was to collect studies that highlight intraspecific variation among coral colonies and their associated microbial communities, as well as to evaluate the consequences of such ecophysiological diversity for the long-term survival of coral species. Here, we summarize the key findings of nine articles that directly address these concepts.

Three studies examined intraspecific variation among reef-building corals. Rodriguez et al. investigated non-contact competitive behavior between three colonies of the hard coral *Porites cylindrica* and five colonies of a soft coral competitor. The fully crossed design pitted each colony against all others, revealing unique behavioral responses depending on the combination of genotypes. Some secretory genes were only expressed by *Porites* in certain pairings, and encoded putative allelopathic toxins. Such individual-level variation in competitive interactions could be an important determinant of reef community dynamics. Marhoefer et al. used a reciprocal transplant design to detect genotype-by-environment interactions among *Pocillopora damicornis* colonies sourced from either the reef slope or reef flat. The performance of clonal fragments varied depending on whether they remained at the source habitat or were transplanted. Experimental heat stress assays indicated that some transplanted fragments began to acclimate to their new habitat, either with or without changes in their symbiont communities, highlighting the role of interactions between hosts, symbionts, and the environment in adaptive responses. Lenz et al. monitored the physiology of *Porites astreoides* colonies at four different reef sites during a

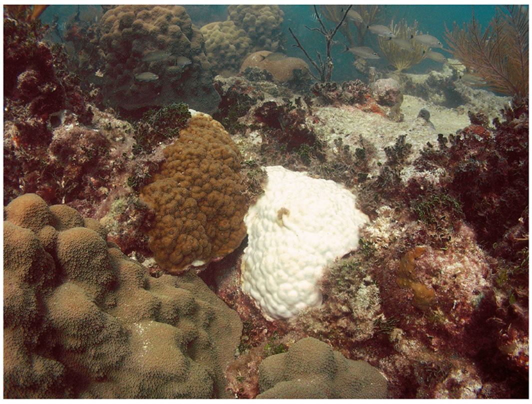

FIGURE 1
An example of intraspecific variation in a coral population: two *Porites astreoides* colonies exhibiting different bleaching responses to thermal stress despite sharing the same environment (and most likely the same Symbiodiniaceae communities). Coral bleaching results when stress breaks down the symbiosis between the host and microalgae, causing a loss of symbionts. The image was captured in the Florida Keys during a warm-water anomaly in October 2015. Photo credit: Ilsa Kuffner, PhD; USGS.

warm-water bleaching event. They identified divergent impacts of heat stress on the different coral populations, as well as unique recovery trajectories at each site. These patterns reflect how prevailing environmental conditions can drive local selection despite gene flow, altering population-level responses to stress and maintaining intraspecific phenotypic variation across a coral species' biogeographic range.

Two contributions to this Research Topic focused on other reef cnidarians. Hsu et al. characterized organismal trait composition in two octocoral species dominated by different Symbiodiniaceae but thriving within the same high-latitude environment. Divergence across multiple physiological traits suggested contrasting performances among *Gerakladium*-associated *Stereonephtya* and *Durusdinium*-associated *Litophyton*. Intraspecific variation in traits indicated a higher possibility for some *Litophyton* individuals to blend heterotropic energy with autotrophically-acquired energy in comparison with *Stereonephtya*. Fuijiwara et al. resolved three Symbiodiniaceae species associating with the zoantharian *Zoanthus sansibaricus* across a depth gradient. They identified intraspecific variation in symbiont community composition across the surfaces of shallow colonies, which suggested a capacity for acclimation via symbiont shuffling. However, after reciprocal transplantation between shallow and deep habitats, symbiont community composition remained stable in most colonies despite the stressful change in environmental conditions.

In addition to associations between hosts and their primary microalgal communities, several authors explored intraspecific variation in the bacterial component of coral holobionts. Yang et al. examined seasonal variation in the prokaryotic communities found within the scleractinian coral *Acropora muricata* at three latitudinal settings influenced by the Kuroshio Current. They observed that local conditions had a great effect on bacterial community dynamics despite exposure to the same water current, driven primarily by the temperature gradient. In corals located at temperate latitudes, specialist bacterial phylogroups outnumbered generalist groups, whereas the opposite was true in tropical latitudes. Van de Water et al. assessed the spatial and temporal stability between the black coral *Antipathella subpinnata* and its bacterial microbiome. They further compared this stability to a sympatric octocoral, *Eunicella cavolini*, which featured a similar arborescent morphology. The black coral's prokaryotic community composition varied across space and time, whereas the octocoral community remained stable. A high degree of flexibility with respect to the microbiome may allow *Antipathella* holobionts to acclimate to a range of environmental conditions, particularly through the occurrence of bacterial taxa putatively involved in nitrogen and sulfur cycling.

One experiment tracked interactions between Symbiodiniaceae and bacteria. Diaz-Almeyda et al. compared the microbial communities associated with three *Symbiodinium* species characterized by contrasting ecophysiologies, levels of interaction with their hosts, and thermal adaptations. Microbial communities were assessed after culturing photosymbionts for 27 days at ambient and elevated temperatures. In addition to identifying a shared set of bacteria common to many Symbiodiniaceae cultures and corals, they showed that among the more variable components of the prokaryotic microbiome, community composition was better predicted by *Symbiodinium* species than by temperature. At elevated temperatures, some species displayed reduced microbial diversity along with greater individual variability in community composition. Overall, these results suggest that bacteria associated with thermotolerant Symbiodiniaceae might play a role in their thermotolerance.

Finally, one study examined how intraspecific variation may scale to impact ecosystem processes. Lin et al. investigated the response of an abundant reef fish species, *Ctenochaetus striatus*, to shifts in benthic composition in the South China Sea. Through DNA sequencing, they showed that fish stomach contents were dominated by macroalgae, filamentous algae, and microalgae. The biomass of *Ctenochaetus* exhibited a positive relationship with short algal turf cover, which tends to be more common on partially degraded reefs. Thus, an increase in fish body condition may be associated with moderate loss in coral cover. The implication is that benthic shifts triggered by the loss of the most susceptible corals could have cascading effects on closely-associated species such as reef fishes. Because *Ctenochaetus* is an important detritivore within reef communities, such shifts could impact the flow of energy in reef systems.

Although they may seem disparate at first glance, the works included in this Research Topic are all focused on intraspecific variability at some level within coral holobionts, from meta-populations to micro-communities. The diverse nature of the studies reflects the organismal diversity found within coral colonies themselves. If we are to gain a truly holistic understanding of coral ecology and evolution, particularly as reef ecosystems respond to climate change in the near future, we must continue to explore variation in coral holobionts at multiple scales.

Author contributions

JEP wrote the first draft of the article. All authors contributed to the article and approved the submitted version.

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