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Nonlinear thermal gradients shape broad-scale patterns in geographic range size and can reverse Rapoport's rule

Adam Tomašových¹, David Jablonski², Sarah K. Berke³, Andrew Z. Krug⁴ and James W. Valentine⁵

¹Geological Institute, Slovak Academy of Sciences, 84005 Bratislava, Slovakia,

²Department of Geophysical Sciences, University of Chicago, 5734 S. Ellis Avenue, Chicago, IL 60637, USA, ³Department of Biology, Siena College, Loudonville, NY 12211, USA, ⁴Flint Hill School, Oakton, VA 22124, USA, ⁵Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, CA 94720, USA

ABSTRACT

Aim Species living at latitudes that have greater annual temperature variations are expected to achieve broader geographic ranges than species living at latitudes that have smaller annual temperature variations, generating a positive relationship between range size and latitude (Rapoport's rule). However, this prediction fails to take into account the greater latitudinal extent of tropical temperatures relative to those at higher latitudes. Here we model the contributions of the broader latitudinal extent of equal-temperature habitats at low latitudes and the greater annual temperature variation at high latitudes to the range size–latitude relationship, and test whether the latitudinal variation in geographic range size in marine bivalves can be explained by models that account for both annual temperature variation and the steepness of latitudinal thermal gradients.

Location Western Pacific, eastern Pacific and western Atlantic.

Methods We use a null model where geographic ranges are placed on the ocean surface independently of thermal gradients, and a range-expansion model where the minimum and maximum temperatures encompassed by the geographic range of a species (macroecological thermal ranges) are positively related to annual temperature minima and maxima at the location where the species originated. We compare results with a database containing 40,820 occurrences of 4760 marine bivalve species.

Result Models incorporating temperature-limited range expansion along realistic thermal gradients predict an inverse relationship between range size and latitude, in opposition to Rapoport's rule. The distribution patterns of marine bivalves match this prediction.

Main conclusions The poleward trend in latitudinal range size is determined by the nonlinearity of the latitudinal gradient of temperature minima and maxima and less by the latitudinal gradient of the local seasonal range in temperatures. Although tropical species do have narrower macroecological thermal ranges than high-latitude species, the nearly constant temperatures over wide areas of the tropics allow tropical species to achieve broad latitudinal ranges.

Keywords

Biogeography, Bivalvia, geographic range, macroecology, Rapoport's rule.

*Correspondence: Adam Tomašových, Geological Institute, Slovak Academy of Sciences, 84005 Bratislava, Slovakia. E-mail: geoltoma@savba.sk

INTRODUCTION

Latitudinal gradients in geographic range size represent a unique source of information on spatial variation in ecological

and evolutionary processes. First, they can reflect gradients in migration, extinction and speciation rates (Case *et al.*, 2005; Price & Kirkpatrick, 2009). Second, they can feed back into evolutionary dynamics by affecting extinction risk (Liow, 2007;

Crampton *et al.*, 2010) and by increasing or reducing speciation rates (Birand *et al.*, 2012). Third, gradients in range size can be coupled with gradients in range overlap, thus indirectly influencing diversity gradients and their relation to environmental gradients (Connolly, 2009; Tello & Stevens, 2012). Spatial variation in geographic range size has been linked to global climatic variation through Rapoport's rule, the hypothesized positive relation between latitudinal range size and latitudinal position (Stevens, 1989). As annual temperature variation generally tends to increase from low to mid latitudes (Clarke, 2009), this positive relationship might occur if annual temperature variation selects for broad thermal tolerances (i.e. the climatic-variability hypothesis; Parmesan *et al.*, 2005; Bozinovic *et al.*, 2011; Quintero & Wiens, 2013). Empirically, species living at temperate latitudes have broad thermal ranges and species inhabiting temporally variable environments possess broad latitudinal ranges (Jackson, 1974; Harley *et al.*, 2003). However, a direct relation between latitude and latitudinal range size seems to be less general. Rapoport's rule mainly applies to terrestrial organisms in the Northern Hemisphere (Rohde, 1996; Fernandez & Vrba, 2005; Whitton *et al.*, 2012), although New World birds, bats and marsupials conform to it along the full tropical–temperate gradient (Blackburn & Gaston, 1996, Lyons & Willig, 1997; Orme *et al.*, 2006). Marine organisms, in contrast, fail to exhibit a clear relationship between range size and latitude (Roy *et al.*, 1994; Hernández *et al.*, 2005; Mora & Robertson, 2005).

As suggested by Gaston & Chown (1999), one factor that can contribute to these mixed results is the nonlinear relationship between temperature and latitude within each hemisphere (at

comparable depths or altitudes), with much weaker spatial variation in annual minimum, mean and maximum daily temperature at low than at mid latitudes in both terrestrial and marine environments (Colwell, 2011). A given mean annual temperature tends to have a smaller latitudinal extent in highly seasonal mid latitudes than in less seasonal lower latitudes, especially along the western margins of ocean basins (top row in Fig. 1 & Fig. A1 in Appendix S1 in the Supporting Information). The spatial extent of the habitat that meets a species' thermal requirements will thus vary latitudinally, such that warm, less seasonal habitats will be more widespread than cooler, more seasonal ones, yielding a latitudinal trend in 'effective habitat area' that runs counter to the pattern expected under Rapoport's rule (Rangel & Diniz-Filho, 2005; Hawkins & Diniz-Filho, 2006; Colwell & Rangel, 2009). Nonetheless, it remains unclear whether the greater latitudinal extent of habitats with a narrow annual temperature variation is sufficient to reverse the relationship between range size and latitude from a positive (postulated by Rapoport's rule) to a negative correlation.

Here, we use a simple model in which species range expansion is determined by annual temperature minima and maxima to quantitatively predict the relationship between latitude and range size. This model effectively translates two assumptions that underlie the process-based explanation for Rapoport's rule into a quantitative prediction for range-size gradients. However, in contrast to the prediction of the climate-variability hypothesis that implicitly assumes a linear relation between temperature and latitude, our temperature-limited model allows for a nonlinear relationship between temperature and latitude in each

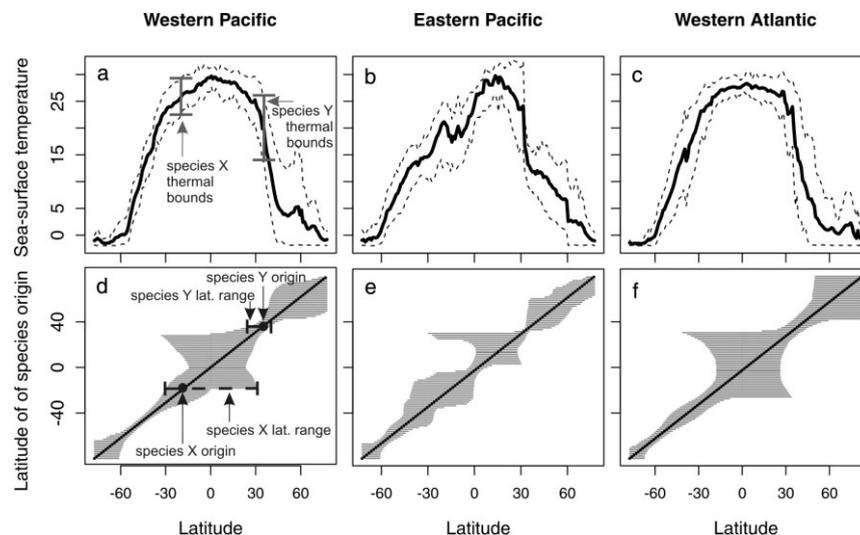


Figure 1 (a)–(c) Annual daily means (solid lines) and annual daily minima and maxima (dashed lines) in sea-surface temperature (SST) exhibit little spatial variation at low latitudes in the western Pacific and western Atlantic. The outcome of the model where ranges are limited by temperature minima and maxima is shown in (d)–(f), with many broad-ranging species in the tropics. Species are placed along a latitudinal transect at 0.1° intervals, starting on the black diagonal line. Species then expand their ranges along the x-axis (grey lines) according to the median temperature-limited scenario. For example, species X has narrow thermal bounds (set by the seasonality at its starting latitude, as shown in (a)), but owing to the distribution of SSTs in the western Pacific its range grows to encompass 45° of latitude (dashed horizontal line). Species Y originated in a location with a high seasonality that imparts very broad thermal bounds (as shown in (a)) but can only expand to a latitudinal range of 20° .

hemisphere. We focus solely on mechanisms associated with range expansion, because virtually all discussions of latitudinal trends in range size, starting with Stevens (1989), emphasize this aspect rather than speciation or local interactions, both of which might also influence range-size patterns (Colwell & Rangel, 2010; Wisz *et al.*, 2013). We also use a null model where geographic range limits are determined purely by geometric and sampling constraints and are not limited by thermal gradients (McClain *et al.*, 2007; Colwell, 2008).

We focus on annual minima and maxima of daily sea-surface temperatures (SSTs) as our climate proxies because Stevens (1989) and others explicitly proposed temperature minima and maxima as the major climatic variables determining gradients in latitudinal range size. Temperature is a key factor in determining latitudinal range size and range limits in marine invertebrates (e.g. Compton *et al.*, 2007; Pörtner *et al.*, 2007; Beaugrand *et al.*, 2013), although many other factors can also play a role (Lester *et al.*, 2007; Šizling *et al.*, 2009; Keith *et al.*, 2013). We find that the temperature-limited model predicts that the relationship between latitude and latitudinal range size is reversed relative to Rapoport's rule under realistic climatic gradients in marine systems, and the empirical distribution patterns of living shallow-marine (< 200 m) bivalves match this prediction.

MATERIALS AND METHODS

Data sets and the spatial scale of analyses

We use marine bivalves as a model system because the group is diverse, widespread and relatively well-sampled, and their diversity patterns mimic those of other groups (Jablonski *et al.*, 2013). At the time of these analyses (downloaded on 19 March 2014), our database of extant marine bivalves along these margins contained 4760 species and 40,820 shelf-depth (< 200 m) occurrences. The median latitudinal resolution of occurrences in these data is 1.2°. We perform separate analyses along the three best-sampled ocean margins – the western Pacific, eastern Pacific and western Atlantic (Fig. A2); these ocean margins share few species ($\leq 16\%$), nearly all at high latitudes. The northern and southern range limits of each species were taken as the occurrences with minimum and maximum latitude, and species were then assigned to each 5° latitudinal band according to their occurrences along each margin. The datasets are available from Data Dryad at dx.doi.org/10.5061/dryad.6n15h.

Latitudinal range size and range limits

Geographic range size as used here is the latitudinal distance between the northern and southern range limits (converted to km). We did not evaluate the longitudinal component of ranges because the tropics have a wider longitudinal extent than high latitudes and longitudinal variation in temperature along the three margins is minor relative to their major latitudinal gradients. Latitudinal range size at the scale of 5° bands is calculated separately along each margin as the median of all

latitudinal ranges that occur in that band (this is similar to Stevens' method based on means). We estimated the slope of the relationship between latitude and log-transformed median latitudinal range size per 5° band separately for each hemisphere and ocean margin. Although the per-band estimates of latitudinal range size are not mutually independent in Stevens' method, we (1) quantify the slope estimates by using generalized-least square models that account for spatial autocorrelation among the per-band estimates of range size, and (2) compare empirical slope estimates with slopes predicted by the temperature-limited model and the null-model (see below). We estimated the slope of the relationship between latitude and log-transformed median latitudinal range size per 5° band separately for each hemisphere and margin. We estimated the Akaike information criterion (AIC) for three types of the correlation structure (exponential, Gaussian and spherical) from the relationship between semi-variance and distance among latitudinal bands (Beguiria & Pueyo, 2009), and fitted the models with the correlation structure having the lowest AIC value (Table S1 & Fig. A3 in Appendix S1).

We measured the clustering of poleward range limits in 5° latitudinal bands by quantifying the proportion of species with poleward range limits in a given latitudinal band relative to the total number of species present in the band (Connolly *et al.*, 2003; McInnes *et al.*, 2010). Latitudinal changes in the steepness of the gradients in mean temperature were quantified by computing absolute differences in mean SST between adjacent 5° latitudinal bands (such changes correlate strongly with changes in the steepness based on minimum and maximum SSTs), proceeding from low to high latitudes for poleward limits (e.g. the first change corresponds to the difference between the 0–5° band and the 5–10° band). We used generalized least squares to evaluate relations between logit-transformed proportions of range limits and absolute change in mean SST between adjacent bands (Table S1 & Fig. A4 in Appendix S1).

Macroecological thermal range

The macroecological thermal range of a species is taken as the interquartile range (IQR) of the annual mean daily SST (the daily mean SST averaged over a full year) encompassed by the full geographic range of that species at a spatial resolution of 1° latitude. Macroecological thermal range limits do not necessarily correspond to critical or lethal limits of individual organisms, but instead are derived from coarse-scale (spatially and temporally averaged) occurrence and environmental data (e.g. Verbruggen *et al.*, 2009; Gouveia *et al.*, 2014). The macroecological thermal range size for each 5° latitudinal band is calculated as the median thermal range for all species that occur in that band. SSTs were obtained at a spatial resolution of 9 km from the Moderate Resolution Imaging Spectroradiometer (MODIS) and scaled to 1° resolution. The macroecological thermal ranges of species measured at 50 and 100 m isobaths significantly correlate with their thermal ranges as estimated from SSTs (Fig. A5 in Appendix S1).

Temperature-limited model for range sizes

With this model, we examine the effects of realistic thermal gradients on distribution patterns generated purely by range expansion, and explore the predictive power of such an approach, assuming that range expansion occurs at shorter temporal scales than speciation dynamics. In contrast to the null model described in the next subsection, no information from the empirical distribution enters into the range-size gradients generated by this model.

Present-day marine ectotherm species show a consistent poleward decrease in both the minima and maxima of their thermal tolerances, and the breadth of their thermal tolerances increases in environments with higher temporal climatic variability (Sunday *et al.*, 2011). We incorporate these observations into our model through two assumptions: (1) that macroecological thermal tolerance minima and maxima are positively related to the minima and maxima of the SSTs at the latitude of their *origination*; and (2) species can expand their geographic ranges up to the latitudes with minimum and maximum SSTs that correspond to their macroecological thermal tolerance minima and maxima (and, as we mentioned above, these tolerances need not correspond to critical or lethal thermal limits). The first assumption was postulated by Janzen (1967) and Stevens (1989); i.e. species originating at latitudes with small annual temperature ranges will only be able to inhabit a narrower range of temperatures than species originating at latitudes with large annual temperature ranges, presumably because these tolerances were inherited from an ancestor that was well adapted to the range of temperatures seen at that latitude. The second assumption holds that range limits are determined by thermal gradients, and this postulate is strongly supported by macroecological and biogeographic analyses of marine ectotherms, which often show links between occupancy, range limits and temperature (Belanger *et al.*, 2012; Buckley *et al.*, 2012).

The minimum and maximum SSTs at each latitude in the model correspond to 5th and 95th quantiles of daily SST (Figs A6 & A7 in Appendix S1), and the difference corresponds to the annual temperature range. The model has two steps. First, individual species were uniformly placed at 0.1° intervals along a latitudinal gradient from the northern shelves of Antarctica (77.7° S) to the northern shelves of the Arctic Ocean (83.5° N), conceptually mimicking new origination events (i.e. 1677 species in total ordered along 167.7 latitudinal degrees; step size does not qualitatively influence the output). Then, each species was allowed to expand its range to adjacent latitudinal bins until it reached SSTs outside its thermal tolerances (defined by the minimum and maximum SSTs at the latitude of its origination). Because little is known of the evolutionary basis of geographic-range expansion, we explore three scenarios that specify the ability of species to expand their ranges into novel temperature habitats (Fig. A8 in Appendix S1).

In the first scenario ('stringent' temperature limitation), species only occur at latitudes where the temperature is never colder than the minimum temperature and never warmer than the maximum temperature at the latitude of their origination.

In the second scenario ('median' temperature limitation), species can expand to latitudes where the temperature is within the minimum and maximum temperature at the latitude of their placement for at least 50% of the year. Thus, species expand their ranges until they reach a median annual temperature colder than the minimum temperature or warmer than the maximum temperature at the latitude of their origination. Two dashed black lines in Fig. 1(d) represent ranges of two species that underwent such range expansions. These two species simply show that (1) species originating in warmer, more constant environments can sometimes achieve broader latitudinal ranges than those originating in variable environments; and (2) the final range midpoint of a species need not correspond to its initial point of origination.

In the third scenario ('relaxed' temperature limitation), species expand to latitudes where the minimum and maximum temperatures fall within the temperature bounds at its latitude of origination for at least 1 month. Although the extreme scenarios may be unrealistic, they represent useful and non-arbitrary end-members likely to bracket the behaviour of most species. We report the results for the second, median temperature-limited scenario because the alternatives resulted in qualitatively similar predictions (Figs A9 & A10 in Appendix S1).

We do not allow discontinuous species ranges in these models. Thus, mid-latitude species placed into the Southern Hemisphere cannot expand their ranges to northern mid latitudes if intervening tropical temperatures are outside their thermal bounds. High-latitude species can theoretically migrate between the Northern and Southern Hemispheres by tracking deeper, and thus colder, habitats at low latitudes. Although such isothermal submergence does occur, the few anti-tropical distributions seen in molluscs appear to be related mainly to past oceanographic events followed by tropical extinction rather than to simple isotherm tracking (Lindberg, 1991). Equatorial submergence affects equatorward rather than poleward range limits (isotherms surface in the poleward direction), and when measuring range limits, we thus focus on poleward range limits. The source code is available in Appendix S2 and at <http://datadryad.org/handle/10255/dryad.68987>.

Null model for range sizes

Geometric and sampling constraints can generate positive or negative relationships between latitudinal range size and latitude, even in the absence of climatic effects (Pineda & Caswell, 1998; Jetz & Rahbek, 2001; Arita *et al.*, 2005; Weiser *et al.*, 2007). Therefore, we compared the empirical relationship between range size and latitude with that expected under a null model where range limits are not determined by climatic gradients. The model also allows us to predict the shape of the relationship between latitudinal and thermal range sizes in the absence of mechanistic links between thermal range and latitudinal range size (Pither & Aarssen, 2005). We use a null model with a spatially explicit random and independent placement of two-dimensional geographic ranges (Taylor & Gaines, 1999) on an equal-area global map that is then folded into a sphere.

Null species ranges were constructed as follows.

1. Range midpoints were randomly placed on a shelf along each margin (Fig. A11 in Appendix S1).
2. Two-dimensional geographic ranges (approximated by a rectangle defined by latitudes and longitudes) were randomly sampled from the frequency distribution of empirical latitudinal ranges along each margin (i.e. the range-shuffling algorithm in Connolly, 2005) and centred on the midpoints. Each empirical latitudinal range has a corresponding longitudinal range that sets the longitudinal dimension of the rectangle.
3. If the northern or southern edge of a given range rectangle fell completely within a continent, the position was discarded and the range midpoint was repositioned, thus conserving the margin-level empirical distribution of latitudinal range sizes (Connolly *et al.*, 2003).
4. Species were sampled in those 1° cells that are present in the empirical database.
5. The latitudinal and macroecological thermal ranges were computed for each species. We repeated this procedure in 1000 runs for each margin, drawing range sizes only from the species pool of a given ocean margin (e.g. species endemic to the eastern Pacific were not used in the simulation of the western Atlantic). The source code is available in Appendix S3 and at <http://datadryad.org/handle/10255/dryad.68917>.

In order to match the spatial resolution of empirical data, the latitudinal and thermal ranges of species were scaled up to 5° latitudinal bands in both models. We focus on aggregated species attributes that allow comparison of predictions of two models with empirical patterns: species were binned (1) into 750-km latitudinal range-size classes in analyses of the interspecific relation between latitudinal and thermal range size, and (2) into 5° latitudinal bands in analyses of gradients in range size and range limits. We did not correct for phylogenetic relatedness owing to a lack of species-level phylogeny, but the amount of variance in latitudinal range size of species explained by higher taxonomic levels is very small (18% in the western Pacific, 7% in the eastern Pacific and 5% in the western Atlantic) in a nested analysis of variance (McGill, 2008).

RESULTS

Relationship between species latitudinal and macroecological thermal range

The temperature-limited model predicts that species macroecological thermal ranges should initially increase with increasing latitudinal range along all three margins, but drop to small values (*c.* 2–3 °C) at latitudinal range sizes > 4500 km in the western Pacific and western Atlantic (Fig. 2a–c). This drop generates a marked non-monotonic relationship between latitudinal and thermal range sizes. Species attaining latitudinal ranges of 4500–6000 km thus have much smaller thermal ranges (by *c.* 2–3 °C) than species with latitudinal ranges of 2000–3000 km, and latitudinal range size explains a small amount of variance in median thermal range size along the western margins ($R^2 = 0.08$ – 0.4 ; Fig. 3a). In contrast, the null model pre-

dicts that median latitudinal range size explains a large amount of variance in median thermal range size ($R^2 > 0.90$) and does not predict the non-monotonic relationship at all (Fig. 3a).

As predicted by the temperature-limited model, the empirical bivalve data along the western margins of ocean basins show that geographically broad-ranging species (> 5000 km) tend to have smaller thermal ranges than intermediate-range species (> 3000 and < 5000 km). The amount of variance in median thermal range size explained by median latitudinal range size is rather small and remains within the confidence envelopes of the temperature-limited model ($R^2 = 0.31$ – 0.47 ; Fig. 3a). Therefore, species with broader latitudinal ranges tend to occupy widespread, relatively constant temperatures, rather than being generalists that occupy a broad temperature range. Although median thermal ranges gradually increase with latitudinal range size in the null model (white circles in Fig. 2d–f), the empirical median thermal ranges are significantly smaller than predicted by the null model in the western Pacific and western Atlantic, especially at larger latitudinal ranges (black circles and grey boxplots in Fig. 2d–f). In the eastern Pacific, deviation from the thermal range expected under the null model is smaller at larger latitudinal ranges, and the amount of variance in median thermal range size explained by median latitudinal range size in the temperature-limited model ($R^2 = 0.90$) and observed in empirical data ($R^2 = 0.79$) is higher than along the western margins.

Geographic variation in latitudinal range

The temperature-limited model predicts that latitudinal ranges will be significantly greater at low latitudes than at high latitudes in the western margins (5000–6000 vs. 1000–3000 km, respectively; light grey squares in Fig. 4a–c), again owing to the very extensive warm-water areas in these regions and narrower latitudinal extent of a given SST in mid latitudes (Table S2 in Appendix S1). For the eastern Pacific, the temperature-limited model shows smaller latitudinal ranges in the tropics (< 3000 km) and maximum range sizes at mid latitudes in the Southern Hemisphere, coinciding with a long stretch of cool upwelling waters. The model predictions change with the location and size of the domain under study. When the southern boundary of the domain is set by land barriers limiting marine organisms or by ocean barriers limiting terrestrial organisms at 25° N (i.e., excludes the tropics), median latitudinal range size increases with latitude in accord with Rapoport's rule because the relation between latitude and temperature becomes linear there (Fig. A12 in Appendix S1).

The empirical patterns also show a tropical maximum in latitudinal range size (i.e. a reverse Rapoport's rule), and this maximum is significantly greater than predicted by the null model in the western Pacific and western Atlantic (Fig. 4d–f). The largest empirical per-band latitudinal ranges are in the western Atlantic (median *c.* 6000 km) and the western Pacific (median *c.* 5000 km), while the eastern Pacific shows the smallest tropical ranges (median *c.* 4000 km) and the weakest differential between tropical and extratropical range sizes. Empirical slope estimates are consistently negative and generally within

the range of slopes predicted by the temperature-limited models, whereas null-model slopes are close to zero (Fig. 3b).

Geographic variation in thermal range

The temperature-limited model predicts that the median per-band thermal range should be narrower at low latitudes ($c. 2\text{ }^{\circ}\text{C}$) than at mid latitudes ($> 5\text{ }^{\circ}\text{C}$) in the western Pacific and western Atlantic, and should be relatively uniform in size in the eastern Pacific (dark grey triangles in Fig. 4a–c). Empirical patterns also show mid-latitude maxima in thermal range ($> 5\text{ }^{\circ}\text{C}$) at northern temperate latitudes (Fig. 4g–i). Therefore, species occurring at low and high latitudes do, in fact, tend to occupy a narrower range of temperatures than do species in the temperate zones (especially in the Northern Hemisphere), and this bimodal pattern is not predicted by the null model.

Geographic variation in range limits

Simply because latitudinal ranges tend to be narrower at high latitudes, their range limits should tend to coincide more frequently. The temperature-limited model thus predicts an increase in the clustering of poleward range limits with latitude

(Fig. 5a–c), and a positive relation between the steepness of the thermal gradient and the clustering of poleward range limits (Table S3 in Appendix S1). Empirical slope estimates are consistently positive and generally within the range of slopes predicted by the temperature-limited models, whereas null-model slopes are close to zero (Fig. 3c).

The temperature-limited model also predicts that the decrease in median per-band latitudinal range size towards high latitudes in the western ocean margins should occur abruptly at the tropical/temperate transition owing to the strong decrease in annual minimum and maximum SST. This abruptness causes a stepwise rather than a gradual increase in the clustering of poleward range limits, with low latitudes containing few poleward limits per latitudinal band (Fig. 5a–c).

In accordance with the temperature-limited models, the clustering of poleward range limits in the empirical data increases abruptly at the tropical/temperate boundary, coinciding with strong changes in annual minimum and maximum SST. Poleward range limits are weakly clustered near the equator and most strongly clustered at $25\text{--}30^{\circ}\text{S}$ and $30\text{--}40^{\circ}\text{N}$ in the western Pacific and western Atlantic (Fig. 5d–f). In the eastern Pacific, where low-latitude thermal gradients are steeper, southern poleward limits cluster at 5°S , i.e. at the southern border of tropical waters along

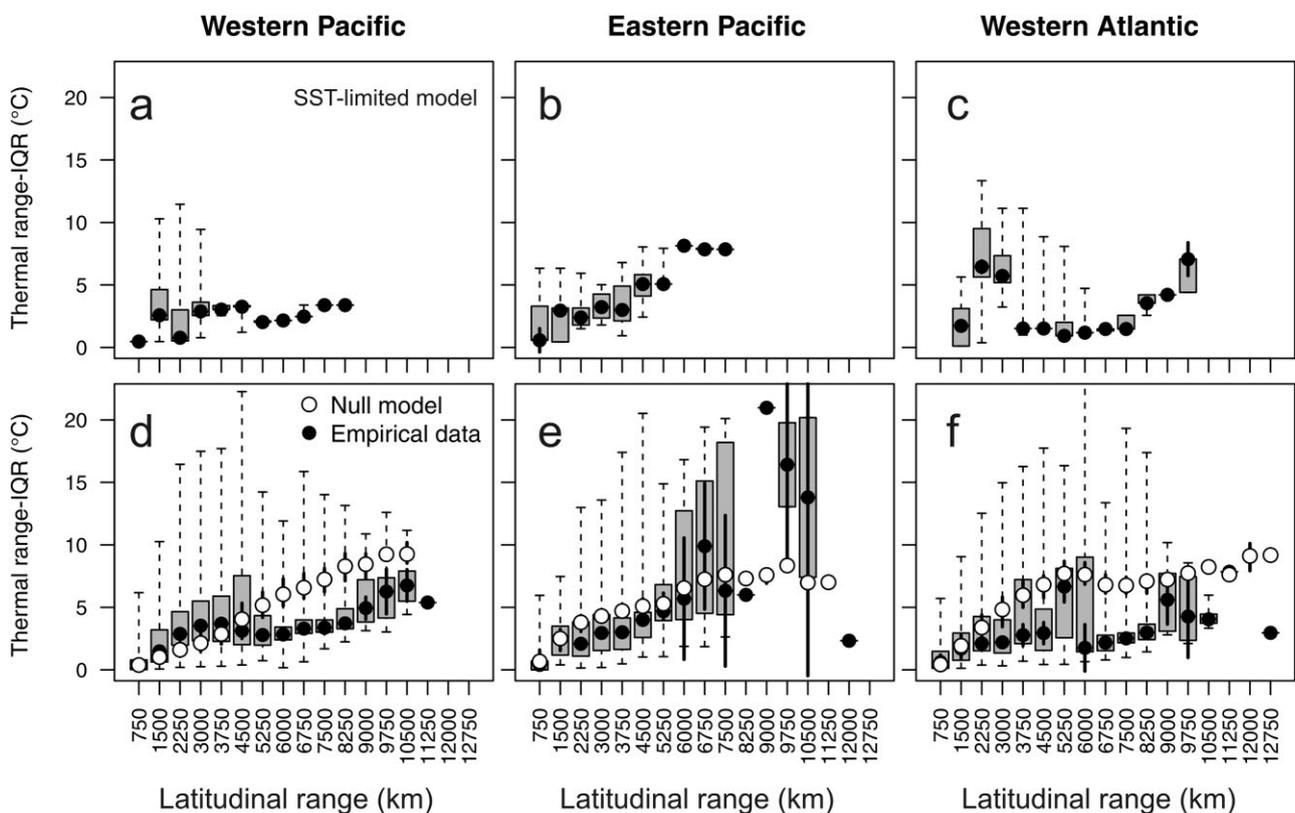


Figure 2 (a)–(c) Temperature-limited models of range expansion predict that species with broad latitudinal ranges have narrower thermal ranges than species with intermediate range sizes along the western margins. (d)–(f) Such a non-monotonic relationship between latitudinal range and thermal range is also expressed by empirical data (black circles). The empirical median thermal ranges of species with broad latitudinal ranges (black circles) are significantly smaller than predicted by the null model (white circles) in the western Pacific and western Atlantic. Boxplots show the 25th and 75th percentiles, whiskers denote the total range and black circles with error bars within boxplots represent medians of modelled and empirical thermal ranges with 95% confidence intervals.

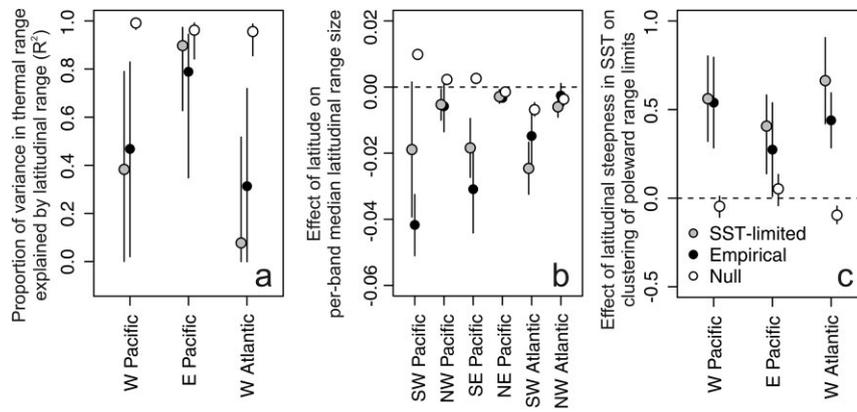


Figure 3 Quantitative comparison of predictions of temperature-limited and null models with empirical distribution patterns. (a) A large amount of variance (R^2) in median species thermal range is expected to be explained by median species latitudinal range under the null model (white circles). The temperature-limited model (grey circles) predicts significant decoupling between thermal and latitudinal ranges, and empirical values of R^2 (black circles) are also significantly smaller than expected under the null model along western margins. (b) The generalized least-squares slope of the relationship between log-transformed per-band median latitudinal range size and latitude tends to be significantly more negative than predicted by the null model, and is similar to the predictions of the temperature-limited model. (c) The generalized least-squares slope of the relationship between the clustering of poleward range limits and absolute latitudinal change in annual mean daily SST is closer to the predictions of the temperature-limited model, and is significantly more positive than predicted by the null model in the western Pacific and western Atlantic.

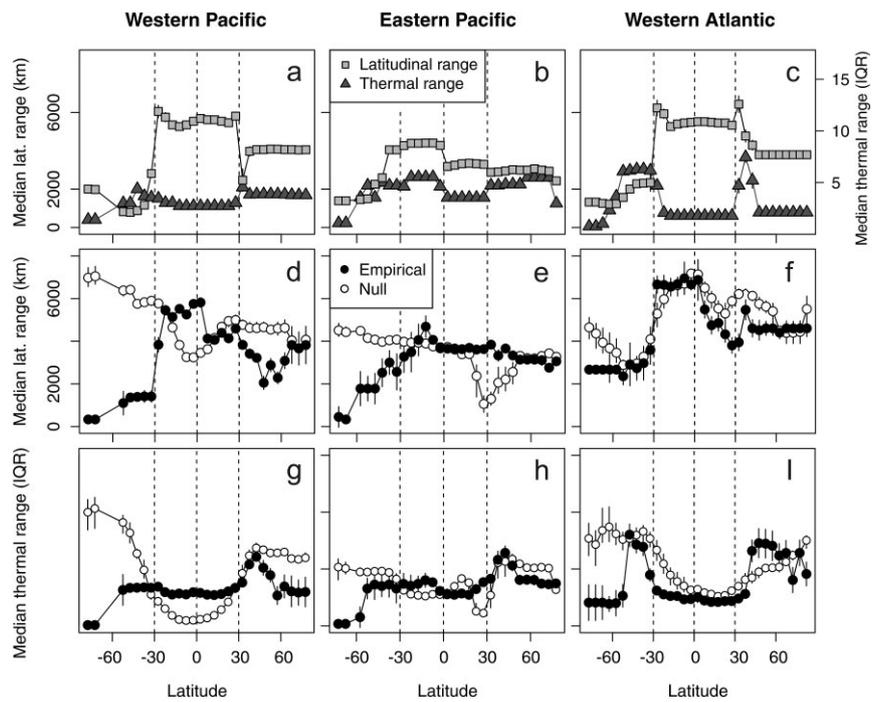


Figure 4 Modelled and empirical gradients in median latitudinal and thermal range size per 5° latitudinal band, measured as the median of all ranges that occur in that band. (a)–(c) Temperature-limited models predict that median latitudinal ranges (squares) are large and median thermal ranges remain low at low latitudes (triangles) in the western Pacific and western Atlantic. (d)–(i) Empirical median latitudinal range is largest at low latitudes (black), in contrast to the predictions of the null model (white). Low-latitude and southern polar bands are dominated by species with small thermal ranges, and northern temperate latitudes are dominated by species with the largest thermal ranges.

this coast, and northern poleward limits cluster at 30° N, as expected from steep declines in temperature at those latitudes.

DISCUSSION

Effects of the availability of thermal habitat on range-size variation

As predicted by the temperature-limited model of range expansion, the greater latitudinal extent of warm-temperature

environments clearly reverses the positive relation between latitude and latitudinal range size predicted by Rapoport's rule in the western Pacific and western Atlantic. Although the temperature-limited and null models differ in their dimensionality, the major differences in their predictions are unlikely to stem from the absence of a longitudinal dimension in the temperature-limited model, because the longitudinal variation in thermal gradients remains small within ocean margins. Support for our one-dimensional temperature-limited model over the two-dimensional null model should

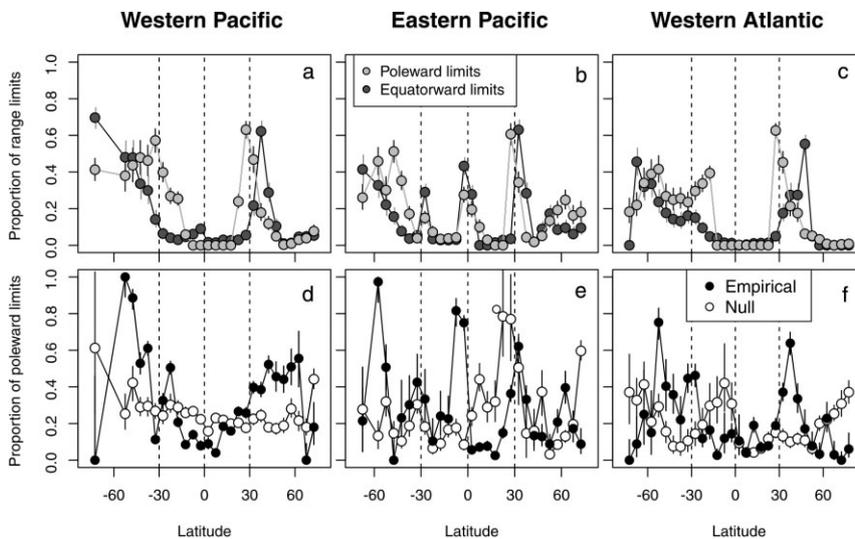


Figure 5 (a–c) Temperature-limited models predict a marked increase in the clustering of poleward range limits at mid latitudes, and minima in their clustering around the equator. (d)–(f) In the western Pacific and western Atlantic, empirical poleward limits (black circles) form minima at low latitudes and cluster at mid latitudes, in contrast to a less regular trends in the clustering of limits in the null model (white circles).

be conservative because the higher dimensionality of the null model should improve its potential to fit the empirical data.

Along the western margins, species inhabiting environments with a narrow annual temperature variation at low latitudes tend to have broader latitudinal ranges, on average, than species inhabiting environments with a broad annual temperature variation at higher latitudes. This negative relation between latitude and latitudinal range size evidently occurs because: (1) warm, low-latitude mean temperatures are the most widespread by far (the modal SST is between 27 and 28 °C, Fig. A13), and (2) temperature maxima at mid latitudes are colder than the mean temperature at low latitudes, so that few mid-latitude species with broad thermal ranges extend into the spatially widespread warm-water habitats at low latitudes or cross the equator into the opposite mid latitudes. Range expansion along gradients that vary in the steepness of their temperature trends may also explain reverse Rapoport's patterns in other marine groups, such as reef fishes and corals (Jones *et al.*, 2002; Connolly *et al.*, 2003). These effects may be a general factor shaping latitudinal gradients in range size, because at the global scale, shallow thermal gradients within the tropics and steep thermal gradients at higher latitudes also characterize some terrestrial environments. However, variation in annual precipitation can further modify range expansion in those settings (Vázquez & Stevens, 2004).

Of course, if annual temperature minima and maxima were always a simple linear function of latitude, then the effect of habitat availability on range-size gradients would vanish because all temperatures would be equally widespread. Although the relation between latitude and temperature becomes more linear in the eastern Pacific, annual temperature variation remains large in the tropics and so latitudinal range size does not increase towards mid latitudes.

Our finding of the reverse Rapoport's pattern does not contradict previous results showing that range size increases with latitude outside the tropics. Most studies finding a positive

relation have focused on northern extratropical latitudes constrained by continental boundaries (Ruggiero & Werenkraut, 2007). If we restrict predictions of temperature-limited models to extratropical regions, we also find that the per-band latitudinal range correlates positively with latitude (Fig. A12 in Appendix S1).

Effects of thermal gradients on poleward range limits

Other factors related to range expansion may also generate an inverse relationship between latitudinal range size and latitude. For example, a decrease in dispersal limitation towards the tropics related to the frequency of species with highly dispersing planktotrophic larvae (Jablonski & Lutz, 1983; Marshall *et al.*, 2012) or the greater longitudinal extent of the tropics (increasing the probability of encountering local conditions favouring a latitudinal range extension) might also generate larger latitudinal ranges at low latitudes. However, the marked clustering of poleward range limits associated with steep mid-latitude thermal gradients and the lack of clustering of poleward limits associated with weak tropical thermal gradients point to the importance of the temperature limitation of range expansion, and thus of latitudinal variation in range size. The role of temperature limitation in setting range limits is also supported by the contrast between the greater maximum range size at low latitudes along the western margins versus the eastern Pacific. The earth's rotation drives warm tropical waters toward the poles along the western margins and polar water toward the equator along the eastern Pacific, where the tropics are further truncated by cold-water upwelling at about 5° S. Therefore, tropical zones with SSTs of 25–27 °C are *c.* 5000–6000 km broad along the western margins but only *c.* 2500–4000 km broad along the eastern margins.

Gaines *et al.* (2009) argued that differences in the strength of clustering for poleward and equatorward limits rule out a significant role for interregional climatic contrasts in setting range

limits. However, the difference in the magnitude of the clustering between poleward and equatorward range limits at the same latitude comes from the temperature-limited models (top row in Fig. 5), because species originating at mid latitudes are expected to have broad macroecological thermal ranges. Such species are expected to be weakly affected by an equatorward steepening of temperature gradients. In contrast, range limits of species with narrow thermal ranges originating at low latitudes are expected to be more concentrated when encountering an equally steep change in temperature in the poleward direction.

Decoupling between latitudinal and thermal ranges

Contrary to most biogeographic models, both the significantly narrower thermal ranges observed in bivalve species with broad latitudinal ranges (> 3000 km) and the broader latitudinal ranges observed in species with narrower thermal ranges imply that many species are widespread not because they have broad thermal tolerances but because they track widespread temperatures. Greater range expansion at low than at mid latitudes thus significantly reduces the correlation between thermal and latitudinal range size along the western margins of ocean basins, as predicted by temperature-limited models. However, although latitudinal ranges of bivalves tend to be larger at low latitudes (and geographic ranges measured as great-circle distance are also larger, see Fig. A14 in Appendix S1) – in direct contradiction to Rapoport's rule – our empirical analyses also show that bivalve species inhabiting seasonally more variable mid-latitude environments do indeed have broader thermal ranges than species inhabiting less seasonal tropical environments, ironically supporting the primary mechanism invoked to explain Rapoport's rule from its inception (Stevens, 1989; see also Addo-Bedaiko *et al.*, 2000). As temperature-limited models show, the small latitudinal extent of habitats with approximately equal temperatures at mid latitudes prevents these broad thermal ranges from translating into very broad latitudinal ranges. Broad thermal tolerances in habitats with strong temporal variability may still contribute to the formation of broad geographic ranges, but this effect is not sufficient to override the nonlinear thermal gradients on the latitudinal gradient in geographic range size. The decoupling between latitudinal and thermal ranges observed along western margins can explain why habitat specialization contributes weakly to extinction risk at geological time-scales (Harnik *et al.*, 2012), because by providing greater scope for range expansion, larger, nearly isothermal habitat areas at low latitudes may provide more opportunities for metapopulation connectivity and rescue effects.

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Additional references can be found at the end of Appendix S1 at {URL}.

SUPPORTING INFORMATION

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

Appendix S1 Supplementary figures and tables.

Appendix S2 Temperature-limited range-expansion model (R language source code).

Appendix S3 Range-shuffling model (R language source code).

BIOSKETCH

Adam Tomašových is interested in processes that generate macroecological and biogeographic patterns of marine ectotherms at multiple spatial and temporal scales.

A.T. and D.J. designed the study, A.T. performed analyses, S.K.B., D.J., A.Z.K. and A.T. collected data, A.T. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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