

Digest: Drivers of coral diversification in a major marine biodiversity hotspot*

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Coral reefs are of great ecological importance for marine wildlife (Knowlton 2001); despite occupying less than 0.1 percent of the surface area of the world's oceans, they provide habitats for at least a quarter of marine species (Spalding and Grenfell 1997). They are fragile ecosystems, under threat from numerous stresses including climate change, ocean acidification, and destructive fishing practices (Pandolfi 2003). Despite their great ecological importance, relatively little is known about the evolution of coral reefs. The mode and tempo of evolution in coral reef systems are poorly understood, with data lacking on the origin and diversification of coral hotspots (Huang and Roy 2015).

In this issue, Huang et al. (2017) utilize a solid phylogenetic framework based on two sets of trees of coral species: one that uses earlier supertree studies incorporating published molecular data (seven mitochondrial DNA markers) and morphological trees, and one that uses an expanded molecular dataset (seven mitochondrial plus two nuclear DNA regions). In both cases, fossil calibrations were used to date the trees. Using these different phylogenetic datasets, they tested the mode of diversification in the Indo-Pacific Coral Triangle (CT) biodiversity hotspot to test competing hypotheses regarding the temporal dynamics of coral species richness.

The Coral Triangle is a geographic area encompassing the oceans around Malaysia, the Philippines, Indonesia, Timor-Leste, Papua New Guinea, and the Solomon Islands. Phylogenetic analyses indicate that diversity within the CT was driven mostly by range expansions of lineages that originated outside the CT. Speciation rates within the CT region itself were lower than surrounding regions, as endemic CT lineages were found to

be older than widespread lineages or those found outside the CT. The drivers of these range shifts are currently unknown, but such shifts could be underpinned by time-dependent variables including changing climatic conditions, as observed in plant (Antonelli et al. 2010; Pérez-Escobar et al. 2017a) and insect (Condamine et al. 2012) lineages.

Diversification patterns of corals in the CT resemble the diversification dynamics of other eukaryotic lineages that are highly diverse in biodiversity hotspots. For example, in Andean orchids (Pérez-Escobar et al. 2017b), asynchronous migrations from adjacent regions followed by rapid diversification have led to extremely high species diversity in montane areas. This contradicts the museum hypothesis, whereby species accumulate at a constant rate over time with little extinction. Huang et al.'s findings posit many puzzling questions for the origin of biodiversity hotspots more generally. For the specific case of the CT, when in time did the wave of migrants move into the CT? Were migrations and recolonizations asynchronous or did they happen simultaneously? The data generated by the authors provide a solid phylogenetic framework to address these questions, and will be helpful to understand in detail the temporal evolutionary dynamics of the CT.

Macroevolutionary analyses (Fig. 1A) on the scleractinian phylogeny of Huang et al. (2017) reveal multiple, asynchronous shifts in diversification rates and a constant increase in net diversification rates through time (Fig. 1D). Additionally, they revealed overall lower tip speciation and extinction rates of endemic CT lineages (Fig. 1B and C) compared with species distributed outside the CT, but also those that are widespread (occurring in the CT and outside). Surprisingly, most of the diversification rate shifts are concentrated toward the Cenozoic, and across clades including both widespread and endemic CT species.

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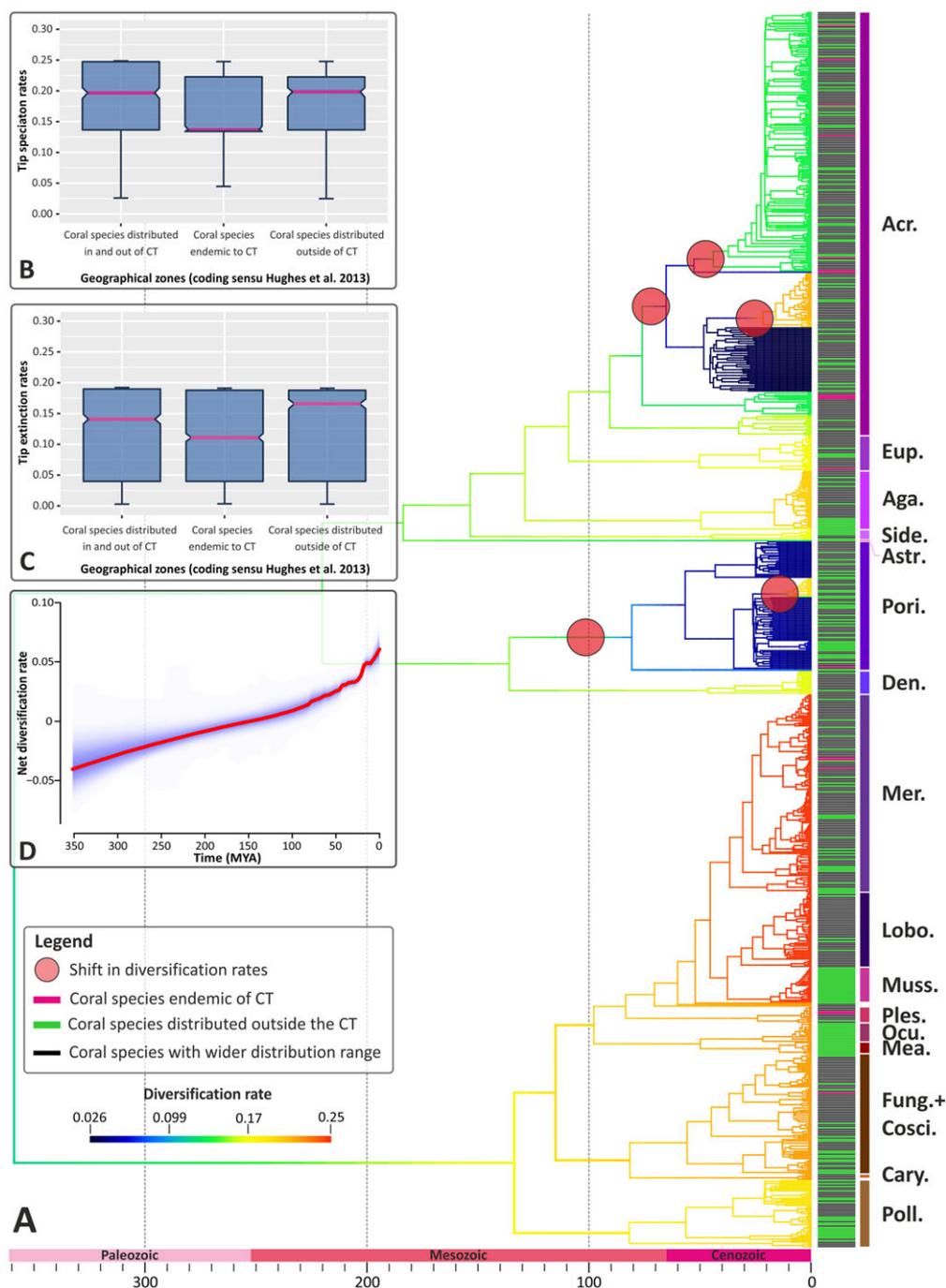


Figure 1. (A) Diversification rate plot (phylorate) of scleractinian reef coral lineages showing changes in diversification rates through time (best configuration shift identified by BAMM, and inferred from a maximum clade credibility tree with common ancestor heights; (Rabosky 2014)). Cold colors represent slower diversification rates, while warm colors indicate faster diversification rates. Red circles on branches represent locations of rate shifts. Geographical ranges (i.e., species endemic to CT vs taxa distributed outside the CT, or widespread) are shown as horizontal bars in front of the terminals. Family members of Scleractinia are color coded: Acr.: Acroporidae; Eup.: Euphylliidae; Aga.: Agariciidae; Side.: Siderastreidae; Astr.: Astrocoeniidae; Pori.: Poritidae; Den.: Dendrophylliidae; Mer.: Merulinidae; Lobo.: Lobophylliidae; Muss.: Mussidae; Ples.: Plesiastreidae; Ocu.: Oculinidae; Mea.: Meandrinidae; Fung.: Fungiidae; Cosci.: Coscinaridae; Cary.: Caryophylliidae; Poll.: Pocilloporidae. Tip speciation (B) and extinction (C) rates of reef coral lineages per geographical range (coding *sensu* Hughes et al. 2013—see Huang et al. supporting online material). Mean rate values are indicated with a pink bar. Note the lower speciation and extinction rates in coral species endemic to CT; diversification rates of widespread and outsider CT taxa, however, are very similar. (D) Net diversification rates of scleractinian reef coral lineages through time shows a constant increase of rates, with an acceleration near the K/T boundary.

This study paves the way for future research where the tempo of diversification of CT lineages can be further investigated. This will help us to understand how diversification rates in coral reef lineages have responded to past climatic and geological changes, as reported in alternative eukaryote lineages (Condamine et al. 2013; Lagomarsino et al. 2016). More importantly, future research will enable the understanding of changes in coral reef species-pump and sink area dynamics through time. Lastly, Huang et al. (2017) highlight the importance of such evolutionary studies for conservation efforts, as the regions surrounding biodiversity hotspots may be as important to conserve as the hotspots themselves.

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