group in a global analysis. For example, Ericson (2012) inferred the ancestor of all passerine birds as "Australasian" based on the position of Acanthisittidae (from New Zealand) and basal songbirds (mostly Australian) in the tree. However, once "Australasia" is divided into its two main continental plates, Australia and Zealandia, successive outgroups are included, and a quantitative analysis is performed, South America becomes a possible ancestral area for Passeriformes (Claramunt & Cracraft, 2015). It remains to be demonstrated whether restricting potential ancestral areas *a priori* improves biogeographic reconstructions or not.

CONCLUSIONS

No one disputes a retraction of many Holarctic biotic elements to warmer and wetter southern areas following the Neogene climate deterioration. Indeed, many years ago one of us wrote extensively about how that might have shaped global vertebrate (and avian) faunas (Cracraft, 1973, 1974). The issue, of course, is that the Neogene event took place long after these major lineages arose and diversified globally, which is the point of our paper. Only by using an integrative quantitative approach can we decipher how that Neogene event may have "overprinted" the historical patterns that developed prior to that time. At present, the fossil record alone is unable to provide that evidence.

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Joel Cracraft[1]* and Santiago Claramunt[1,2]*

[1]*Department of Ornithology, American Museum of Natural History, New York, NY 10024, USA,* [2]*Department of Natural History, Royal Ontario Museum, Toronto, ON M5S2C6, Canada*

**E-mails: jlc@amnh.org; sclaramunt@rom.on.ca*

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Biogeographical homogeneity of Caribbean coral reef benthos

ABSTRACT

Caribbean reef benthic assemblages have been considered biogeographically homogeneous at regional scales, but this concept was recently challenged by Williams *et al.* (2015, *Journal of Biogeography*, **42**, 1327–1335). These authors concluded that benthic assemblages exhibit considerable biogeographical variability at regional and smaller scales, that rugosity and wave exposure play key roles in structuring assemblages, and that homogenization has yet to occur at a regional scale. We reassess their conclusions using recently published benthic and fish surveys that targeted sites either protected from fishing or intensively overfished. For sponges, regional variation in assemblages is mostly attributable to the removal of chemically undefended species by sponge-eating

fishes at sites protected from overfishing. We maintain that Caribbean benthic assemblages are remarkably homogeneous when compared to reefs in other tropical regions, and were likely more homogeneous before the localized effects of intensive fishing resulted in top-down ecosystem alterations in benthic assemblages.

Keywords endemism, global comparison, macroecology, overfishing, spatial scales, sponges, top-down

In a recent article, Williams *et al.* (2015) used data from benthic surveys of 546 fore-reef transects across the Caribbean to examine spatial variability in species richness, composition and relative abundance for corals, sponges, and octocorals at four hierarchical spatial scales ranging from transects (metres) to regions (hundreds of kilometres). Using PERMANOVA analyses, they found that variation in species richness for all three taxa was not significant at the regional scale but was significant below that spatial level. Species composition and relative abundance were significantly variable across all spatial scales for all three taxa. The variability in species composition was partially explained (< 5%) by wave exposure and reef rugosity for corals and octocorals, but not for sponges, and the variability in relative abundance was partially explained by wave exposure and rugosity for octocorals, but not corals and sponges. The authors' main conclusions were that (1) contrary to the general view that Caribbean reefs are biogeographically homogeneous at a regional scale, benthic assemblages exhibit considerable variability at all scales 'when more responsive community attributes are used', (2) variability at the level of site (kilometres) can be attributed to the effects of environmental factors such as rugosity and wave exposure, and (3) within-site variability not explained by rugosity and wave exposure may be explained by anthropogenic disturbances such as runoff and sedimentation. The authors went on to speculate that the considerable variation in species composition they documented suggests that homogenization of biodiversity across Caribbean reefs has yet to occur.

We recently published our own benthic and fish survey data for 69 fore-reef sites across the Caribbean (Loh & Pawlik, 2014; Fig. 1; Loh *et al.*, 2015), with a similar survey depth profile and in many of the same reef areas surveyed as in Williams *et al.* (2015, Fig. 1). Our surveys focused on sponges at the species level, but included other components of the benthos as well as selected fish species above the reef, and were designed to test the hypothesis that the predatory activities of sponge-eating fishes (angelfishes and parrotfishes) alter sponge assemblages by removing chemically undefended sponge species. We took advantage of historically intensive fishing practices (fish-trapping) to compare sites where sponge-eating fishes were mostly absent to sites that were protected from fishing, either because the latter category of sites were remote and less affected by fishing or designated as marine protected areas (MPAs). Contrary to Williams *et al.* (2015), we found that the species composition of the sponge community depended more on the abundance of sponge-eating fishes than on geographical location (Fig. S1 in Loh & Pawlik, 2014). Although we have not been provided access to the raw data used by Williams *et al.* (2015) to perform analyses that include fish abundance for locations where our surveys overlap, we believe it is likely that much of the variation in sponge community assemblages reported by Williams *et al.* (2015) can be attributed to spongivore abundance and fishing intensity.

We were surprised that Williams *et al.* (2015) dismissed the relative effects of predation when embarking on their study, writing 'At regional scales, historical and geographical factors are unlikely to account for spatial variability in regions with low species richness such as the Caribbean, and biological interactions are weak drivers in non-equilibrial communities such as coral reefs (p. 1328, references omitted)'. This statement is contradicted by considerable evidence for the effects of fish and invertebrate consumers on coral and seaweed communities on coral reefs worldwide, research that was recently reviewed by two of the co-authors of the study in question (Roff & Mumby, 2012). For Caribbean sponges, fish predators have a demonstrable effect on fast-growing, chemically undefended species in small-scale manipulative field experiments (Loh & Pawlik, 2009; Leong & Pawlik, 2010), as well as the region-scale, long-term manipulative experiment imposed by differential fishing practices (Loh & Pawlik, 2014). We note that sponges were an important driver of variance in analyses of the entire benthic community (corals, sponges, and octocorals) in Williams *et al.* (2015), but it is also well known that parrotfishes have species- and size-dependent effects on corals and seaweeds that may have affected the variance in the data, either directly (parrotfishes eat corals) or indirectly (parrotfishes eat seaweeds that compete with corals).

The foregoing should not be interpreted to suggest that we discount the importance of the abiotic effects of turbulence from wave or storm exposure or reef topography in structuring benthic reef communities, particularly at smaller spatial scales. Sponges, in particular, are strongly influenced by turbulence and storm damage, and sponge assemblages on fore-reefs that are affected by hurricanes or that face the swell of the open sea may be structured by water motion to depths of 10 m or deeper; nevertheless, the biotic factors of competition and predation should not be dismissed (Pawlik *et al.* 2015; Fig. 4).

The larger issue is biogeographical homogeneity. Williams *et al.* (2015) conclude that Caribbean benthic assemblages exhibit 'considerable' variability at regional and smaller scales, but this variability is not placed in context relative to coral reefs in other parts of the tropics. For example, it is generally accepted that reefs of the Indo-Pacific region have much greater species richness and localized endemism of benthic fauna than the Caribbean (Paulay, 1997). Indeed, it has been suggested that endemism is a particularly useful measurement of biodiversity for the purpose of conservation (Lamoreux *et al.*, 2006). Coral reefs in regions such as the Eastern Pacific certainly rank lower in many metrics for biodiversity than parts of the Indo-Pacific, but the Caribbean is notable for its low species richness, low endemism, and relative homogeneity (Paulay, 1997), and evidence of the connectivity between Caribbean reefs has been amply demonstrated by the rapid spread of diseases (e.g. long-spined sea-urchin die-off) and invasive species (e.g. lionfish) across the region.

Sponges have the greatest species diversity of the macrobenthic fauna in the Caribbean (Diaz & Rützler, 2001), yet most species are widespread within the region. From our surveys of 69 reef sites, we found that the 10 most common sponge species constituted 51% of sponge cover Caribbean-wide (Loh & Pawlik, 2014). This is in marked contrast to the Indo-Pacific, where less than 5% of sponge species are widely distributed and a large component of the very high species richness can be attributed to endemics that are limited to specific embayments, remote island groups, and isolated patch reefs (Hooper & Levi, 1994). More recent assessments have confirmed high levels of dissimilarity and endemism of the sponge fauna across the Indo-Pacific; for example, between the north and south portions of the Great Barrier Reef, between

the Great Barrier Reef, Vanuatu and New Caledonia (Wörheide *et al.*, 2008), and across French Polynesia, where approximately one-third of the sponge species in the Marquesas and Society Islands are endemics (Hall *et al.*, 2013). Recent assessments of biodiversity for other tropical reef areas, while not focusing on sponges in particular, have also noted high levels of endemism among benthic fauna (Red Sea: DiBattista *et al.*, 2016; Western Indian Ocean: Wilson & Kirkendale, 2016).

Williams *et al.* (2015) argued that 'the considerable variability in species composition' implied that homogenization had yet to occur at a regional scale on Caribbean reefs (p. 1333). On the basis of our past studies, we propose that Caribbean reef sponge assemblages were more homogeneous and less species rich in the past, before intensive fishing in some reef locations resulted in predator-release of chemically undefended, fast-growing sponge species that now compete to a greater degree with corals (Loh *et al.*, 2015; Fig. S1).

We maintain that Caribbean coral reef benthic assemblages are remarkably homogeneous in terms of biodiversity when compared to shallow tropical reef systems of similar geographical scale elsewhere on the planet, and this is true when considering other diverse macrobiotic benthic taxa as well. Unfortunately, the paucity of comparable survey data for most of these taxa, and for most tropical reefs in the Indo-Pacific, makes it difficult to provide more specific quantitative contrasts with Caribbean reefs.

Joseph R. Pawlik* and Tse-Lynn Loh

Department of Biology and Marine Biology and Center for Marine Science, University of North Carolina Wilmington, Wilmington, NC 28409, USA
E-mail: pawlikj@uncw.edu

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