



Decoupling of latitudinal gradients in species and genus geographic range size: a signature of clade range expansion

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ABSTRACT

Aim Clade range size is a function of species range sizes but also depends on the geographic deployment of species: clade range expansion should therefore depend partly on the tendency of a clade to produce new species. Previous work has shown empirically that species-rich clades are more likely to expand outside their present distributions, i.e. to overcome niche conservatism, than species-poor ones. This pattern can follow from a neutral probabilistic model of clade-level range expansion arising from differences in net species diversification between clades. We show that predictions of this model discriminate between weaker and stronger climatic niche conservatism, and compare these predictions with range-size patterns of marine bivalves at the species and clade (genus) level.

Location Western Pacific, eastern Pacific and western Atlantic.

Methods We decompose the latitudinal and thermal distribution of genera into within-species and among-species components. We use a neutral model in which species range expansion does not vary with latitude and descendants originate within the ranges of their ancestors (model with spatial dependency) or where descendants originate independently of ancestral ranges (model without spatial dependency).

Result In accord with model predictions: (1) genus latitudinal range size is weakly related to the latitudinal range sizes of congeneric species, but strongly depends on per-genus species richness; (2) among-species latitudinal distances correlate positively with per-genus species richness; and (3) genus latitudinal and thermal range sizes increase towards higher latitudes because genera that are species rich anywhere within their range increase in proportion towards higher latitudes.

Main conclusions Application of the neutral probabilistic model to marine bivalves shows that tropical niche conservatism is only moderately strong, and that species diversification plays a significant role in range expansion of bivalve genera to new latitudes and climates, even when thermal range sizes and limits of congeneric species show significant correlations, and are thus conserved to some degree.

Keywords

Biogeography, geographic range, macroecology, niche breadth, niche conservatism hypothesis, out-of-the-tropics hypothesis, palaeobiology, Rapoport's rule, species–genus ratio.

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INTRODUCTION

Hypotheses for the origin and maintenance of broad-scale diversity gradients, such as the out-of-the-tropics (OTT) hypothesis and the tropical niche conservatism hypothesis, differ in predictions about the dynamics of range expansion, phylogenetic niche conservatism and regional phylogenetic structure (Jablonski *et al.*, 2006; Wiens *et al.*, 2006; Smith *et al.*, 2012; Jansson *et al.*, 2013). However, they also share some similarities and are not mutually exclusive (Jablonski *et al.*, 2013; Kerkhoff *et al.*, 2014). Both hypotheses assume that clades diversify more in the tropics, regardless of whether higher tropical diversity is driven by greater accommodation of species at ecological time-scales or by diversification of species over longer time-scales (Crame, 2000; Jablonski *et al.*, 2013; Hurlbert & Stegen, 2014; Rolland *et al.*, 2014; Antonelli *et al.*, 2015; Duchene & Cardillo, 2015). However, the OTT model assumes preferential, albeit infrequent, expansion of clades from low to high latitudes (Jablonski *et al.*, 2006, 2013; Marchant *et al.*, 2015), with little flow of taxa in the opposite direction, and thus assumes that clades that originated in the tropics are evolutionarily *less* conservative than those that originated at higher latitudes. Models postulating climatic niche conservatism (CNC) are less specific about the latitudinal gradients in range expansion and allow expansion out of the tropics or into the tropics (Kennedy *et al.*, 2014), depending on whether niche conservatism increases or decreases towards high latitudes (Kozak & Wiens, 2007; Cooper *et al.*, 2011). Thus, CNC and OTT are not mutually exclusive, unless clades originating at higher latitudes have higher probabilities of range expansion to novel climates. To clarify the multiple predictions and consequences of these hypotheses, it becomes important to explore the effects of species range expansion and species diversification on clade range expansion (Quenouille *et al.*, 2011; Luiz *et al.*, 2012; Cowman & Bellwood, 2013; Dornburg *et al.*, 2015; Leprieur *et al.*, 2016; Prinzing *et al.*, 2016; Tittensor & Worm, 2016).

In this study, we explore whether the weaker conservatism of tropical clades relative to high-latitude ones can arise via a neutral scenario in which tropical and extratropical clades have equivalent abilities to expand to new climatic zones on a per-species basis (either by within-species expansion or by production of new species) but net diversification is higher in the tropics: species-rich clades in the tropics will simply have more opportunities for successful expansion than species-poor clades at high latitudes. That is, species-rich clades will be more likely to produce species that spread across climatic barriers ('bridge species') or to speciate into new regions than species-poor clades (Roy *et al.*, 2009; Jablonski *et al.*, 2013). Under this probabilistic model, the probability of the expansion of clades to new climatic zones is not only a function of per-species climatic niche conservatism but also of the number of species generated by the clade, and the frequency distribution of range shifts at clade level should be skewed towards the poles. Therefore, this

model exemplifies the simplest version of the OTT model because it predicts preferential expansion of clades to higher latitudes, rather than the reverse, purely on the basis of species-richness trends. This probabilistic model provides a neutral baseline for more complex versions of OTT models, e.g. where tropical clades (1) have a higher per-species probability of expansion to new climatic zones than extratropical clades, or (2) have a lower per-species probability of expansion than extratropical ones (e.g. if specialist species diversify at a higher rate than generalist species, generating higher tropical species richness; Rolland & Salamin, 2016), but are more likely cross to new climatic zones overall owing to their higher number of species. This model is also consistent with CNC scenarios where tropical niche conservatism is not very strong. In the absence of strong climatic niche conservatism, this richness-based probabilistic model predicts: (1) significant decoupling of species and clade range size (in clades with more than one species), and (2) a positive dependence of a clade's range size on its species richness, even when climatic niche evolution does not actively promote speciation events. Both relations have been observed in marine clades (Jablonski, 2007; Krug *et al.*, 2008; Harnik *et al.*, 2010). Under strong climate niche conservatism (e.g. Rangel *et al.*, 2007; Hawkins *et al.*, 2011), the coupling of species-defining novelties within individual clades with expansions to novel climates will be sufficiently rare that we expect only small differences between per-clade species range sizes and clade range sizes, and weak effects of a clade's species richness on its range size. However, it remains unclear whether the positive relation between clade range size and species richness can be explained by this purely probabilistic model, and whether clade range size can be explained by the geographic (or environmental) deployment of constituent species.

Here, we develop the predictions of such a probabilistic range-expansion scenario where low- and high-latitude species do not differ in the probability of expanding to higher or lower latitudes, and compare these predictions with empirical data, using marine bivalve species and genera. Morphologically defined bivalve genera tend to correspond to molecularly defined units and latitudinal range sizes of bivalve 'morphogenera' significantly correlate with those of molecularly defined clades (Jablonski & Finarelli, 2009). First, we assess the contributions of per-genus species range size, and the spatial separation among congeneric species, to genus range size, and their relation to per-genus species richness. Second, we compare empirical gradients in latitudinal and thermal range sizes of species and genera, evaluate whether these gradients differ owing to the dependence of genus range size on per-genus species richness, and compare them with the gradients in genus range size and per-genus species richness predicted by the probabilistic range-expansion model. In accord with this model, we find that: (1) the range sizes at species and genus levels are decoupled, suggesting that the rate of clade expansion is partly related to within-genus introduction of species into new latitudes; (2) latitudinal distances among congeneric species increase with

per-genus species richness; and (3) the proportion of genera that are species rich (anywhere within their range) increases towards higher latitudes, significantly modulating gradients in genus latitudinal and thermal range size. Our study also has consequences for analyses addressing species-level distribution patterns on the basis of genus-level patterns in range size, because it shows that species range-size gradients do not correlate with genus range-size gradients.

MATERIALS AND METHODS

Data

Marine bivalves represent a diverse, widespread and relatively well-sampled group of benthic invertebrates (Jablonski *et al.*, 2013; Huang *et al.*, 2014). Our database contains shelf-depth (< 200 m) localities from all the major bivalve clades. Present-day species-level occurrences were compiled from the literature and museum collections, primarily collected during the 20th century. We perform analyses separately along the three best-sampled ocean margins: the western Pacific (WP; 3170 species and 22,598 occurrences), eastern Pacific (EP; 928 species and 11,240 occurrences) and the western Atlantic (WA; 1035 species and 8795 occurrences) (database download of 25 August 2015). These three oceanic regions share a small number of species mainly restricted to the highest latitudes, with 114 species shared between the WP and WA, 145 species shared between the WP and EP and 152 species shared between the WA and EP. To account for sampling effects, we use range interpolation, i.e. species are assumed to occur in all latitudinal bands between the latitudinal range endpoints of the species. The changes in the results are minor when we use raw data. When measuring geographic range size, we focus on latitudinal ranges because we investigate clade expansion along latitudinal gradients, and climatic boundaries tend to be parallel with latitude along ocean margins. Analyses performed with full geographic ranges (measured with great-circle distances) show similar results. When measuring environmental range, we focus on thermal ranges, because temperature represents one of the predominant correlates of the distribution and diversity of shallow-water marine ectotherms (Tittensor *et al.*, 2010; Sunday *et al.*, 2011; Belanger *et al.*, 2012; Buckley *et al.*, 2012; Sanciangco *et al.*, 2013; Woolley *et al.*, 2016). We measure latitudinal and thermal range size as (1) total range and as (2) dispersion that measures the geographical spread of all occurrences relative to the range centroid. Although the first measure efficiently summarizes the maximum range, the second measure summarizes the distance by which every occurrence differs from the range centroid, and is thus less affected by single extreme occurrences. The datasets are available at Data Dryad (dx.doi.org/10.5061/dryad.23cn7).

Total latitudinal and thermal range size

The total latitudinal range size of species and genera is defined as the latitudinal distance between northern and

southern limits. The total macroecological thermal range of a taxon is defined as the total range of mean annual daily sea-surface temperature (SST) encompassed by the full geographic range of that taxon at 1° resolution. Total thermal range thus corresponds to the thermal range encountered by a given taxon at broad spatial scales (e.g. Verbruggen *et al.*, 2009; Gouveia *et al.*, 2014; Schweiger & Beierkuhnlein, 2016). SSTs were obtained at 1° resolution from MODIS (<http://modis.gsfc.nasa.gov/>).

Latitudinal and thermal dispersion

Genera can achieve broad geographic ranges by containing one or more widespread species or by containing narrow-ranging species that are widely separated in space. These two modes of range formation can be quantified by additive partitioning of genus latitudinal ranges into the dispersion of occurrences within species (within-species dispersion) and the dispersion of species within genera (among-species dispersion; Foote *et al.*, 2016). The total within-species dispersion corresponds to the sum of squared latitudinal (or thermal) distances of species occurrences from the species centroids. The total among-species dispersion corresponds to the sum of squared latitudinal (or thermal) distances of species centroids from the genus centroid (weighted by the number of species occurrences). The total within-genus dispersion corresponds to the sum of squared latitudinal (or thermal) distances between the genus centroid and all occurrences of its species. An occurrence here is any 25,000 km² equal-area cell containing at least one locality where a given species occurs; thus, a cell containing 50 closely spaced records of a species counts as a single occurrence in the analysis. In all instances, the geographical centroid corresponds to the point where the line drawn from the centre of the earth to the average of latitudes and longitudes of individual occurrences transformed to Cartesian coordinates intersects the surface of the earth, and the thermal centroid corresponds to the average of the SSTs of individual occurrences. The within-species dispersion, among-species dispersion and genus dispersion correspond to the square roots of total dispersions divided by the number of occurrences. Such latitudinal and thermal dispersions correlate closely with total latitudinal and thermal ranges (see Fig. S1 in the Supporting Information).

Relationship between per-genus species range size, genus range size and species richness

We (1) assess whether the dispersion of genera is determined by the range size of their constituent species (within-species dispersion) or by among-species dispersion in each transect and (2) measure the strength of bivariate relations between per-genus species richness on the one hand and genus dispersion, within-species dispersion and among-species dispersion on the other, using Spearman rank correlations. Genus dispersion cannot be smaller than within-species dispersion, and so some amount of variation in genus dispersion must

inevitably be explained by within-species dispersion. Therefore, to assess the significance of these relations in empirical data, we use a bootstrapping test to determine whether genus dispersions can be predicted from within-species dispersion or among-species dispersion beyond this constraint (i.e. within the triangular space where any values are allowed). Each genus dispersion was resampled (with replacement) independently for each genus, and resampled species dispersion components were required to be smaller than or equal to the corresponding value for resampled genus range size. A null estimate of rank correlation was then calculated on the resampled data set 1000 times, and compared with the observed rank correlation (Novack-Gottshall & Miller, 2003).

Latitudinal gradients in latitudinal and thermal range size

We estimate species and genus range size per latitudinal band as the median of all the ranges (total ranges or dispersions) that occur in that latitudinal band (the method of Stevens, 1989). We partition genus range-size gradients according to per-genus species richness, thus evaluating gradients in range size for monospecific genera, genera with two species, and genera with more than two species. We use generalized least squares to measure the slope of the relationship between median total latitudinal range size and latitude to minimize the correlation among the residuals due to the spatial structure within the data (Table S1) (Pinheiro *et al.*, 2013). We used five alternative functions to fit the relationship between the variance in the residuals and between-band latitudinal distance in semi-variograms (linear, Gaussian, spherical, exponential and rational quadratic functions; Beguería & Pueyo, 2009). We determined the Akaike information criterion (AIC) for models incorporating each of these five functions, and selected the best-fitting model for each of the respective analyses.

Latitudinal gradients in per-genus species richness

The range size of a genus occurring at high latitudes is determined by occurrences of its constituent species anywhere within its latitudinal range. To account for latitudinal variation in per-genus species richness, we measure the contribution of per-genus species richness to median genus range size at each latitude with mean per-genus species richness. The mean per-genus species richness is the number of species that occur anywhere within the range of those genera that occur at the given latitude, divided by the total number of genera at a given latitude (Foote, 2012; Maruvka *et al.*, 2013). This measure differs from a species–genus ratio, where only species that occur in a given latitudinal band are divided by the number of genera in that band (Krug *et al.*, 2008).

Probabilistic model of species range expansion

To quantify the net range shift of clades that undergo preferential tropical diversification and to assess whether such a

shift also generates a latitudinal gradient in genus range size and in mean per-genus species richness, we use a model which assumes that: (1) species are more likely to originate at low than at high latitudes and (2) species have equal probability of equatorward or poleward range expansion. The first assumption is in accord with theory and observations on the origin and maintenance of diversity gradients (Hawkins *et al.*, 2003; Currie *et al.*, 2004; Brayard *et al.*, 2005; Allen & Gillooly, 2006; Tello & Stevens, 2010), and with empirical observations implying higher rates of origination of invertebrates in the tropics (Goldberg *et al.*, 2005; Jablonski *et al.*, 2006; Krug *et al.*, 2009; Kiessling *et al.*, 2010). Although the second assumption is unlikely to be strictly accurate if species range-limiting factors vary with latitude (Papacostas & Freestone, 2016), it can be difficult to predict the net effects of a variety of range-limiting factors (Holt & Keitt, 2000; Early & Sax, 2011; Louthan *et al.*, 2015; Boucher-Lalonde *et al.*, 2016) on latitudinal gradients in species range expansion. On the one hand, tropical species may face weaker predation and competitive pressure at high latitudes, allowing easier invasion of tropical species to higher latitudes (Freestone *et al.*, 2013). On the other hand, high-latitude species can have broader thermal tolerances or can track isotherms to deeper environments, and so will be more likely expand to low latitudes. We use this latitudinal symmetry in range expansion at species level as the simplest model.

First, we place the midpoints of geographic ranges on the continental and island shelves so that the probability of species placement increases towards the tropics, selecting one ancestor species for each genus present in each transect (e.g. 772 ancestor species in the WP with 3134 species and 772 genera). We use the grid with 1° resolution, and range-size data are scaled to 5° latitudinal bands. We use the exponential dependence of speciation rate on latitude-specific SST expected under the metabolic theory of ecology (Brown *et al.*, 2004; Allen *et al.*, 2006), although any negative and monotonic relation between latitude and net diversification, underlain by other factors (e.g. greater eradication of shelf-habitat at the highest latitudes during glacial maxima; Clarke & Crame, 2010), should generate qualitatively similar model outcomes with respect to gradients in genus range size and per-genus species richness. Second, the range size of this ancestor is randomly sampled from the frequency distribution of empirical latitudinal and longitudinal ranges (i.e. the range-shuffling algorithm in Connolly, 2005), thus mimicking random species expansion along a latitudinal gradient. Third, ancestors produce descendants either within their range (the scenario with spatial dependency) or anywhere along the latitudinal gradient (the scenario without spatial dependency). In the first case, where spatial dependency between ancestors and descendants implicitly imposes some degree of niche conservatism, the range midpoints of the descendant are sampled from the 1° cells occupied by the ancestor. Given the size of the grid cells, this scenario need not imply sympatric speciation, but can also incorporate allopatric separation along, for example, bathymetric,

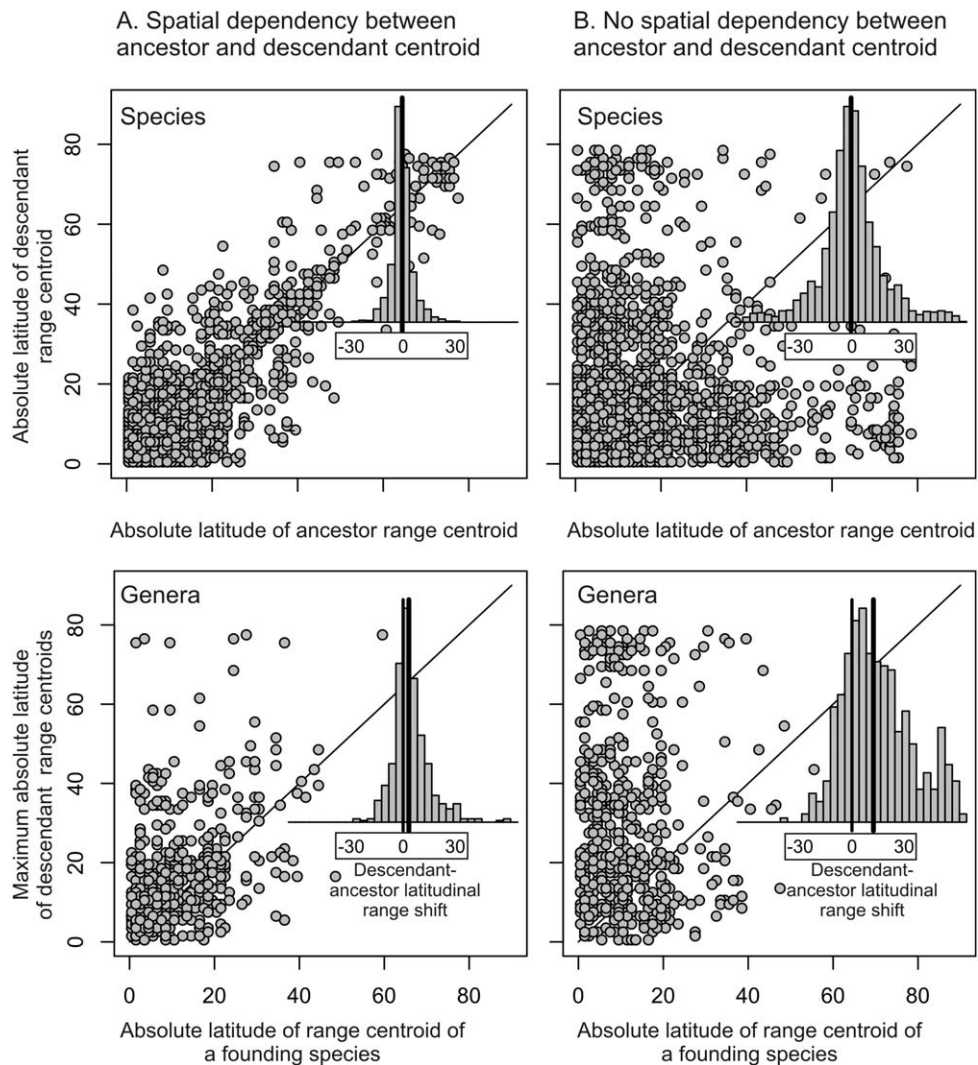


Figure 1 The relationship between the latitudinal range centroid of ancestors and their descendants as predicted by the range-expansion model, with (a) and without (b) spatial dependency of the position of the descendant range on ancestral ones, shows a symmetric distribution of descendant–ancestor range shifts at the species level (top row) but an asymmetric distribution of descendant–ancestor range shifts at genus level (bottom row), modelled for the Western Pacific. Insets show frequency distributions (in degrees of latitude) of descendant–ancestor range shifts at species and genus level, i.e. differences in the latitude of the range-centroid between descendant and ancestor species (top row), and differences in the latitude of the range-centroid between a descendant species with a maximum range-centroid latitude and a founding congeneric species (bottom row). The thick solid black line represents the median shift in range location. The median shift at species level is 0°. The median shift at genus level is 4° under spatial dependency and 15° in the absence of spatial dependency.

productivity or salinity gradients or discontinuities. In the second case, the end-member scenario without niche conservatism, range midpoints of the descendant are drawn from all 1° cells in the given transect. The descendants come from the last ancestors in the sequence of congeneric species, not from the original ancestor.

Fourth, range sizes of descendants are randomly sampled from the frequency distribution of empirical ranges. Thus, low- and high-latitude species have equal chances of obtaining broad ranges, and therefore in extending poleward or equatorward. This process of within-genus speciation is repeated until the number of new descendant species equals

the species richness of the genus minus one (assuming that the ancestor species persists with its descendants). This approach conserves both the empirical distribution of latitudinal range sizes (Connolly *et al.*, 2003) and the distribution of per-genus species richness within each oceanic margin. We repeated this procedure in 1000 runs for each oceanic margin. Under this procedure, the frequency distribution of range shifts between descendants and ancestors (i.e. the differences in the location of their range centroids) is symmetrical at the species level, i.e. the absolute latitude of descendants is not preferentially shifted equatorward or poleward and the median range shift equals 0 in all transects

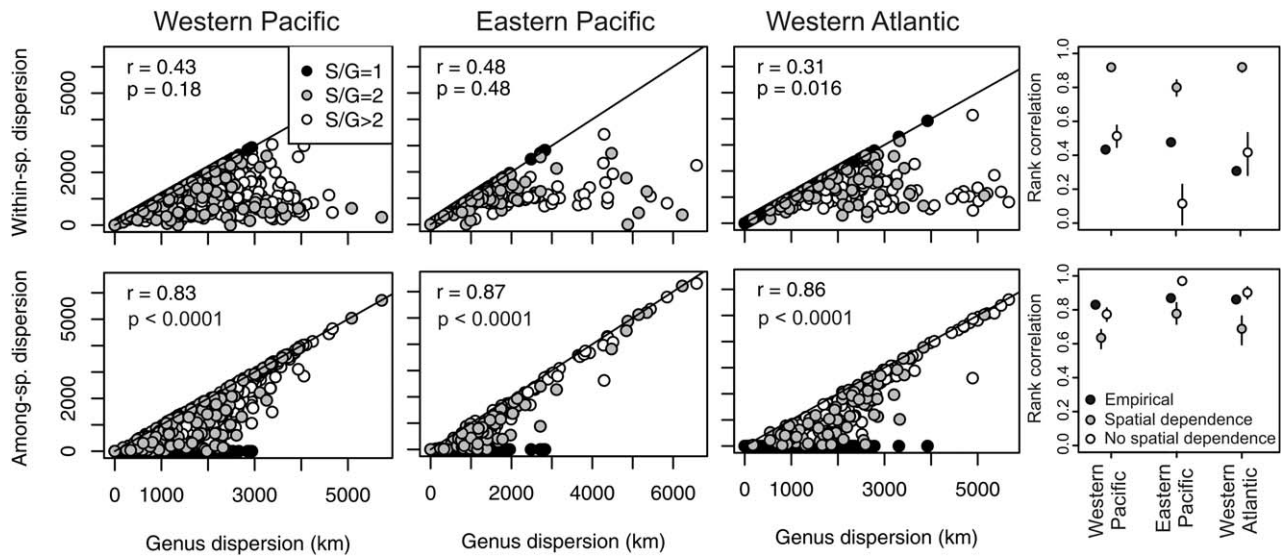


Figure 2 Top row: with the exception of the constraint that genus range size cannot be smaller than species range size, genus latitudinal dispersion is unrelated to within-species latitudinal dispersion. Bottom row: genus latitudinal dispersion is significantly related to among-species latitudinal dispersion. Spearman rank correlations (r) are shown for genera with more than one species ($S/G > 1$). The rightmost plots show that models without spatial dependency (black circles) predict a relatively weak correlation for within-species latitudinal dispersion and a relatively strong correlation for among-species latitudinal dispersion, similar to what is observed in the empirical data. Error bars represent bootstrapped 95% confidence intervals.

(top row in Fig. 1). In contrast, the frequency distribution of range shifts is asymmetrical at the genus level, i.e. the absolute latitude of the genus tends to be shifted poleward relative to the absolute latitude of the founding species (bottom row in Fig. 1). This asymmetry is less pronounced in the scenario with spatial dependency (median range shift between 4° and 8° ; Fig. 1a) than without spatial dependency (median range shift between 15° and 20° ; Fig. 1b). The source code for the model in R 3.2.1 (R Core Team, 2015) is available at Data Dryad ([dx.doi.org/10.5061/dryad.23cn7](https://doi.org/10.5061/dryad.23cn7)).

The scenario assuming no spatial dependency of the descendant range location on the location of the ancestor is effectively equivalent to random aggregation of species ranges into genera (up to aggregating a single polar species and a single tropical one into a genus), while conserving (1) the higher species richness in the tropics, (2) the distribution of latitudinal range sizes, and (3) the distribution of per-genus species richness. This scenario represents a simple approach for detecting whether niche conservatism is stronger than expected under the probabilistic range-expansion dynamic at species level.

RESULTS

Empirical and predicted decoupling between genus range size and species range size

Genus latitudinal dispersion correlates weakly and insignificantly with within-species latitudinal dispersion in genera with more than one species [r (WP) = 0.43, $P = 0.19$; r (EP) = 0.48, $P = 0.48$; r (WA) = 0.31, $p = 0.02$, insignificant after a Bonferroni correction at $\alpha = 0.05$; Fig. 2]. Therefore, the signature of species range size is obliterated at the genus level: broad-

ranging bivalve genera are not collections of widespread, successful or ecologically generalized species. In contrast, genus latitudinal dispersion correlates strongly with among-species latitudinal dispersion ($r = 0.83$ – 0.87 , all $P < 0.0001$; Fig. 2). The scenario with spatial dependency predicts a stronger contribution of within-species latitudinal dispersion to genus latitudinal dispersion than does the scenario without spatial dependency. Thermal range size is less decoupled between species and genus levels: the correlations between genus thermal dispersion and within-species thermal dispersion are moderately high and significant [r (WP) = 0.67, $P < 0.0001$; r (EP) = 0.73, $P < 0.0001$; r (WA) = 0.81, $P < 0.0001$). However, genus thermal dispersion correlates even more strongly with among-species thermal dispersion ($r = 0.84$ – 0.89 , all $P < 0.0001$; Fig. S2) than with within-species thermal dispersion ($r = 0.67$ – 0.81 , all $P < 0.0001$; Fig. 2).

Empirical and predicted relation between per-genus species richness and genus range size

In marine bivalves, empirical data match the model predictions in many aspects. Per-genus species richness shows a moderately high correlation with genus latitudinal dispersion ($r = 0.57$ – 0.58 , all $P < 0.0001$; Fig. 3), similar to expectations under the range-expansion models, which give slightly higher correlations (~ 0.7 in models with spatial dependency and ~ 0.8 in models without spatial dependency; Fig. 3). Per-genus species richness (1) does not correlate or correlates only very weakly with within-species latitudinal dispersion ($r = -0.01$ to 0.21 , $P < 0.0001$ in the WP only; Fig. 3), and (2) correlates moderately with among-species latitudinal dispersion ($r = 0.36$ – 0.41 , all

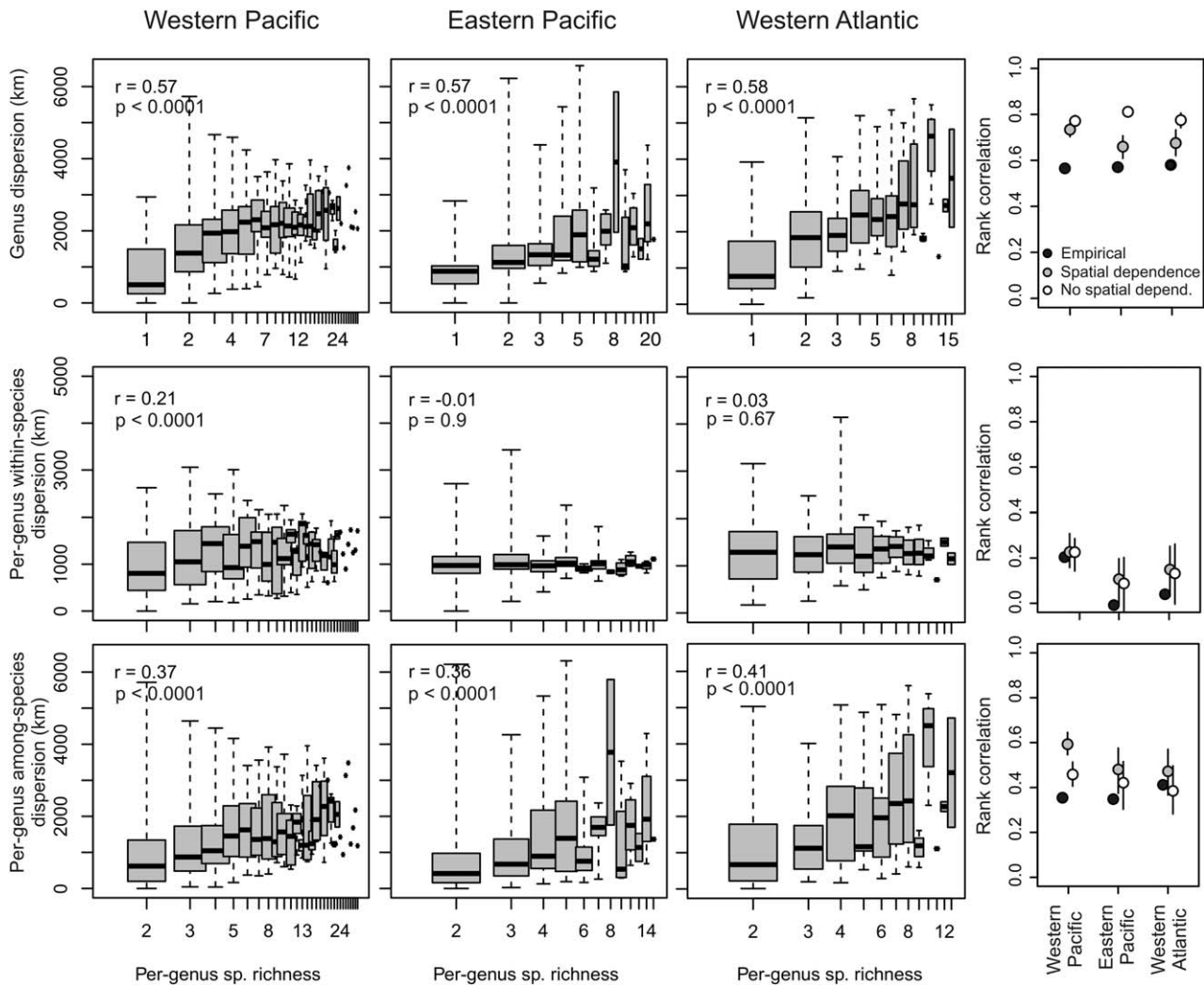


Figure 3 Top row: species-rich genera have significantly broader latitudinal dispersion than species-poor genera. Middle row: species-rich genera show a very weak propensity for containing species with broader latitudinal ranges than species-poor genera. Bottom row: genera with many species tend to have a broad among-species latitudinal dispersion. The rightmost plots show that models with and without spatial dependency predict a strong correlation between genus dispersion and species richness, weak correlations between within-species latitudinal dispersion and species richness, and moderate correlations between among-species latitudinal dispersion and species richness. Model predictions are not very sensitive to the degree of spatial dependency between ancestor and descendant range locations. r = Spearman rank correlations. Error bars represent bootstrapped 95% confidence intervals. Among-species dispersion in monospecific genera is forced to be zero and the contributions of within- and among-species dispersions to per-genus species richness are thus assessed for genera with more than one species.

$P < 0.0001$; Fig. 3), as predicted by the range-expansion models. Thermal dispersions show similar patterns as latitudinal dispersions: per-genus species richness correlates weakly with within-species thermal dispersion ($r = 0.17$ – 0.25 , all $P < 0.0001$), very strongly with among-species thermal dispersion ($r = 0.76$ – 0.91 , all $P < 0.0001$) and moderately highly with genus thermal dispersion (0.41 – 0.46 , all $P < 0.0001$).

Gradients in latitudinal range size at species and genus level

Median species latitudinal range increases towards the tropics, while median genus latitudinal range increases

towards high latitudes (Fig. 4). This shift from negative to positive slope in the range-size/latitude relationship is generated purely by species-rich genera, whereas monospecific genera show the same pattern as species (Fig. 5, Table S1). Model predictions also show an increase in genus range size towards higher latitudes, especially in the WP and WA (Fig. 6). The diversification hotspot in the EP is narrower, and so the potential for expansion is reduced under spatial dependency. However, the latitudinal increase in genus range size becomes stronger in the absence of spatial dependency between the range location of ancestors and descendants, as also observed along the empirical gradients. Within-species latitudinal dispersion is also at a maximum in the tropics

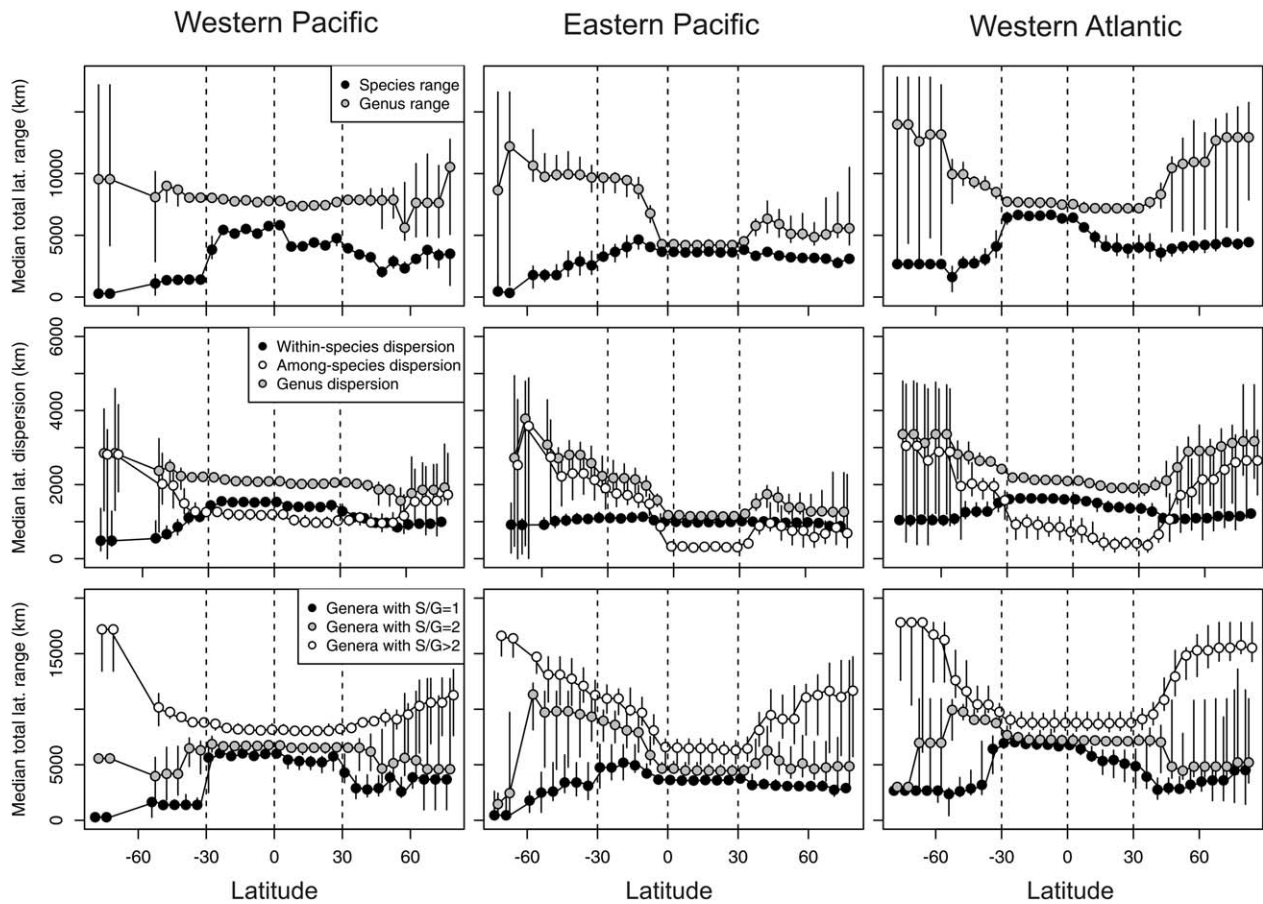


Figure 4 Top row: median latitudinal range size at the species level (black points) increases towards low latitudes along three oceanic margins. In contrast, median latitudinal range size at genus level (grey points) increases towards high latitudes. Middle row: median per-genus within-species latitudinal dispersion is greatest at the lowest latitudes whereas median genus latitudinal dispersion is smallest in the tropics or latitude-invariant in the Western Pacific. Among-species latitudinal dispersion is smallest in the tropics. Bottom row: the reversal in the range-size gradient is driven by genera containing more than one species ($S/G > 1$) along each of the three oceanic margins. Error bars represent bootstrapped 95% confidence intervals.

and genus dispersion is either smallest in the tropics or latitude invariant, and is primarily associated with a greater among-species dispersion in the tropics (Fig. 4). Full frequency distributions of total range size show that broad-ranging genera occur at all latitudes, whereas narrow-ranging

genera occur mainly in the tropics, i.e. they are nested geographically within broad-ranging, almost cosmopolitan genera (Fig. A3). Thus, although the location of the smallest median genus range at low latitudes superficially conforms to the Rapoport pattern, this pattern is not related to the

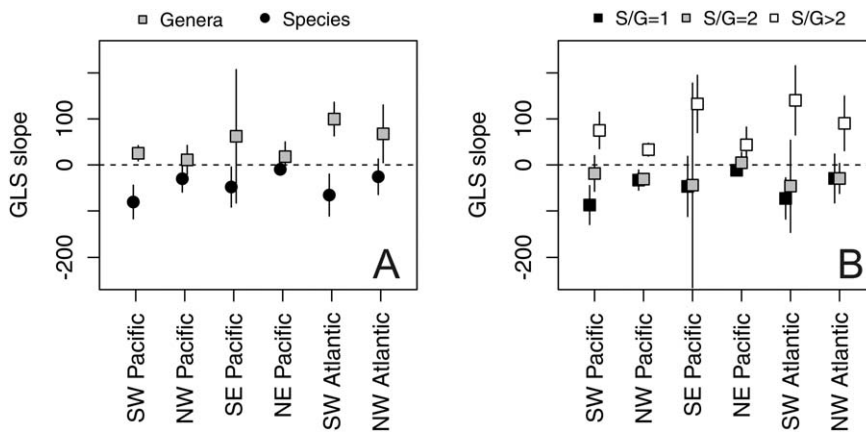


Figure 5 (a) Slopes of the relation between latitude and total latitudinal range size measured by generalized least-square (GLS) models change from negative at the species level to positive at the genus level. (b) The slope of the relation between latitude and total latitudinal range size is negative when monospecific genera are included, but becomes positive in genera containing more than two species. Error bars represent 95% confidence intervals.

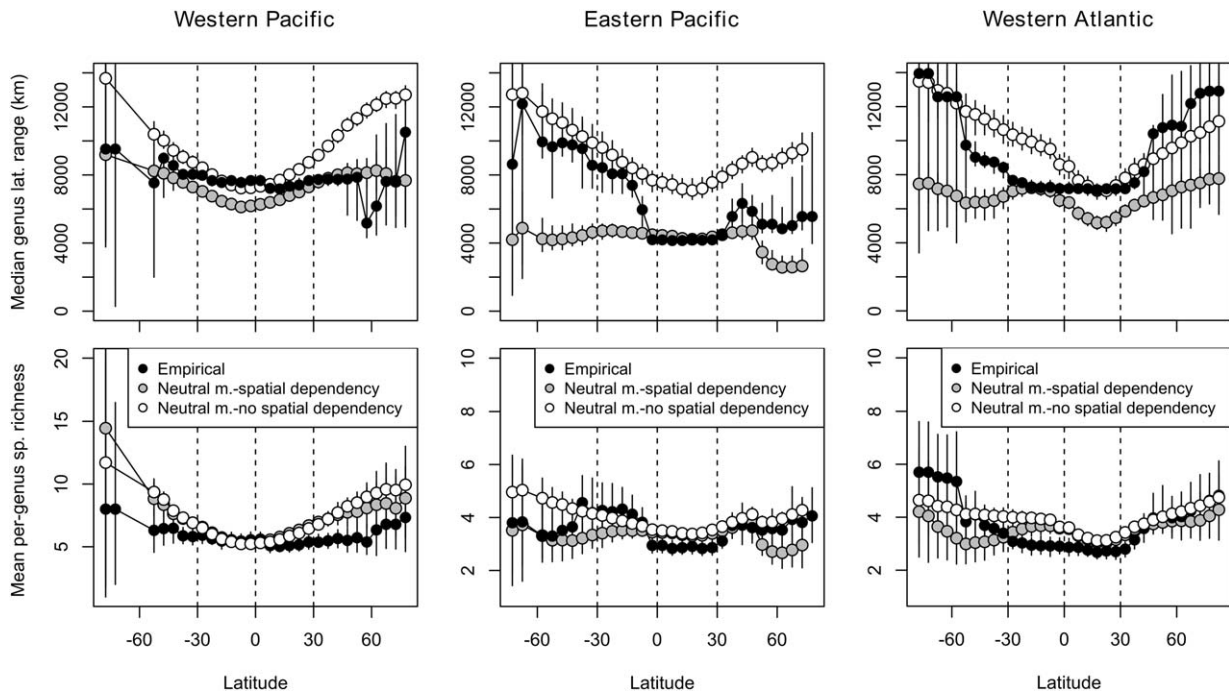


Figure 6 Top row: range-expansion models predict an increase in range size towards higher latitudes, especially without spatial dependency between ancestor and descendants. Bottom row: empirical data and a model of range expansion at the genus level driven by higher species richness in the tropics (with genus range expansion being most probable in species-rich clades) both show increases in mean per-genus species richness towards higher latitudes. Error bars represent bootstrapped 95% confidence intervals.

replacement of narrow-ranging by broad-ranging genera towards higher latitudes.

Gradients in per-genus species richness

Per-genus species richness increases towards higher latitudes, even though both species and genus richness increase towards the tropics. The per-genus gradient arises because monospecific and species-poor genera along the western transects are proportionally more frequent at low latitudes. In contrast, high-latitude bands are dominated by cosmopolitan genera, which have few species in polar seas but tend to have more species on a global basis (Fig. 6). This excess of species-rich genera at high latitudes is predicted by the diversity-dependent probabilistic model of range expansion at genus level (Fig. 6), i.e. the richest genera are evidently the ones most likely to expand their ranges out of the tropics.

Gradients in thermal range size at species and genus level

Although genus thermal dispersions correlate with within-species thermal dispersions, latitudinal gradients in genus and species thermal range sizes are different. Species total thermal ranges and within-species dispersions peak at temperate latitudes, are relatively low in the tropics and are smallest at polar latitudes (Fig. 7). Genus total thermal ranges and dispersions remain small in the tropics but markedly increase towards polar latitudes (with the exception of southern polar latitudes in the WP). This change from

species- to genus-level gradients is underlain by a latitudinal increase in among-species thermal dispersion (Fig. 7), i.e. genera at high latitudes consist of species with widely different thermal midpoints, across many different latitudinal bands. The poleward increase in thermal range size is thus caused by genera that reach the polar seas and thus tend to have the broadest latitudinal ranges (and thus encompass the broadest range of temperatures).

DISCUSSION

The geographic range sizes of marine bivalve genera are not a simple function of the range sizes of their constituent species, but are positively related to the species richness of the genus: widespread genera do not consist of widespread species, but tend to contain more species than do spatially restricted genera, and species-rich genera tend to contain species separated by larger latitudinal distances than species-poor genera, supporting the predictions of range-expansion models. These findings have several empirical and theoretical implications.

Decoupling between genus and species latitudinal range sizes

With decreasing spatial dependency in range location between ancestors and descendants (one proxy for climate niche conservatism), the contribution of among-species latitudinal dispersion to genus range size is expected to increase. In accord with this, marine bivalves show that among-species

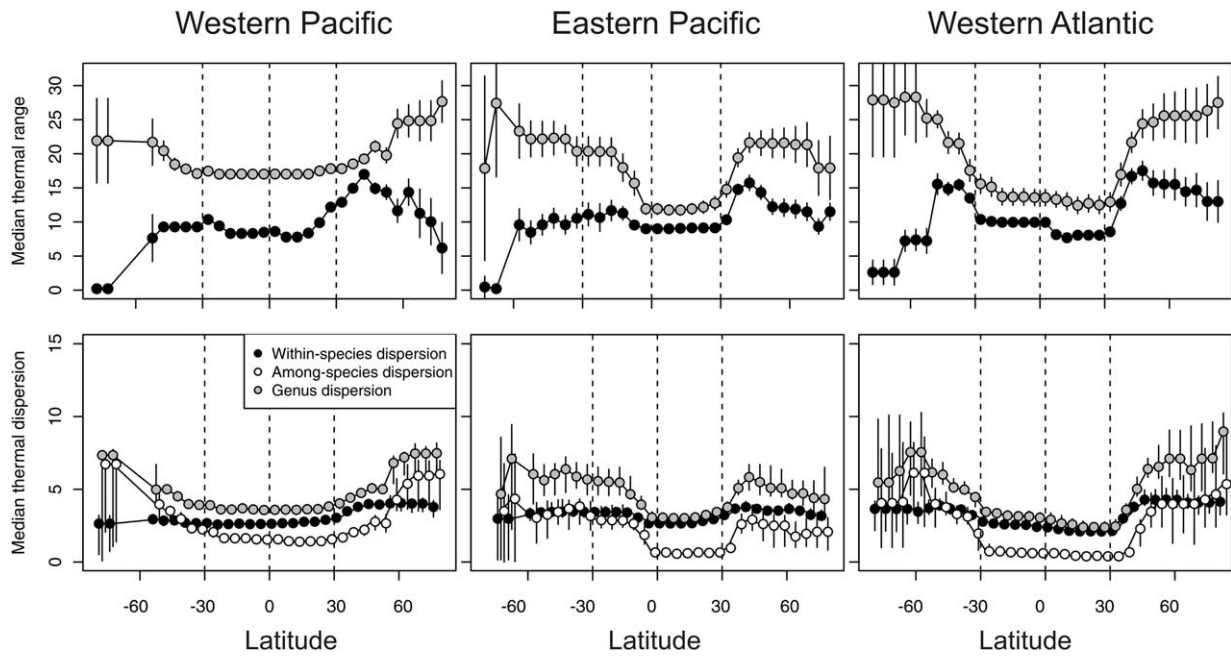


Figure 7 Top row: species thermal range size (black symbols) peaks at intermediate latitudes (especially in the Northern Hemisphere), whereas thermal ranges of genera (grey symbols) peak at polar latitudes. Bottom row: genus thermal dispersion is smallest in the tropics and greatest at polar latitudes. This gradient is underlain by the latitudinal increase in among-species thermal distance towards the polar latitudes. The increase in within-species thermal dispersion towards the polar latitudes is weak.

latitudinal dispersion contributes more to genus latitudinal range size than within-species latitudinal dispersion (Fig. 2). However, despite these observations that congeneric species can occur at different latitudes, strong correlations between genus and within-species thermal dispersions show that thermal range size is still generally conserved among congeneric species of marine bivalves (Fig. S2). Within-genus differences in thermal tolerance minima and maxima are significantly smaller than among genera (Fig. S4), and thermal limits are thus also conserved among species at the genus level (Roy *et al.*, 2009). Nonlinearity of latitudinal gradients in temperature explains the observation that gradients in thermal dispersions are similar but gradients in latitudinal dispersions differ between species and genera: even when some genera show high among-species latitudinal dispersion, their among-species thermal dispersion will be still low in the tropics, where temperatures are nearly constant throughout. However, the contribution of among-species thermal dispersion to genus thermal dispersion is even higher than that of within-species thermal dispersion, and the nonlinearity thus does not completely explain the difference. A relatively high number of congeneric species inhabiting similar thermal regimes can outweigh the few species that shifted their ranges to new thermal regimes, so that the thermal range size among congeneric species is greater than expected by chance. High correlations between genus and species thermal dispersions are thus not mutually exclusive with the observation that some congeneric species inhabit different latitudes and thermal regimes, and thus distinct climatic zones. Such relations reconcile the relationship between the OTT and CNC

models: thermal niche conservatism can be coupled with the preferential poleward range expansion of clades, because under conditions when only a few species in a clade manage to cross the tropical/temperate boundary, conservatism still persists. The effect of per-genus species richness on genus ranges is thus compatible with some degree of conservatism in latitudinal range limits and in thermal niche, as also documented in other studies of molluscs (Saupe *et al.*, 2014).

Genus distribution patterns probably provide a better surrogate for species-level patterns under stronger genus climatic niche conservatism, i.e. when new clades do not expand into new climatic zones and show species-level range-size heritability (Jablonski, 1987; Waldron, 2007; Borregaard *et al.*, 2012), especially in terrestrial clades (Hawkins *et al.*, 2011; Duchene & Cardillo, 2015). For example, Carotenuto *et al.* (2010) found that midpoint locations of sister species are similar and that genus range size of Pliocene large mammals is mainly determined by range expansion at the species level, rather than being the sum of individual species ranges. Nonetheless, our findings indicate that genus range size will often be a poor proxy for species distributions or environmental tolerances. The relation between species and clade range size is of much palaeobiological interest because genera tend to be applied with greater taxonomic consistency (Harcourt, 2000) and are better sampled in the fossil record than species (Robeck *et al.*, 2000; Hadly *et al.*, 2009; Harnik *et al.*, 2012; Foote, 2014; Hendricks *et al.*, 2014; Hopkins *et al.*, 2014). Biogeographic analyses have also sometimes been performed at higher taxonomic levels because they discriminate among provinces as well or better than analyses based purely

at the species level (Kreft & Jetz, 2013; Proches & Ramdhani, 2012; Pierrat *et al.*, 2013; Rueda *et al.*, 2013). Our data show that extrapolations from species to genus range size, or conversely to from genus to species range size, are problematic, especially when genera are species rich. Among many other macroevolutionary implications, these results suggest that extinction selectivity of genus-level clades on the basis of geographic range size during background (Jablonski, 1986; Payne & Finnegan, 2007; Janevski & Baumiller, 2009; Harnik *et al.*, 2012) and mass extinctions (Jablonski, 1986, 2005) are not simply related to the range sizes or environmental tolerances of their constituent species. By the same token, temporal changes in per-genus species richness can generate significant temporal changes in genus range size in the absence of any change in species ecology (Foote *et al.*, 2008).

Relationship between genus latitudinal range size and species richness

The positive relation between a clade's species richness and its range size has been reported in both marine and terrestrial systems (Ricklefs & Latham, 1992; Krug *et al.*, 2008; Tomašových *et al.*, 2016) and is predicted by the probabilistic range-expansion model, with or without spatial dependency, implying that differences in genus range size among genera are partly related to differences in within-genus species diversification. The relation holds even with a fixed probability of placing a new species outside the existing climate envelope of the clade per speciation event. The decomposition of genus range size into within- and among-species latitudinal dispersion shows that in bivalves at least, among-species latitudinal dispersion correlates very strongly, whereas within-species latitudinal dispersion correlates weakly, with per-genus species richness. These patterns are rather insensitive to the degree of spatial dependency between ancestor and descendant range locations, and imply that species diversification into novel latitudes and climates is largely responsible for creating broad genus ranges.

It is possible that among-species latitudinal dispersion can arise from fragmentation and associated vicariant speciation of an initially broad latitudinal range of a single species (possibly also associated with extinction of some species within that range). In such cases, a broad genus range size (and high among-species dispersion) would not be a function of speciation associated with range expansion to novel environments, but rather a function of species range expansion prior to range fragmentation. However, this scenario is probably infrequent because: (1) it requires very broad thermal ranges at species level, whereas few species of marine bivalves extend their range from tropics to cool-temperate and polar latitudes, and (2) genus latitudinal range size exceeds per-genus maximum species latitudinal range size by a median of >1000 km in all transects (excluding monospecific genera). The probabilistic range-expansion model does not assume that species range expansion to novel latitudes or climates

directly triggers speciation (Kozak & Wiens, 2010). Such an active association between species range expansion and speciation would further strengthen the relation between among-species dispersion and per-genus species richness.

Species range-size gradients

Strong temporal environmental variability might select for generalized species with broad geographic ranges in temporally variable environments at high latitudes (Stevens, 1989; Dynesius & Jansson, 2000; Colles *et al.*, 2009; Bell, 2010), but other processes, such as selection for mobile dispersal strategies or continuity of effective habitat area, can reverse such effects (Rosenzweig & Sandlin, 1997; Gaston & Chown, 1999; Travis & Dytham, 1999; Goldberg *et al.*, 2011; Birand *et al.*, 2012; Gross & Snyder-Beattie, 2016). The gentler environmental gradients in tropical environments allow broader geographic ranges in the tropics whereas the steep temperature gradients at high latitudes can impede full occupation of that space (Pintor *et al.*, 2015; Tomašových *et al.*, 2015). This nonlinearity of climatic gradients gives rise to an inverse Rapoport pattern in bivalves: species latitudinal range size increases towards the tropics owing to flat climatic gradients at low latitudes (Tomašových *et al.*, 2015). In contrast, species thermal range size does not peak in the tropics because tropical species achieve broad latitudinal ranges even when they are thermally specialized (Fig. S5). Species latitudinal ranges also tend to be largest in the tropics, and also show weaker clustering of range limits there in other marine clades, including teleosts and corals (Jones *et al.*, 2002; Connolly *et al.*, 2003; MacPherson, 2003), implying the marine species often tend to follow an inverse Rapoport pattern. Although the OTT scenario predicts higher origination rates (or more time for origination) in the tropics, it does not necessarily predict narrower species ranges in the tropics (*contra* Spano *et al.*, 2015) because marine species ranges can evidently expand more broadly or more rapidly in the thermally homogeneous low latitudes than in high latitudes.

Genus range-size gradients

An increase in genus latitudinal and thermal range size towards higher latitudes is tightly coupled with a latitudinal increase in mean per-genus species richness because: (1) genus range size is more closely related to among-species latitudinal dispersion; (2) monospecific genera do not show the Rapoport pattern, whereas genera containing two or more species show an increasingly strong Rapoport pattern, and the species-rich genera that range fully or nearly from tropics to poles become an increasingly larger fraction of the taxa in each successive latitudinal band; and (3) per-genus species richness positively correlates with both genus latitudinal range and thermal range. Therefore, high latitudes are inhabited by globally species-rich, nearly cosmopolitan genera that consist of few species that also occur at low latitudes and others that are restricted to high latitudes. Rohde *et al.* (1993) and Hausdorf (2006) described other examples where

an apparent Rapoport pattern is generated by geographically nested ranges rather than by Stevens' (1989) stepwise latitudinal turnover of species having increasingly broader ranges. We thus suggest that species-rich genera are statistically more likely than species-poor genera to expand their ranges out of the tropics, as predicted by the probabilistic range-expansion model. This model exhibits diversity-dependent expansion to higher latitudes at genus level owing to greater species richness at low latitudes. It predicts asymmetry in range expansion at the genus level, an increase in genus range size towards higher latitudes, and an increase in global species richness in the genera reaching higher latitudes, all matching the bivalve data. Assuming that the species extinction rate does not decrease towards higher latitudes (Rivadeneira *et al.*, 2015), this range-expansion mechanism ensures that latitudinal and thermal ranges of such genera also increase as they reach high latitudes. Such genera become increasingly eurytopic overall even when they consist of thermally specialized species.

The positive relation seen in some fossil clades between latitude and genus range size (Powell, 2007) and between macroecological niche breadth and genus geographic range size (Miller, 1997; Heim & Peters, 2012) is also a predictable consequence of a probabilistic range-expansion scenario, and thus may be unrelated to processes determining environmental tolerances and range limits at the species level. This scenario is independently supported by spatially and temporally explicit analysis of the evolutionary history of bivalves: since the Late Miocene, bivalve genera that appear first in the tropics later expand to extratropical regions while keeping their tropical presence (Jablonski *et al.*, 2006). The higher proportion of genera that originate in the tropics over the late Cenozoic and a lag between genus origination and extratropical expansion (Jablonski *et al.*, 2013) suggest that the configuration of ranges observed in extant genera evolved over millions of years, despite higher-frequency climate fluctuations. This dynamic leaves its signature in a latitudinal increase in the median age of extant genera along the three ocean margins. As in genus range-size–frequency distributions, geologic age–frequency distributions at low latitudes are mixtures of narrow-ranging young and broad-ranging old genera, whereas age–frequency distributions at high latitudes are dominated by old, broad-ranging genera, many of which probably originated in the tropics, that also occur at low latitudes (Jablonski *et al.*, 2013; Berke *et al.*, 2014). Even for geologically young bivalve genera that originated in the tropics and currently also inhabit higher latitudes, extant genera in the tropics still tend to be on average younger than at higher latitudes, providing further support for high tropical origination rates, especially in the WP (Fig. S6) (Jablonski *et al.*, 2006).

CONCLUSIONS

Although some macroevolutionary and biogeographic patterns, such as spatial and temporal diversity trends, can be

directly extrapolated from species to genus levels, and vice versa, biogeographic patterns in range size may not warrant such extrapolation. We show that: (1) genus latitudinal range size in marine bivalves is decoupled from species ranges, and thus partly decoupled from species-level ecological and biogeographic processes that affect species range size and limits, and (2) genus latitudinal and thermal range size is mainly determined by per-genus species richness. Both findings are predicted by a simple probabilistic scenario that implicitly allows some degree of climate niche divergence—as appears to be required by the data—and assumes higher within-genus species diversification at low latitudes coupled with subsequent expansion of the genus out of the tropics. The probabilistic model can serve as a neutral baseline for more complex models that explain non-random gradients in range size because it corresponds to a simple version of the OTT model and is consistent with CNC models with weak to moderate niche conservatism. The geographical nestedness of ranges at the genus level, with endemic genera occurring mainly within the tropical portions of other, latitudinally widespread, genera, and the latitudinal increase in genus range size towards high latitudes, are thus predictable when species preferentially arise in the tropics and spread or speciate poleward over geological time, carrying their genera with them. Thus, latitudinal gradients in species-level diversification can propagate into latitudinal gradients in range size via non-random clade range expansion.

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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:

Table S1 The relation between median latitudinal range size and latitude at species and genus level for three oceanic margins, separately for total ranges and dispersions, show that negative slopes at species level tend to be reduced or even change to positive values at genus level.

Figure S1 Total latitudinal and thermal genus ranges strongly correlate with latitudinal and thermal genus dispersions.

Figure S2 Genus thermal dispersion correlates moderately strongly with within-species thermal dispersion and very strongly with among-species thermal dispersion.

Figure S3 Range-size–frequency distributions of species and genera and frequency distributions of per-genus species richness in the Western Pacific and Western Atlantic show that the apparent Rapoport pattern at the genus level is caused by the presence of narrow-ranging tropical genera in the tropics within the geographic ranges of latitudinally broad-ranging genera

Figure S4 The median difference between among-genus differences in the sea-surface temperature minima and maxima of individual species and differences in the minima and maxima of congeneric species significantly exceed the difference expected in the absence of genus conservatism in these thermal limits.

Figure S5 The relation between latitudinal and thermal ranges is constrained to be positive because species with the smallest range cannot have a broad thermal range whereas species with broad ranges cannot have zero thermal range.

Figure S6 Latitudinal gradients in median genus age with bootstrapped 95% confidence intervals, showing that median genus age tends to be higher at high latitudes in northern hemispheres, and tends to be smallest in the tropics. The genus ages are derived from Huang *et al.* (2014).

BIOSKETCH

Adam Tomašových is interested in the mechanisms that generate macroecological and biogeographical patterns of marine ectotherms in time and space.

A.T. and D.J. designed the study and collected data, A.T. performed analyses and wrote the first draft of the manuscript, and both authors contributed to revisions.

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