RESEARCH PAPER

Geographic patterns of diversification and the latitudinal gradient of richness of rocky intertidal gastropods: the 'into the tropical museum' hypothesis

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ABSTRACT

Aim To evaluate the existence of a latitudinal gradient of richness (LGR) in rocky intertidal gastropods and the role of evolutionary processes in shaping the LGR.

Location The entire eastern Pacific coast, from Alaska to Tierra del Fuego, encompassing ca. 120° latitude.

Methods The LGR was assessed using field surveys and a comprehensive literature dataset from 308 rocky intertidal sites, representing 328 species and 159 genera. The importance of geographic patterns of diversification in shaping the LGR was assessed using three complementary approaches. First, we used the fossil record to evaluate the region of origination of genera (tropical vs. extra-tropical). Secondly, we used a nestedness analysis to compare present-day biogeographic distributions of genera with their region of origin. Finally, we evaluated the importance of biogeographic dynamics for shaping the LGR using a projection matrix and estimating transition probabilities among different biogeographic states.

Results Eastern Pacific rocky intertidal gastropods follow the canonical latitudinal gradient of richness (higher richness in the tropics). Originations were similar in the tropics and extra-tropics, a pattern that was robust to geographic differences in fossil sampling. The biogeographic distribution of genera was significantly nested, irrespective of the region of origin of genera. The distribution dynamics model accurately reproduced the LGR and showed that key-transitions are low extinction in the tropics and high dispersal of taxa from the extra-tropics to the tropics.

Conclusions The existence of a canonical LGR in rocky intertidal gastropods can be explained by the combined effect of reduced extinction rates in the tropics and the range expansion of taxa from the extra-tropics toward the tropics, in what we have called the 'into the tropical museum' hypothesis.

Keywords
Biodiversity, dispersal, diversification dynamics, extinction, fossil record, origination.

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INTRODUCTION

The latitudinal gradient of species richness (LGR) is one of the most prominent patterns in macroecology and biogeography. Hundreds of studies have evaluated the LGR in a variety of taxa and ecosystems at multiple spatiotemporal scales (Pianka, 1966; Rohde, 1999; Willig *et al.*, 2003; Wiens & Graham, 2005), including several meta-analyses that confirm the pervasiveness of the canonical pattern of the LGR, which is characterized by increasing diversity from the poles towards the tropics (Willig *et al.*, 2003; Hillebrand, 2004a,b).

Causes of the LGR pattern have been intensely debated for decades (Rohde, 1999), with a recent focus on the creation of integrative and explanatory conceptual frameworks (Wiens &
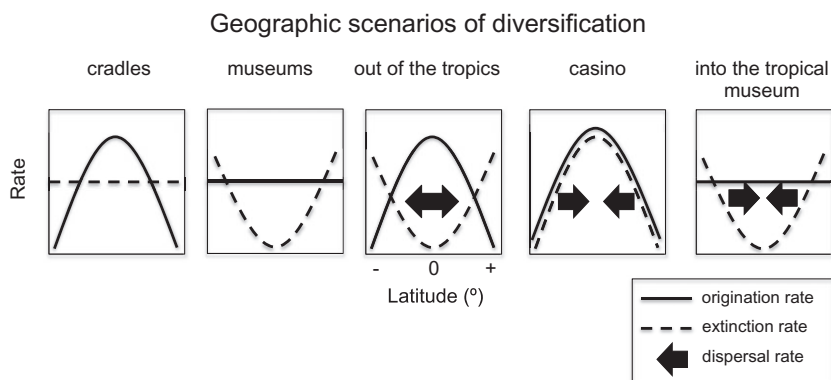
Geographic scenarios of diversification

Figure 1 Different geographic scenarios of diversification proposed to explain the LGR phenomenon.

Graham, 2005; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007). Evolutionary (or historical) explanations pose that geographic variation in diversification rates (origination, extinction and dispersal) forced by past climatic, geologic, and biotic events, may shape the LGR (Fig. 1). More classic evolutionary hypotheses only considered the dichotomy of tropics as 'cradles' (i.e. higher origination rates in the tropics), or 'museums' (i.e. lower extinction rates in the tropics) (Chown & Gaston, 2000). More recently, Jablonski *et al.* (2006, 2013) have postulated the 'out of the tropics' hypothesis, which assumes that tropics are both 'cradles' and 'museums', but also sources of dispersal of taxa towards higher latitudes. A 'casino' model, based on stochastic simulations of range shifts and originations, predicts that dispersal from the extra-tropics towards the tropics combined with a geometric mid-domain effect suffice to produce the LGR (Arita & Vázquez-Domínguez, 2008). Indeed, empirical evidence (Buzas & Culver, 2009) shows that dispersal 'into the tropics' can produce the LGR, even if origination rates are not higher in the tropics.

Rocky intertidal studies have a long tradition of fueling ecological theory (Menge & Branch, 2001), but surprisingly few studies have assessed the LGR in these habitats. Early studies were based on data comprising few sites, or with little replication between temperate and tropical areas, showing mixed results supporting or rejecting higher tropical diversity (Spight, 1977; Coates, 1998). Later studies with more robust replication and spatial extension, have reported different shapes for the LGR (Okuda *et al.*, 2004; Schoch *et al.*, 2006; Cruz-Motta *et al.*, 2010). Moreover, patterns seem scale-dependent, tending to disintegrate at smaller spatial scales (Rivadeneira *et al.*, 2002; Okuda *et al.*, 2004; Schoch *et al.*, 2006). Indeed, a meta-analysis confirms that the LGR is less pronounced in marine benthic coastal habitats (Hillebrand, 2004a).

Eastern Pacific (EP) rocky intertidal gastropods offer an excellent study system to assess the role of evolutionary processes in shaping the LGR for several reasons, including: (i) their good fossil record, allowing for explicit tests of diversification dynamics in shaping the LGR, (ii) the very long tradition of ecological and taxonomic studies in this marine habitat, (iii) relative ease of access to field sites, making this habitat less prone to sampling bias, (iv) the high diversity and dominance of this taxonomic group, and (v) the EP is predominantly north-south trending,

with intertidal habitat (almost exclusively rocky or sandy shore) spanning nearly the whole length of the globe. This relatively simple coastal geometry is in stark contrast to other inter-hemispheric coastlines, such as the western and eastern Atlantic or along the Indian Ocean and western Pacific. These coastlines can have major longitudinal trends (e.g. Eurasia, western sub-Saharan Africa) and/or island clusters (e.g. Indo-Pacific, Caribbean) which can complicate tests of the LGR for coastal systems, including constraints on the availability of north-south sampling locations and ecological and evolutionary processes generally unrelated to latitude, such as island biogeography. Indeed, the EP intertidal represents a natural transect of the globe, making its denizens ideal for tests of the ecological and evolutionary processes underlying the LGR.

Here we evaluate: a) the existence of the canonical LGR across the entire Pacific coast of the Americas, from Alaska to Tierra del Fuego, and b) the importance of geographic patterns of diversification shaping the LGR. We show the validity and robustness of the canonical LGR phenomenon along the eastern Pacific rocky intertidal, highlighting the role of evolutionary processes contributing to its origination and maintenance, embodied in what we have named the 'into the tropical museum' hypothesis. Our study represents the first to assess the role of evolutionary processes contributing to the LGR in rocky intertidal habitats at an inter-hemispheric scale.

METHODS

Rocky intertidal data

We collected information for gastropod diversity inhabiting rocky intertidal assemblages along the entire eastern Pacific coast, encompassing at least five marine biogeographic provinces (Fig. 2). We gathered 6,123 occurrences, representing 1,479,000 individuals in 428 local assemblages (308 unique georeferenced sites; Fig. S1). The spatial extent of each site was variable, but in the order of 10's of meters, as customary in rocky intertidal studies. The database included 328 species, 159 genera, and 64 families in 5 orders (Caenogastropoda, Heterobranchia, Neritimorpha, Patellogastropoda and Vetigastropoda), collected over more than 40 years (1972 to 2013). Only forms with external hard-shells were included, because of its higher potential for
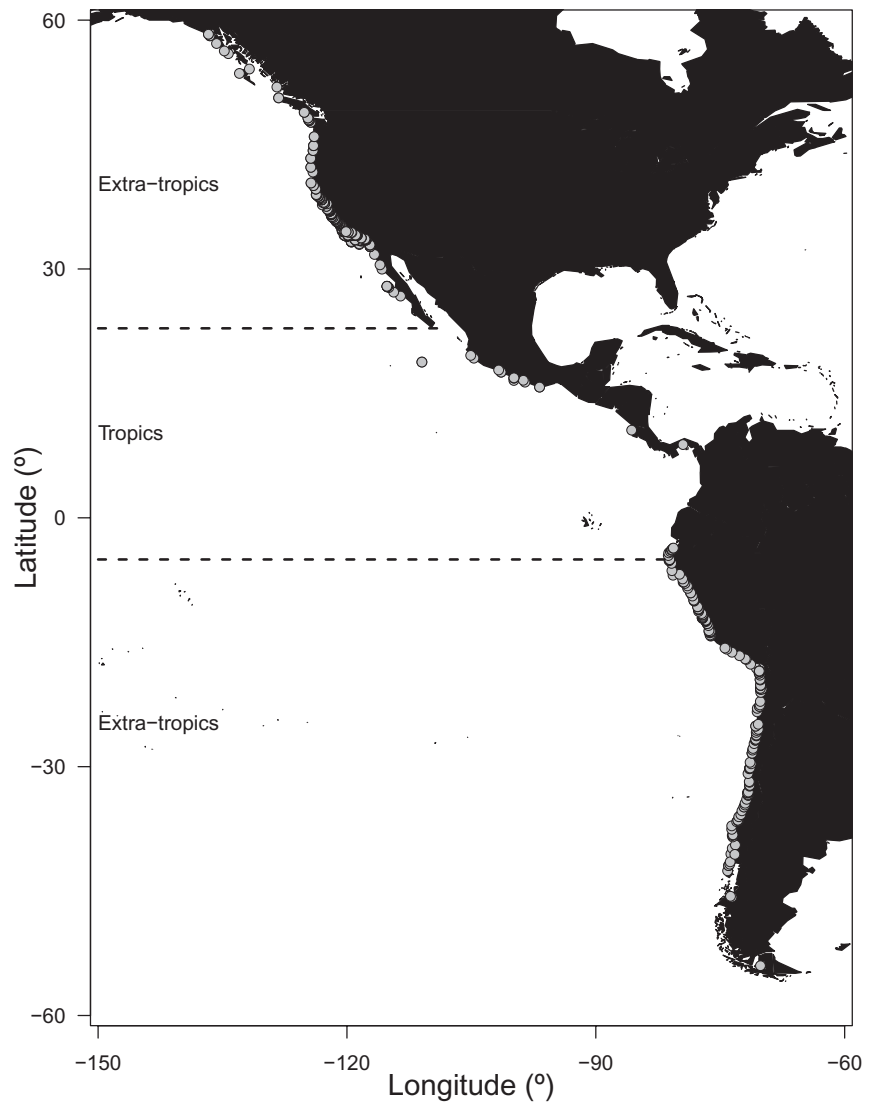
Figure 2 Map of the study region along the eastern Pacific coast, showing the locations of the 308 rocky intertidal sites and the tropical and extra-tropical zones as delimited by the Tropical Eastern Pacific biogeographic province from 22°N-5°S (but other classification schemes are possible; see Table 1).

fossilization. Collection methods and sources are detailed in Appendix S1 in Supporting Information.

Assessing the LGR

We assessed the LGR at different spatial (regional, local, pixel) and taxonomic (genera, species) scales, correcting for the possible incompleteness of sampling using rarefaction methods. We estimated the regional (i.e. province level) species and generic richness using the Chao 2 non-parametric extrapolation index, based on site occurrences across each province (Chao & Lee, 1992). Marine provinces were delimited following the scheme of Spalding *et al.* (2007). Local richness was also estimated at the species and generic level using the observed values. For a subset of sites, where abundance data were available, we estimated the rarefied species and generic richness to account for the broad differences in sampling protocols that would likely introduce bias in the estimation of local richness, using the expression recently proposed by Chao & Jost (2012). Rarefied richness was

estimated using n = 100, 500, and 1000 individuals, and all of these estimations were strongly correlated (r > 0.94, $P < 0.0001$ in all cases). The completeness of local inventories was evaluated using the $\hat{c}$ expression proposed by Chao & Jost (2012) to estimate sample coverage, where values close to 1 indicate a high coverage (i.e. few missing taxa in the inventory). Rarefied richness was averaged in cells of 0.5° to account for the effect of heavily sampled regions (i.e. temperate northeastern Pacific).

Inferring diversification dynamics

Further analyses were carried out at the generic rather than species level because the fossil record is mostly available at this taxonomic level. Three approaches were used to assess the importance of diversification dynamics in the LGR: region of first appearance of genera, nestedness analysis, and a distribution dynamics model. We used 23,837 worldwide fossil occurrences to evaluate the region of origin of 123 out of 159 modern

genera (77%) inhabiting the eastern Pacific coast, obtained from the Paleobiology database (http://www.fossilworks.org). Genera with a fossil counterpart represented 92% of all modern occurrences. Fossil occurrences were classified as either tropical or extra-tropical. Because a clear tropical/extra-tropical distinction depends on the region and time bin, we used three possible boundaries: a) 10° latitude (north and south) (Vilhena & Smith, 2013), b) 23° latitude (north and south) (e.g. Jablonski *et al.*, 2006), and c) the limits of the modern Tropical Eastern Pacific province (22° N and 5° S, Fig. 2). Because the fossil record in tropical areas are known to be less complete compared to temperate areas (Krug *et al.*, 2009) a face value comparison would likely be biased to conclude a temperate place of origin for most genera. In order to reduce this bias we re-sampled the total number of occurrences in both tropical and extra-tropical regions using an equal sampling scheme and 'oversampling' the tropical zones in which we doubled the number of occurrences sampled in the tropical zone. Because fossil occurrences in temperate regions are at least 2-fold higher than in the tropics, the tropical oversampling scheme represents a reverse of this scenario. In addition, the resampling scheme considered the differences in the age frequency distribution of occurrences between regions because the temporal distribution of fossil occurrences are different in tropical and temperate areas (Vilhena & Smith, 2013; Fig. S2A). To this end, the resampling probability in the extra-tropical region was made dependent on the age frequency distribution of occurrences in the tropics, and vice-versa. For instance, occurrences between 60–100 Ma in the extra-tropics had a minimum chance of being selected because the tropics had virtually no occurrences during that period; conversely the method also corrected for the excess of Neogene occurrences in the tropics (Fig. S2A). Indeed, this procedure created similar temporal trends in fossil occurrences between the tropics and extra-tropics (Fig. S2B). At each run, we calculated the percentage of genera appearing first in tropical or temperate areas. The models were run 10,000 times to build 95% CI for each tropical/extra-tropical classification boundary and sampling type. The stratified resampling analyses were implemented in the library 'sampling' in R (Tillé & Matei, 2012).

Nestedness was originally introduced to investigate distribution patterns in ecological communities within the same biogeographic region (Atmar & Patterson, 1993), and its existence was attributed to extinction/colonization dynamics (Ulrich *et al.*, 2009). More recently, nestedness has been used to infer the role of evolutionary dispersal/extinction at much larger spatial scales for shaping latitudinal or bathymetric gradients of species richness (Rivadeneira *et al.*, 2011). Assuming that taxa originated in a single biogeographic region, the only way taxa could be shared among regions is via dispersal. If dispersal is absent, then the number of shared taxa between regions should be zero (i.e. low degree of nestedness). On the contrary, high dispersal between regions would lead to a high degree of nestedness. These patterns could be reinforced or masked by regional extinction (i.e. emigration), depending on its spatial variability. Hence, a nested pattern of distribution would be caused by dispersal and/or extinction dynamics. We used the nestedness metric based on the overlap and decreasing fill (NODF) index to evaluate the degree of nestedness in a genus-province matrix, using the 'quasiswap' algorithm (i.e. preserving both province richness and generic frequencies) in 10,000 null matrices. Z-score values lower than expected by the null model are an indication of strong nestedness, suggesting extinction/colonization dynamics over evolutionary timescales. Because sampling effort was not uniform across provinces, we re-ran the analysis using a uniform sampling scheme; we re-sampled a fixed number of modern occurrences (n = 100) within each province, and re-ran the NODF analysis in 10,000 matrices. Analyses were carried out using the library 'vegan' in R (Oksanen *et al.*, 2013). We also estimated the degree of nestedness by comparing modern biogeographic distributions of genera appearing first in the tropics or extra-tropics separately (see above), under different tropical/extra-tropical classification boundaries and sampling type. If the region of origin of genera is important in shaping modern biogeographic structure, then we should expect different nestedness patterns for genera appearing first in the tropics vs. extra-tropics. On the contrary, if processes other than origination (i.e. extinction, dispersal) are driving the biogeographic structure, nestedness should be observed irrespective of the region of origin of genera.

Finally a distribution dynamics model (DDM) was used to evaluate the impact of changes in the geographic distribution of taxa on the LGR. In the DDM, the modern distribution of each genus can be in any of three states: tropical endemic, extra-tropical endemic, and 'bridge' (i.e. present in both regions, *sensu* Jablonski *et al.*, 2013). Because of the strong differences in the total number of occurrences between tropical and extra-tropical zones (see above), the proportion of genera in extra-tropical endemic or bridge states would likely be inflated. To avoid this problem, the biogeographic state of each genus was established by using a stratified re-sampling scheme (n = 500 occurrences at each region) in 10,000 runs. The modern biogeographic state was the state more frequently selected across all runs ('majority rule'). For the fossil data, we considered the biogeographic state at the time of first appearance, and hence only two states were allowed (tropical endemic and extra-tropical endemic). The biogeographic states of each fossil genus was defined using the 'majority rule' criteria based on the output derived from the analyses of the region of first appearance, using three sampling types and three tropical/extra-tropical boundaries. The fossil and modern biogeographic states defined for the 123 genera were used to build a projection matrix based on the transition probabilities. The temporal change in number of genera at each state G from t to $t+1$ can be modeled as:

$$G_{(t+1)} = D_{G,t} * G_{(t)}$$

Where D is the projection matrix

$$D = \begin{bmatrix} 0 & P_{E \to B} & P_{T \to B} \\ 0 & P_{E \to E} & P_{T \to E} \\ 0 & P_{E \to T} & P_{T \to T} \end{bmatrix}$$

And $G_{(t)}$ is the initial vector with number of genera at each biogeographic state. Each entry of the D represents the probability of transition between states (from → to, E: extra-tropical endemic, B: bridge, T: tropical endemic). The number of genera at each state can be obtained from the left eigenvector of the dominant eigenvalue obtained at equilibrium (set at $t = 10$ since the dynamic quickly stabilizes). We compared the final estimated proportion of genera at each state vs. the observed one using a G^2 likelihood ratio test. We also calculated the initial and final ratio of tropical vs. extra-tropical genera, where the total generic-richness in each region is simply the sum of endemics + bridge genera. We also carried out an elasticity analysis (Caswell, 2001) to evaluate the impact of each element of the projection matrix on the overall biogeographic dynamic.

The DDM is akin to the one proposed by Goldberg *et al.* (2005), but it differs in its three major assumptions: i) there are no origination or global extinctions, i.e. all dynamics are produced only by dispersal, and no genera enters or leaves the pool, ii) only the initial and final states are of interest, i.e. the absolute age of origin of a genus and previous paleobiogeographic dynamics are irrelevant in the model, and iii) the final (modern) biogeographic state is invariant across oceans (i.e. eastern Pacific coast is representative of the biogeographic state at a global scale). Analyses were carried out using the library popbio (Stubben & Milligan, 2007) in R (Team, 2014).

RESULTS

Regional (extrapolated) generic richness is one order of magnitude and up to 8-fold higher in the tropics compared to extra-tropical provinces, and it is remarkably invariant across temperate provinces in both northern and southern hemispheres (Fig. 3a). The extrapolated species richness at the provincial scale showed the same pattern, with tropical richness being 3–6 fold and one order of magnitude higher than extra-tropical areas (Fig. 3a). Comparing temperate areas, species richness in the northern hemisphere was slightly higher than in the southern hemisphere. The observed species richness reaches maximum values in the tropics (72 species), around 10–15°N, where it was consistently higher than the vast majority of any other temperate site (Fig. 3b). The completeness of local inventories was very high for both species and genus levels ($\hat{c}$ 95% CI: 0.99–1.00 in both cases). Mean rarefied generic richness (S_{500}) at a pixel scale (0.5° resolution) followed the same pattern as observed species richness (r = 0.92, n = 78, $P > 0.001$). Most of the variability of observed species richness and rarefied generic richness occurs at very large geographic scales (i.e. tropics vs. extra-tropics), as evident by the very low and non-significant autocorrelation values at meso-scales, but negative and significant autocorrelation at distances of *ca.* 5000 km (Fig. S3, Appendix S1 in Supporting Information).

After correcting for differences in sampling effort between the tropics and extra-tropics, tropical endemics represented 53–63% (the range representing 95% CI) of total diversity, compared to 23–29% of extra-tropical endemics, and 13–21% of bridge genera. The observed genus-province presence-
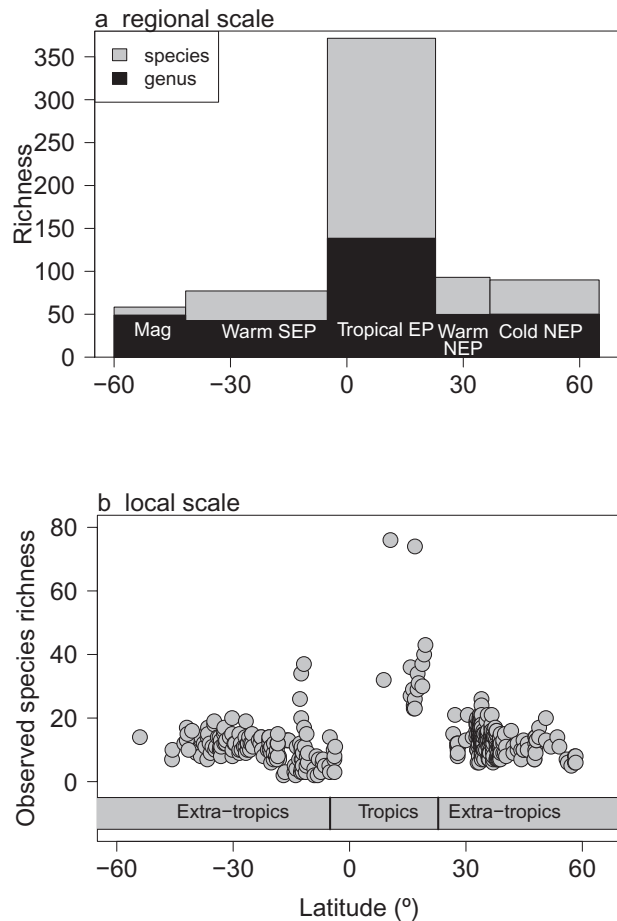

Figure 3 Latitudinal gradient of diversity of rocky intertidal gastropods along the eastern Pacific coast. (a) Extrapolated (Chao 2 non-parametric index) species and generic-richness for each marine biogeographic province, (b) Observed species richness at local sites, indicating the limits of tropical (22°N-5°S) and extra-tropical zones.

absence matrix showed a significant degree of site-nestedness (NODF = 28.761, Z-score = −12.333, $P < 0.0001$). Controlling for differences in sampling effort across provinces did not alter results (Z-scores, 95% CI = −14.163 to −3.782; P-values < 0.05 in 100% of runs). Modern biogeographic distributions of genera showed a high degree of nestedness, independent of the tropical/extra-tropical origin of genera and under different sampling scenarios (Table 1).

Analyses of the fossil dataset showed that the percentage of genera originating in the tropics vs. extra-tropics was variable according to the definition of tropical/extra-tropical boundaries and sampling type (Table 1). Face-value estimations showed that most originations occurred in the extra-tropics (66–85%). Differences between the tropics and extra-tropics tended to be minimized after accounting for sampling bias (equal sampling), especially when the 23°N/°23°S was used to define the tropical/extra-tropical boundaries. Origination was slightly higher in the tropics when these were 'oversampled' in comparison to extra-tropics, although differences were minimal (Table 1).

Table 1 Testing the region of first appearance for the 123 genera that inhabit the study area and have a Phanerozoic fossil counterpart worldwide. Estimations (median and 95% CI) are based on 10,000 runs. Also shown is the degree of nestedness (NODF) based on the modern biogeographic distribution of genera across five biogeographic provinces for genera originating first in the extra-tropics or tropics. Significant NODF values ($P < 0.01$) in bold.

Tropical/extra-tropical boundaries	Sampling type	Region	# Occurrences	% Genera making a first appearance (95% CI)	Nestedness (NODF, Z-score)
10° N; 10° S	Face-value	Extra-tropics	19823	85	**−16.3**
		Tropics	4014	15	**−6.4**
	Equal sampling	Extra-tropics	4000	59 (54–64)	**−13.9**
		Tropics	4000	41 (37–46)	**−12.2**
	Tropics oversampled	Extra-tropics	2000	47 (41–56)	**−13.9**
		Tropics	4000	53 (45–57)	**−13.5**
23° N; 23° S	Face-value	Extra-tropics	15393	66	**−16.5**
		Tropics	8444	34	**−5.4**
	Equal sampling	Extra-tropics	8000	51 (47–54)	**−11.9**
		Tropics	8000	49 (46–53)	**−9.1**
	Tropics oversampled	Extra-tropics	4000	40 (35–44)	**−12.7**
		Tropics	8000	60 (56–65)	**−9.9**
22° N; 5° S	Face-value	Extra-tropics	16652	76	**−16.7**
		Tropics	7185	24	**−5.7**
	Equal sampling	Extra-tropics	7000	54 (52–58)	**−12.9**
		Tropics	7000	46 (42–48)	**−10.4**
	Tropics oversampled	Extra-tropics	3500	45 (40–49)	**−12.0**
		Tropics	7000	55 (52–60)	**−10.7**

The DDM showed a strong temporal change in the tropical/extra-tropical genus ratio, from ratios lower or close to 1 (i.e. a flat or even inverse LGR) to ratios of between 2.43–3.97, similar to the present day observed value of 2.19 after ten steps in the model (Fig. 4a). The final (present-day) observed proportion of genera at each state was not different than predicted by the DDM (G^2 likelihood ratio test, $P > 0.05$ in all cases, Table 2 and S1). For the equal sampling scenario, the two largest transition probabilities were the recurrence of the tropical endemic state ($P = 0.70$ to 0.80) and the shift from extra-tropical to tropical endemic ($P = 0.53$–0.58) (Table 2, Fig. 4b). The elasticity analyses indicated that recurrence of the tropical endemic state was the most important transition determining the dynamic ($P = 0.62$–0.82). Similar trends were observed under other sampling scenarios (Table S1). Overall, these results suggest the LGR can be generated by a low extinction rate in the tropics and net dispersal of taxa from the extra-tropics into the tropics.

DISCUSSION

Our analyses confirm the existence of a canonical LGR pattern for rocky intertidal gastropods across the entire eastern Pacific, which are robust to sampling bias and highlight the importance of evolutionary processes for shaping the LGR (Wiens & Graham, 2005; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007; Mannion *et al.*, 2014).

Previous studies have shown the existence of the LGR in marine gastropods, but using much larger scales of spatial resolution, over multiple marine habitats and depths (Roy *et al.*, 1998; Valdovinos *et al.*, 2003; Linse *et al.*, 2006). Importantly,

our study shows that the LGR is not monotonic; that is, there is no latitudinal trend in the local richness along temperate areas and both species and generic richness showed very low and non-significant autocorrelation values at distances smaller than 5000 km. Previous studies in rocky intertidal assemblages have shown that the LGR is less pronounced, or even disappears at smaller spatial scales (Rivadeneira *et al.*, 2002; Okuda *et al.*, 2004; Schoch *et al.*, 2006). Indeed, the observed LGR is only evident at very large geographic scales (i.e. tropical vs. extra-tropical areas), as shown by the existence of negative and significant autocorrelation values at larger distances (i.e. ca. 5000 km, Fig. S3). The inverse LGR previously observed for southeastern Pacific prosobranch gastropods (Vermeij, 1996; Valdovinos *et al.*, 2003; Linse *et al.*, 2006) was not mirrored by our dataset, suggesting that it may be due to inclusion of subtidal assemblages as seen in peracarid crustaceans (Rivadeneira *et al.*, 2011). This observation highlights the importance of controlling for habitat in assessments of the LGR.

Global patterns of biodiversity ultimately arise from the balance between rates of origination, extinction and dispersal across space (Chown & Gaston, 2000; Mannion *et al.*, 2014) (Fig. 1). Our analysis of fossil data suggests that the LGR of eastern Pacific rocky intertidal gastropods can be formed by the combined effect of low extinction rates in the tropics, and a net dispersal of taxa from the extra-tropics towards the tropics, a novel dynamic that is not entirely consistent with previously described models of latitudinal diversification (Fig. 1) (Chown & Gaston, 2000; Arita & Vázquez-Domínguez, 2008; Mannion *et al.*, 2014). We have named this evolutionary dynamic the 'into
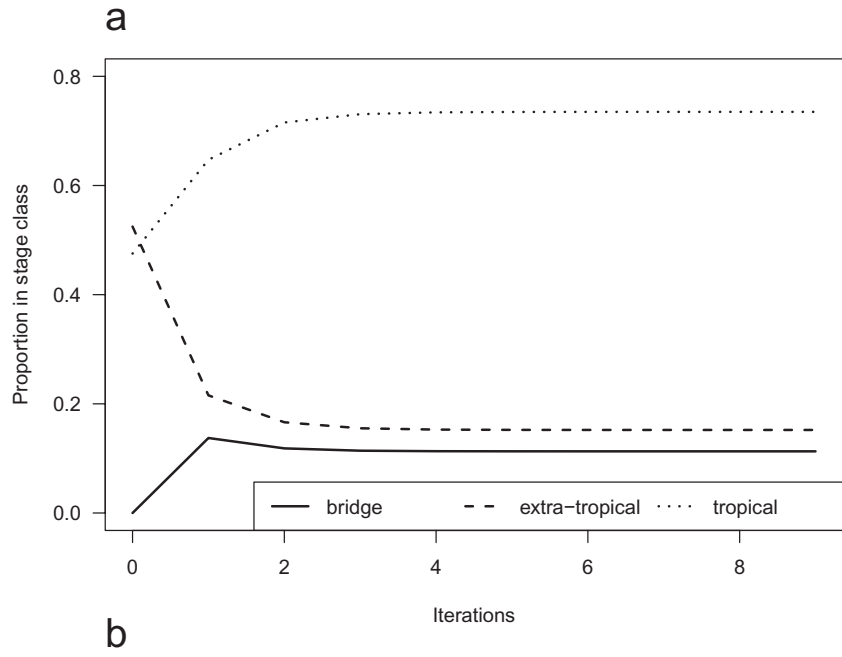
Figure 4 The distribution dynamics model (DDM). (a) Projected changes in the relative abundance of genera at each biogeographic state (tropical endemic, extra-tropical endemic, and bridge) after 10 time steps. (b) Estimated transition probabilities among the three biogeographic states. The output corresponds to the tropical/extra-tropical classification boundary set at 22°N and 5°S, with equal sampling between regions. See Table 2 and S1 for results corresponding to the other tropical/extra-tropical classification boundary schemes and sampling types.

Table 2 Summary of the distribution dynamics model (DDM), showing the transition probabilities and elasticities associated to the projected matrices, after accounting for differences in sampling differences between regions (i.e. 'equal sampling' Table 1), and under three schemes of classification of tropical/extra-tropical boundaries. Also shown are the observed and predicted tropical/extra-tropical genus ratios. The likelihood-ratio test G^2 evaluates differences between final observed and estimated ratios. B: bridge (i.e. tropics and extra-tropics); E: extra-tropical endemics; T: tropical endemics. The highest transition probabilities and elasticities are highlighted in bold.

Tropical/extra-tropical boundary	Tropical/extra-tropical genus ratio					Transition probabilities (elasticities)					
	Starting observed	Final estimated	Final observed	G^2	P-value	E→B	E→E	E→T	T→B	T→E	T→T
10°N, 10°S	0.68	3.97	2.19	5.66	0.06	0.15 (0.00)	0.32 (0.04)	**0.53** (0.07)	0.12 (0.00)	0.07 (0.07)	**0.8** (0.82)
23°N, 23°S	1.10	2.43	2.19	0.18	0.92	0.17 (0.00)	0.25 (0.06)	**0.58** (0.16)	0.11 (0.00)	0.19 (0.16)	**0.7** (0.62)
22°N, 5°S	0.91	3.10	2.19	1.76	0.42	0.17 (0.00)	0.3 (0.06)	**0.53** (0.11)	0.1 (0.00)	0.13 (0.11)	**0.77** (0.73)

the tropical museum' hypothesis. This model differs from the 'museum' hypothesis because of the role of dispersal from the extra-tropics to the tropics. Dispersal is also considered in the 'out of the tropics' (Jablonski *et al.*, 2006, 2013) and 'casino' models (Arita & Vázquez-Domínguez, 2008), but they both highlight higher rates of origination in the tropics.

Contrary to the widespread notion that tropics are 'cradles' of diversity (Chown & Gaston, 2000; Mannion *et al.*, 2014) our analyses showed that genera did not tend to appear first in the tropics, even after controlling for the incompleteness of fossil sampling in tropical areas. Recent studies have shown that first appearance of Neogene and Pleistocene bivalves tend to occur preferably in tropical regions (Jablonski *et al.*, 2006, 2013). On the contrary, our analyses show the origination of new forms is markedly similar between tropical and extra-tropical regions. Buzas & Culver (2009) reported similar results for foraminifera of the Atlantic continental margin of North America, i.e. the LGR occurs despite more than 60% of species originate in the extra-tropics. In addition, the DDM showed that tropical endemic genera had higher probability of survival (70–80%, Table 2 and S1) than extra-tropical endemics (25–32%). The reduced extinction rate of tropical endemic genera is, according to the elasticity analysis, the most relevant transition in the DDM; the survival and maintenance of tropical endemics is thus pivotal for the LGR.

The 'tropics as a museum' allegory (Chown & Gaston, 2000; Mannion *et al.*, 2014), however, is insufficient to fully understand the generation of the LGR. Two lines of evidence suggest that biogeographic range dynamics are crucial to create the LGR. First, the geographic distribution of genera was significantly nested, implying some sort of extinction/dispersal dynamic (Ulrich *et al.*, 2009). Moreover, nestedness was concluded independent of the region of origin of genera, reinforcing the idea that originations are not playing a major role in shaping the biogeographic structure of eastern Pacific rocky shore gastropods. Secondly, the transition of extra-tropical endemics to tropical endemics was the second most important transition in the DDM, implying that geographic range shifts may have a profound effect on the LGR. This mechanism based on a net dispersal of taxa from extra-tropical to tropical regions has also been proposed to explain the LGR in foraminifera of the Atlantic (Buzas & Culver, 2009). A different dynamic null model assuming stochastic originations and range shifts combined with geometric constraints has also concluded the relevance of dispersal dynamics, i.e. dispersal into the tropics can produce the LGR despite the tropics having higher extinction and origination rates (Arita & Vázquez-Domínguez, 2008). The DDM showed that the combined effect of reduced extinction and high dispersal towards the tropics could reproduce the LGR (i.e. tropical/extra-tropical genus ratio), despite the initial conditions (i.e. a flat latitudinal gradient of richness). The DDM is, however, an oversimplification of evolutionary processes (i.e. ignoring the role of originations and global extinctions, e.g. Goldberg *et al.*, 2005), and its implementation requires a significant amount of fossil data. Further tests of the different geographic diversification hypotheses (Fig. 1) may be based on

analyses of phylogenetic data (Jansson *et al.*, 2013; Moreau & Bell, 2013). However, these are currently not amenable for our study model because of the lack of phylogenic information for the vast majority of species.

More than two centuries of research, starting with Alexander Von Humboldt, have produced a myriad of plausible explanations for the LGR phenomenon (Pianka, 1966; Rohde, 1992; Willig *et al.*, 2003; Brown, 2014). Whether the 'into the tropical museum' can be a general process explaining the LGR at a global scale for the clade remains an open question. However, a similar process seems to explain the high diversity of reef fishes in the Indo-Australian Archipelago, where richness is not driven by origination within the region, but by the dispersal and subsequent maintenance of taxa originated in peripheral areas over evolutionary time (Bowen *et al.*, 2013; Dornburg *et al.*, 2014). In addition, we do not know the ultimate mechanisms explaining the geographic differences in the diversification pattern, including the role of paleoenvironmental changes (e.g. rise of the Isthmus of Panama, onset of coastal upwelling in temperate zones) and life-history traits of species. While our results validate the role of evolutionary processes, they do not exclude the parallel importance of ecological factors maintaining the LGR, as suggested by previous studies (Fraser & Currie, 1996; Hawkins *et al.*, 2003; Buckley & Jetz, 2007; Tittensor *et al.*, 2010; Jetz & Fine, 2012). Further analyses, combining both ecological and evolutionary proxies, preferably carried out at local spatial scales, may shed light into the relative role of ecological versus evolutionary forces shaping the LGR.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Supplementary methods, tables and figures.

BIOSKETCH

The authors are interested in understanding the processes that shape marine biodiversity through a range of approaches, including paleontology, phylogeography, population and community ecology along the eastern Pacific coast. Their studies incorporate a wide diversity of taxa in the quest to uncover the factors influencing the distribution of these organisms.

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