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Scope for latitudinal extension of reef corals is species specific

In a recent paper, Muir et al. (2015) demonstrate that the maximum depths of staghorn coral assemblages are shallower at higher latitudes, a trend that correlates with winter light levels. Based on these findings, the authors hypothesize that light availability limits the current latitudinal extent of the group and will constrain future range expansion. Here we reanalyze their data and show that depth-latitude relationships vary substantially among species, and that most species show either no significant pattern or the opposite pattern. In so doing, our reanalysis highlights a common misinterpretation of mixed-effects models: the fallacy of the average. Muir and colleagues' hypothesis is also inconsistent with fossil and contemporary observations of coral range-shifts. The factors that limit the current range extent of corals remain elusive, but they are likely species-specific and will require much further research to elucidate.

Identifying the factors that define the geographic range limits of species, and their capacities to expand their ranges in response to environmental change, are key goals of climate change research. Species-energy theory postulates that energy availability drives broad-scale patterns in taxonomic richness and has led to hypotheses that link biodiversity patterns to various forms of energy (Clarke and Gaston 2006) through distinct mechanisms (Hawkins et al. 2003, Currie et al. 2004). Energy used by biota comes in many forms, including solar radiation, molecular kinetic energy (as indexed by temperature), and chemical potential energy stored in biomass (Hawkins et al. 2003, Clarke and Gaston 2006). A growing body of literature suggests that the importance of specific climatic variables to persistence varies among taxa and with spatial scale (Helmuth et al. 2002, Evans et al. 2006, Keith et al. 2014).

Indeed, many studies have highlighted the central role of temperature in influencing species-specific distributions, with marine species, in particular, closely tracking thermal conditions (Tittensor et al. 2010, Sunday et al. 2012). Latitudi-nal range shifts have been documented for hundreds of species (Parmesan and Yohe 2003, Parmesan 2006). Recent work suggests that the leading range edges of marine species that have responded to climate change have shifted poleward at a mean velocity of 72.0 ± 13.5 km per decade (Poloczanska et al. 2013), which is an order of magnitude faster than for terrestrial species (6.1 ± 2.4 km per decade; Parmesan and Yohe 2003). Reef corals are no exception. Some reef coral species' geographic ranges have expanded pole-ward in both hemispheres in recent decades (Precht et al. 2004, Baird et al. 2012), in Japan as fast as 14 km per year (Yamano et al. 2011).

Fossil data demonstrate that such range expansions have occurred in the past in response to warming oceans. For example, tropical sea surface temperatures (SSTs) during the last interglacial period (LIG), 125 ka (McKay et al. 2011), were likely to have been at least $0.7°C$ warmer than today, and sea levels were 2-6 m higher (Lambeck et al. 2002). Latitudinal diversity patterns in scleractinian corals are characterized by a tropical plateau today, but during the warmer SSTs of the LIG they were characterized by a pronounced equatorial trough as species distributions shifted away from the equator along trailing edge margins, while simultaneously expanding poleward along their leading edge margins (Kiessling et al. 2012). These LIG dynamics were particularly striking along the western Australian coastline (Greenstein and Pandolfi 2008), where vibrant Pleistocene reefs extended all the way to the Margaret River region at $34°S$ latitude. These fossil reefs had a similar species composition to modern reefs, which are now limited at their southern margin to the Houtman Abrolhos Islands, some 550 km further north. Pleistocene coral assemblages have also been found at other high latitude locations, including some in eastern Australia (Pickett 1981). Finally, reef development throughout the Phanerozoic (past 600 my) has often extended substantially beyond tropical settings (Kiessling 2001). Therefore, range expansions are to be expected in response to ongoing ocean warming.

Muir et al. (2015) analyzed a global dataset of maximum depth of occurrence as a function of latitude for 104 staghorn reef coral species. Based on their quantile regression analysis, they propose that species of this group adhere to a general U-shaped depth-latitude relationship such that maximum depth (as indexed by the 97.5% quantile) is shallower at higher latitudes. They further propose that this pattern reflects light limitation because photosynthetically available radiation during winter exhibits a higher correlation with their U-shaped relationship than three other environmental variables that have been posited to limit distributions of reef coral species (i.e., sea surface temperature, aragonite saturation, salinity). However, the analysis of Muir et al. (2015), and their interpretation, entails the implicit, and as yet untested, assumption that all species exhibit identical depth-latitude responses. Evaluating this assumption is key to determining whether all staghorn species are expected to respond similarly to future climate change, as Muir et al. (2015) assume, or whether responses are instead expected to be species-specific.

Here we evaluated this key assumption of Muir et al. (2015) by reanalyzing their data using the same mixed-effects quantile regression technique, but by assuming a different structure for 'random' effects, which correspond to species-specific deviations from overall trends. In their analysis, Muir et al. (2015) implicitly assume that all species adhere to the same maximum depth-latitude relationship by treating latitude as having only 'fixed' effects, and by treating species as having a random effect on only the intercept (corresponding to absolute depth at fixed latitude). We can evaluate this implicit assumption by comparing the model of Muir et al. (2015) (A in Table 1) to a more complex model (B) that incorporates two additional parameters, corresponding to random differences among species in the linear and quadratic effects of latitude. Results of this comparison yield compelling evidence that depth-latitude relationships vary substantially among species (AIC difference: 622, Table 1; likelihood ratio test: $\chi^2 = 720.6$, $p < 10^{-100}$, $df = 2$), contrary to the implicit assumption of Muir et al. (2015).

Having established that depth-latitude relationships vary significantly among staghorn reef corals as a group using a mixed-effects modeling approach, we now characterize these trends on a species by species basis by treating species effects on the intercept and the linear and quadratic coefficients for latitude as being fixed (using *quantreg* in R). Results of this analysis, which was conducted for the subset of 50 species with > 100

Table 1. Quantile regression models characterizing maximum depths of occurrence (defined as 97.5% quantile) for staghorn species (S) as linear and quadratic functions of latitude (L and L^2). Muir et al. (2015) treat quadratic effects of latitude as fixed (model A), allowing intercepts (I) to vary among species (I|S). We show here, however, that incorporating random species-level variation in the quadratic relationships (model B) results in a substantial improvement in model fit (ΔAIC=622 for models A versus B), implying substantial variation in depth-latitude relationships among species. Treating species effects on depth-latitude relationships as fixed (model C), by incorporating interactions for the intercept (I:S) and linear and quadratic terms for latitude (L:S, L^2:S), allows depth-latitude relationships to be independently estimated for each species (yielding the thin curves depicted in Fig. 1). The thin curves are essentially the same when analyzing each species in separate models. Models A and B were fitted using all of the data of Muir et al. (2015) (14208 observations and 104 species), whereas model C was fitted only to data for the subset of 50 species with >100 observations (*n*=12173) to increase statistical power; therefore, the AIC for model C is not comparable to that of the first two models. The documented R analysis is available at: https://github.com/jmadin/muir_comment

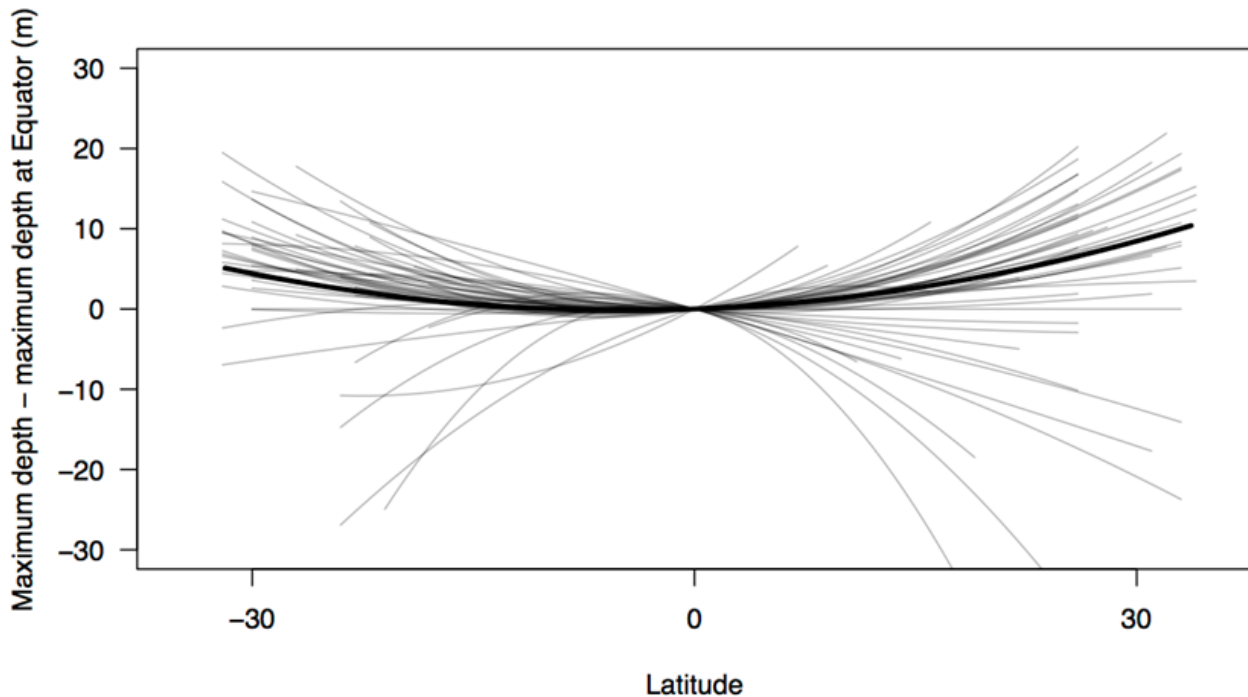|	Fixed	Random	LL	df	AIC
(A) Random variation among species in intercepts	$I + L + L^2$	I|S	-55357	5	110725
(B) Random variation among species in depth-latitude relationships	$I + L + L^2$	$(I + L + L^2)$|S	- 54997	7	110008
(C) Fixed variation among species in depth-latitude relationships	$S + L{:}S + L^2{:}S$	None	-46417	150	107638

Figure 1. Latitudinal gradient in the maximum depth of staghorn coral species. The thick line shows the model fit for random variation among species in intercepts as per Muir et al. (2015) (Table 1A). The thin lines show the fixed variation among species in depth-latitude relationships (Table 1C). Each line has been normalized to be relative to maximum depth at the equator and extends from a species' southern-most to its northern-most observed occurrence.

observations to increase statistical power, confirm that depth-latitude relationships vary substantially among species (model C in Table 1). Furthermore, while 34% of species indeed showed a significant U-shaped pattern (as indicated by positive coefficients for the quadratic terms based on two-tailed t-tests with $p < 0.05$), 8% had significant hump-shaped patterns (negative quadratic coefficients, $p < 0.05$), and the remaining 58% showed no significant quadratic trend ($p > 0.05$, Fig. 1).

Mixed-effects modeling approaches can be incredibly powerful, but can yield models that are grossly misinterpreted, which is the case in Muir et al. (2015), due to the fallacy of the average. Specifically, the authors estimated an average trend across species, which can always be calculated, but failed to recognize that few species actually followed this trend. Our reanalysis highlights striking differences among species in how their depth distributions vary with latitude. The implication is that trait differences among coral species should not be ignored when attempting to forecast changes in their distributions in response to climate change, as they should not be ignored when attempting to explain current biogeograph-

ical patterns in assemblage structure (Sommer et al. 2014, Keith et al. 2013, Keith et al. 2015). For instance, species differ in the amount of energy acquired by heterotrophy relative to autotrophy, and therefore their reliance on light. Species also differ in morphological plasticity, and therefore their capacities to maximize light interception in low light environments.

Muir et al. (2015) go on to correlate depth-latitude relationship and winter light levels, and conclude that low winter light is limiting current coral distributions. However, this is not a logical inference. The preferred light environments for all deep-water tropical species are present in temperate locations; they just occur at shallower depths. If anything, tropical *shallow-water* species would be limited by low winter light, but the authors show that there is no decline in richness in this group until latitudes markedly higher than for deep- and mid-water species (Fig. 4A in Muir et al. 2015). As the authors acknowledge, the factors that prevent a deep-water tropical species moving to shallower depths at high latitudes are numerous, and include wave energy, lack of appropriate substrates and competition with algae. Therefore,

low winter light is not the sole factor limiting current staghorn distributions, and it is unlikely to hinder range expansion in the future. The factors that limit the current range extent of corals remain elusive (Veron 1995), but they are likely species-specific and will require much further research to elucidate.

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