

Convergence, divergence, and parallelism in marine biodiversity trends: Integrating present-day and fossil data

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Paleontological data provide essential insights into the processes shaping the spatial distribution of present-day biodiversity. Here, we combine biogeographic data with the fossil record to investigate the roles of parallelism (similar diversities reached via changes from similar starting points), convergence (similar diversities reached from different starting points), and divergence in shaping the present-day latitudinal diversity gradients of marine bivalves along the two North American coasts. Although both faunas show the expected overall poleward decline in species richness, the trends differ between the coasts, and the discrepancies are not explained simply by present-day temperature differences. Instead, the fossil record indicates that both coasts have declined in overall diversity over the past 3 My, but the western Atlantic fauna suffered more severe Pliocene–Pleistocene extinction than did the eastern Pacific. Tropical western Atlantic diversity remains lower than the eastern Pacific, but warm temperate western Atlantic diversity recovered to exceed that of the temperate eastern Pacific, either through immigration or in situ origination. At the clade level, bivalve families shared by the two coasts followed a variety of paths toward today's diversities. The drivers of these lineage-level differences remain unclear, but species with broad geographic ranges during the Pliocene were more likely than geographically restricted species to persist in the temperate zone, suggesting that past differences in geographic range sizes among clades may underlie between-coast contrasts. More detailed comparative work on regional extinction intensities and selectivities, and subsequent recoveries (by in situ speciation or immigration), is needed to better understand present-day diversity patterns and model future changes.

biogeography | diversification | extinction | latitudinal diversity gradient | marine biodiversity

Biodiversity is spatially structured at many scales. Biogeographic realms and provinces, the partitioning of species among environments within biogeographic units, and genetic population structure within species are all manifestations of the ecological and evolutionary processes that generate and maintain diversity in terrestrial and marine systems. For most terrestrial and marine organisms, the first-order global diversity pattern is the latitudinal diversity gradient (LDG): the increase in the number of species and higher taxa from the poles to the tropics (1). This gradient, as seen today, has been shaped by a combination of origination, extinction, and past geographic shifts of taxa; all of these variables might differ among clades, functional groups, and land masses or ocean basins (2–7), even when the overall LDG is similar. Thus, a mechanistic understanding of the present-day LDG in general, and along specific equator–pole transects, for distinctive regional faunas, and for individual clades, cannot be divorced from its history.

The need for historical data is underscored by the differences and similarities among related clades that broadly conform to the LDG. As in many evolutionary questions (8), process-based interpretations of similarities and differences in diversity at local

and regional scales require separation of parallelism and convergence, and data on the timing and context of divergences. However, present-day data alone may not be able to determine whether similar latitudinal trends represent common histories—i.e., parallel diversity trajectories from similar starting points—or convergence from different starting points. Similarly, different latitudinal trends might reflect either long-standing contrasts or recent divergences driven by clade- or region-specific contrasts in origination, extinction, and/or range shifts. Thus, the pervasive emphasis on the approximate fit of taxonomic diversity trends (e.g., refs. 9–11) and biogeographic structure (e.g., ref. 12) to present-day environmental factors, and present-day similarities of diversity of a single clade in multiple regions (e.g., ref. 13), captures only part of the underlying story. Owing to difficulties in accurately quantifying extinction and the timing of most past distributional shifts, exclusively present-day data can be actively misleading when attempting to reconstruct biotic histories (14–17).

Here we use intertidal and shelf-depth marine bivalves, a group with a well-documented LDG in modern oceans and a rich fossil record, to explore how an integrative approach can provide a direct, comparative window into the temporal and spatial dynamics of clades along the LDG. We do this by comparing two of the best-sampled coastlines, the Northern Hemisphere section of the American coasts (hereafter, E Pacific and W Atlantic), which show broadly similar LDGs that differ in detail and have different Late Cenozoic environmental and evolutionary histories. The differences between these coasts appear to involve all three components of diversity dynamics: origination, extinction, and spatial

Significance

The fossil record can reveal the complex history behind present-day diversity patterns. For marine bivalves, similarities and differences in species diversity within lineages among regions are better explained by past extinction, origination, and immigration than by contrasts in today's climates alone. A signature of more severe extinction in the western Atlantic relative to the western Pacific coast is still evident in the tropics, but not in the temperate zone, where more prolific diversification and/or immigration has allowed the western Atlantic to match or surpass eastern Pacific diversities for many lineages. Species persistence in the temperate zone is associated with broad geographic range prior to an extinction pulse ~2–3 My ago, underscoring the importance of history for understanding modern biodiversity patterns.

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shifts. By focusing on the Pliocene bivalves in the two best-sampled temperate regions along each coast [California and the Carolinas–Virginia region (hereafter termed Virginia), both at ~32°N–40°N], living at a time when extratropical temperatures were warmer and latitudinal temperature gradients gentler than today (18–20), we can begin to tease apart the complex roles of regional extinction and range expansion in shaping present-day patterns of species richness (hereafter termed diversity). For comparison, we summarized modern diversity within the same latitudinal bins, rather than using the natural provincial boundaries, to assess local extinctions from Pliocene to Recent.

Results

Modern SSTs. The LDGs of the two coasts are significantly correlated when resolved to 1° latitudinal bands (Fig. 1A; Spearman rank correlation coefficient $r_s = 0.89$, $P < 0.001$). Both coasts also exhibit the genus-level out-of-the-tropics (OTT) dynamic that has been documented for bivalves on a global scale for the past ~12 My (Fig. S1A): genera tend to originate in the tropics and expand to higher latitudes without losing their tropical occurrences. The coasts show different, albeit nearly monotonic, sea surface temperature (SST) trends with latitude (Fig. S1B), and, given the significant temperature–diversity correlations reported for bivalves and other marine groups (9, 12, 21), we might expect to find predictable differences in diversity along the two coasts. However, the diversity differences at a given latitude are complex (Fig. S1C): the first differences of the two LDGs are not significantly correlated for 1° latitudinal bins (Pearson’s correlation coefficient $r_p = 0.02$, $P = 0.88$), and the diversity divergences across latitudes only loosely correspond to the SST differences between the two coasts [Fig. 1B; using first differences of the two variables, $r_p = 0.01$, $P = 0.92$, and in an Ordinary Linear Model (OLM), $R^2 = -0.01$, $P = 0.92$]. The diversity contrasts are most striking in the tropics [where extinction has long been implicated (22–25)] but are also seen in the temperate zones, where we can best analyze temporal trends because of a good fossil record. Given the failure of present-day differences in SSTs to fully explain the richness differences, we consider two different historical explanations: phylogenetic composition and effects of past extinctions.

Phylogeny. Overall, the two coasts are nearly identical at the taxonomic level of families, sharing 90% (56 out of 62) of the extant North American bivalve families. Thus, interregional differences in clade representation at this level cannot underlie the between-coast contrast. The diversities of individual families are also generally correlated between the two coasts ($r_s = 0.83$, $P < 0.001$), but clades show differing levels of between-coast discordance in diversities, without always mirroring the overall pattern of the whole-fauna comparisons. For the nine families most diverse on the two coasts today, most are more diverse in the E Pacific tropics, although the Lucinidae shows roughly equal diversity on both tropical coasts. In the warm midlatitudes (~25°N–40°N), more families tend to have similar diversities on the two coasts, with the W Atlantic tending to have higher values where deviations are present (Fig. S2). Again, the diversity differences observed for the nine families do not correlate with present-day SST differences between the two coasts at a given latitude, and diversity values often differ strongly at a given SST (Fig. S3 and Table S1).

Some studies have found a significant effect of taxon age or clade age on the LDG (10, 26), so we assess whether the two coasts’ faunas sampled different portions of the bivalve evolutionary tree. Neither coast shows a significant difference in the steepness of the LDG between young and old cohorts of bivalve genera, using the Eocene–Oligocene boundary (33.9 My) as the cutoff between old and young genera (as in ref. 10), and calculating the steepness by fitting an OLM to the tropics–temperate diversity drop from the difference in median diversity in tropical

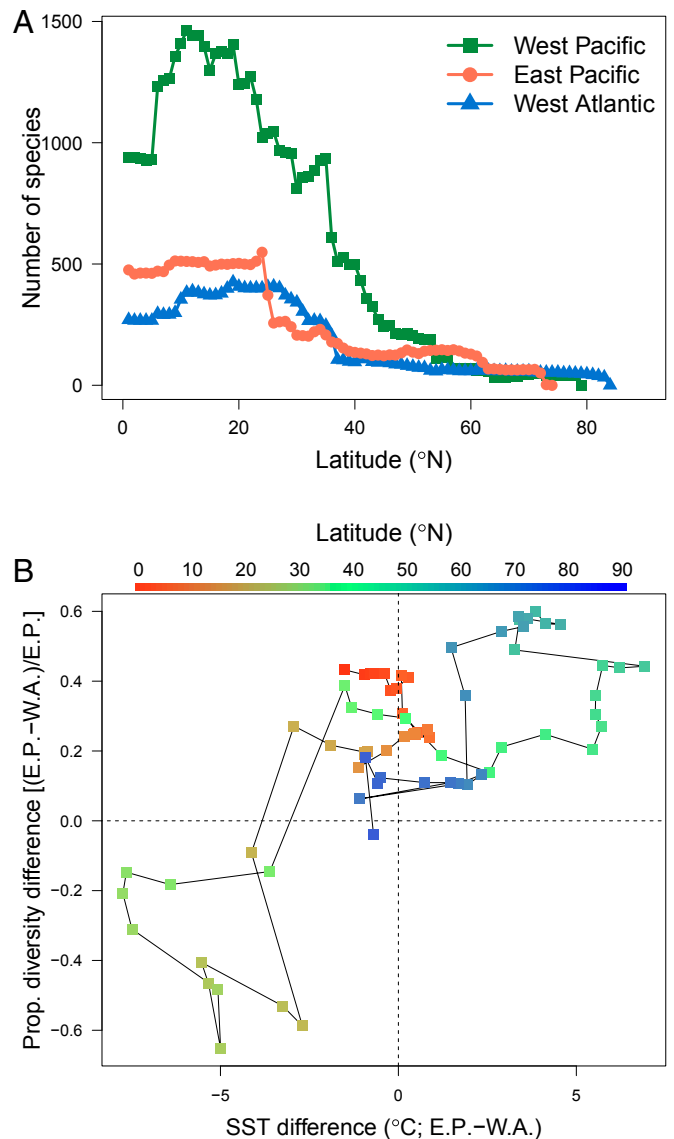


Fig. 1. Present-day diversity of marine bivalves on Northern Hemisphere coastlines. (A) Bivalve diversity patterns along the focal coasts (E Pacific and W Atlantic), with W Pacific included for scale. (B) Proportional diversity differences between the two coastlines do not correspond to SST differences for the same latitudinal bins (solid line connects successive latitudes). Thus, diversity is roughly 30% greater in the E Pacific (E.P.) than the W Atlantic (W.A.) across a range of conditions: when the E Pacific SST differs from the W Atlantic by -3 °C, 0 °C, and $+5$ °C; locations having similar temperatures can exhibit a range of diversities, e.g., where the E Pacific is ~ 3 °C cooler than the W Atlantic, its biota can have 50% less, 10% less, and 30% more diversity than the W Atlantic.

(20°N–25° N) and midtemperate (40°N–45°N) bins [W Atlantic: 93 old versus 127 young genera, Kolmogorov–Smirnov test, $P = 0.76$; E Pacific: 91 old versus 162 young genera, $P = 0.97$; we omit the few genera that originated before the end-Cretaceous mass extinction, which reset the evolutionary rates and biogeographic patterns of bivalves (27, 28)]. Therefore, the diversity differences between the two coasts are unlikely to derive from differing age distributions of the lineages occurring there.

Regional History. We next consider how past extinctions and subsequent rebounds have shaped the latitudinal trends in species richness today. Our two focal Pliocene faunas experienced net

decreases in both mean SST [estimated mean Pliocene–Recent difference for California: 2.1 °C; for Virginia: 2.9 °C (18, 20)] and diversities; regional extinctions have also been documented on both coasts, although their direct connection to climate change is debated and other factors may also have been involved (20, 23–25, 29). Consistent with the previous work cited above (e.g., refs. 20, 23, and 25), the observed temperature drops are at least indirectly associated with regional extinctions of bivalve species (regionally extinct species in California: $57 \pm 6\%$; in Virginia: $75 \pm 5\%$; 95% binomial confidence interval), often involving range contractions toward the south and resulting in net reductions in regional diversity from the Pliocene to the present day (California: $12 \pm 4\%$; Virginia: $8 \pm 3\%$). Thus, Virginia was more severely affected by the Pliocene–Pleistocene extinctions, but subsequent origination and immigration compensated such that the net diversity drop from the Pliocene to the present day is statistically indistinguishable from California, and the warm temperate W Atlantic fauna now harbors more species than corresponding E Pacific latitudes. In other words, Virginia has experienced a larger turnover in diversity since the Pliocene (Jaccard similarity coefficient for Virginia is 0.17, and for California is 0.34, corrected for sample sizes following ref. 30).

For the 49 families shared by both Pliocene faunas, rank orders in species richness are significantly correlated between the California and Virginia faunas, both in the Pliocene ($r_s = 0.77$, $P < 0.001$) and today ($r_s = 0.83$, $P < 0.001$), and between the Pliocene and today in both faunas (California: $r_s = 0.88$, $P < 0.001$; Virginia: $r_s = 0.84$, $P < 0.001$). However, although the species diversities of families tend to be similar in California and Virginia in the Pliocene, they tend to be lower in present-day California (OLM slopes of Californian on Virginian richness: Pliocene, 1.10 ± 0.08 ; today, 0.76 ± 0.04 ; both $P < 0.001$, but a significantly shallower slope today). Focusing on the nine most diverse families discussed above to eliminate the noise inherent in low-diversity families, diversity was correlated in the Pliocene between California and Virginia ($r_s = 0.75$, $P = 0.02$), but not today ($r_s = 0.53$, $P = 0.14$). Among those taxa, both the Pliocene (sometimes weaker) correlation and the lack of Recent correlation remain when we truncate the data to exclude either the best- or poorest-preserved family, or both. (Without Pectinidae, which has greater preservation potential owing to its more robust shell mineralogy, the Pliocene $r_s = 0.67$, $P = 0.07$, and the Recent $r_s = 0.52$, $P = 0.20$; without Mytilidae, which has poorer preservation potential owing to the high organic content of its shell, the Pliocene $r_s = 0.79$, $P = 0.02$, and the Recent $r_s = 0.37$, $P = 0.37$; excluding both, the Pliocene $r_s = 0.72$, $P = 0.07$, and the Recent: $r_s = 0.36$, $P = 0.44$.)

Differential extinction clearly underlies some of the between-coast contrasts in species richness within and among families. Measured by the proportion of species recorded from the California and Virginia Pliocene that are absent from those regions today, we find that regional extinction was more severe in the W Atlantic than in the E Pacific for most families (Fig. 2). Families that evidently lost most or all of their Pliocene species over the past 3 My have generally recovered by evolution or immigration, although one low-diversity family (Gryphaeidae) was permanently lost from California, and five were lost from Virginia (Condylocardiidae, Glossidae, Mesodesmatidae, Placunidae, and Psammobiidae), despite persisting farther to the south. The 11 families with at least five Pliocene species in each fauna show no correlation of extinction intensity between California and Virginia (Fig. 24; $r_s = 0.5$, $P = 0.12$). However, extinction alone cannot account for between-coast differences, as the between-coast difference in today's diversities among the nine most diverse families analyzed above is not correlated with the differences in extinction intensity ($r_s = -0.13$, $P = 0.73$; excluding Pectinidae, $r_s = -0.20$, $P = 0.65$; excluding Mytilidae, $r_s = 0.18$, $P = 0.67$; excluding both, $r_s = 0.14$, $P = 0.78$). Thus, subsequent speciation and invasion were important factors in shaping the present-day faunas.

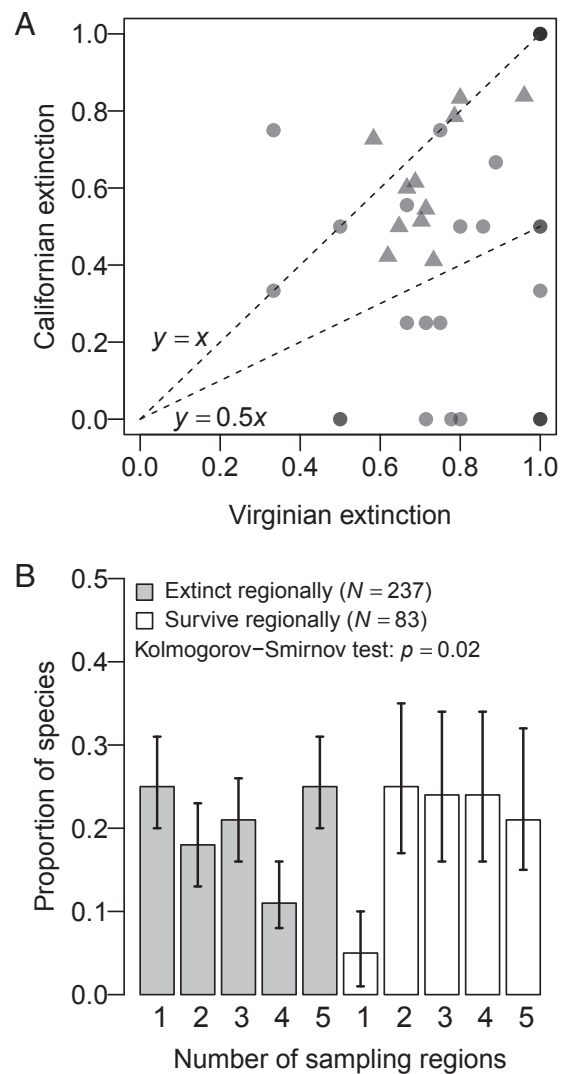


Fig. 2. Pliocene–Recent extinction patterns. (A) Combined regional and global extinction within each bivalve family is generally more severe in the Virginian region than in California. The dashed lines represent $y = x$ and $y = 0.5x$, triangles represent families having more than five species on both coasts, and darker symbols indicate multiple families showing the same patterns. (B) In the Virginian region, species that became extinct (gray bars) were significantly less widespread than those that persisted in the area (open bars; a Kolmogorov–Smirnov test shows the two distributions are significantly different, $P = 0.02$). Geographic range is quantified as the number of sampled regions in which a species occurred (following ref. 53); results are insensitive to alternative binning schemes.

Even families with similar diversities on the two coasts today can have contrasting histories. For example, the clade with the best preservation potential, the Pectinidae, has 11 species in California today, and 13 in Virginia, but California contains 10 local survivors from the Pliocene and 1 later addition (via speciation or immigration), whereas Virginia had only 2 local survivors and 11 additions. More generally, local survivors are a larger fraction of species diversity of families in California, such that most families have larger diversities in Virginia than expected for their proportion of local survivors, corroborating the importance of differential origination or immigration in determining current diversity differences (Fig. S4).

In sum, just in the few million years encompassed here, the 48 bivalve families shared between California and Virginia have had markedly different histories of extinctions and recoveries (Fig. 3).

Using a simple 10% difference criterion (see *SI Materials and Methods*), 25 families had different Pliocene diversities on the two coasts. Of those, nine have since converged in their modern diversity, by a variety of pathways: of the two most diverse families, the Semelidae mostly via immigration and speciation, and the Pectinidae by both extinction and immigration/speciation. Of the 16 families that remained significantly different in their regional diversities, 6 suffered similar extinction intensities on the two coasts, while 10 suffered differential extinction intensities on the two coasts without converging in diversity. Conversely, of the 23 families that had similar Pliocene diversities on the two coasts, 9 have diverged today, including the Cardiidae and the Arcidae. Among others that show similar Pliocene and present-day diversities, three families underwent differential extinction compensated by origination/immigration on the two coasts, including most notably, the Veneridae (the most diverse living family outside the deep sea). The nine most diverse families noted above also show a variety of diversity pathways (Table S1).

Discussion

The contrast between the post-Pliocene diversity dynamics of the two coasts of North America is surprising, given that they were connected by a shared tropical seaway until ~3.5 My ago (31), and both show an OTT dynamic over the past 12 My. However, since the tropical connection was severed, and well before that in the temperate zones, the coasts have had different oceanographic histories (for tropics, see refs. 25 and 31; for temperate zones, see refs. 22, 23, 32 and 33). In the temperate zones, the overall regional diversities were evidently shaped by extinction and subsequent recovery through origination and immigration, with clades showing a variety of divergent, convergent, and parallel trajectories between coasts. Thus, similar diversities today for a given clade in different regions are no guarantee of a shared history or similar rates of diversification (as noted in refs. 10 and 13). Conversely, today's interregional diversity contrasts might reflect geologically recent developments rather than deep evolutionary differences.

The general differences between coasts, clades, and time intervals documented here are most likely real; incomplete sampling of both modern and fossil faunas requires caution in reading precise diversity levels and other fine details, but sampling alone is unlikely to drive the general patterns. Especially robust measures likely include the significant contrasts in present-day regional and clade diversities, and the temporal shifts in rank order diversities through time. Regarding the present-day contrast, extant species are still being described in both regions (34, 35) but at approximately the same rate, providing no evidence that the Caribbean biota is likely to catch up with, let alone surpass, that of the tropical E Pacific.

The greater diversity drop that we record in the W Atlantic is also consistent with prior work finding more severe Plio-Pleistocene extinction in that region, particularly the Caribbean, relative to the E Pacific (22–25). This extinction probably accounts for the most striking present-day difference between the coasts: the higher diversity in the E Pacific tropics despite the fivefold greater shelf area in the tropical W Atlantic (calculated in ArcGIS 10.2.1), and the greater variety of marine habitats associated with its past and present Caribbean coral reef systems, commonly viewed as important multipliers of regional marine biodiversity (36). The different extinction histories may be only indirectly related to climate change, with changes in primary productivity and habitat types also implicated (23, 25, 31). The spatial configuration of the two provinces may also have contributed to their contrasting histories: The N and S coasts of the Caribbean largely trend longitudinally, whereas the tropical E Pacific today, with the more diverse fauna, occupies a narrow, northwest–southeast trending shelf. Climatic and environmental changes related to the uplift of Panama would have caught the longitudinal array of Caribbean

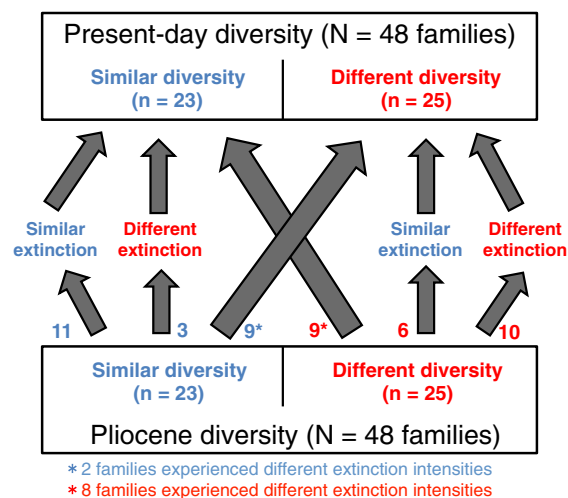


Fig. 3. Convergent, divergent, and parallel pathways in diversity of the 48 families shared by the two coasts, from the Pliocene to the present day. Numbers by arrows are the number of families that follow each path. Blue numbers are similarities at that step; red numbers are differences at that step. Among the two sets of nine families that follow the paths crossing in the center of the diagram, two families that started with similar diversities, and eight families that started with different differences, experienced different extinction intensities since the Pliocene. See *Results, Regional History* for details.

shelves in enfilade, affecting all of the faunas along their lengths. A similar set of changes along the narrow Panamanian shelf would affect a far smaller area at a time, and could be ameliorated by latitudinal shifts in geographic ranges of species, as commonly found in the fossil records along the continuous Pacific coastal shelf (37). Thus, in contrast to analyses of terrestrial diversity patterns (38, 39), present-day habitat area is a poor predictor of large-scale marine diversity patterns within major climate zones (40), and, equally important, the tropical faunas from which OTT taxa emerged into temperate zones each had distinctive histories.

In the temperate zone, our data show that the Virginia fauna has suffered more severe extinction than that in California, as the Caribbean did relative to the tropical E Pacific, but that the net result was greater diversity in the warm temperate W Atlantic, in contrast to the tropics (Fig. 1A). Further, the diversity differences among the regionally dominant families are not correlated with Pliocene–Recent extinction intensities, indicating that post-Pliocene speciation and immigration were also involved in shaping present-day biotas. Such a scenario is consistent with previous suggestions (3, 40) that the milder temperature gradients along the W Atlantic owing to the northward flow of the Gulf Stream have been more conducive to northward expansion of species over the past 5 My (the E Pacific receives cool water via the California Current and localized upwelling, both potential barriers to the northward spread of species). This hypothesized contrast in the biotic dynamics of western and eastern boundaries of ocean basins, with a stronger flow of species and clades out of the tropics in the W Atlantic, may account for the rapid recovery of diversity in that region, even as in situ diversification rates in the Caribbean left its diversity lagging behind that in the tropical E Pacific. The oceanographic contrast and its biotic consequences also imply that diversity will be higher, and will more readily rebound following extinction, along the temperate margins of the W Pacific than along the margins of the E Atlantic, a prediction supported by the high diversities recorded in southern Japan and southeast Australia (40).

Despite the extensive fossil sampling in our focal regions, absolute extinction values should be treated cautiously, owing to the lack of comprehensive information about differential preservation in the two regions. However, results were qualitatively unchanged when

we excluded the most diverse families having unusual sampling and preservation potential [Pectinidae (scallops), having dissolution-resistant shell mineralogy, and Mytilidae (mussels), having disintegration-prone shells (41–43)], suggesting that the first-order patterns are robust, including different intensities of post-extinction speciation and/or immigration. Separating in situ speciation from immigration over such brief time intervals is difficult in the fossil record, particularly with less complete sampling in our tropical source regions; molecular data may be informative here, as we expect very young species to be more readily detectable via short branch lengths of a time-calibrated molecular phylogeny than via fossil morphospecies. Newer models such as GeoSSE (44), which aims to infer region-dependent rates of speciation, extinction, and range evolution from a phylogeny of extant species, may be useful in this context, although the validity of such approaches has recently been questioned (45, 46). Biogeographic approaches integrating phylogenies with spatially explicit fossil data can also be effective tools here (47).

The differences in bivalve family dynamics on the two coasts remain poorly understood. They may reflect the contrasting histories of the regions beyond the few variables that we have incorporated in our study, and differences among clades on a single coast may reflect intrinsic differences (see differential family-level extinction patterns over time in ref. 48). Extinction selectivity on factors such as morphological variation and body size has been detected in specific families in our study areas (29, 49), but more extensive analyses are lacking.

Another potentially general factor may be variation in the size of geographic ranges among Pliocene species; extinction risk has proven to be inversely related to geographic range size in many paleontological analyses (50, 51). For the Virginian faunas, Pliocene species that are now regionally or globally extinct had significantly narrower ranges than those that persisted in the region (Fig. 2B), as is also reported for California Pectinidae during the Pliocene–Pleistocene extinction event (29). The data suffer from relatively limited spatial coverage, but regional geographic ranges of marine bivalve species are significant proxies for the total geographic ranges of those species (52). Thus, our data suggest that the strongest predictors for the extinction term in the regional biodiversity equation will be found by direct paleontological analysis, and that Pliocene geographic range size played a role—an important factor that can cut across family-level phylogeny and functional groups, and is difficult to retrieve from present-day biogeographic or molecular data owing to subsequent climate-driven range-size fluctuations (37).

Our data also appear to contain post-Pliocene range expansions that involve more than the simple temperature tracking that appears to predominate in marine ectotherm biogeography (e.g., refs. 7, 20, and 53). At least 22 species in the modern Virginian fauna evidently ranged only as far north as Florida in the Pliocene. These species may represent bridge species (3) that have recently expanded their climate tolerances, although further investigation of their systematics relative to extant congeners is also warranted. If genuine, these data pinpoint species that have expanded poleward in the face of severe cooling, and so would be interesting targets for comparative analysis of physiological evolution. Such data would also represent direct evidence for interspecific differences in rates of climate niche evolution, hypothesized predictors of responses to future global change (54). In any case, assuming that these species actually ranged to our focal area in the Pliocene, but were not sampled or recognized (unlikely given the intensity and quality of the work there), would only strengthen the differential extinction pattern in Fig. 2B.

The primary kinds of historical data available for the present-day biota absent the fossil record, i.e., phylogenetic topology and relative timing of lineage splits, generate patterns that contrast with those recorded here. In part, this contrast is because many biogeographic analyses based solely on present-day biotas assume

that lineages have relatively stable distributions through time, and (necessarily) omit past extinctions and environmentally driven range dynamics that must have helped shape modern-day biodiversity patterns, perhaps most markedly over the past 3 My. For example, inferring patterns through deeper time via phylogenies, basal clades of birds but more derived clades of mammals tend to be more diverse in the tropics (10), and another analysis of mammal phylogeny found that “the New World tropics are a diversity cradle whereas the Old World tropics are a museum of old diversity” (26). In contrast, bivalve LDG steepness is unrelated to the ages of genera or families (see also ref. 55), although bivalve orders that originated in the early Paleozoic do show shallower LDGs than orders that originated in the middle to late Paleozoic, despite the subsequent intervention of three of the Big Five mass extinctions (6). Further, both New and Old World tropics serve as simultaneous diversity generators and diversity accumulators for bivalves (refs. 3 and 4 and, for mammals, ref. 56). These contrasts may signal genuine differences among animal groups, but they could also reflect the use of different metrics, violation of model assumptions, and the lack of robust data on extinction and past geographic range shifts for the terrestrial groups. For example, mammals in the New World tropics evidently suffered significantly more severe Late Pleistocene extinction than in the Old World tropics (57), and the impact of this difference in extinction intensity on the apparent cradle–museum pattern has not been tested; indeed, little direct evidence is available on Pleistocene extinction intensities of tropical mammals relative to tropical birds. Our results suggest that such data may be crucial for understanding their apparent contrast in evolutionary dynamics. More generally, our analyses add to the wide array of studies that have drawn a richer understanding from the geologic record into the nature and origins of present-day diversity patterns (3, 4, 6, 25, 36, 51, 55).

Conclusion

The modern diversity patterns of bivalves along the American coasts have a complex history. The variables most readily accessible for extant species—current environmental conditions, present-day occurrences, and phylogenetic relationships—do not fully capture these dynamics. Paleontological data are also incomplete in isolation, but integrating extinctions and past distributional shifts (i.e., regional extinction) with modern biogeography and phylogeny can provide key evidence for testing hypotheses of convergence, divergence, and parallelism in the diversity trajectories of clades and whole biotas along disparate coasts. Many taxa lack sufficient fossil records for this integrative approach, but model systems such as marine bivalves can be used to develop methods that can be applied more broadly, and can provide insights into limitations and potential improvement of current models. The richer understanding of diversity dynamics that comes from paleontological data will shape theory and can provide a framework for anticipating biotic changes in the face of accelerating global change. The future of the fossil record lies partly in its potential to trace the roots of present-day diversity in time and space, and to shed light on the paths that biodiversity will follow from here.

Materials and Methods

Data on extant bivalves were obtained from an existing database ([Dataset S1](#); described in refs. 3 and 50; September 5, 2014 download). SST data were drawn from the HADISST1.1 database, UK Met Office Hadley Centre, averaged over 1998–2008 (3, 7, 12). Pliocene data for our focal regions were based on refs. 58–60, which extend through the entire Pliocene Epoch (61), updated and taxonomically standardized to the extant-species database. Further details on data and analytical methods are provided in [SI Materials and Methods](#).

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