



Cenozoic latitudinal response curves: individualistic changes in the latitudinal distributions of marine bivalves and gastropods

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Abstract.—We use a Gaussian logistic regression model to characterize epoch-to-epoch and stage-to-stage changes in the latitudinal response curves of Cenozoic marine bivalve and gastropod genera along the global latitudinal gradient, and analyze these changes to understand the mode and tempo of changes in latitudinal distribution. A ubiquitous “hollow curve” pattern is apparent, wherein smaller changes in response-curve parameters are much more common than larger changes. Curves are strikingly consistent in terms of the average level of change exhibited, despite the many unique environmental and biological changes documented between each of these intervals. This implies that the pace and magnitude of changes in the latitudinal distribution of marine mollusks are not controlled, in aggregate, by time-period-specific conditions. Additionally, we find no evidence for long-term migration from tropical to extratropical latitudes. Our results instead favor a model of either equatorward migration or no general trend. This likely reflects the tendency of genera to maintain their highest concentrations in the tropics even if their ranges become extended out of the tropics over time.

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Introduction

Miocene–Pleistocene marine bivalve genera tend to occur first in the tropics, whereas last occurrences tend to cluster in the extratropics (Jablonski et al. 2006, 2013; Krug et al. 2009). One potential explanation for this finding is that latitudinal distributions preferentially move in a poleward direction over a genus’s evolutionary history. If this is correct, then a number of important questions naturally arise. First, is there a detectable overall pattern of latitudinal migration, poleward or otherwise, over the course of the entire Cenozoic? Second, is any such latitudinal migration primarily driven by the expansion of a genus’s geographic range, or do genera maintain a fairly consistent range size and instead shift the center of their distribution? Third, what is the proportion of larger to smaller changes in latitude, and can changes in latitudinal distribution be linked to specific geologic events? Fourth, are there variations in the rates of these changes; i.e., do they vary in magnitude when considered among successive stages, successive epochs, or nonadjacent epochs?

To address these questions we first characterize the distributions of marine bivalve and gastropod genera as unimodal response curves (Whittaker 1967) along the global latitudinal gradient for different Cenozoic time intervals. We parameterize these curves and calculate a latitudinal tolerance and preferred latitude parameter for each taxon in each time interval (Fig. 1). Preferred latitude represents the central position of the response curve, and latitudinal tolerance reflects the width of the curve. We apply this method to all Cenozoic marine bivalve and gastropod genera in the Paleobiology Database (PaleoDB; <http://paleobiodb.org>) and assess changes in parameter estimates between successive stages, successive epochs, and nonadjacent epochs.

We begin by following the method outlined in Holland and Zaffos (2011), where correlation coefficients are used to compare the covariation of latitudinal tolerance and preferred latitude between intervals. In addition, we compare the slope of the best-fit regression line of these scatter plots as a measure of poleward vs. equatorward drift, and latitudinal tolerance expansion vs. contraction. We

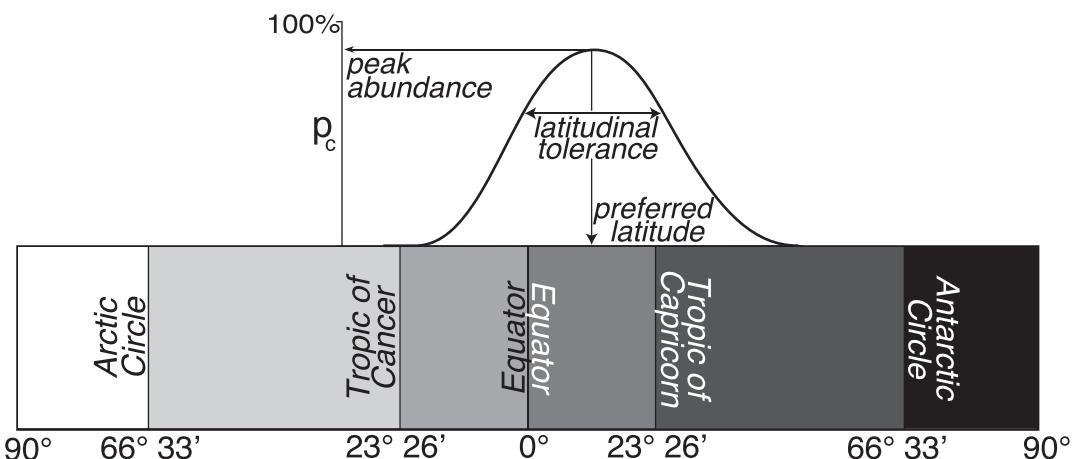


FIGURE 1. A schematic representation of a latitudinal response curve. Gradient theory (Whittaker 1967) predicts that the abundance (probability of collection, p_c) of a genus will rise and fall symmetrically along an environmental gradient. The parameter peak abundance measures the maximum probability of collection and the preferred latitude parameter measures the latitude where this maximum occurs. The latitudinal tolerance parameter reflects the width of the distribution, but is not identical to the entire range of the curve; instead, it is more analogous to a standard deviation north and south of the preferred latitude (ter Braak and Looman 1986), and can be interpreted as representing the core zone of a taxon's latitudinal distribution. Modified from Holland and Zaffos (2011).

conclude by comparing the changes in each parameter for each genus between intervals to create a distribution of larger vs. smaller changes (first differences), and we assess the extent to which these distributions fluctuate throughout the Cenozoic.

Analytical Methods

Gaussian logistic regression (GLR) is used to estimate each genus's preferred latitude, peak abundance, and latitudinal tolerance (ter Braak and Looman 1986; Coudun and Gégout 2006). GLR is a form of the generalized linear model in which the link function is the logit: $\ln[\frac{p}{(1-p)}]$, where p is the probability of collection. It differs from the more common linear logistic regression in that it fits a quadratic curve to the data rather than a straight line:

$$\ln\left[\frac{p}{(1-p)}\right] = b_0 + b_1x + b_2x^2.$$

The y -coordinate of the function's vertex represents the genus's *peak abundance* (Max), and the x -coordinate represents the *preferred latitude* (Opt), where the peak occurs. *Latitudinal tolerance* (Tol) is an approximation of the curve's width. The latitudinal tolerance and preferred latitude parameters are used in the analyses, but, because abundance is not

relevant to the themes addressed in this paper, peak abundance is calculated only to identify poorly fit response curves. The three response curve parameters are calculated using the following equations (ter Braak and Looman 1986):

$$Opt = \frac{-b_1}{2b_2}$$

$$Max = e^{(b_0 + b_1 Opt + b_2 Opt^2)}$$

$$Tol = \frac{1}{\sqrt{-2b_2}}$$

Once parameters are estimated, they are compared among intervals to examine the degree of change. This is achieved in two different ways. In the first, a scatter plot of parameter values is used, where the older of the two intervals is plotted on the x -axis, the younger on the y -axis, and the Pearson's correlation coefficient and least-squares linear regression slope are calculated. A very high correlation coefficient and a slope near unity would indicate a lack of latitudinal migration. Other combinations might suggest a change in latitudinal distribution, but, depending on the intensity and direction of the relationship between pairs of parameters for the two

intervals, the interpretation will vary. For example, a strong correlation coefficient ($>50\%$ variance explained) and a slope well above unity indicate ubiquitous migration toward the poles, whereas a weak correlation and broad scatter would indicate random migration, regardless of the calculated slope. The intercept of the regression is not considered because its meaning is ambiguous: it may shift because of an increase (or decrease) in the average size of latitudinal tolerance or preferred latitude, or because of changes in the slope without any corresponding change to the mean. In our second set of analyses, we measure the number of degrees by which a genus shifts its preferred latitude or latitudinal tolerance between two intervals. We plot the absolute value of these first differences in normalized rank order to diagnose the proportion of greater to lesser changes; these plots are analogous to rank abundance diagrams used in community ecology (see McGill et al. 2007).

We also ask whether observed changes in these parameters are smaller or larger than would be expected by chance, given the reconstructed latitudinal gradient. A bootstrapping procedure is used to address this question for each of the distributions of first differences. For each possible pair of epochs (stage-to-stage comparisons are not bootstrapped), the response curve parameters of each genus in the younger of the two epochs are reshuffled (sampled without replacement) 1000 times and the mean of the first differences recorded for each iteration. This maintains the mean, median, and mode of each epoch's distribution, but changes how the parameter values are matched between epochs. The actual observed mean of the first differences is then compared against the resampled distribution of potential means, and instances where the observed average falls in the upper or lower 5% of the resampled distribution are considered statistically significant.

Data

Global occurrences of marine bivalve and gastropod genera come from the PaleoDB, and are organized by Cenozoic epoch and stage (downloaded 9 October 2013). The raw data

set contains 2958 unique genera, represented by a total of 124,701 occurrences. The downloaded data files are available in un-culled form at datadryad.org (see Supplementary Materials). Occurrences are binned by paleo-latitude, as determined by Scotese's paleo-coordinate rotations (scotese.com), which are provided when data are downloaded. Latitudinal binning can be conducted at a variety of sizes ranging from 0.1° to 10.0° bins. Finer scaling of the bins provides more statistical power by increasing the number of samples, but bins will exhibit lower diversity as a result. Broader bins are less sensitive to this bias, but they have lower statistical power. In other words, there is a trade-off between the number of samples and the quality of samples. Here, results are presented at the intermediate scale of 1.0° bins, but the results reported here are robust within the range of 0.1° – 5.0° bins, suggesting that this trade-off is not critical (Supplementary Fig. 1).

At 1.0° binning, a total of 790 genera remain after removing small samples and rare taxa (minimum diversity of a bin = 5, minimum number of occurrences for a genus = 5), freshwater and terrestrial genera, and genera without an assigned family in the database because they are considered to be of dubious taxonomic quality. Results are robust, however, if these culling requirements are loosened to allow less diverse samples and rare genera (Supplementary Fig. 2). In addition, genera with physically impossible GLR parameter results indicative of a poor curve fit are removed: tolerances greater than 180° , preferred latitudes in excess of 90° , and probabilities of collection equal to one or zero. Poor fits are symptoms of small sample sizes (Coudun and Gégout 2006), multi-modal distributions of occurrences (Oksanen and Minchin 2002), or edge effects caused by occurrences clustered near the terminus of the latitudinal gradient (ter Braak and Looman 1986). An average of only 5% of genera per epoch are affected by this final culling step.

Model Accuracy

The validity of GLR has been questioned in the past because it assumes a spatially symmetric (Gaussian) distribution of taxon

occurrences, an assumption that is commonly violated (Austin 2002; Oksanen and Minchin 2002), and because it is sensitive to sample size (Coudun and Gégout 2006). We therefore also used canonical correspondence analysis (CCA) to estimate each genus's preferred latitude, as it does not require the assumption of a symmetric distribution and can incorporate rare species (Palmer 1993; ter Braak and Verdonschot 1995). CCA is a variant of the multivariate ordination technique, correspondence analysis, which is commonly used to estimate the central position of response curves along environmental gradients. Correspondence analysis orders samples along a gradient on the basis of their relative similarity to one another in terms of the present taxa. CCA differs in that additional exogenous information about the possible order of samples along the gradient is incorporated into the analysis beforehand, and coefficients of regression are used to find an optimal compromise solution between the exogenously defined order of samples and the order of samples based on taxonomic similarity. In this case, the paleolatitude of the samples/bins was used to constrain the possible ordering of samples in the ordination (i.e., it provides the exogenously defined sample order). Estimates of preferred latitude based on GLR and CCA were strongly correlated ($\bar{r} = 0.84$; $\bar{p} << 0.01$), demonstrating that the assumption of symmetry does not substantially distort the results from GLR for preferred latitude. The accuracy of the latitudinal tolerance parameter has similarly been questioned in the past (Coudun and Gégout 2006; Holland and Zaffos 2011). We therefore compared the total sampled latitudinal extent of each genus (its northernmost known latitude minus its southernmost known latitude in the data set) with the latitudinal tolerance parameter. The two range estimates were also highly correlated ($\bar{r} = 0.79$; $\bar{p} << 0.01$).

Results

Linear regression slopes for epoch-to-epoch comparisons of preferred latitude and latitudinal range are always less than 45° , and in many cases are nearly flat (Fig. 2). A slope below unity for preferred latitude indicates a

tendency for equatorward migration. A slope below unity for latitudinal tolerance indicates a convergence toward intermediate range sizes; in other words, smaller ranges are expanding and larger ranges are contracting. Because the majority of regression slopes are below unity and statistically significant at $\alpha = 0.05$ these results could be interpreted as strong evidence for both ubiquitous equatorward drift and convergence toward an average geographic range size. The correlation coefficients tend to be on the weaker side (preferred latitude $\bar{r} = 0.30$; tolerance $\bar{r} = 0.28$), however, generally explaining less than 10% of the variance. Therefore, we suggest that looking directly at the first differences of preferred latitude and latitudinal tolerance values may be more illuminating.

If the first differences of adjacent epochs are plotted in normalized rank order the distributions universally follow a hollow curve (see McGill et al. 2007), wherein smaller changes are far more common than larger changes. For example, as a general rule, approximately 80% of genera in an epoch change less than 25° in preferred latitude and latitudinal tolerance in the subsequent epoch (Fig. 3). Preferred latitude curves exhibit higher first differences, on average, than latitudinal tolerance curves (two-tailed *t*-test $p = 0.02$), but only by a small amount (difference of means, 1.6°). That said, there is a substantial distinction between the three Paleogene comparisons (Paleocene-Eocene, Eocene-Oligocene, and Oligocene-Miocene) and the two post-Paleogene comparisons (Miocene-Pliocene, Pliocene-Pleistocene). Paleogene comparisons show on average more change in both preferred latitude (4.9°) and latitudinal tolerance (5.6°) than seen in post-Paleogene comparisons (two tailed *t*-tests $p << 0.01$).

Because the distribution of first differences always takes the shape of a hollow curve, wherein smaller changes dominate the distribution, it might be inferred that response curve parameters are fairly stable over geologic time. However, there are many ways to produce a hollow curve by chance, and such curves are common in ecological (multiplicative) data (McGill 2003). Therefore, we also performed a bootstrapping procedure to ask

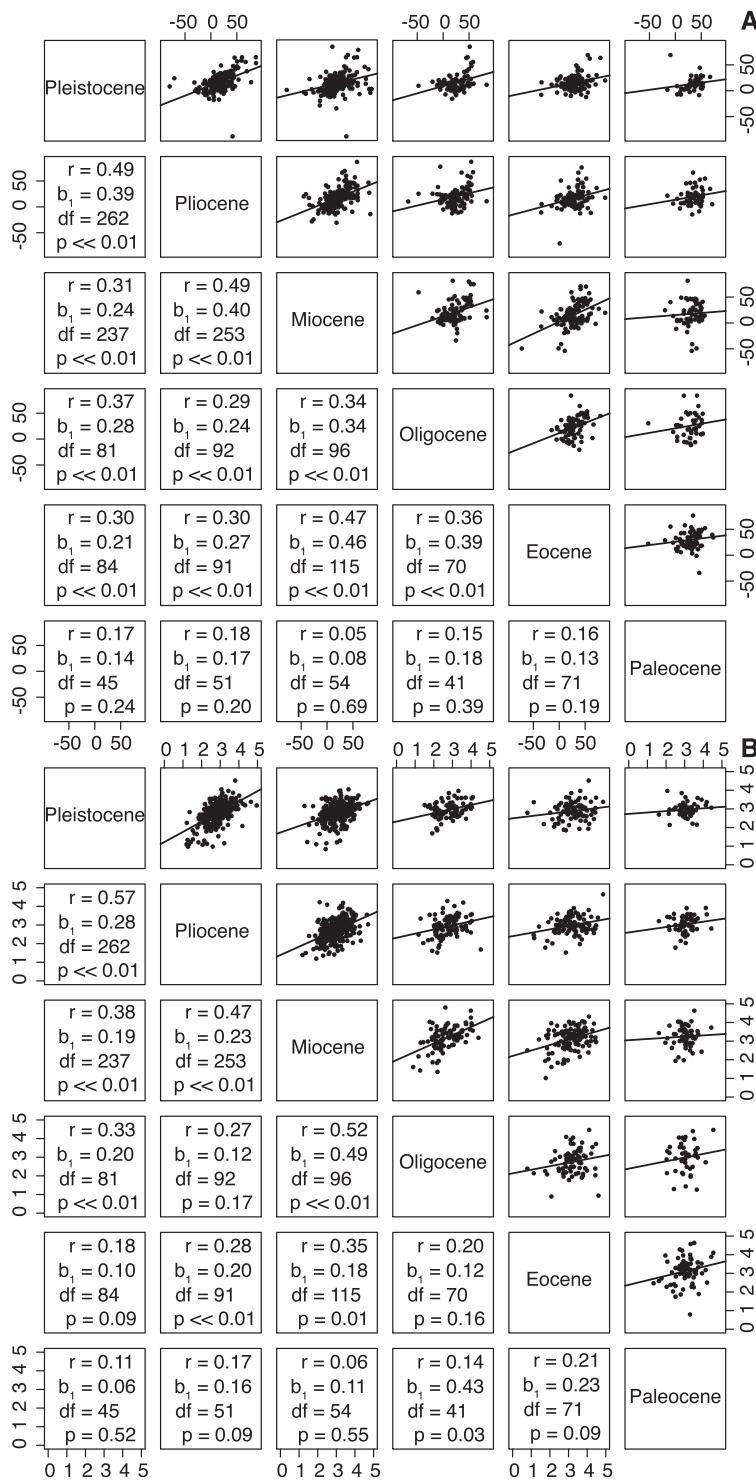


FIGURE 2. Values of preferred latitude (A) and latitudinal tolerance (B) cross-plotted for all shared taxa in each combination of Cenozoic epochs. The Pearson's r value (r), linear regression slope (b_1), degrees of freedom (df), and linear regression p -value (p) for each comparison are provided on the mirror side of each plot. The axes for preferred latitude (A) are in degrees of latitude, but the axes for latitudinal tolerance (B) are presented on a log-scale for clarity.

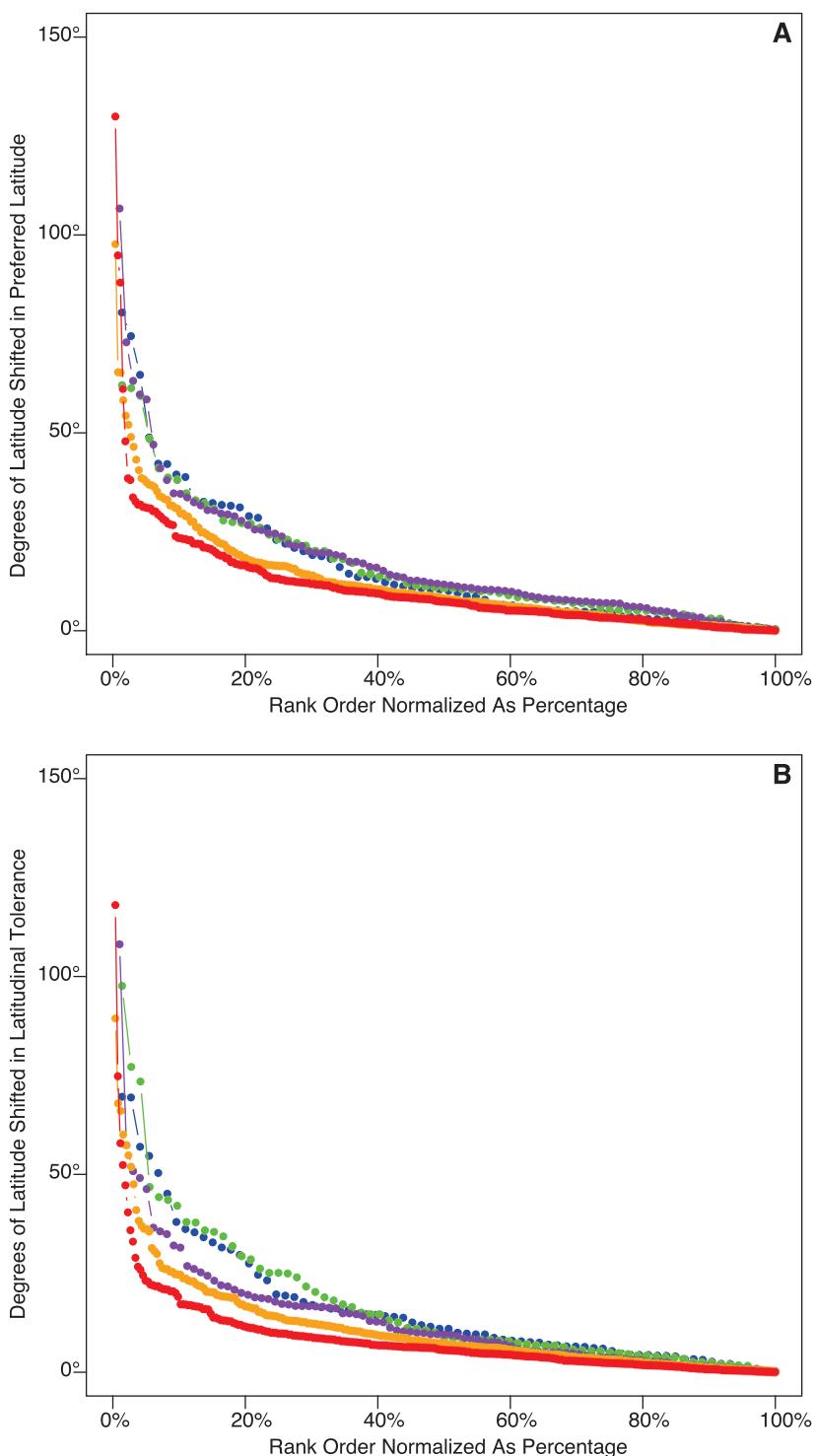


FIGURE 3. The change in preferred latitude (A) and latitudinal tolerance (B) between adjacent epochs (first differences) in normalized rank order. Each curve represents the following epoch-to-epoch comparisons: Paleocene-to-Eocene (blue), Eocene-to-Oligocene (green), Oligocene-to-Miocene (purple), Miocene-to-Pliocene (orange), and Pliocene-to-Pleistocene (red). All first differences conform to a hollow curve shape.

TABLE 1. A table of the original mean of the first differences and the average bootstrapped mean of first differences. The original mean is always lower than the average bootstrapped mean for both preferred latitude (top) and latitudinal tolerance (bottom). All intervals are statistically significant at $\alpha = 0.05$.

Interval	Original mean	Bootstrapped mean	p-value
Pliocene to Pleistocene	10.87°	17.66°	0.000
Miocene to Pliocene	12.20°	18.97°	0.000
Oligocene to Miocene	17.14°	23.33°	0.000
Eocene to Oligocene	16.06°	21.04°	0.000
Paleocene to Eocene	15.79°	19.06°	0.000
Pliocene to Pleistocene	8.40°	11.87°	0.000
Miocene to Pliocene	11.01°	14.15°	0.000
Oligocene to Miocene	13.42°	23.33°	0.000
Eocene to Oligocene	17.05°	19.57°	0.013
Paleocene to Eocene	16.14°	17.93°	0.049

whether the average first difference of any curve is higher or lower than would be expected by chance. In all cases the observed average first difference is lower than the bootstrapped average (Table 1). Collectively, these bootstrapping results and a visual examination of the curves suggest a striking level of consistency across all epoch-level comparisons.

The stage-level curves are more difficult to interpret given the much smaller sample sizes involved, and many stages are omitted from the analysis because of insufficient sample size. For example, setting a minimum of five occurrences per latitudinal bin and five occurrences per taxon, as is done in the epoch-level analysis, leaves no samples for the Selandian stage of the Paleocene and Langhian stage of the Miocene. Poorly sampled stages exert a cascading effect on the analysis because even sufficiently sampled stages must be omitted if the preceding and succeeding intervals are insufficiently sampled.

Despite these sampling difficulties, a ubiquitous pattern of hollow curves remains visible even at the stage level (Fig. 4) that is strikingly similar to the pattern observed at the epoch level, with generally 80% of genera shifting less than 25° between stages. Nevertheless, there are several differences between the stage-level and epoch-level analyses. Preferred latitude curves no longer exhibit larger first differences than latitudinal tolerance curves (two-tailed t -test $p = 0.32$). Similarly, a visual comparison of the curves suggests that there is no noticeable distinction between

Paleogene and post-Paleogene intervals, as the Zanclean–Piancenzian transition of the Pliocene strongly overlaps the Lutetian–Bartonian and Bartonian–Priabonian transitions of the Eocene, although this cannot be confirmed quantitatively because the Zanclean–Piancenzian is the only Neogene comparison available. The primary difference between the stage- and epoch-level analyses is that stages exhibit lower maximum levels of change. No stage-level transition exhibits a response-curve parameter shift greater than 84°, as compared to a maximum of 129° in the epoch-level analysis.

Considering these results in the context of the original questions, we conclude that no definitive pattern of either ubiquitous poleward or equatorward migration is apparent. Evidence, however, is especially weak for poleward drift, with no regression slope at or above unity (Fig. 2). There are instances of large shifts (tens of degrees) in both preferred latitude and latitudinal tolerance, but preferred latitude shifts are on average slightly larger than changes in tolerance at the epoch level. Taken at face value this suggests that marine genera are slightly more likely to shift the center of their distribution than widen it. On the other hand, the small size of this difference and the fact that such a difference is not visible at the stage level suggest that neither parameter is meaningfully more likely to change than the other. Smaller changes are much more common than larger changes, as evidenced by the hollow curves and the bootstrap results. The magnitude of change appears comparable across all three temporal

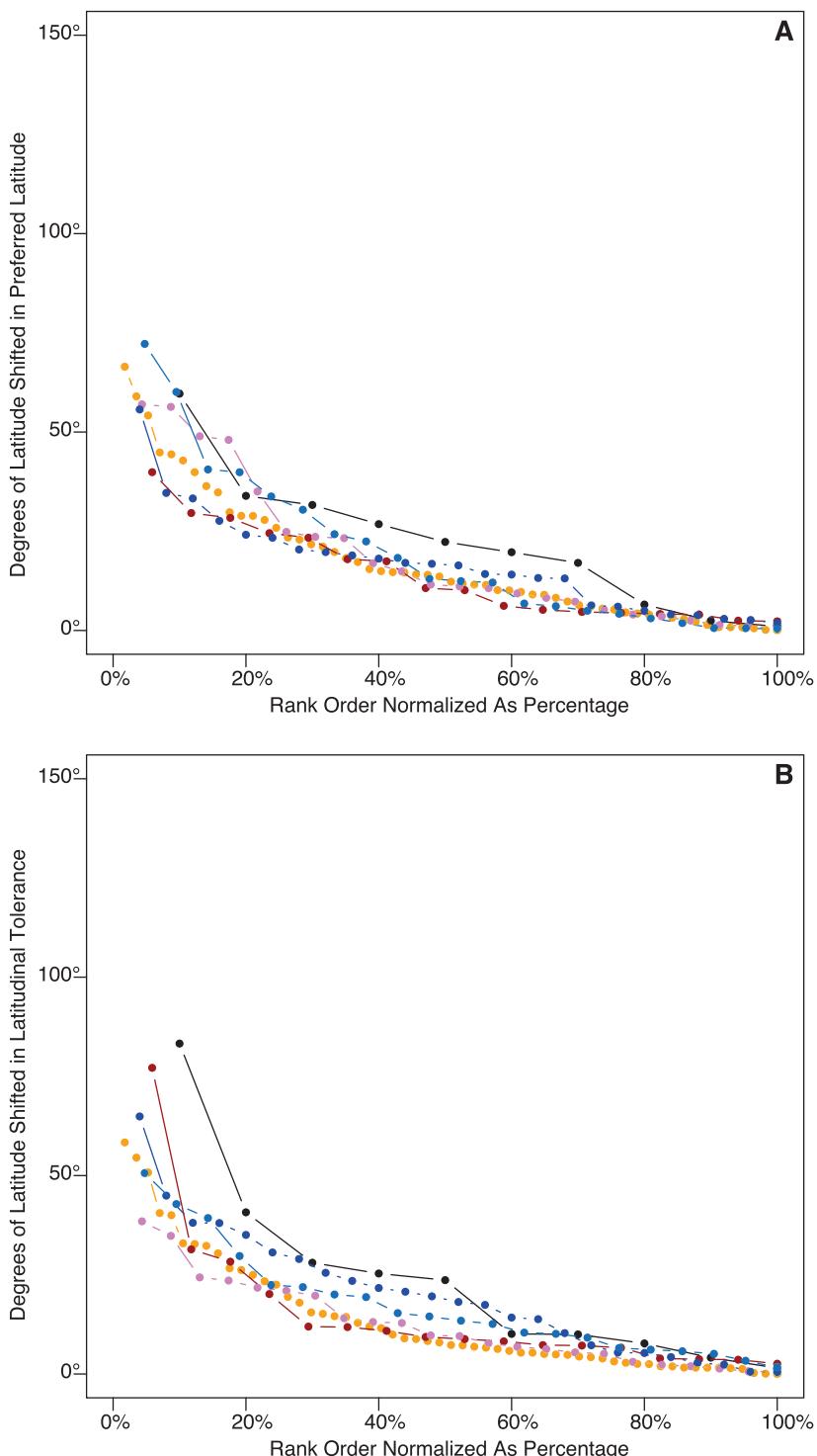


FIGURE 4. The change in preferred latitude (A) and latitudinal tolerance (B) between adjacent Cenozoic stages (first differences) in normalized rank order. Each curve represents the following stage-to-stage comparisons: Ypresian-to-Lutetian (black), Lutetian-to-Bartonian (brown), Bartonian-to-Priabonian (violet), Priabonian-to-Rupelian (dark blue), Rupelian-to-Chattian (light blue), and Zanclean-to-Piancenzian (orange).

scales (between successive stages, between successive epochs, and among nonadjacent epochs), and relatively large changes (tens of degrees) are still observed in some instances among stages.

Discussion

No Evidence for Poleward Migration.—We propose four possible explanations for the apparent dissonance between our results (Fig. 2) and other studies that have proposed a tendency for poleward migration in fossil (Jablonski et al. 2006, 2013; Krug et al. 2009) and modern (Walther et al. 2002; Yamano et al. 2011) taxa. First, our results could reflect disproportionate sampling at temperate northern latitudes, which has been suggested previously as a fundamental bias in the PaleoDB (see Krug et al. 2009). Specifically, migration might have an equatorward bias if sampling in the tropics improves over time, thus pulling the position of the average occurrence for a typical genus toward the tropics. We do not favor this explanation, because the ratio of extratropical to tropical occurrences in the data set changes irregularly between epochs (Fig. 5). Furthermore, even if the data are subsampled such that the number of tropical occurrences is always made equal to the number of extratropical occurrences, the results remain comparable, though Paleogene sample sizes are much smaller as a result (Supplementary Fig. 3).

Second, there may be a genuine long-term trend of equatorward migration during most of the Cenozoic (Fig. 2). Recent studies demonstrate shifting centers of peak latitudinal diversity throughout the Phanerozoic and the general equatorward movement of those peaks over the latter half of the Cenozoic (Renema et al. 2008; Powell 2009; Powell et al. 2012). This observation dovetails well with the results presented here, but they are not co-dependent because changes in diversity are also functions of extinction and origination, as well as of changes in geographic distribution. Another possible explanation for genuine equatorward migration is the longstanding hypothesis that climatic cooling drives extratropical taxa toward warmer latitudes (see Bennett et al. 2012). Although this model is

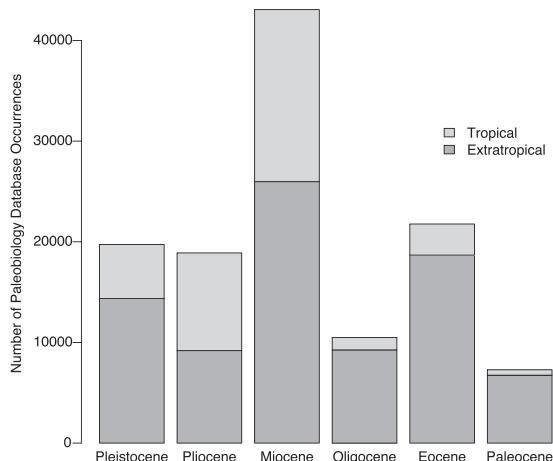


FIGURE 5. A histogram of occurrences in the Paleobiology Database data set for each epoch. Tropical occurrences are less well sampled in the Paleogene than in the post-Paleogene, but the ratio of tropical (-25° to 25°) to extratropical occurrences changes irregularly from epoch to epoch, and tropical occurrences even slightly exceed extratropical occurrences in the Pliocene.

generally invoked specifically in relation to Quaternary glaciations, it is extendable to the entire Cenozoic. If cooling forces migration toward lower latitudes, then the long-term cooling trend following the early Eocene (Zachos et al. 2001) could have caused a longer-term, general shift of latitudinal distributions toward the equator. The ubiquity of the hollow curves seen here does not support this hypothesis, however, as the general shape of the curves is remarkably consistent across both the stage- and epoch-level comparisons (Figs. 3, 4), despite the numerous climatic shifts that have occurred throughout the Cenozoic (Zachos et al. 2001). Even if the Paleogene to post-Paleogene divide is emphasized, it is the cooler and more volatile post-Paleogene that exhibits less change, on average, in preferred latitude and latitudinal tolerance than the warmer Paleogene—suggesting, if anything, that climatic cooling is less likely to force greater or accelerating changes in latitudinal distributions relative to warming.

Third, there may be a time-averaging effect resulting from the relatively coarse temporal scales (epochs and stages) of this analysis. If response curves move abruptly poleward only toward the latter portion of a genus's life span,

then earlier lower-latitude occurrences will be time-averaged with later higher-latitude occurrences. This would dampen apparent changes in latitudinal distribution and might obscure patterns of poleward drift. On the one hand, we consider this possibility to be plausible, considering the many abrupt, extreme shifts in geographic distribution documented in Quaternary studies (e.g., Lyons 2003; Chen et al. 2011; Poloczanska et al. 2013), and the reported general time lag, measured in millions of years, between the tropical origination of a marine bivalve genus and its expansion into extratropical latitudes (Jablonski et al. 2013). On the other hand, the temporal resolution of our analysis (epochs and stages) is broadly comparable to that of other studies reporting unidirectional movement out of the tropics (Jablonski et al. 2006, 2013; Krug et al. 2009), which suggests that such latitudinal redistribution should also be visible in our analysis. Unfortunately, we do not have the necessary temporal resolution to test this hypothesis with the data at hand.

Last, marine bivalve genera expand into the extratropics from the tropics via constituent “bridge species” that originate in the tropics and subsequently widen their ranges into extratropical settings (Jablonski et al. 2013). This model of poleward migration by no means, however, precludes the possibility that the core zone of the genus’s distribution (Fig. 1) remains centered in lower latitudes, reflecting a continued concentration of occurrences in the tropics even as the genus’s latitudinal limits extend poleward. We believe that this explanation dovetails well with the observations of Jablonski et al. (2013). First, bridge species that originate at the periphery of the tropics tend to extend equatorward into the core of the tropics even as they extend poleward into the extratropics. This means not only that bridge species maintain a presence in the tropics, but also that this presence may actually increase over time. Second, if extinction rates are lower and origination rates higher in the tropics, meaning that the tropics are both a “cradle” and “museum” of biodiversity (Jablonski et al. 2006), then, over time, the greatest latitudinal concentration of constituent species and,

therefore, occurrences for a genus might not only stay centered in lower latitudes, but actually move equatorward as endemic tropical species continue to accumulate (Fig. 2).

The Significance of Ubiquitous Hollow Curves.—Each epoch-to-epoch comparison of changes in preferred latitude and latitudinal tolerance exhibits a hollow curve distribution (see McGill 2003), wherein smaller changes are much more common than larger changes (Figs. 3, 4). Furthermore, the average level of change for each curve is less than would be expected by chance (Table 1). Taken at face value, this implies a tendency toward biogeographic conservatism, as opposed to lability, at least in a latitudinal context. This is unsurprising given both the theoretical predictions of niche theory (*sensu* Hutchinson 1957) and empirical observations of the natural world. On the theoretical front, niche theory distinguishes between the fundamental niche, the geographic space that a species can physiologically tolerate, and the realized niche, the space where a species is actually observed. A basic proposition of niche theory is that the realized niche is generally smaller than the fundamental niche, because of barriers (e.g., interspecific competition, mountain chains, propagule motility) to dispersal. These barriers should, in turn, impede a taxon from frequently or continuously altering its biogeographic distribution. This prediction is supported by several empirical patterns: the lag-time, associated with thermal barriers, between the origination of a tropical genus and its expansion into the extratropics (Jablonski et al. 2013); the observation that species do not occupy all geographic areas where they could survive (Pearson and Dawson 2003); and the heritability of geographic range size (Jablonski 1987; Hunt et al. 2005; Waldron 2007).

It is important, however, to recognize that biogeographic conservatism is not synonymous with stasis. For example, over 85% of all epoch-to-epoch shifts in preferred latitude are actually greater than 2° (Fig. 2A). Furthermore, the mean level of latitudinal migration of marine organisms in the face of modern climate change is about 30 to 72 km per decade, depending on the definition of geographic distribution used (Poloczanska et al.

2013). Considering that a degree of latitude is, on average, about 111 km, there is plenty of accommodation for this level of climatic response in our analyses. Similarly, even the average reported range shift of mammals during the climatically volatile Pleistocene, 1200–1400 km (Lyons 2003) is not greater than the average level of latitudinal change seen here (Table 1; ~1600 km). In other words, the fact that the average levels of directional change observed are lower than predicted by chance is not the same as claiming that change does not happen or that levels of change are low in absolute terms.

A second notable aspect of the hollow curves is their striking similarity to one another. For example, the Eocene–Oligocene transition encompasses a marine mass extinction (Prothero 1994) driven by dramatic cooling (Ivany et al. 2000; Lear et al. 2008), yet it is visually indistinguishable from the Paleocene–Eocene transition (Fig. 3), which records the highest temperature and rate of temperature rise in the Cenozoic (Zachos et al. 2001). Collectively, this remarkable similarity implies that biogeographic conservatism is rather ubiquitous, and that extinction, origination, climate change, and other environmental or biological conditions that vary among epochs (see Blois and Hadly 2009) do not appreciably affect this pattern.

Perhaps this is unsurprising given increasing evidence that taxa tend to respond individualistically to perturbations and commonly shift geographic distributions in directions, at speeds, and over distances that are unique from one another (Graham et al. 1996; Lyons 2003; Hofreiter and Stewart 2009; Poloczanska et al. 2013). If this is the case, then it makes sense that, in aggregate, the pattern converges toward an average, particularly over the time scales assessed here. Furthermore, changes in range size are more easily identified at the periphery of the range than at its core (Blois and Hadly 2009). Considering that the metrics used here are fundamentally measures of change in the core zone of latitudinal distribution, rather than fluctuations of the outer tails of the response curve (Fig. 1), it makes sense that changes in

these response curve parameters are similarly conservative across all comparisons.

Conclusion

1. No long-term, overall trend of either poleward or equatorward shifts in the latitudinal distribution of marine genera is evident among Cenozoic marine bivalve and gastropod genera. Evidence is weakest for a model of gradual expansion from the tropics into extratropical latitudes.
2. There are many possible explanations for the absence of a poleward shift in response curve parameters. Our favored explanation is that, although the outer tails of a marine genus's response curve may well expand from tropical settings into higher latitudes, the majority of latitudinal occurrences remain tropical, thus keeping the peak probability of collection centered in lower latitudes.
3. Shifts in the preferred latitude parameter are on average slightly larger than changes in the latitudinal tolerance parameter at the epoch level. Although this comparative difference is statistically significant, it is not very large, nor is it visible at the stage level of analysis.
4. The overwhelming consistency and ubiquity of hollow curve distributions of first differences across all epoch-to-epoch and stage-to-stage comparisons suggest that the underlying geographic conservatism of genera has been impervious to many of the unique epoch-to-epoch environmental and biological perturbations that characterize each of these intervals. This is a direct departure from models predicting, for example, systematic poleward migration during warming and equatorward migration during cooling.

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