



Evolutionary dispersal drives the latitudinal diversity gradient of stony corals

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The diversity of stony corals displays one of the most exemplary latitudinal gradients on the planet, yet the evolutionary dynamics that produced this pattern remains unclear. Using both paleontological and distributional data, we compare the origination, extinction and immigration levels between low and high latitudes since the earliest proliferation of the group during the mid-Triassic. Altogether, first and last occurrence localities in the fossil record do not support a positive preference towards either latitudinal bin. Nonetheless, considering past and present scleractinian fauna, the process of extinction has been apparently more pronounced at higher latitudes based on face values and correlation coefficients. Far above these differences, immigration of extant taxa has been substantially higher towards the tropics than to temperate regions. While the net dispersal toward low latitudes persists in all temporal intervals, the gradient of diversity was largely built up during the Cenozoic Era and only becomes significantly steep from the Neogene Period onwards. This dynamic supports the 'into the tropical museum' model, which suggests that tropics have historically acted as a center of accumulation for marine biodiversity.

The pronounced upsurge in species richness from the poles to the tropics is one of the oldest and yet most famous large-scale pattern in ecology (Pianka 1966, Hawkins 2001). With few exceptions, the latitudinal diversity gradient (LDG) is strikingly persistent regardless of the biota's taxonomic affiliation, geographic context or even time domain (Willig et al. 2003, Hillebrand 2004). A consequence of this same universality is that in recent decades numerous studies have accumulated a vast variety of hypotheses addressing the primary causes underlying this pattern (Krug et al. 2009). Thus far, consensus remains elusive among ecologists about the actual mechanism that gave rise to the modern distribution of biodiversity.

In this context it is undoubtedly apparent that evolution of lineages must have played a pivotal role to set and shape the present-day LDG (Mittelbach et al. 2007). As we gather more information about the past, evolutionary and historical explanations have been expanding the traditional ecological framework to a more long-term progression of natural events over the diversification rates. Currently, most evolutionary hypotheses ascribe the higher number of taxa in the tropics to a higher rate of speciation or a lower extinction rate compared to temperate zones (Mittelbach et al. 2007). While these simplified scenarios may occur, this dichotomy is misleading and contradicts most of the biogeographic data

that show large distributional changes over time (Jablonski et al. 2006, Roy and Goldberg 2007). In marine bivalves, for instance, more than half of the genera that originated in the tropics have extended their geographic range towards higher latitudes, evidence used by Jablonski et al. (2006) to suggest an 'out of the tropics' (OTT) dynamic. Linking evolutionary and ecological processes through a spatially explicit approach, this model poses that 'taxa preferentially originate in the tropics and expand toward the poles but without losing their tropical presence'. Although the OTT model was tested in marine organisms, phylogenetic information on terrestrial clades also confirmed these predictions over the tropical conservatism hypothesis (Jansson et al. 2013). In fact, dynamic model simulations of range shifts and diversification processes have shown that extratropical regions may act not only as a macroevolutionary sink but as a dispersal source as well (Goldberg et al. 2005, Arita and Vázquez-Domínguez 2008). Either way, results consistently indicate that speciation and extinction cannot fully explain the canonical LDG, thus it seems quite likely that historical dispersion plays a central role in the current distribution of taxa (Goldberg et al. 2005, Jablonski et al. 2006, Roy and Goldberg 2007, Arita and Vázquez-Domínguez 2008, Escarguel et al. 2008, Soria-Carrasco and Castresana 2012).

Stony corals (order Scleractinia) are the world's primary reef-builders, one of the most productive and biologically diverse ecosystems on the planet (Moberg and Folke 1999). Given that not all species form massive calcareous skeletons, genera are often characterized based on whether or not they contribute to the framework of reefs (hermatypic and ahermatypic corals, respectively) or interact with zooxanthellae (Schuhmacher and Zibrowius 1985). This remarkable diversification in response to different ecological requirements is well imprinted on its modern distribution, scleractinian representatives being found from shallow tropical waters to the great depths near the poles (Keller 1976). The vast majority of stony corals, however, are currently located in tropical latitudes and, more precisely, between the 30° north and south of the equator (Stehli and Wells 1971, Veron 1995, Keller 1998, Cairns 2007). Since Darwin's first monograph about coral atolls, this particular LDG has caught the attention of marine biogeographers for years and it has been even used as an historical indicator of tropical conditions (Jablonski 1993, Bellwood and Hughes 2001, Hughes et al. 2002, Connolly et al. 2003, Bellwood et al. 2005). Veron (1995) explained this spatial pattern as a 'progression of layers of detail', where the family-level distribution determined by major global and climatological changes such as the continental movements and extinction events, is passed down as a template to generic groups defined by more recent geological events, especially the obliteration of the Tethys Sea and the closure of the Central American Seaway. As an outcome of the post-Pliocene climate, the highest species richness is nowadays concentrated in the Indonesian/Philippines archipelago due to a combination of environmental and geometric constraints (Kleypas et al. 1999, Bellwood and Hughes 2001, Connolly et al. 2003, Bellwood et al. 2005). This area commonly known as the 'Coral Triangle' comprises thirty-two functional seascapes, eleven different ecoregions and is today acknowledged as the global center of marine biodiversity (Green and Mous 2008).

While most Scleractinia ancestors date back from the Middle Triassic (Veron 1995), the historical variability of the gradient slope as well as the evolutionary dynamic that built up their present distribution remains largely untested (but see Kiessling et al. 2007). As a group, stony corals fulfill all the criteria to address each of the OTT predictions directly (i.e. possesses a distinguishable LDG, a fossil record fairly sampled and its taxonomy is well standardized across groups). Like no other major type of ecosystem, coral reefs imprint paleoclimatic events through massive ramparts of rock which are a direct product of the environmental conditions (Veron 2008). Although we cannot completely rule out a spatial bias, these geological structures have been sampled nearly worldwide (including non-reef-building corals). Given its ecological and socioeconomic importance (Moberg and Folke 1999), coral taxonomy has been comprehensively reviewed in popular textbooks (Veron 2000), specialized journals (e.g. Coral Reefs) and online projects (< www.coralosphere.org/index >). Scleractinia phylogeny is also currently undergoing an extensive revision that has frequently revealed little coincidence between the skeleton morphology and the evolutionary history of its major clades (Romano and Palumbi 1996, Huang et al. 2011, Budd et al. 2012). Though results from molecular techniques are

similarly under intense debate (Kitahara et al. 2014), we acknowledge some of the taxonomic limitations the fossil record might have. Still, the present study assesses the latitudinal diversity gradient of stony corals throughout geologic time. Following Jablonski et al.' (2006, 2013) approach, here we: 1) test the fidelity and sampling bias of the fossil record, 2) estimate the origination, extinction and migration levels on a spatially explicit scenario, using modern latitudinal distribution and paleontological data of the first and last occurrence of corals genera, 3) evaluate the historical strength of the canonical LDG, and 4) discuss the role of low and high latitudes in the light of the spatiotemporal dynamic underlying the modern scleractinians diversity gradient.

Methods

Paleontological and distributional data

As most paleontological studies, we used the genera level (henceforth termed taxa) as the unit of analysis owing its representativeness to macroecological processes, completeness of fossil record and robustness against sampling artifacts common at lower levels (Campbell and Valentine 1977, Jablonski and Finarelli 2009). All living stony corals were identified through the World Register of Marine Species (WoRMS, September 2014) and subsequently verified in the *CoralloSphere* web application (< www.coralosphere.org/ >, September 2014). To determine the first and last occurrence in the fossil record (the latter only for extinct taxa), about 32 000 occurrences data of Scleractinia were downloaded from the Paleobiology Database (PBDB, accessed on 26 August 2014). Of the 30 extant families, only one completely lacks a fossil record (Coscinaeidae), therefore, a total of 29 families and 223 genera were finally included in the comparative analysis between past and present distributions. Modern geographic ranges were projected through the Ocean Biogeographic Information System (OBIS, September 2014) and refined using the Corals of the World information base (Veron 2000).

Sampling bias and fidelity of the fossil record

Spatial bias occurs, among other reasons (Vilhena and Smith 2013), due to sampling effort varying non-randomly between geographic locations. Even though this study considers spatial bins large enough to minimize this effect, fossil records tend to be more frequent in temperate latitudes and sometimes higher from what is expected from the canonical LDG (Krug et al. 2009, Rivadeneira et al. 2015). In order to assess this deviation, we used three different approaches: First, we evaluate some conditions as possible predictors for the absence of genera in the fossil record (hereafter missing taxa). Usually they do not represent a random sample of the clade but rather tend to be related to certain ecological and life-history traits mirroring the rarity of the taxa (Cooper et al. 2006, Valentine et al. 2006). Features such as date of description, geographic range and taxon's size were assessed based on their representativeness within each genus without a fossil record, broadly weighing the level of bias forced by the

accessibility of the samples. Secondly, we use the proportion of living genera known from the fossil record within each family as a sampling gauge. In case there was no substantial bias, the relationship between the proportion of living taxa that first occur at low latitudes and the taxa known from the fossil record ought to be positive as a direct result from the latitudinal gradient ("The better the fossil record of a family, the higher the proportion of its genera that first occurs in the tropics"; Jablonski et al. 2006). Finally, the aggregation of the occurrence data within spatial bins was quantified through Green's coefficient of dispersion (Kiessling et al. 2007). This variance to mean ratio measures the sampling distribution, indicating an overall equitable allocation with low values or a possible spatial bias toward a particular geographic bin when over 0.5 (Kiessling et al. 2007, Clapham et al. 2009).

Diversification dynamics

The rates of origination, extinction and immigration were estimated in a two-box model, using the 30°N and S of the equator as the foremost boundary between the regions of low and high latitudes (based on the post-Neogene tropical and extratropical categorization; see also Supplementary material Appendix 1, Fig. A1). In order to quantify the evolutionary dynamic, we use all records of stony corals that originated or went extinct in the last 247 Ma (i.e. since the Middle Triassic). First, the origination rates were determined based on the place of first occurrence for each taxon in the fossil record. Paleocoordinates and localities assignment in one of the two spatial bins was carried out through the GPlates rotation model implemented in the PBDB Navigator (Wright et al. 2013). Due to lack of evidence to prove local extinction processes, the last occurrence data were used to estimate the fluctuation of global extinction in Scleractinia as well as the temporal strength of the LDG based on the latitudinal generic richness ratio (L/H ratio). In this case we also included extinct families, adding a total of 356 taxa according to the Global Biodiversity Information Facility (GBIF, October 2014). Biogeographic data was then incorporated to measure the extent of historical immigration between latitudinal bins through the present-day maximum range limits (i.e. degree of dispersal of tropical taxa in the extratropics, and vice versa). Categorization of modern distribution between tropical and extratropical regions was defined using the 95% of the genus occurrence records. Finally, all statistical analyses were performed in R (R Development Core Team).

Results

Of the 223 extant genera considered in the comparative analysis, almost one-third has no fossil record (Table 1). Generally, missing taxa vary around 20% of the family and only in Coscinaraeidae and Stenocyathidae outnumbered the genera with fossil record. Following the three-step approach to assess the spatial bias, our analyses revealed that: First, 26% of all missing taxa have a restricted geographic range (i.e. confined to one biogeographic province) and only 15% have been recently described (i.e. after the inventory

Table 1. Families of Scleractinia with their respective number of genera and the percentage without fossil record. Classification according to WoRMS database; the recently described family Coscinaraeidae Benzoni, F., Arrigoni, R., Stefani, F., Stolarski, J., 2012, is not included.

Family	No. genera	Missing genera, %
Acroporidae	7	29
Agariciidae	7	14
Anthemiphylliidae	1	0
Astrocoeniidae	4	0
Caryophylliidae	41	41
Deltocyathidae	1	0
Dendrophylliidae	21	29
Diploastreidae	1	0
Euphylliidae	7	29
Flabellidae	10	30
Fungiacyathidae	1	0
Fungiidae	15	33
Gardineriidae	2	50
Guyniidae	1	0
Lobophylliidae	11	18
Meandrinidae	4	0
Merulinidae	24	33
Micrabaciidae	4	50
Montastraeidae	1	0
Mussidae	10	10
Oculinidae	7	14
Pocilloporidae	3	0
Poritidae	4	50
Psammocoridae	1	0
Rhizangiidae	4	0
Schizocyathidae	3	33
Siderastreidae	2	0
Stenocyathidae	3	67
Turbinoliidae	23	43
Total	223	30

of Veron 2000). Yet, 35 out of the 66 genera lacking a fossil record proved to be monotypic, which means that 53% of all missing taxa contain single species. Secondly, the relationship between living corals originated at low latitudes and the quality of the fossil record was directly proportional (Fig. 1). In general terms, this tendency would indicate that there is no significant evidence to support a strong bias toward temperate areas because of its heavier sampling effort. Finally, the spatial independence of the fossil record was upheld in most intervals and only at the edges of the timeline (i.e. Middle Triassic, Pliocene and Pleistocene) Green's coefficients become critical (Fig. 2). Even so, the mean range was relatively low (~0.2), suggesting that data aggregation would not generate a major bias in our analysis.

The origination distribution of stony corals has been very variable over time (Table 2). Considering only living genera, 83 and 74 first occurrences took place at low and high latitudes respectively. Overall, there is no significant difference in the origination rate between both spatial bins ($p = 0.7546$; one-way ANOVA). By including extinct families the variance considerably increases as origination differences get even larger. Two of the four temporal intervals with significant differences between latitudinal regions match the epochs where the fossil record seems to be more aggregated according to Green's coefficient (i.e. Middle Triassic and Pliocene; Table 2). This correlation remains true for the subset of extant taxa, with geographic significant differences

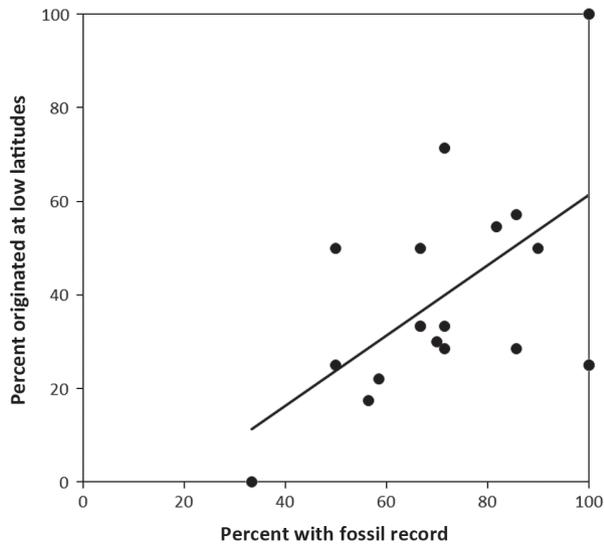


Figure 1. Sampling quality at low latitudes in stony coral families since the start of the Middle Triassic (ca 247 Ma); only extant families having three or more first occurrences within that interval were consider in this analysis ($R^2 = 0.309$, $p = 0.0018$; OLS regression).

noticed only during the Quaternary (Fig. 3E). Without ignoring that these data are likely undersampled, the remarkable variability of the location of first occurrence implies that there is no substantial origination preference toward any particular climatic region.

Global records of last occurrence frequencies outline a bimodal curve apparently defined by the end Triassic (205 Ma) and end Cretaceous (65 Ma) mass extinctions (Supplementary material Appendix 1, Fig. A2). This last interval brings together 24% of all extinct taxa and nearly 50% when considering the entire Cretaceous period. No epoch showed significant differences in the proportion of

extinctions between spatial bins (Table 2). Assuming face values though, 50 exclusively low-latitude genera went extinct in comparison with the 92 genera that were only found above the 30° boundary. When comparing local origination trends with global extinction, there is also a greater correlation between these historical processes at higher latitudes ($r = 0.35$, $n = 430$, $p = 0.2278$) than in the equatorial zone ($r = 0.02$, $n = 439$, $p = 0.9558$). Taking into account the same cautions as for the previous results, some of these differences suggest that ultimately the extinction may have played a more preponderant role than origination in order to passively shape the scleractinians LDG.

Contrary to the predictions of the OTT model, biogeographic data show a far greater tendency to immigrate toward the tropics than temperate regions. Even considering pre-Neogene conditions, most high-latitude genera expanded their geographic distribution by several degrees of latitude toward the equator (Fig. 3). Conversely, the vast majority of the taxa originated in this region did not spread beyond the 35° latitude, exhibiting a significantly lower propensity to immigrate compared to extratropical corals ($p < 0.0001$; Pearson's χ^2 test). Summing over the entire 247 Ma interval, only 23 (28%) of the 83 low-latitude genera expanded their geographic range toward temperate regions compared to 70 (95%) of the 74 high-latitude genera that are currently also distributed in the tropics. While the maximum origination levels varied among spatial bins, this immigration drift toward low latitudes persisted through all geological periods, being even more evident in older taxa and especially during the Cretaceous-Paleogene (K-Pg) boundary. Furthermore, the L/H ratio shows that the modern LDG strengthens in the Cenozoic and becomes significantly pronounced from the Miocene onwards (Fig. 2). Considering the 30° N and S of the equator as boundaries, our estimations indicate that during this period the number of tropical stony corals started to double those in extratropical latitudes.

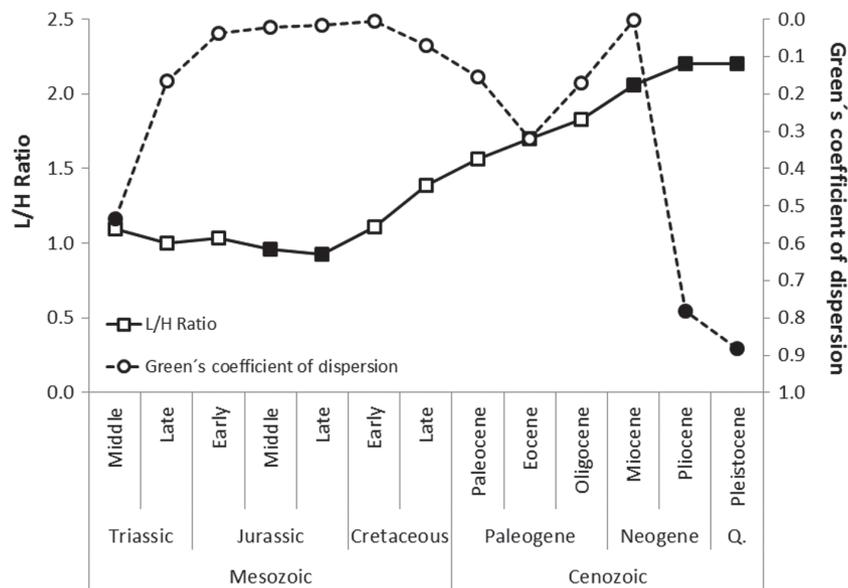


Figure 2. Temporal trends in the data aggregation (Green's coefficient of dispersion for occurrences) and the strength of the LDG (L/H ratio); filled-in squares indicate significant chi-square values ($p < 0.01$) and filled-in circles indicate coefficients above 0.5. Because smaller values of the Green's coefficient indicate less data aggregation, the axis is inverted to display smaller values at the top.

Table 2. Latitudinal differences in the percentages of origination and extinction of stony coral genera. Significant χ^2 values ($p < 0.01$) are highlighted in bold.

Period	Epoch	Origination			Extinction		
		Low latitudes	High latitudes	χ^2	Low latitudes	High latitudes	χ^2
Triassic	Middle	88	12	12.30	75	25	1.32
	Late	78	22	10.74	56	44	2.23
Jurassic	Early	61	39	1.03	45	55	0.02
	Middle	51	49	0.24	47	53	0.00
Cretaceous	Late	33	67	12.09	42	58	0.41
	Early	50	50	0.51	43	57	0.49
Paleogene	Late	48	52	0.73	46	54	0.01
	Paleocene	57	43	0.07	44	56	0.05
Neogene	Eocene	36	64	4.22	44	56	0.04
	Oligocene	31	69	2.87	44	56	0.01
Quaternary	Miocene	52	48	0.10	52	48	0.34
	Pliocene	100	0	6.76	50	50	0.01
Quaternary	Pleistocene	80	20	4.02	50	50	0.03

Discussion

Fossil record reveals that despite its early Mesozoic origin, the canonical LDG in Scleractinia is actually not that old. In fact, the diversity gradient was largely built up after the end

of the Cretaceous mass extinction and only became significantly steep from the Neogene period (see also Buzas et al. 2002). The evolutionary dynamic that induced this pattern also does not meet the OTT model in at least two of its three main predictions (i.e. higher tropical origination, lower

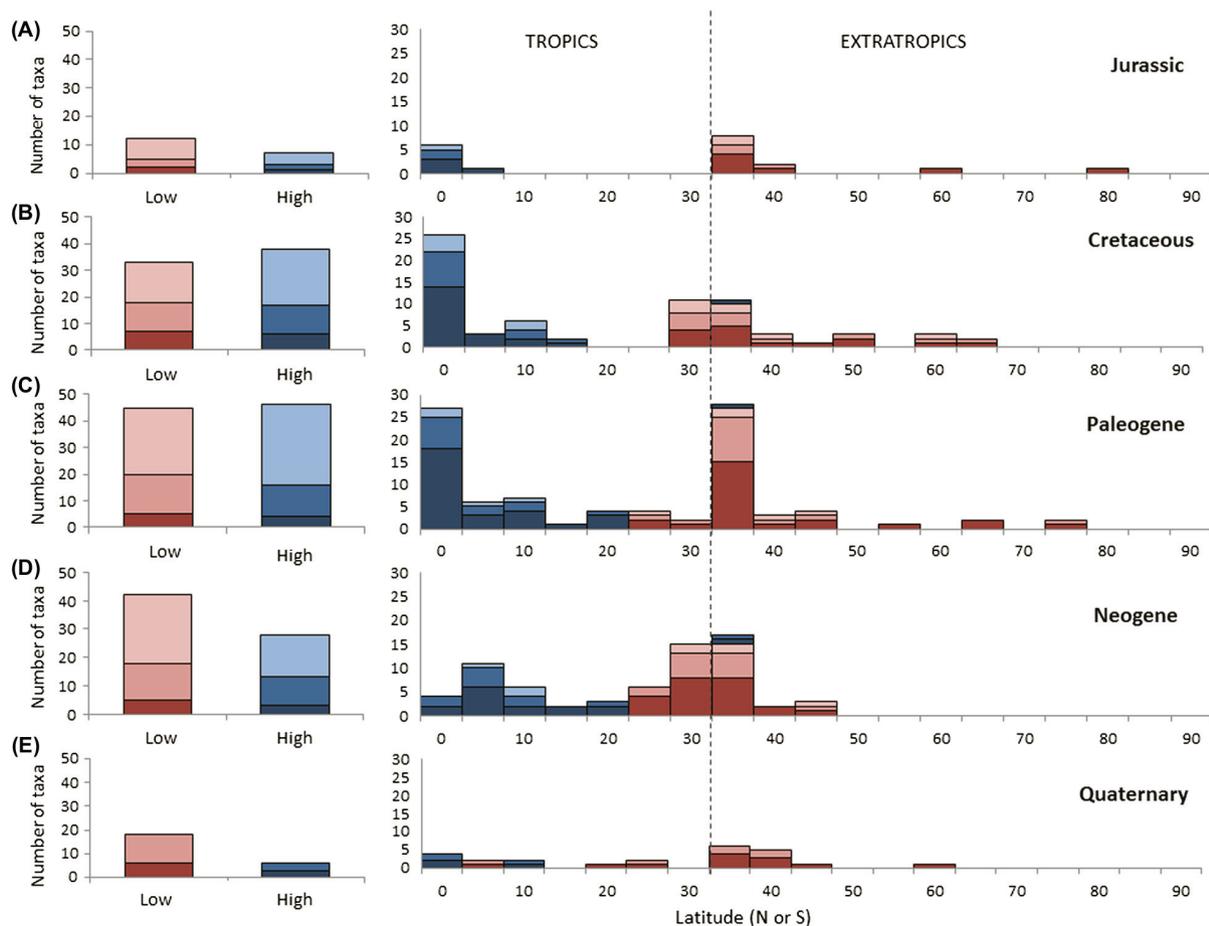


Figure 3. Spatial distribution of the first occurrences of stony corals genera in the fossil record (left) and their corresponding present-day geographic range limits (right). Bars of taxa originated at low (red) and high (blue) latitudes are subdivided according to the quality of the fossil record, showing from the bottom up families with $\geq 90\%$ (dark colored), $\geq 70\%$ (normal color) and $\geq 50\%$ (light colored) of their living taxa known as fossils. With the exception of the Quaternary, there is no significant difference between the frequencies of first occurrence by spatial category [(A), $p = 0.18$; (B), $p = 0.76$; (C), $p = 0.58$; (D), $p = 0.06$; (E), $p = 0.01$; exact binomial test].

extratropical extinction and a net immigration towards the tropics). Although we cannot overlook the impact that sampling restrictions may have in these conclusions, the fossil record in Scleractinia not only is fairly complete but consistent enough to firmly reject the origination and dispersal premises (Fig. 3). Even assuming the underestimation certainty of the paleontological data, the results were upheld throughout different sampling quality segments, showing no substantial spatial bias and a 'pull of the Recent' influence of less than 10% (Jablonski et al. 2003). Quite the opposite, Green's coefficient indicates that geographic sampling distribution tends to be poorer after the Pliocene interval (Fig. 2). In fact, more than half of the taxa without a fossil record are comprised by single species, many of which are derived from other genera and are likely from a recent origin. Overall, stony corals proved to be a suitable model system to test evolutionary hypotheses and thus evaluate the spatiotemporal dynamic that shaped the macroecological patterns of their current biodiversity.

The high biotic richness in the tropics has traditionally portrayed this region as a 'cradle' or a 'museum' of taxa depending on whether this condition is attributed to a higher origination or a lower extinction rate, respectively (Chown and Gaston 2000). The main goal of Jablonski's et al. (2006, 2013) alternative model was not to propose yet another hypothesis to explain the LDG, but rather argue that this exclusion paradigm is not coherent with paleontological data or present-day distribution patterns. Even though the OTT dynamic does not always apply in relation to the diversification rates (Mannion et al. 2014, and references therein), phylogenetic reconstructions and simulation studies have repeatedly recovered the strong influence of geographic range shifts in the modern latitudinal gradient (Arita and Vázquez-Domínguez 2008, Escarguel et al. 2008, Soria-Carrasco and Castresana 2012). In benthic Foraminifera, for instance, origination occurs worldwide and, therefore, differences in the species richness seem to be primarily caused by a temperate-tropical interchange in favor of the latter (Buzas and Culver 2009). While this may be also the case in stony corals, our results additionally reveal a somewhat preponderance of extinction process at higher latitudes (Table 2). Wallace (1878) initially reasoned that this contrast presumably caused by the exposure to climatic fluctuations ultimately made the difference in the diversification process, with the equatorial zone relatively less vulnerable to natural disasters than temperate regions (as is presumed from the correlation coefficients). The substrate stability not only would have been crucial for the proliferation of shallow-water corals but could also explain the high diversity of deep-water azooxanthellate Scleractinia at lower latitudes (Cairns 2007). Accordingly to the fossil record, the combined effect of high immigration with low rates of extinction has led scleractinians to accumulate in the tropics in a more or less uninterrupted fashion. Unlike marine bivalves, this variant to the 'out of the tropics' model has been recently reported for rocky intertidal gastropods under the 'into the tropical museum' (ITM) hypothesis (Rivadeneira et al. 2015). To date, stony corals represent the first taxon to explicitly exhibit this evolutionary trend as the potential leading cause of its modern geographic distribution.

While the diversity gradient of stony corals appears to be fairly pronounced, the generality of this pattern often

depends on the scale at which it is observed (Hillebrand 2004). Indeed, recent studies have demonstrated that the canonical LDG is mostly recognized at large geographic scales (e.g. at tropical vs extratropical areas; Rivadeneira et al. 2015) and especially during the last 30 Ma (Mannion et al. 2014). As in other marine invertebrates, the slope of the latitudinal differences in scleractinians has also undergone severe changes over time presumably due to major oceanographic shifts (Buzas et al. 2002, Crame 2002, Kiessling et al. 2007, Powell 2007). For example, Schwartz et al. (2012) showed that the rapid ecological radiation of Caribbean 'faviid' corals coincided with high productivity periods of the water column during the late Miocene and early Pliocene (see also Fig. 2). Assuming that tropical genera are less prone to extinction, it is expected that the strengthened of the LDG was largely determined in the Cenozoic by the accumulation of older taxa around the equator given the more stable suitable-conditions. Average ages, however, seems to decrease with diversity (Stehli and Wells 1971) even though most Mesozoic corals live in the tropics and molecular phylogenies indicate that the soft-bodied ancestor came from somewhere off the Tethys Ocean (Stanley 2003, Stolarski et al. 2011, Kitahara et al. 2014). Due to the autocorrelation restrictions of age-frequency distributions, indirect tests may provide a more dependable way to respond some of these predictions and thus have better resolution of the evolutionary dynamic of individual taxa (Jablonski et al. 2006). Currently, one of the most promising approaches to do so is through model-based historical biogeographic inferences that rely on maximum-likelihood (Ree et al. 2005, Ree and Smith 2008). This emerging field provides a powerful alternative to assess the ancestral geographic ranges from an evolutionary perspective, progressively integrating the entire diversification process (i.e. dispersal-extinction-cladogenesis model) with both paleontological and neontological data along each divergence event (Ree and Smith 2008, Pyron 2011, Ronquist et al. 2012).

Unlike the OTT dynamic, the ITM model does not predict that endemism should increase toward the equator. On the contrary, biogeographic data from living taxa strongly suggest that the tropics act more as a natural reservoir than as source of species for temperate regions (Veron 2000, Hughes et al. 2002). According to the World Wide Fund for Nature (WWF), almost 80% of the world's coral species are found in the Coral Triangle but only 2% of them are regionally endemic. Interestingly, this pattern is nearly transversal whether or not they are zooxanthellate (Cairns 2007). Several hypotheses have been proposed to explain the causal mechanism (Bowen et al. 2013), however, the noted contribution of peripheral habitats to biodiversity hotspots particularly supports the 'center of accumulation' model. Concomitant with our results, Jokiel and Martinelli (1992) ascribed the high diversity of coral reefs to a net dispersal of taxa caused by prevailing currents toward tropical latitudes, which may occur via 'bridge species' or isolated deep-water colonies (Roberts et al. 2006, Jablonski et al. 2013). Moreover, this hypothesis has not only been put forward for stony corals but also for reef associated organisms such as the ember parrotfish, the yellow tang, the tropical sea cucumber and the holocentrid fishes (Eble et al. 2011, Fitzpatrick et al. 2011, Skillings et al. 2011, Dornburg et al. 2014).

As Hughes et al. (2002) pointed out, centering most conservation efforts on localized hotspots for immediate reasons may be ineffective in the mid and long term. For this purpose, being able to understand what shapes macroecological patterns as the latitudinal diversity gradient is crucial if we want to determine the actual role of climatic regions and thus model the biotic responses to future changes. Recent analyses have highlighted that far more than interspecific interactions, the environmental filtering is the most relevant factor for the community organization of scleractinian corals (Sommer et al. 2014). More and more evidence is revealing how these populations and especially reef-building species are being increasingly endangered by human impact, one-third of them currently facing an elevated risk of extinction (Carpenter et al. 2008). Even independently of local anthropogenic disturbances, the projected ocean acidification has by itself the potential to trigger a mass extinction event by the end of this century (Veron 2008, Kiessling and Simpson 2011). Additionally, several models also alert that the rise of the global temperature over the next 40 yr significantly exceed the conditions under which most corals have flourished over the past half-million years (Hughes et al. 2003, Hoegh-Guldberg et al. 2007). These very rapid changes not only appear to surpass their adaptive capacity but also seem to have a multiplicative deleterious effect in the early planktonic stages (Anlauf et al. 2011). Yet, the part that dispersion will play in a globally threatened marine environment is extremely important, especially when the fossil record suggests it is one of the main drivers of the diversification process (see also Tager et al. 2010). Contrary to most post-Paleozoic marine invertebrates (Jablonski 1993), evolutionary novelties in corals are indeed more concentrated at the edge of their distributions than within the diversity hotspots (Budd and Pandolfi 2010). These range boundaries are likely to change over time, however, past references and environmental predictors indicate that they will be far more restricted than today (Kiessling et al. 2007, Muir et al. 2015). As the tropics progressively become a less suitable place to preserve marine biodiversity, fossil data forecasts that future climate change will have a direct impact on the corals evolutionary trajectory.

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Supplementary material (Appendix ECOG-01855 at <www.ecogeography.org/appendix/ecog-01855>). Appendix 1.