The sampling and estimation of marine paleodiversity patterns: implications of a Pliocene model

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Abstract.—Data that accurately capture the spatial structure of biodiversity are required for many paleobiological questions, from assessments of changing provinciality and the role of geographic ranges in extinction and originations, to estimates of global taxonomic or morphological diversity through time. Studies of temporal changes in diversity and global biogeographic patterns have attempted to overcome fossil sampling biases through sampling standardization protocols, but such approaches must ultimately be limited by available literature and museum collections. One approach to evaluating such limits is to compare results from the fossil record with models of past diversity patterns informed by modern relationships between diversity and climatic factors. Here we use present-day patterns for marine bivalves, combined with data on the geologic ages and distributions of extant taxa, to develop a model for Pliocene diversity patterns, which is then compared with diversity patterns retrieved from the literature as compiled by the Paleobiology Database (PaleoDB). The published Pliocene bivalve data (PaleoDB) lack the first-order spatial structure required to generate the modern biogeography within the time available (<3 Myr). Instead, the published data (raw and standardized) show global diversity maxima in the Tropical West Atlantic, followed closely by a peak in the cool-temperate East Atlantic. Either today's tropical West Pacific diversity peak, double that of any other tropical region, is a purely Pleistocene phenomenon—highly unlikely given the geologic ages of extant genera and the topology of molecular phylogenies—or the paleontological literature is such a distorted sample of tropical Pliocene diversity that current sampling standardization methods cannot compensate for existing biases. A rigorous understanding of large-scale spatial and temporal diversity patterns will require new approaches that can compensate for such strong bias, presumably by drawing more fully on our understanding of the factors that underlie the deployment of diversity today.

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Introduction

Understanding the evolution of biodiversity patterns requires knowledge of the origination, extinction, and migration events that have shaped them. Because these processes have operated within constantly shifting environmental settings, dissecting them requires spatial as well as temporal and taxonomic information. Methods exist for estimating diversification rates from molecular phylogenies in younger time bins, but they require simplifying assumptions that can bias the relative contributions of originations and, particularly, extinctions through time (Quental and Marshall 2009; Losos 2011; Morlon et al. 2011), and require additional assumptions to assess immigration, which has been a major contributor to diversity for many regions

today and in the past (e.g., Jablonski 1998; Vermeij 2001; Jablonski et al. 2006; Krug and Patzkowsky 2007; Fisher et al. 2010). Spatial dynamics must be reconstructed from the fossil record, which provides the only direct evidence of the distribution and environmental contexts of species, clades, and communities in past time intervals. However, paleontological results can be compromised by inadequate or biased spatial coverage, particularly if analyses span time frames that encompass spatial shifts in sampling intensity or preservation. Such spatial and temporal biases in the fossil record are well documented, and in many cases are difficult to overcome. Statistical treatments of fossil samples may permit comparisons among temporal and spatial bins, but many of these

treatments involve degrading fossil data sets to a common level of sampling, by standardizing either sampling size or the underlying abundance distribution among samples. Such procedures can mask actual diversity peaks and patterns arising from oceanographic and climatic factors that create strong interregional variation in diversity even at similar latitudes and temperature regimes (see below).

A growing number of studies focus on explaining *present-day* diversity patterns in terms of processes and specific events in the past (e.g., Ricklefs 1987, 2007; Little and Vrijenhoek 2003; Wiens and Donoghue 2004; Jablonski et al. 2006; Krug et al. 2009a,b; Kiel and Nielsen 2010). We fully endorse that general approach, but contend that the flow of information can be bidirectional. Here we develop a set of estimates for marine Pliocene biodiversity patterns by using an actualistic approach, bringing present-day observation to bear on paleontological problems, rather than traditional "fossil only" methods. Latitudinal diversity gradients (LDGs) were probably a dominant feature of north-south-trending continental shelves throughout the Cenozoic, and have been detected in a general way as far back as the Ordovician (Crame 2001; Novack-Gottshall and Miller 2003), although their strengths and differentials among oceanic coastlines have varied over time. Thus, an understanding of the environmental factors associated with coastal LDGs and their inter-ocean variation today can be valuable in assessing biotic patterns and their sampling biases in the geologic past. For modern marine environments at shelf depths, LDGs correlate strongly with environmental parameters such as sea surface temperature (SST) that have strong latitudinal gradients themselves. Although the causal mechanisms underlying diversity patterns remain hotly debated, there is no reason to suppose that the strong and well-established diversity–environment correlations recently arose de novo—more likely, they have characterized shelf faunas throughout geologic time. Therefore, we argue that these relationships should inform and constrain attempts to infer past biodiversity patterns. We illustrate this view by using databases of fossil and living marine bivalves to infer shallow-sea LDGs along the major coastlines for a relatively recent interval of geologic time, the Pliocene (5.3 to 2.6 Ma). The close proximity of our target interval to the present day provides a particularly informative basis for evaluating approaches to estimating past diversity patterns, because the Pliocene fossil record must credibly give rise to the modern diversity pattern within just 2.6 Myr.

We show that invertebrate marine shelf diversities based on compilations of fossil taxa analyzed via widely used paleontological protocols differ strongly from our Pliocene estimates based on an actualistic evaluation of modern and fossil data. The similarities and differences between these reconstructions reveal the strengths and weaknesses of fossil data in capturing first-order biogeographic patterns, with implications for establishing global and regional diversity patterns through time. From the inception of modern research on large-scale diversity trends (Newell 1952, 1967; Valentine 1969), emphasis has been placed on developing adequate samples of the paleontological literature. Instead, we argue that, because an unbiased or even complete sample of the literature on invertebrate fossils is not necessarily equivalent to an unbiased sample of the fauna that lived in a target interval, robust reconstructions of ancient marine diversity patterns require applying principles and lessons from the modern world to the past, and cannot rely solely on increased sampling and compilation of fossil data. As a step toward developing novel approaches to bridging this conceptual and methodological gap, we use present-day marine biogeography to develop a model for Pliocene diversity patterns, and suggest how this exercise can inform reconstructions of biodiversity deeper in the past.

A Review of Modern Marine Biodiversity Patterns

As modern marine biogeography presents the underpinnings for our model of Pliocene diversity, we must first review the major features of the modern oceans and the biological and environmental processes that govern them. Most major taxonomic groups
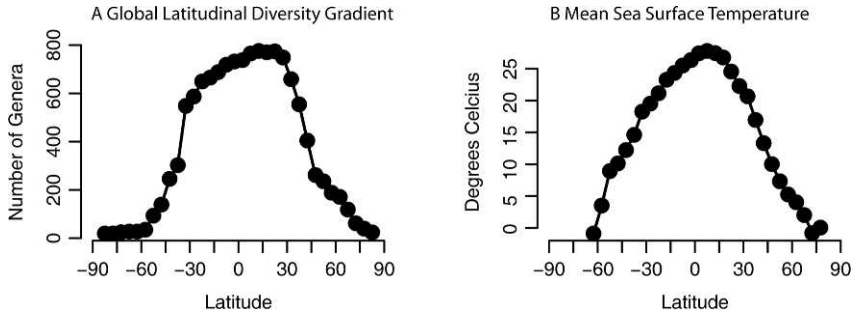
FIGURE 1. Global bivalve genus-level diversity gradient (A) and mean sea surface temperature (B) within 5° latitudinal bands. Modern SST data were obtained from the UK Meteorological Office Hadley Center (Rayner et al. 2003; Met Office Hadley Centre 2006–2010).

exhibit two first-order diversity patterns: (1) the LDG (e.g., Fig. 1A) and (2) longitudinal variation in taxonomic richness, especially well displayed within the tropical belt of maximum diversity, characterized by a diversity hotspot in the Indo-West Pacific (Hillebrand 2004a,b; Tittensor et al. 2010). These patterns in the modern oceans form the basis of our estimate for first-order Pliocene patterns.

The major ocean surface currents are largely wind driven (see reviews in Munk 1950 and Niiler 2001). Air warmed near the surface in low latitudes rises and flows poleward; it cools and descends in midlatitudes, returning equatorward in the meridional Hadley cell. Owing to the Coriolis effect, this returning air is deflected to the right in the Northern Hemisphere and to the left in the Southern Hemisphere, forming the great subtropical gyres. The thermal expansion of ocean waters that are warmed by the sun in low latitudes elevates the sea surface there, and gravity causes the water to flow from the warmer highs down isobars toward cooler lows. Coriolis affects this flow, helping form a clockwise gyre beneath the northern meridional atmospheric cell and a counterclockwise gyre in the Southern Hemisphere, further defining the temperature patterns that dominate the tropics and subtropics. The thermal equator lies north of the geographic equator in the Atlantic and East Pacific (Fig. 1B). Finally, Earth's spin imposes a planetary vorticity—rotational force—on ocean currents that is strongest near the poles, decreasing to zero at the equator. Poleward-flowing segments of the

gyres thus pick up increasing vorticity that adds to their velocity, while equatorward-flowing segments of the gyres lose vorticity, damping their velocity (Stommel 1948). As a result, currents on the western sides of these major oceanic gyres—western boundary currents—flow faster than those on the eastern side. To conserve mass, western boundary currents are therefore narrower than eastern boundary currents, and the centroids of the warm-water pool inside each gyre are shifted significantly to the west. Coastal upwelling zones of cool water are more common among the more sluggish eastern boundary currents, where the thermocline is shallower and warm surface waters tend to drift offshore owing to the Coriolis force and wind stress.

The basic features of ocean circulation and temperature we outline here should hold, in some form, so long as the sun was shining and Earth was spinning. Of course, different climate states and continental configurations should have important effects on oceanic and atmospheric circulation patterns, and on the distribution of associated environmental parameters. Thus the continental configurations in the Mesozoic and particularly in the Paleozoic, coupled with different atmospheric conditions, had to have supported quite different circulation patterns than today's (Herrmann et al. 2004 show that even minor shifts in the estimated $p\mathrm{CO_2}$ of the atmosphere can produce different models of Paleozoic circulation). But the configuration of continents in the Pliocene was similar to today, and north-south boundary currents of contrasting width and velocity, and stable, warm-cored

subtropical gyres, are all likely to be present in some form throughout the Neogene (see below).

The first-order oceanographic features play a major role in structuring the distribution of the marine biota. The huge warm-water pool of the tropical West Pacific harbors the richest diversity at shelf depths today. Provinciality on the western sides of ocean basins tends to be less well defined than on eastern sides because warm western boundary currents drift poleward into subtropical and warm-temperate provinces, carrying a subset of tropical taxa with them. Thus, barring regional complications, tropical elements are more common in the western extratropical provinces, reducing their distinctiveness (as observed for marine bivalves, see Harnik et al. 2010). During cooler climatic episodes the latitudinal changes in SSTs steepen and are localized at changes in surface current patterns over the shelf.

A Review of Biogeographic Patterns for Marine Bivalvia

Bivalves have modern biogeographic and diversity patterns that are representative of the shallow-sea fauna (0–200 m) as a whole (Briggs 2007; Hoeksema 2007; Reaka et al. 2008; Krug et al. 2009a,b; Roy and Witman 2009), and have a good fossil record. Our database includes 43,687 Recent occurrences of 5614 living species from 2646 shelf-depth localities (as of December 2011) of all major bivalve families from all latitudes and all oceans, gleaned from the literature and from museum collections and vetted to a common genus-level taxonomy. Our fossil data include a list of the first paleontological occurrences in time and space of each living bivalve genus, a common taxonomic level in marine paleobiogeography, again drawn from the literature and museum collections (see Supplementary Information online), and thus heavily modified and updated from Sepkoski (2002) and other sources. We have omitted several families of minute bivalves whose sampling and systematics are especially incomplete (the galeommatoidean and cyamioidean families, plus Gaimardiidae and Neoleptonidae), a conservative decision for our results. Much

of the known diversity for these groups is tropical West Pacific (e.g., Bouchet et al. 2002 and Paulay 2003, who find Galeommatidae to be the most diverse family in their respective faunas, in contrast to even the best-sampled high latitudes, e.g., Higo et al. 1999; Coan et al. 2000), and so this omission reduces the difference among tropical peaks, and weakens the LDG. We also omitted the wood-boring teredinids, whose "natural" biogeography has been massively disrupted by human transport (e.g., Carlton 2009).

Latitudinal Patterns.—Modern marine bivalve diversity in the shelf benthos reaches its peak near the equator on all coastlines. The peak is displaced northward in both the Atlantic and Pacific (Fig. 1A), tracking a similar offset in the thermal equator (at least in the Atlantic and eastern Pacific, Fig. 1B) but perhaps also influenced in part by some combination of sampling and the unequal hemispheric distribution of tropical shelf environments. This general latitudinal diversity pattern is pervasive among major marine taxa (Hillebrand 2004a,b; Field et al. 2009).

As summarized above, oceans differ in their hydrography, and their eastern and western boundary currents have contrasting ecological and biogeographical effects. Therefore, we have compiled separate bivalve LDGs for the shelves of four oceanic coastlines, the West Pacific (excluding the Indian Ocean and central Pacific, which are essentially attenuated samples of the core West Pacific), East Pacific, West Atlantic, and East Atlantic, together with the corresponding gradients in sea surface temperatures (SSTs) (Table 1, Figs. 2, 3). All modern coastlines show strong LDGs in both Northern and Southern Hemispheres at the genus level (and even stronger ones at the species level [e.g., Krug et al. 2009b]). These genus-level LDGs show a tropical plateau in diversity, with sloping shoulders that extend into warm-temperate latitudes and that are strongest along western boundaries of ocean basins, before declining steeply into cold-temperate regions. Sampling of the shelves is best in the Northern Hemisphere, but the major north-south hemispheric differences in LDGs apparent in the figures are likely to be real and indeed are seen in most

TABLE 1. Linear regressions of mean annual sea surface temperature and species richness (log-transformed for this analysis) along the four major coastlines. All correlations are significant to $p > 0.0005$. Spatial autocorrelation not factored out, following Hawkins 2012.

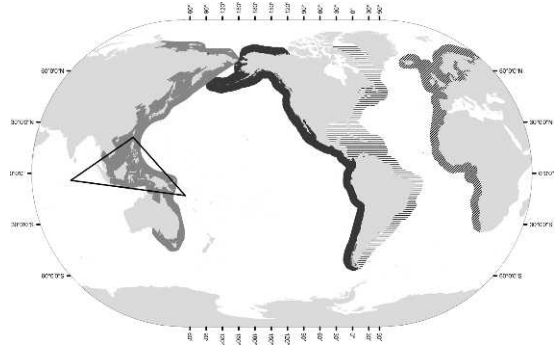|	Slope	R^2
West Pacific	0.1	0.74
East Pacific	0.08	0.62
West Atlantic	0.06	0.89
East Atlantic	0.07	0.89

FIGURE 2. The four coastlines examined here for marine bivalve diversity patterns (Figs. 3, 4), and the global diversity maximum, the Coral Triangle. Note that Coral Triangle is comparable in dimensions to conterminous United States.

major marine clades (Hillebrand 2004b; Tittensor et al. 2010). Although their diversity peaks are impressive, the tropics are significantly less well sampled than are extratropical latitudes, as attested by large numbers of undescribed or previously undetected species recorded whenever detailed faunal analyses are performed (e.g., Bouchet et al. 2002; Bouchet 2006; Glover and Taylor 2007; Knowlton et al. 2010). Thus, corrections for sampling errors should increase the steepness of the latitudinal gradients shown here.

Longitudinal Patterns.—Today, the tropical diversity peaks vary significantly among coastlines, with by far the greatest contrast presented by the West Pacific global maximum. Bivalve genus-level diversity in the tropical West Pacific exceeds that of the tropical regions of the East Pacific and of the Atlantic by more than a factor of two (Fig. 3), and for the species level by about a factor of four, a pattern of interoceanic and intercoastal diversity that has evidently been in place since at least the Early or Middle Miocene (e.g., Crame and Rosen 2002; Renema et al. 2008). More generally, although latitudinal diversities correlate with temperature, longitudinal diversities do not.

The high diversity of the West Pacific province today may result partly from the great environmental heterogeneity along the fragmented shelf-depth habitats there (Rosen 1984; Crame and Rosen 2002; Renema et al. 2008; Williams and Duda 2008), a legacy of the complex plate-tectonic history of the region, coupled with the broad east-west extension of warm waters; when shelf-depth provinces have important longitudinal extensions they show unusually high provincial diversities in tropical and temperate settings alike (Valen-

tine 2009). Major West Pacific elements occur as far west of the Philippines-Indonesia core region (sometimes termed the "Coral Triangle"; see Fig. 2) as East Africa, and as far east as Hawaii and Easter Island in the central Pacific, but these extensions harbor relatively few endemic genera. Thus the Indian Ocean shelves contain about 540 genera in our database, but only nine are endemic (<2%), and the scattered central Pacific islands support an increasingly attenuated fauna, with just three endemic genera out of 181 (also <2%). The other tropical regions are separated from one another by land or water barriers that have promoted taxonomic divergence to varying degrees. The present north-south disposition of continental coastlines are obvious barriers separating major ocean basins, and the >5000 km of open water between the Line Islands (~150°W) and the west coast of South America (~80°W) also constitutes a nearly impermeable East Pacific Barrier (Darwin 1859: pp. 347–348; Ekman 1953; Vermeij 1987; for rare exceptions and general discussion see also Emerson 1967, 1978, Vermeij 2001, and Lessios and Robertson 2006).

Tropical provinces are generally not as well sampled as temperate ones, and the tropical West Pacific is probably the most poorly sampled as a fraction of its total diversity (see sampling references cited above). Interregional differences in tropical shelf diversity are thus almost certainly greater than current-

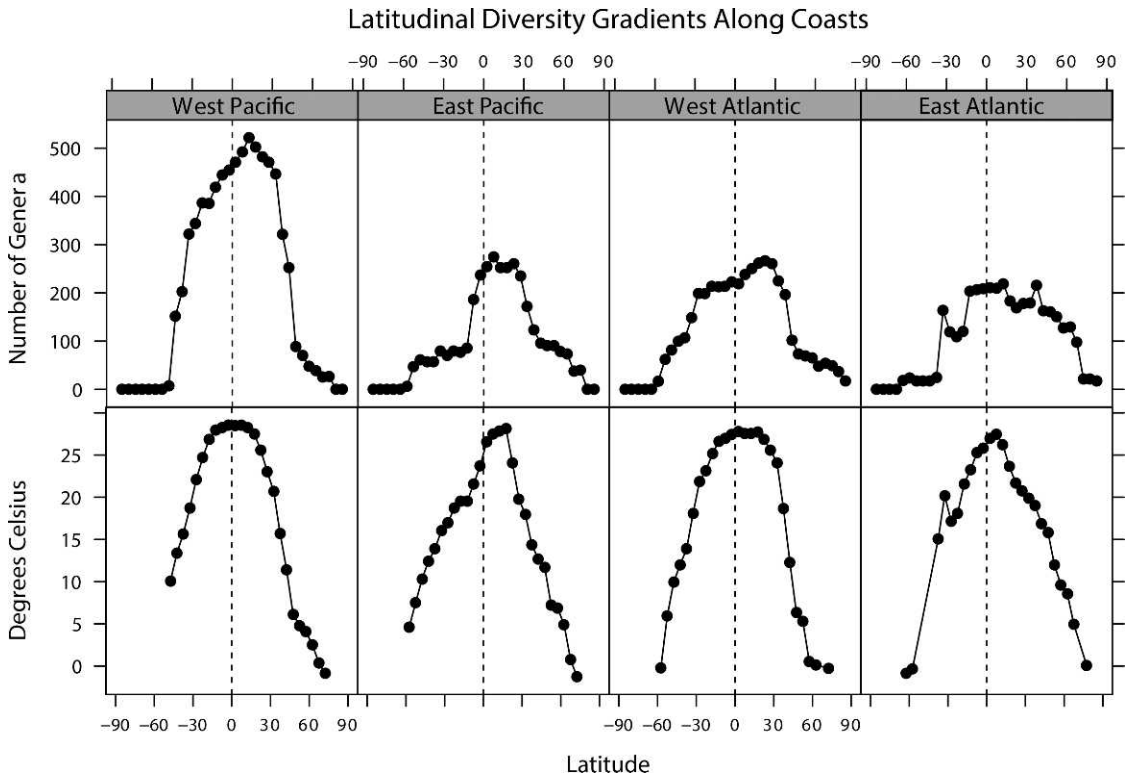## Latitudinal Diversity Gradients Along Coasts

FIGURE 3. Latitudinal diversity gradients and corresponding temperature gradients along the shelves of transects of the four major coastlines.

ly recorded. Given the extreme amount of diversity harbored in the West Pacific today, and the available fossil data on its recent history, this province must have been a major factor in global diversity in the world ocean for most or all of the late Cenozoic. The "Coral Triangle" within the broad West Pacific province is a formidable feature: by most definitions its east-west base extends from western Indonesia to Papua New Guinea and its northern corner reaches the northern Philippines, Taiwan, or the Ryukyu Islands (e.g., Wells 2002; Briggs 2005; Hoeksema 2007; for a different geometry but similar size, with the base shifted to extend from Java to the Solomon Islands, see Veron et al. 2009); it is thus as wide as the United States and as deep as the United States and Mexico combined. The presence of such a commanding feature in today's oceans indicates that identifying the position of this and other such peaks in past

time intervals is vital to any understanding of past marine diversity patterns.

As in the tropics, the extratropical provinces show dramatic diversity differences. Much of this variation is latitudinal, but there is significant longitudinal variation among coasts that is demonstrably unrelated to shelf area. These interprovincial differences are partly predicted by proximity to the tropical maxima along western margins of oceans (Harnick et al. 2010), presumably owing to the poleward flow of warm currents that permits greater spread of tropical taxa along these shelves. As in the tropics, isolated extratropical islands, for example in sub-Antarctic latitudes, tend to support depleted or mixed faunas that add little to global diversity at the genus level.

Most of the genera in temperate (and polar) provinces evidently originated in the tropics and have spread poleward in an out-of-the-tropics (OTT) dynamic (Roy et al. 1998;

Jablonski et al. 2000, 2006; Krug et al. 2007, 2008, 2009a,b; Roy and Goldberg 2007; Valentine 2009; Valentine and Jablonski 2010). Lineages that expanded from the tropics generally retain a tropical presence—110 of the 113 living genera that demonstrably originated in the tropics over the past 11 Myr are still there today (Jablonski et al. 2006). The ubiquity of the Neogene OTT pattern should allow us to infer past distributions of genera present but not directly sampled in the Pliocene but whose geographic ranges are known from the Recent.

Relationships with Temperature.—The variable most often correlated with diversity is temperature, which has been shown to be a first-order predictor of diversity at various geographic scales in both the terrestrial and marine realms (e.g., Hillebrand 2004a,b; Krug et al. 2009a; Tittensor et al. 2010), although whether the relationship is directly causal is uncertain (for the potential role of increasing poleward seasonality, with its influence on the variability in productivity, see Valentine et al. 2008, Valentine 2009, and Krug et al. 2009b). Despite the uncertainty on causality, temperature is an appealing variable because it correlates with the present-day latitudinal diversity of so many taxa, is well measured today, and is associated with energy flow into the biosphere. Indeed, bivalve genus and species diversity is highly correlated with the latitudinal sea surface temperature (SST) gradient along each of the four coastlines (Table 1). Although similar SSTs occur in all of the tropical provinces, diversity is much higher in the West Pacific, indicating that temperature per se is not the sole factor in LDG regulation. Nonetheless, the consistent correlations between diversity and SST do imply that range limits of species and genera expand along warmer coastlines, thus conforming to large-scale temperature trends, as is well supported for various marine ectotherms, including bivalves (e.g., Compton et al. 2007; Roy et al. 2009; Sunday et al. 2011). Thus, expansion of tropical conditions along a coastline should be accompanied by increasing local diversity of the tropical flanks.

Inferring Pliocene Diversity Patterns

Pliocene LDGs Inferred from Evolutionary and Biogeographic Dynamics.—Because temperature is useful in predicting biogeographic patterns across latitudes, we use Pliocene temperature reconstructions together with our data for bivalves to generate a hypothesis of the expected differences in diversity patterns between the Pliocene and Recent oceans. The PRISM3D reconstruction of SST gradients during a mid-Piacenzian time slice (3.264 to 3.025 Ma) is summarized in Figure 4 (see Dowsett et al. 2009, 2010, and references therein). PRISM reconstructions are based on a broad array of paleoclimatic evidence, including geochemical, isotopic, and microfossil data, and climate modeling. Pliocene temperatures were generally warmer than today's, and Piacenzian temperatures appear to represent a local peak of late Pliocene warmth within a general Pliocene cooling trend that culminated in the Pleistocene glaciations; they represent our best data for Pliocene marine climates. These data are drawn from a much narrower time bin than the Pliocene records in the Paleobiology Database (PaleoDB; paleodb.org) or our data on genus first-occurrences, but they provide an oceanographic and biogeographic state useful for comparisons to the present day.

In the West Pacific, Piacenzian temperature proxies indicate tropical SSTs much like today's or slightly higher, whereas East Pacific temperatures were significantly higher than today's. These results imply a weaker E-W thermal contrast in the Pliocene, with the West Pacific warm pool extending farther east. In the Atlantic, western tropical shelves had Piacenzian temperatures close to or slightly higher than today's, but warm-temperate zones had significantly warmer temperatures, which extended farther north along the Carolinian and Virginian shelves and farther south along the Brazilian coast.

Modeling and microfossil data suggest that both the Pacific and Atlantic gyres were displaced poleward in the Piacenzian relative to today, and thus that tropical zones were generally broader latitudinally than at present (Dowsett et al. 2010; see also Lutz 2011).
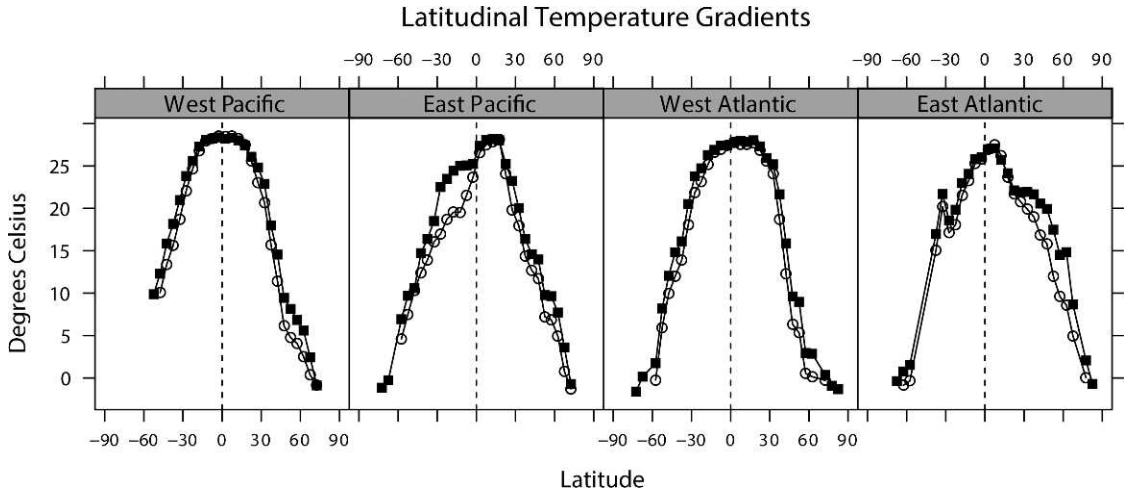
FIGURE 4.   Comparison of present-day (open circles) and Pliocene (filled squares) temperature gradients along the four major coastlines.

Modeling also finds that extratropical marine temperatures along nearly all coastlines were higher than today at a given latitude. The Arctic Ocean enjoyed mostly ice-free Piacenzian summers (Matthiessen et al. 2008; Robinson 2009), while around Antarctica the polar front was displaced southward (Barron 1996; Dowsett et al. 2010).

Whether Piacenzian LDGs were correlated to temperature patterns as highly as modern LDGs is uncertain; diversities might have been more loosely tied to the SST patterns. However, it is reasonable to assume from first principles that the ~3 Myr since the Piacenzian has been inadequate for a massive global reorganization of marine diversities to have occurred, particularly given the large median ages of extant bivalve genera (33.9 Myr along Pacific coasts, 37.2 Myr along Atlantic coasts). Thus, the Pliocene LDGs should roughly resemble those of today, after accounting for latitudinal range shifts associated with Neogene cooling and modest regional genus-level extinctions around the Plio-Pleistocene boundary (we estimate ~7% globally). In many regions, climate fluctuations during post-Pliocene glaciations, having been accommodated by changes in the latitudinal ranges of species, were accompanied by relatively few extinctions at the genus (or even species) level (e.g., Valentine and Jablonski 1993).

Of the 610 bivalve genera recorded from the tropical West Pacific today, 491 (80%) are known to have been extant somewhere during the Pliocene (Table 2). This is a much larger diversity gap than on the other coasts, but the 100+ genera today in the tropical West Pacific that lack a fossil record of any kind could well have existed in that region in the Pliocene—many of them are small and/or thin-shelled and/or rare, and thus have a low likelihood of discovery in this poorly sampled region (see Harper 1998, Cooper et al. 2006, and Valentine et al. 2006 on controls on bivalve preservation and sampling; Jackson and Johnson 2001, Vermeij 2001, and Krug et al. 2009b on poor sampling in the West Pacific Neogene). The median ages of genera and the near ubiquity of the Neogene out-of-the-tropics dynamic (see above) also suggest that these genera were probably present in the tropics during the Pliocene; they are extremely unlikely to have migrated from temperate regions, and molecular phylogenies are increasingly yielding phylogenies indicating that tropical West Pacific genera lacking a fossil record are likely to have originated deep in the Neogene or even Paleogene (e.g., *Scaeochlamys*, *Troendelina*, *Funafutia* [Alejandrino et al. 2011; Taylor et al. 2011]). Even if most of the taxa in the tropical West Pacific are Pliocene or older, we lack direct paleontological evidence that they were all present in the region during the Pliocene.

TABLE 2. Ratio of Pliocene diversities using different data types, compared with Recent pattern, treating the tropical West Atlantic as the best-sampled region. Expected PaleoDB diversity estimates for the tropical West Pacific region are derived by accepting the tropical West Atlantic as correct, then using the ratio of diversities (a) observed today in the two regions or (b) observed using just genera older than Pleistocene in each region. Shortfall is the difference between the expected PaleoDB diversity and the diversity recorded from that region in the PaleoDB.

	No. of genera		
Data type	Tropical West Pacific	Tropical West Atlantic	Ratio WPac:WAtl
Recent	610	316	1.9:1
Extant in region, older than Pleistocene	491*	290	1.7:1
PaleoDB Pliocene	131	243	0.54:1
PaleoDB Pliocene, SQS estimates	45.8 (u = 0.6)	61.9 (u = 0.6)	0.74:1 (u = 0.6)
	85.4 (u = 0.8)	106.6 (u = 0.8)	0.8:1 (u = 0.8)
Expected PaleoDB Pliocene, estimate W Pacific accepting W Atlantic diversity as correct, using (a) ratio today or (b) ratio using just genera older than Pleistocene in each region	(a) 462 (shortfall = 331) (b) 413 (shortfall = 282)		
Absolute diversity estimates using SQS ratios and PaleoDB data for Tropical West Atlantic	180 (u = 0.6, shortfall = 282) 194 (u = 0.8, shortfall = 267)		
Extant in Pliocene + globally extinct	495*	301	1.6:1

* Underestimates, owing to poor sampling in tropical West Pacific Pliocene.

However, if they are post-Pliocene immigrants, the only real possibilities are that they entered from the tropical Indian Ocean and/ or the tropical Eastern Pacific. We will evaluate each of these possibilities.

There is no evidence that present-day West Pacific forms were derived in any numbers from the East Pacific over the past few million years. As noted above, the West Pacific provincial fauna shows a diminishing diversity gradient to the east, from its high-diversity core to the relatively impoverished faunas on tropical archipelagoes in the south-central Pacific such as the Marquesas and isolated islands like Easter and Pitcairn; few taxa manage to bridge the East Pacific Barrier. Furthermore, there is no paleontological hint of a migration of Panamanian or Caribbean bivalves into the West Pacific (Emerson 1967; Vermeij 1987, 2001), and phylogenies of West Pacific molluscan taxa are rarely rooted in the New World tropics except at very deep nodes that represent ancient vicariance events rather than branchings associated with the Pleisto-cene–Recent invasions (e.g., Paulay and Meyer 2002; Meyer 2003; Schiaparelli et al. 2005; Williams 2007; Frey and Vermeij 2008; Chen et al. 2011; Cunha et al. 2011).

To the west, the West Pacific fauna continues across the Indian Ocean to the Red Sea and tropical East Africa, and those regions are

commonly joined with the West Pacific province that we discuss here into a single Indo-West Pacific (IWP) provincial complex (e.g., Valentine 1973; Briggs and Bowen 2012). As noted above, <2% of Indian Ocean bivalve genera are endemic today, and the available fossil record suggests similar values in the Pliocene and Pleistocene (e.g., Cossmann 1924; Cox 1927, 1929, 1930; Abrard 1942; Eames and Cox 1956; Freneix et al. 1971; Crame 1984), apparently ruling out that region as a source for a major post-Pliocene flood of taxa to pump West Pacific diversity to its present levels. A connection from the IWP through the Mediterranean region to the East Atlantic tropical fauna was severed ca. 16 Ma (see Renema et al. 2008 and Vermeij 2012a), and these faunas are now quite distinct; in any case, 88% of the extant genera today with tropical affinities were locally extinct in the Mediterranean by the end of the late Miocene (Vermeij 2012a: Table 1), also ruling out this region as a source of post-Pliocene West Pacific diversity.

We also note that the warm waters of the East Pacific and the East and West Atlantic are an unlikely source of a hypothetical, massive post-Pliocene rise in West Pacific diversity, as they each contain only about half the diversity of the West Pacific peak (Tables 2, 3, Fig. 3); each region—the East Pacific and the East and

TABLE 3. Ratio of Pliocene diversities using different data types, compared with Recent pattern, treating the Northeast Atlantic Pliocene as the best-sampled region. Expected PaleoDB diversity estimates for the tropical West Pacific region are derived by accepting the Northeast Atlantic as correct, then using the ratio of diversities (a) observed today in the two regions or (b) observed using just genera older than Pleistocene in each region. Shortfall is the difference between the expected PaleoDB diversity and the diversity recorded from that region in the PaleoDB. The northeast Atlantic has lost 56 genera to regional or global extinction to the Pliocene, but improved sampling and immigration brings its present-day diversity back to the Pliocene level; by our count (unpublished data), northeast Atlantic Pliocene diversity was 226 genera, well above the present-day value.

Data type	No. of genera			Ratio WPac:NEAtl	Ratio W Atl:NE Atl
	Tropical West Pacific	Northeast Atlantic	Tropical West Atlantic		
Recent	610	156	316	3.9:1	2.03:1
Extant in region, older than Pleistocene	491*	155	290	3.2:1	1.9:1
PaleoDB Pliocene	131	157	243	0.8:1	1.5:1
PaleoDB Pliocene SQS estimates	45.8 (u = 0.6) 85.4 (u = 0.8)	59.6 (u = 0.6) 93.1 (u = 0.8)	61.9 (u = 0.6) 106.6 (u =0.8)	0.77:1 (u = 0.6) 0.92:1 (u = 0.8)	1.01:1 (u = 0.6) 1.15:1 (u = 0.8)
Expected PaleoDB Pliocene values, and shortfalls	(a) 612 (shortfall = 481) (b) 502 (shortfall = 371)		(a) 319 (shortfall = 76) (b) 298 (shortfall = 55)		
Absolute diversity estimates using SQS ratios and PaleoDB data for NE Atlantic	121 (u = 0.6, shortfall = 491) 144 (u = 0.8, shortfall = 468)		159 (u = 0.6, shortfall = 160) 181 (u = 0.8, shortfall = 138)		
Extant in Pliocene + globally extinct	495*	163	301	1.6:1	1.8:1

* Underestimate, owing to undersampling of tropical West Pacific Pliocene.

West Atlantic—has its own history with considerable evidence for regional extinctions but little for extensive post-Pliocene intertropical migrations (e.g., Todd et al. 2002; Renema et al. 2008; Vermeij 2012a). In light of the evidence and arguments of the preceding paragraphs, we conclude that the relative heights of peaks of Pliocene LDGs along the major coastlines, including the tropical West Pacific, were probably notably similar to those of today.

We give two rough estimates of Pliocene tropical diversity patterns, without claiming any precision for absolute values (Table 2). One estimate is simply a tally of all genera present today in a given region that are recorded—anywhere—in Pliocene or older strata; it indicates a modest change in the ratio of tropical West Pacific to tropical West Atlantic diversities, from today's 1.9:1 to 1.7:1 in the Pliocene. The second estimate adds globally extinct taxa whose youngest recorded occurrences are in the Pliocene or Pleistocene of a given region; it finds a further change in the ratio of tropical West Pacific to West Atlantic diversity, to 1.6:1. These data, while suggesting weaker diversity differences among tropical Pliocene provinces than today, must be viewed cautiously. The first estimate is distorted by poorer sampling in the Pliocene tropical West Pacific relative to the tropical West Atlantic. The second estimate is even more distorted by such undersampling, because extinction-prone endemics are most likely to be unsampled (see Bromfield and Pandolfi 2011 for extinction in West Pacific coral genera in the late Pliocene–Pleistocene). Thus the ratios in Table 2 must be taken as extreme minima, and should almost certainly be corrected upward, placing them closer to present-day values.

Accurate Pliocene diversity estimates are difficult for the warm-temperate zones flanking the tropics. The increased breadth of the Pliocene tropics and the increased warmth of their flanking temperate zones, relative to today, suggest that tropical Pliocene latitudinal ranges were on average greater than those of today, and that the shoulders and flanks of the LDG peaks were wider, carrying fairly high diversities into higher latitudes. This

condition should have been most important along western boundary currents. Upwelling compartments, especially along eastern boundary currents, may have created or enhanced barriers between provincial regions as climates cooled and ocean circulation intensified (see Vermeij 2012a). A steepening of the LDGs must have accompanied the increasing latitudinal temperature gradients as the poles cooled into the Pleistocene, restricting the latitudinal ranges of stenotherms and enhancing latitudinal provinciality. As noted above, regional diversity losses could have been substantial as generic ranges contracted into the tropics.

LDGs of similar height and shape can harbor different total diversities if they differ in taxonomic turnover. Today, the most widespread sea surface temperatures are 27–28°C, so that even stenothermal species adapted to such a narrow temperature range can and do range widely latitudinally (Tomašových et al. 2011). Given that Pliocene tropical marine temperatures were more widespread and latitudinal ranges of tropical species likely wider than today's, the extensions of lineages into the tropical flanks should have maintained a high standing diversity there, despite the lowered overall provinciality. Provinciality, however, is an important multiplier of global diversity (Valentine 1968, 1973; Holland 2010). Still unresolved, then, is whether (1) extratropical endemic bivalve species and genera are more numerous today than in the Pliocene, (2) the contribution of endemics to the global diversity of modern bivalves is greater or less than their contribution during the Pliocene, and (3) tropical and extratropical diversities during the Pliocene summed globally to more or fewer bivalve genera and species than encountered today. For the last question, both possibilities have been entertained (see discussion in Hall 2002).

Pliocene Diversity Patterns Recorded by Fossils

The biogeography that we have estimated for the Pliocene by combining the modern pattern, the ages of extant genera, and obvious differences in climatic conditions, is, unsur-prisingly, qualitatively similar to that of modern oceans. This result is intuitive and seemingly unspectacular until it is compared with even the best diversity estimates derived directly from the fossil record. With the rise of interest in major macroevolutionary and macroecological patterns, biogeographic data from the fossil record have become a priority, and paleobiologists have attempted to capture, from the vast literature and from rich but unpublished museum collections old and new, occurrence data that include information on the precise locations and taxonomic associations found in marine invertebrate fossil collections though the Phanerozoic. Many of these data are incorporated into the PaleoDB, a remarkable and steadily growing online resource that provides a massive compilation of published fossil occurrences (see Alroy et al. 2008; Alroy 2010a,b).

Here, we compare the diversity estimates of our simple model of Pliocene diversity with raw and sample-standardized diversity estimates derived from the literature, as inventoried by the PaleoDB (accessed 4 September 2011) (Tables 2, 3, Fig. 5). All marine bivalve genera from the Pliocene were queried (excluding genera assigned by the PaleoDB to the smaller-bodied families; see above) and parsed by coastline and climate zone. The lower taxon numbers reported in the raw literature are unsurprising—the fossil record is incomplete and the PaleoDB does not claim comprehensiveness—but the qualitative differences with the Pliocene model are striking, with a spatial pattern far removed from that expected from modern diversities—even when various sample standardization methods are applied. These raw data show the tropical Atlantic as the global diversity maximum for Pliocene bivalves, followed by the warm-temperate northwest Atlantic and the cool-temperate northeast Atlantic. The tropical West Pacific contains roughly half, rather than roughly twice, the diversity of the tropical West Atlantic.

The mismatch between modeled and recorded fossil Pliocene diversities persists even when sample standardizing procedures are applied (Alroy 2000; Alroy et al. 2008), including the recently developed Shareholders

A Unstandardized Diversity
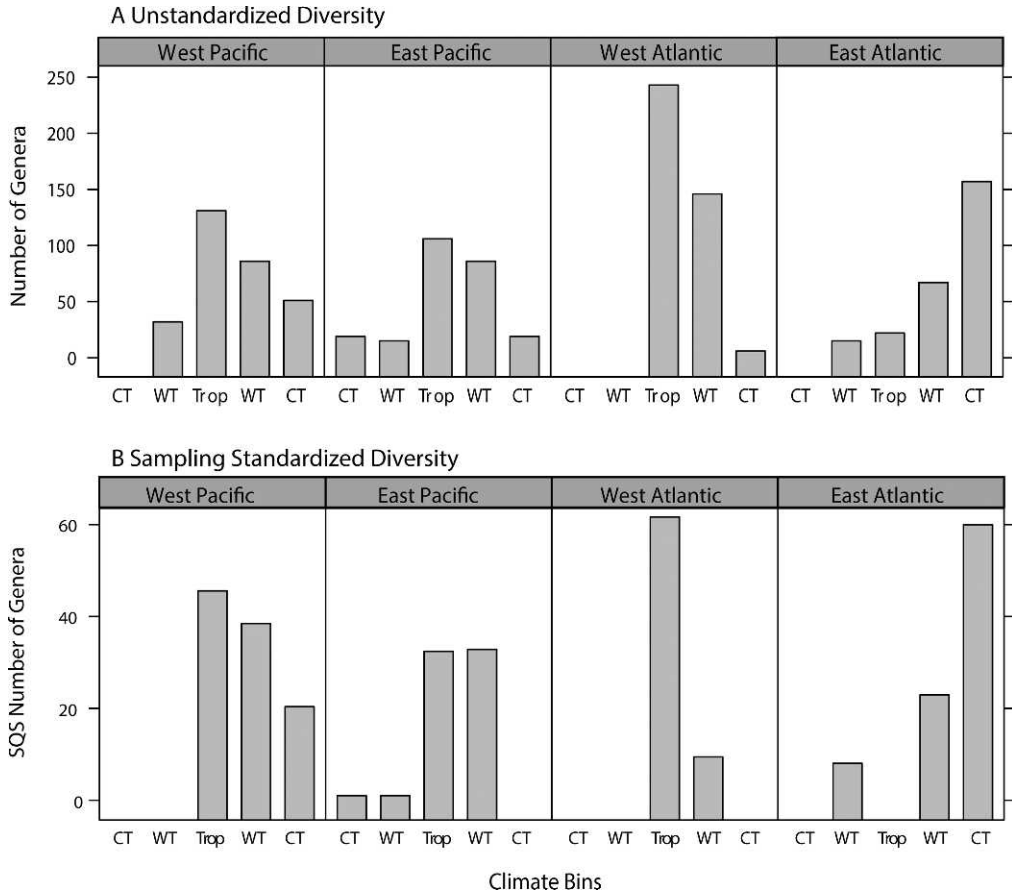

B Sampling Standardized Diversity

FIGURE 5. Unstandardized (A) and sampling standardized (B) marine bivalve diversity gradients for the Pliocene as derived from literature data, downloaded from the PaleoDB 4 September 2011. Sampling standardizations were performed on the data in A using the Shareholders Quorum Subsampling Method (Alroy 2010a), with u = 0.6. Climate-zone abbreviations: CT, cool-temperate; WT, warm-temperate; Trop, tropical.

Quorum Subsampling (SQS) Method (Alroy 2010a,b) (see Fig. 5B), which standardizes samples to a common proportion of the underlying frequency distribution of those samples, regardless of the sample size required to do so. This method is an improvement over more traditional sampling standardization methods that standardize to a common number of occurrences because it is more likely to capture rare taxa and therefore to capture real diversity differences through time. In the case of Pliocene biogeography, however, SQS implies that the Pliocene tropical West Pacific was 20–25% less diverse than the West Atlantic (Table 2), depending on the sampling level used.

The ratio of West Pacific to West Atlantic tropical diversity today is 1.9:1. If we adopt a conservative approach and only include genera within each region that are Pliocene or older, and therefore almost certainly present within these tropical regions in the Pliocene, the ratio shrinks slightly to 1.7:1 (Table 2). Assuming these ratios bracket the relative diversities of the tropics during the Pliocene, we can use them to estimate a range of absolute diversities for these regions. Due to its superior sampling, the unstandardized Pliocene tropical West Atlantic sample of 243 bivalve genera likely captures more of the actual diversity present than the West Pacific does, and is therefore used as the baseline for our first set of diversity calculations (with the understanding that any absolute diversity determined by using direct counts of fossils must be an underestimate). Using this base-

line, the present-day West Pacific to West Atlantic diversity ratios predict a tropical West Pacific Pliocene diversity of between 413 and 462 genera (see Jackson and Johnson 2001 for a similar estimate based on a broader range of taxa derived from the Panama Paleontology Project collections), 282–331 greater than the 131 genera documented in the region in the literature (the "shortfall" category in Table 2). Using the ratio predicted by sampling standardization (between 0.74:1 and 0.8:1; Table 2), the 243 tropical West Atlantic genera predict a West Pacific diversity of 180–194 genera, still at least 267 genera shy of that predicted by modern diversity ratios. As discussed above, an increase of that magnitude within that brief time frame is exceedingly improbable. The general result from sampling-standardized PaleoDB data is a strong downgrading of diversity in the West Pacific in favor of the Atlantic, in stark contrast to our expectations based on the evolutionary and biogeographic history of the modern fauna, as described previously. If the tropical West Pacific samples were roughly equivalent to those of the Western Atlantic, or if SQS was able to compensate for differences, we would not expect the significant shortfalls in these calculations.

A second assessment derives from the observation that sampling-standardization (SQS) of the PaleoDB data returns a cool-temperate Northeast Atlantic diversity that is virtually equal to that of the tropical West Atlantic (Fig. 5). Such equality is unlikely to have been the case even during the warmer part of the Pliocene: the very heavily sampled Northeast Atlantic Pliocene fauna contains 63 genera that are now absent from the region, a number insufficient to have brought that fauna into parity with the tropical West Atlantic. Therefore, we must conclude that even the tropical West Atlantic Pliocene is undersampled relative to the Northeast Atlantic, despite the spectacular efforts of the Panama and Dominican Republic projects (Budd et al. 2001, 2008). This undersampling is perhaps to be expected given the long tail of rare taxa that typifies tropical biotas (e.g., Bouchet et al. 2002), although SQS aims to minimize this effect.

These findings indicate that the cool-temperate Northeast Atlantic data in the PaleoDB is the best sampled region by far, and the 157 genera found within this region should therefore be the most appropriate baseline for predicting diversity in both the West Pacific and West Atlantic. In modern oceans, the ratio of West Pacific to Northeast Atlantic genus diversity is 3.9:1 (Table 3). The ratio of tropical West Atlantic to Northeast Atlantic diversity is 2.03:1. With the conservative step of subtracting genera lacking a fossil record that is Pliocene or older (although this lack probably derives from tropical undersampling), the ratios become 3.2:1 and 1.9:1, respectively. These ratios, combined with the 157 genera found in the Pliocene Northeast Atlantic, predict diversities between 502 and 612 genera in the West Pacific and between 298 and 319 genera in the West Atlantic. Ratios derived from SQS values predict a Pliocene diversity between 121 and 144 genera for the tropical West Pacific and 159–180 genera for the tropical West Atlantic (depending on the sampling cutoff; Table 3). This result again reverses the expected region of greater diversity—the West Atlantic comes out as significantly more diverse than the West Pacific, and gives absolute numbers that are far short of the present day; more than 450–500 genera would have had to migrate into or originate in the tropical West Pacific (and more than 135 genera in the tropical West Atlantic; see "shortfall" rows in Table 3) within the past 2.6 Myr to produce present-day genus richness in those areas.

The steepness of the flanks of the Pliocene LDG is not well established by fossil evidence. For example, we do not yet know when OTT genera actually entered a given extratropical region, only that they were extant within a given time bin, so modern temperate occurrences of genera may overestimate Pliocene diversities in those regions. However, the PRISM data and models do corroborate the overall impression drawn from macrofossils that the temperate zones have cooled since the Pliocene (Fig. 4). Further, although regional extinction estimates from well-sampled extratropical Pliocene faunas vary (Fig. 6A), all suggest that temperate standing diversities
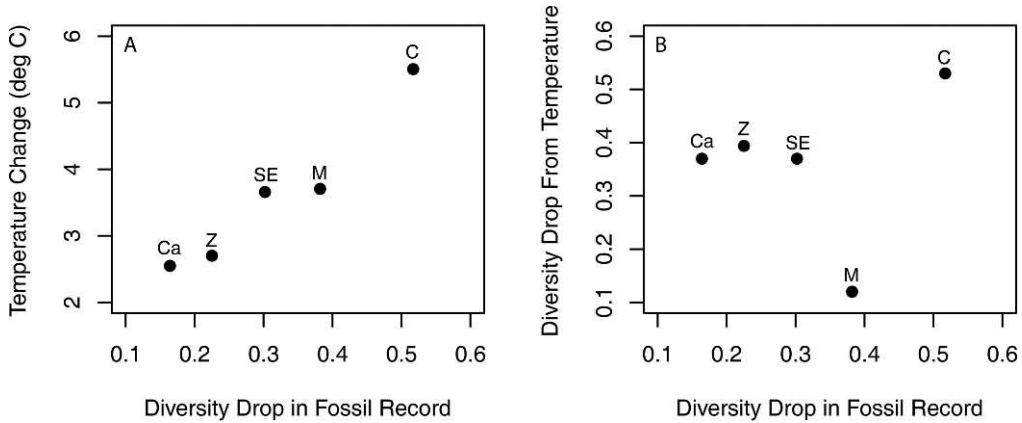
FIGURE 6. Regional extinction intensities (incorporating both global extinction and contraction of geographic ranges) of genera in well-sampled temperate-zone Pliocene bivalve faunas following taxonomic standardization plotted against temperature decline from the Pliocene to the Recent (A) and the expected drop in diversity for each region given the magnitude of the temperature change and the modern correlations between temperature and diversity (Table 1) (B). Main sources: M (Mediterranean) – Monegatti and Raffi 2001; C (Chile) – Rivadeneira and Marquet 2007; Kiel and Nielsen 2010; Z (New Zealand) – Beu 2004, 2006; Beu and Raine 2009; Maxwell 2009; SE (Southeast United States) – Campbell 1993; Ca (Californian Province) – Hall 2002; Smith and Roy 2006.

were indeed higher in the Pliocene and that the limbs of the Pliocene LDG began to collapse toward modern levels during the Pliocene cooling. Those regional extinction intensities are significantly correlated with the magnitude of temperature changes since the Pliocene (Fig. 6A; Spearman's rho = 1, $p = 0.017$). However, because regional standing diversity is the net outcome of extinction, origination, and immigration, and the relationship between temperature and diversity in modern oceans varies between hemispheres and among coastlines (Table 1), the regional changes in SST do not predict the expected change in diversity given the present-day correlation between temperature and latitudinal diversity (Fig. 6B; Spearman's rho = 0.2, $p = 0.74$). This discordance between predicted extinction and predicted net outcome suggests that additional factors besides simple temperature declines drive the evolution of modern gradients (see also Todd et al. 2002, Crampton et al. 2006, and Kiel and Nielsen 2010), so that simple temperature correlations are insufficient guides to regional or global diversity dynamics.

Implications for the Reconstruction of Fossil Biodiversity Patterns

The use of statistical methods to standardize sampling inequities may not yield accurate, or even improved, estimates of diversity for regions, coastlines, or the globe. Here we have used our understanding of modern biogeography and its first-order oceanographic underpinnings to provide a rank-order expectation for Pliocene diversity values along the major coastlines. The raw and SQS PaleoDB data on Pliocene fossil bivalves diverge dramatically from these expectations. The magnitude and spatial pattern of these inter-regional discrepancies indicate that they are more likely to arise from pervasive sampling biases than from massive, undocumented post-Pliocene diversifications and/or invasions. There is, however, a great difference in the time spans represented by the Pliocene (~3 Myr) and modern (a few centuries) data sets, and in the regions from which they have been drawn. Possible time-averaging effects of those differences on the pattern in Figure 5 therefore deserve comment.

Time-averaging could artificially produce the diversity peaks in the Pliocene of the Caribbean or the cold-temperate Northeast Atlantic if (a) evolutionary turnover was higher, (b) environmental heterogeneity was greater, or (c) range expansions/local extinctions occurred more readily in these regions. The pattern in Figure 5 could not arise via (a) evolutionary differences among regions, be-

cause the higher origination rates in the tropics (Crame 2000, 2001; Jablonski et al. 2006; Kiessling et al. 2010) should, if anything, inflate Pliocene tropical diversity relative to higher latitudes (Foote 2000). First occurrences in the tropical West Pacific over the past 11Myr were roughly twice those in the tropical West Atlantic (61 versus 26 genera respectively [D. Jablonski unpublished data]), so that Caribbean diversity could not have been inflated by time-averaging of origination rates. The pattern in Figure 5 could not arise via (b) environmental heterogeneity, because the tropics contain most of the terrigenous-clastic depositional environments seen at high latitudes (>75% of Late Cenozoic tropical shelves are terrigenous or mixed carbonate-terrigenous in composition [Walker et al. 2002; Best et al. 2007]) plus a richer array of marine carbonate environments, including biotically rich reef-associated settings. The remaining possibility, that (c) binning the biogeographic dynamics during the Pliocene inflated diversity in the Northeast Atlantic and Caribbean to a level significantly exceeding that of the Indo-West Pacific, would require a quintupling or quadrupling of diversity in the northeast Atlantic, and more than a doubling of diversity in the Caribbean. Given the relative homogeneity of extratropical faunas at the genus level, such inflation could not have been accomplished by shifting faunas within the north Atlantic. The influx of taxa into the North Atlantic from the North Pacific was not close to the necessary numbers (see Vermeij 2001) and there is no evidence for a massive short-lived influx of taxa from the tropics into the northeast Atlantic during the Pliocene. Creating the Pliocene northeast Atlantic–Indo-West Pacific diversity imbalance by biogeographic time-averaging would require that such well-studied faunas as the Coralline Crag and Kattendijk Formation contain >70% tropical genera, which is not the case (see Marquet 2005; Williams et al. 2009; Long and Zalasiewicz 2011). Such biogeographic shifts are equally unlikely to account for the apparent inflation of Caribbean diversity in Figure 5 relative to the tropical West Pacific. The differential dynamics of regions and potential consequences of strong-

ly unequal temporal bins are certainly worth considering in large-scale diversity analyses, but do not underlie the patterns reported here.

Clearly, the mismatch between any plausible actualistic estimate for the deployment of Pliocene diversity on the one hand and the most extensive compendium of the past half-century of paleontological literature on the other indicates that non-critical sampling exclusively from the literature is insufficient to extract an accurate biogeographic signal, even after sampling standardization. Any standardization algorithm must assume, a priori, that the primary diversity patterns in time and space are contained in some minimal fashion by the raw data.

We emphasize here that we draw on PaleoDB data not to criticize this important enterprise, but to underline the value of using models of marine climates and their biological implications, based on well-studied modern systems, to provide first-order estimates for *expected* diversity patterns in the younger geologic record, which can then be compared with paleontological patterns documented for that interval. A mismatch between model expectations and paleontological observations could signal either a genuine biotic anomaly or problems with the data; we focus on a sufficiently young interval where the latter is far more likely than the former.

The PaleoDB has important potential in the reconstruction of provincial regions, which play fundamental roles in biogeographic and biodiversity patterns. However, modeling of those patterns may be the only viable approach for more accurately inferring spatial and temporal diversity trends through the Cenozoic, at least until major new sampling efforts in the tropical West Pacific bear fruit (see Johnson et al. 2011). For example, new analyses using information theory have found that unstandardized (raw) data track sea level and other environmental signals in a fashion that indicates determination by a common cause rather than sampling biases (Hannisdal and Peters 2011). These results do not, however, indicate that reverting to analyses of raw data will be a panacea for biased data collection when the raw data are so distorted spatially as to reduce the largest diversity

peak on the globe to third or fourth rank among regions.

Accurately assessing the biogeographic structure of the world's oceans through time is important for a number of questions besides the history of global diversity per se, including the role of tectonics and other factors in the waxing and waning of provinciality, the effect of climate shifts on regional faunas, and spatial patterns in the origins of evolutionary novelty. For example, the tropical West Pacific is a center for both wide- and narrow-ranging species and genera, and poor samples in the late Cenozoic will lose not only large numbers of endemics but also significant geographic range extensions into that area, distorting estimates of interregional differentiation relative to other provinces and other time bins. Although we cannot restore such data, barring further faunal descriptions, an actualistic approach can make qualitative statements on how certain large-scale estimates should be revised. Such biases will also affect the sizes of geographic ranges, a key variable in analyses of extinction and origination rates (e.g., Jablonski and Roy 2003; Foote et al. 2008; Jablonski 2008; Birand et al. 2012). Spatial variation in turnover rates may be similarly affected, as sampling must truncate both bases and tops of stratigraphic ranges in the late Cenozoic of the tropical West Pacific more severely than in other tropical and extratropical regions. For that matter, if the tropical West Pacific was an important generator of morphological as well as taxonomic diversity during the Cenozoic (e.g., Vermeij 2012b), then even inventories of novelties or temporal and spatial patterns of morphospace occupation must be revised upward for the late Cenozoic, or for clades that flourished then, relative to better-sampled regions and time intervals.

Of course, the only direct data on the geographic position of genera through time are from the fossil record, but given the limitations of the published record (which may prove to be the limitations of the rock record itself), climatic and oceanographic principles can be used to inform estimates of taxonomic or phenotypic diversity for undersampled regions. Correcting diversity estimates by using hydrographic principles is obviously complicated by ever-changing continental configurations and climatic conditions. However, even a coarse-grained understanding of broader climatic patterns can be useful. Should fossil data of those times show dramatic differences from the most plausible location of latitudinal and longitudinal diversity peaks, such discordances should indicate important areas for further investigation. Data standardization can commonly detect latitudinal trends given some minimum sampling of tropical high-diversity areas, but cannot compensate for the levels of mismatch between sampling intensities and diversity hotspots that exist for the late Cenozoic. Indeed, at those times during the Phanerozoic when mismatches among coastlines or across latitudes are similarly large, time-averaging will be similarly insensitive to the diversity pattern and preclude studies of diversity levels or biogeographies.

Acknowledgments

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