

Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient

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Latitudinal diversity gradients are underlain by complex combinations of origination, extinction, and shifts in geographic distribution and therefore are best analyzed by integrating paleontological and neontological data. The fossil record of marine bivalves shows, in three successive late Cenozoic time slices, that most clades (operationally here, genera) tend to originate in the tropics and then expand out of the tropics (OTT) to higher latitudes while retaining their tropical presence. This OTT pattern is robust both to assumptions on the preservation potential of taxa and to taxonomic revisions of extant and fossil species. Range expansion of clades may occur via “bridge species,” which violate climate-niche conservatism to bridge the tropical-temperate boundary in most OTT genera. Substantial time lags (~5 Myr) between the origins of tropical clades and their entry into the temperate zone suggest that OTT events are rare on a per-clade basis. Clades with higher diversification rates within the tropics are the most likely to expand OTT and the most likely to produce multiple bridge species, suggesting that high speciation rates promote the OTT dynamic. Although expansion of thermal tolerances is key to the OTT dynamic, most latitudinally widespread species instead achieve their broad ranges by tracking widespread, spatially-uniform temperatures within the tropics (yielding, via the nonlinear relation between temperature and latitude, a pattern opposite to Rapoport’s rule). This decoupling of range size and temperature tolerance may also explain the differing roles of species and clade ranges in buffering species from background and mass extinctions.

biodiversity | biogeography | climate | macroecology | macroevolution

The latitudinal diversity gradient (LDG), meaning the decrease in the number of species and higher taxa from the equator to the poles, is as pervasive among marine organisms as it is on land (1, 2). Although the marine LDG is increasingly well documented, we are only beginning to understand the evolutionary and biogeographic dynamics of speciation, extinction, and distributional shifts that generate and maintain it. Here we evaluate these dynamics in marine bivalves, a group that not only parallels diversity patterns of the overall marine biota (1–3), but permits the integration of biogeographic, phylogenetic, and spatially explicit paleontological data (4, 5) and has thus become a model system for macroecological and macroevolutionary analysis. Extending our previous work, we show that clade origination in the tropics and range expansion out of the tropics [the OTT model (5)] are major factors in the origin and maintenance of the bivalve LDG. We reanalyze and update paleontological data on the OTT dynamic and present evidence that at least some bridge species, whose ranges cross the tropical/extratropical boundary, are important in the expansion of lineages along the LDG. Although bridge species violate niche conservatism with their expanded thermal ranges, we find that species with narrow thermal ranges often achieve unexpectedly broad distributions, an effect particularly

strong in the tropics. The nonlinear relationship between temperature and latitude may account for several large-scale biogeographic and evolutionary patterns, including the inverse relation between range size and latitude and the contrast in clade survivorship between background and mass extinctions.

Bivalves as a Model System

The present day marine biota contains ~8,000 bivalve species, ranging from detritus and suspension feeders to parasites, carnivores, and photo- and chemosymbiotic taxa; free-living and attached burrowers and surface dwellers whose mobility ranges from permanent cementation to episodic swimming; and adult sizes ranging from <1 mm to >1 m. The group has a rich fossil record whose biases are increasingly understood and thus can often be taken into account (6–10). The poor paleontological sampling of the Indo-West Pacific relative to other regions is a significant problem for all clades throughout the Cenozoic (5, 11–14), but the sampling biases run counter to several of the key results discussed here, so that our conclusions should be conservative.

The extant bivalve fauna contains ~1,300 genera and subgenera, and we treat them all as genera representing distinct clades, following previous work (15). We have informally attempted to avoid paraphyletic taxa, but some uncertainty remains owing to a lack of detailed phylogenetic data. Morphologically defined molluscan genera generally map well onto molecular phylogenies, and the correspondence is particularly robust among clades for macroecological variables such as body size and geographic range (16). See *SI Materials and Methods* for additional details on the materials and methods.

The bivalve LDG is strong at both species and genus levels, globally and along each continental margin, with a biodiversity hotspot in the tropical West Pacific, where bivalve generic diversity exceeds the other tropical regions by about a factor of 2 (and species diversity by about a factor of 3) (Fig. 1; Fig. S1). Marine bivalves have exhibited an LDG at least since the Mesozoic (4, 17), although the history of today’s longitudinal patterns, such as the

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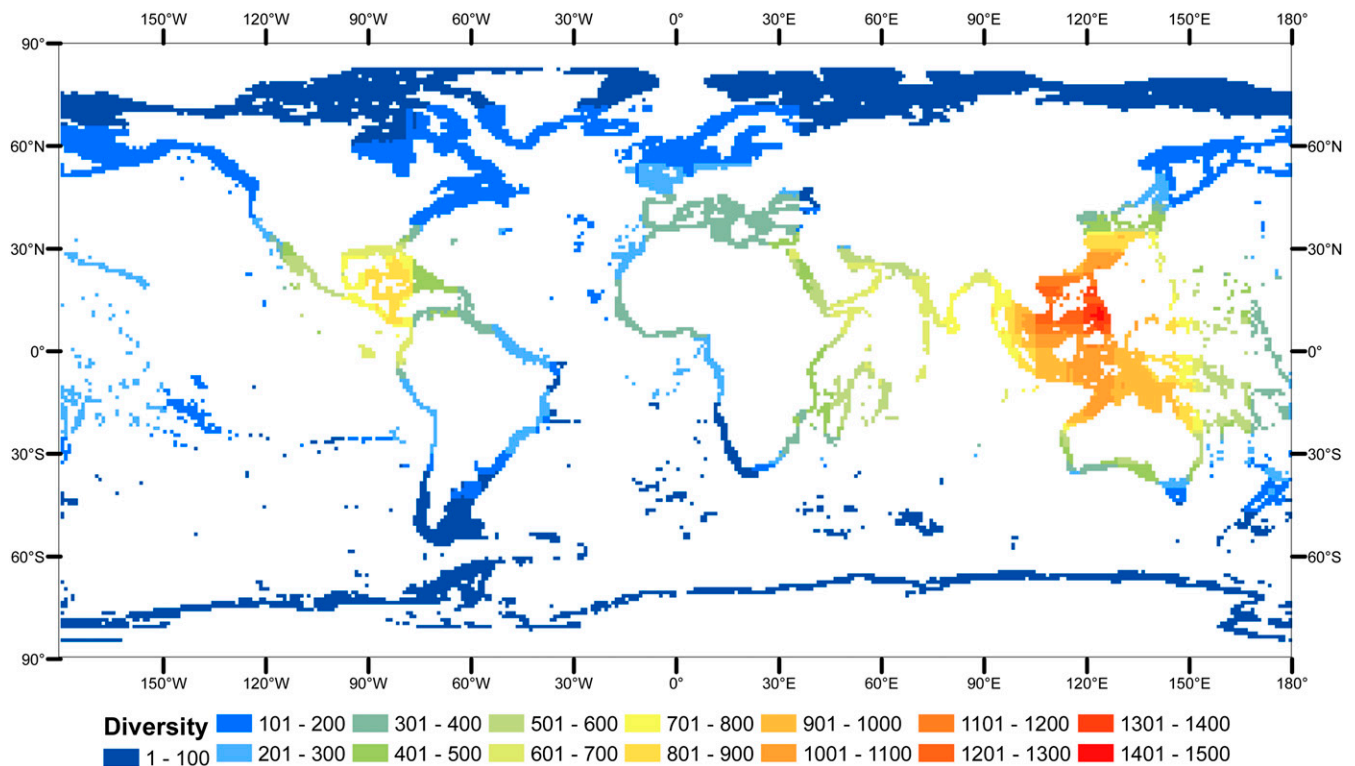


Fig. 1. Species richness of present-day marine bivalves occurring at continental shelf depths (< 200 m).

West Pacific diversity maximum, is less clear. The relative magnitude and geographic position of tropical diversity peaks have probably shifted through the Phanerozoic, owing to changing continental, oceanic, and climatic configurations (18, 19), but the present configuration evidently dates at least to 20 Mya (19). The role of regional extinction in shaping second-order aspects of the LDG, such as anomalously high or low regional diversities, and the steepening of the LDG during later Cenozoic polar cooling, is only now being clarified, and considerable work is still needed (14, 19–22).

Clade Origin and Expansion

The LDG is built and maintained by regional variations in origination, extinction, and shifts in geographic distribution, but the relative roles of these components may vary among higher taxa and perhaps between marine and terrestrial systems (5, 12, 23–28). For marine bivalves, roughly twice as many well-preserved genera first appear in the tropics as in extratropical regions in each of three successive time bins encompassing the last 11.6 My (henceforth the study interval), suggesting that differential origination patterns predominate in this system (Fig. 2). Only extant families having $\geq 75\%$ of their genera known as fossils are considered sufficiently well preserved for analysis (5), but the results are not sensitive to this threshold (*SI Materials and Methods*). The values in Fig. 2 surely underestimate tropical/extratropical differences in origination, owing to the undersampling of the tropical fossil record, particularly in and around the Indo-West Pacific diversity maximum; this sampling bias makes rigorous per-taxon calculations difficult. However, except for the East Atlantic, where the late Cenozoic tropical fossil record is “woefully meager” (29), each major coastline in the world ocean exhibits preferential tropical origination (Fig. S2).

The strong tendency for genera to first appear in the tropics over the study interval has proven to be robust to ongoing taxonomic revisions and new molecular phylogenetic data. No significant

change in the overall pattern is seen from the previous analysis (5) despite the addition of 31 genera and removal of 47 genera from the time bins analyzed in Fig. 2. Additions are primarily because of revised assessment of previously described fossil species (7), whereas removals are largely because of reassessments of fossils that push a clade’s first occurrence into an older time bin, phylogenetic analyses that merge some genera, and the relegation of three families to poor preservation status by the description of new genera not yet known as fossils (documented in ref. 30).

Clade expansion OTT has been pervasive in marine bivalves. Using the 75% preservation threshold (as in the rest of this paper), 77% of the 103 genera whose first fossil appearances are in the tropics during the study interval have expanded to higher latitudes over time, and, as noted above, some fraction of the genera that first appeared in the temperate zones during the study interval must also have originated in the tropics but entered the fossil record only on reaching well-sampled extratropical regions. In fact, when tropical first occurrences of bivalve genera over the last 12 My are standardized to the number of tropical vs. extratropical bivalve occurrences over this time interval in the Paleobiology

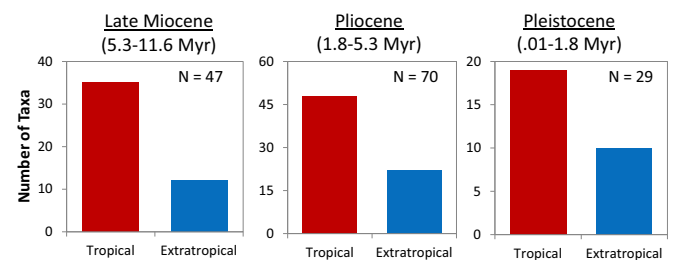


Fig. 2. First occurrences of bivalve genera in the tropical and extratropical fossil record for three successive geologic time bins. All pairs differ significantly ($P = 0.001$, exact binomial tests).

database (<http://paleodb.org/>, 4 September 2011 download), as a rough measure of sampling intensity across latitudes, tropical originations occur at least four times more frequently per fossil occurrence than in the extratropics, for both New and Old World transects (14).

This OTT process has evidently shaped the biogeographic and evolutionary profile of the LDG at the genus level since at least the start of the Cenozoic era ~65 My ago (31) [a modeling approach corroborates these results and may help to clarify processes in clades lacking a rich fossil record (32,33)]. Thus, the tropics contain both widespread and endemic genera, but most temperate genera are shared with lower latitudes—narrow-ranging genera are uncommon outside the tropics. In evolutionary terms, the frequency distributions of geological ages of genera vary significantly with latitude: the tropics show a steeply right-skewed hollow curve, with many young genera and a long tail of old ones, whereas the polar latitudes have a dearth of young taxa and a shallower hollow curve that shares most of the genera in the right-skewed tail of older forms with the tropics (Fig. S3). The lower median age of tropical genera therefore captures the Cenozoic origination dynamic but does not reflect the presence of old genera shared between tropics and poles. At the genus level, the tropics are thus both cradle and museum of diversity, whereas the poles are primarily a museum, mainly harboring genera that evidently originated at mid and low latitudes (5). A few high-latitude taxa clearly originated in situ, but primarily in cool-temperate zones such as the North Pacific (34) rather than in polar waters.

Genera that expand out of the tropics, whether via their founding species or by later ones, often show significant lags between their first occurrence in the tropics and their entry into the extratropical fossil record. Along the temperate coasts of North America, where the late Cenozoic faunas are documented in synoptic, taxonomically standardized compendia (35, 36), the median lag time is 4.8 My ($n = 22$ genera including mid-Miocene taxa to increase statistical power; Fig. 3A). The sample size is small but suggests that the biotic or physical events that permit genera to expand outside their initial climate zone are relatively infrequent per taxon. Biotic factors that promote the OTT process are uncertain (see below), but OTT clades in our study interval have significantly more tropical species today than clades of the same age that originated in, but are now restricted to, the tropics, and a comparable differential is seen between older widespread genera and tropics-only genera (Fig. S4).

Bridge Species in Marine Biogeography

For the genera that first appeared in the late Miocene-Pleistocene tropics, and thus demonstrably participated in the OTT dynamic, extratropical diversity is dominated today, by a factor of 4, by species that occur in both tropical and extratropical zones, here termed bridge species (Dataset S1). For all genera today found in both tropical and extratropical regions, regardless of age, the ratio of bridge species to extratropics-only species is ~2:1, suggesting that bridge species have been a major factor in the spatial dynamic of this larger pool of taxa as well. In fact, ~95% of the genera today shared between tropics and extratropics contain at least one living bridge species, and the number of bridge species exceeds the number of exclusively extratropical species in those genera in most 5-My cohorts through the entire Cenozoic (Fig. 3B). A similar value is seen for the warm-temperate/cool temperate boundary (639/688 genera worldwide = 93%). These data appear to contradict a model where species straddling the tropical-temperate boundary are simply transient stages in the speciation-driven range expansion process (37).

The present day distribution of bridge species cannot determine where those species originated. However, for the 48 OTT genera in the study interval whose first fossil occurrence in the tropics is assigned to an extant species, 69% of those species are bridge species today (Dataset S1), suggesting that

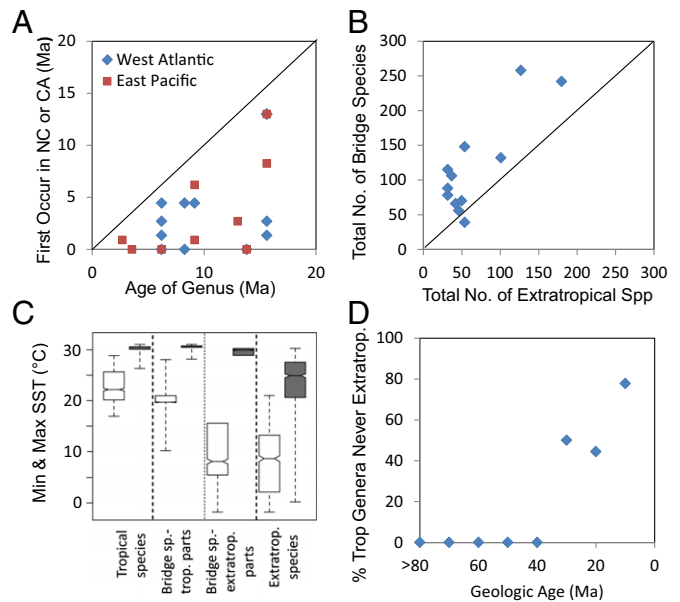


Fig. 3. Spatial and temporal dynamics underlying the OTT process. (A) Lag between time of tropical origination (geologic age of genus) and entry into the temperate-zone fossil record (lag = distance below 1:1 diagonal) in North America, using only taxa that today extend at least as far as North Carolina or California ($n = 22$, Middle Miocene-Pleistocene genera). (B) For genera today occurring in both tropics and extratropics, the number of bridge species equals or exceeds the number of entirely extratropical species, regardless of genus age for 5-My cohorts back to 60–65 My. Diagonal = 1:1 line. (C) Minimum (white) and maximum (shaded) SSTs occupied today by tropics-only and extratropics-only species in the West Pacific compared with the tropical and extratropical parts of bridge species ranges. See Fig. S5 for further examples. (D) Percentage of genera today endemic to the New World tropics but having extratropical fossil occurrences, as a function of the geologic ages of the genera.

many bridge species originate in the tropics and expand to higher latitudes, thereby carrying their genera out of the tropics. The first occurrences of the extant bridge species are evenly split between the tropical core and its margins, and regardless of their oldest location, all but three of those bridge species today extend into the core tropics. Accordingly, the maximum sea surface temperatures (SSTs) in the tropical portions of bridge species today do not differ significantly from those occupied by tropics-only species. The minimum SSTs occupied by bridge species, even within the tropics, are significantly lower than those occupied by tropics-only species, along coastlines and in the four most diverse families analyzed separately (Fig. 3C; Fig. S5). Caution is needed owing to less complete tropical sampling, but these data all suggest that bridge species have significantly expanded thermal ranges relative to their ancestral states rather than originating exclusively in cooler waters within or at the margins of the tropics. Further evidence for changes in thermal ranges is seen outside the tropics, where the minimum SSTs occupied by the extratropical portions of bridge species often do not differ significantly from those occupied by extratropics-only species in the Western Pacific, unlike the pattern in the Eastern Pacific, where bridge-species temperature minima are significantly warmer than in the extratropics-only taxa; Fig. S5); these results are complicated by differential diversification of extratropical species in warm-temperate vs. cool-temperate settings, and more detailed analyses would be useful here. Thus, bridge species evidently tend to expand their temperature ranges compared with related species (via an expansion of their lower limits) rather than simply shifting their temperature preferences.

Geographic Range Sizes and Thermal Ranges

Geographic ranges of species are set in part by barriers to larval dispersal, substratum availability, and other physical and biotic factors (38), but temperature tolerances are clearly important range determinants in marine invertebrates (39). The biogeographic structure of the marine bivalve fauna can be predicted with 89–100% accuracy by SST plus salinity and productivity (the last two having lesser but significant effects), without additional biological or physical data (40). Given such temperature effects, nonlinear changes in SST with latitude should strongly influence the deployment of geographic ranges across the globe (41–43). Latitudinally widespread species tend to occupy significantly narrower thermal ranges than expected from a null model where placement of geographic ranges is independent of climatic gradients (Fig. 4A). Those widespread species evidently achieve their broad latitudinal ranges by occupying the most common SSTs on the continental shelves. The distribution of SSTs by continental shelf area is strongly bimodal, but the latitudinally and longitudinally most continuously extensive SSTs are 27–28 °C. Consequently,

(i) tropical species tend to be significantly more widespread than

expected for their thermal ranges under the null model, and (ii) species tend to occupy unexpectedly high median temperatures even as latitudinal ranges extend beyond 8,000 km (Fig. 4B; Fig. S6). Inevitably, the few truly cosmopolitan species (e.g., *Hiatella arctica*) encompass a broader thermal range and have lower mean SSTs than the widespread tropical species, but even the cosmopolitans have significantly smaller thermal ranges and higher means than expected for their gargantuan spatial distributions (Fig. 4C). Consequently, latitudinal ranges in marine bivalves tend to decrease in size toward the pole, contrary to Rapoport's rule, which contends that latitudinal ranges tend to narrow in the tropics (44–46).

The frequency distributions of latitudinal range sizes vary among coastlines because the warm, poleward-flowing currents along the western boundaries of ocean basins promote more prolific spreading of species to higher latitudes than seen on eastern boundaries, which are characterized by cooler equatorward flows and more cool-water upwelling zones (14). Therefore, tropical conditions encompass ~51–52° of latitude along western coastlines, centered roughly on the equator, but only about ~36–38° along the East Pacific and East Atlantic, with a strong asymmetry about the equator, and extratropical gradients in annual SST are gentler along western boundaries. Presumably in response to this intercoastal contrast, Western Hemisphere clades that originated in the tropics in our study interval have extended significantly further north in the Western Atlantic than in the Eastern Pacific (Fig. S7).

Discussion

OTT Dynamic: Clades. A complete, multilevel description of the spatial and temporal dynamics underlying the LDG will require combined molecular and paleontological analysis at an unprecedented scale (20). A working hypothesis that is compatible with the data for marine bivalves is that genera tend to originate in the tropics and expand to higher latitudes, generally remaining present in the tropics as they do so. This OTT dynamic is especially striking because it has demonstrably operated over an 11-My interval dominated by the steepening of the global temperature gradient, culminating in extensive high-latitude Pleistocene glacial cycles and thus requiring increasingly greater temperature adaptation within the clades expanding poleward. Equatorward contraction of existing ranges must also occur when the poles cool (Fig. 3D), steepening the LDG by local extinction even as new clades leave the tropics.

Although clades often track temperature and other environmental factors over time, range expansions across climate zones is a constant theme in Phanerozoic biogeography, and a biogeographically important subset of speciation events is related to changes in thermal range. Such shifts in climate niche are evidently rare in bivalves on a per-clade basis, as indicated both by the evolutionary lag between tropical origin and entry into the extratropical fossil record shown here and by the significant phylogenetic signal in the position of geographic range endpoints and thus of thermal ranges (47). Despite this overall phylogenetic conservatism, our results corroborate observations that the boundaries between climate zones (tropical/temperate) are not loci where congeneric species, sisters or not, regularly meet (48–50), as would have been expected if those boundaries were key sites of speciation or if competitive exclusion often limited shifts across those boundaries. In any case, the OTT dynamic clearly violates the general tendency toward niche conservatism often used to explain the LDG (51–53).

The first occurrence of bivalve genera in the tropical fossil record and their subsequent expansion to higher latitudes is likely to be robust to sampling, and the numbers are conservative, because the Cenozoic tropical fossil record is severely undersampled relative to the temperate zones (5, 11–14). Further, continued sampling and taxonomic standardization has not changed the OTT

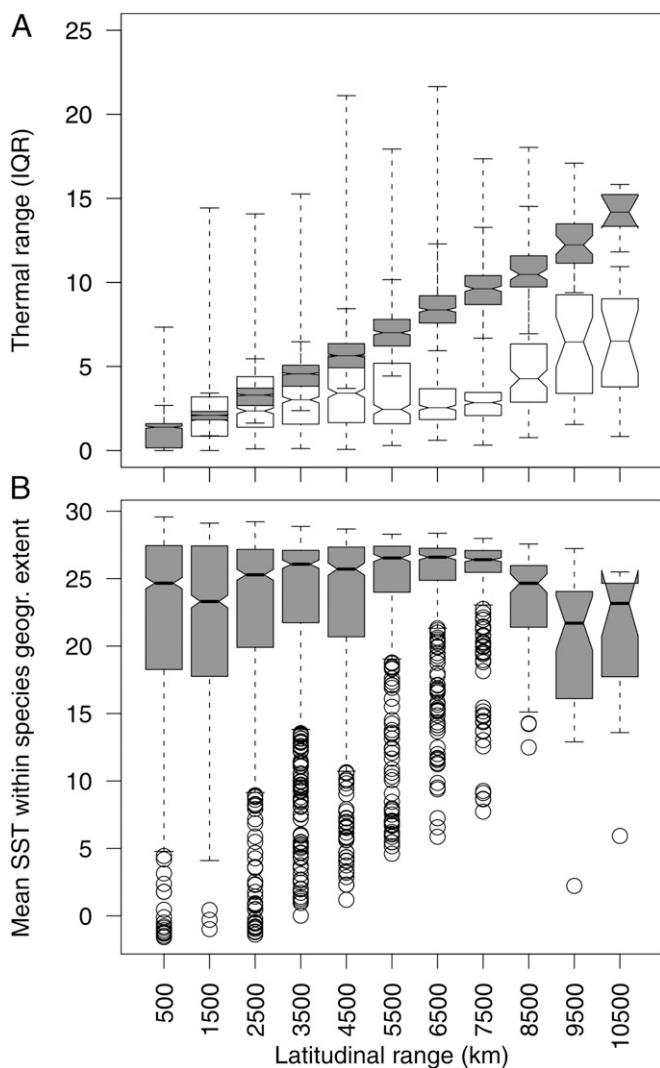


Fig. 4. (A) Geographic ranges of bivalve species (white boxes) encompass narrower temperature ranges than expected from a null model (gray boxes; see SI for details); IQR, interquartile range. (B) Mean annual SSTs encompassed by geographic ranges-size classes of bivalve species, showing that widespread species tend to occupy warm temperatures.

pattern, and the results are also robust to changes in the inclusion of clades based on their preservation potential. In fact, the proportion of genera known to have originated in the tropics and expanded to higher latitudes is likely to increase with further study, for at least two reasons. First, improved sampling and taxonomic standardization of the tropical fossil record is likely to detect more first occurrences than in the already heavily studied temperate zones. Second, more detailed analysis of the extratropical fossil record is likely to reveal that some of the taxa restricted to the tropics today had brief extratropical excursions—i.e., some tropical endemics will prove to be former OTT genera that later contracted their ranges. Of the 51 genera that have a fossil record and are today restricted to the New World tropics, at least 28 (55%) occurred extratropically at some point in the geologic past. The proportion of genera that are exclusively tropical now but occur in the extratropical fossil record increases with increasing genus age (Fig. 3D), and it remains formally possible that this pattern reflects an extratropical origin for some genera, followed by invasion of the tropics and loss of extratropical occurrences [the “tropics-as-museum” scenario (54)]. Some phylogenetic analyses do indicate an into-the-tropics history for some marine genera (55), but numbers are too sparse to seek trends. Other genera may have had more complex histories of zonal originations and extinctions, appearing in tropical and extratropical latitudes multiple times; such cases are difficult to find for marine bivalves but may be more common in terrestrial clades (56). Overall, the most parsimonious reading of our analyses involves tropical origins, expansion, and contraction back to the tropics (57); temperate origins and expansion into the tropics are evidently rare for bivalves.

To extend these analyses further back through the Cenozoic, more elaborate sampling-standardization approaches will be required, owing to the imbalance between tropical and extratropical records. A different dynamic may apply to the greenhouse worlds of the early Cenozoic, when warm climates reached beyond 40° N and S (58). Some data suggest that an OTT dynamic operated during the recovery from the end-Cretaceous extinction (59, 60), but a more comprehensive analysis is needed.

OTT Dynamic: Species. Bridge species are remarkably pervasive in marine bivalves and are also known in terrestrial clades (61, 62); their evolutionary and biogeographic role deserves investigation. However, caution is needed when inferring process from present day species distributions, as species have almost certainly been repositioned by repeated, extensive reshuffling in response to Pleistocene climate fluctuations in both marine and terrestrial settings (63, 64). Detailed integration of molecular phylogenies and spatially explicit paleontological data are needed to confirm whether bridge species (*i*) are generally the vehicle for clade expansion out of the tropics, so that extratropical species are a monophyletic group within each genus, or (*ii*) are secondary phenomena, drawn from multiple invasions of congeneric species directly from the tropics and perhaps accumulated during high-amplitude climate oscillations. Hybrid models are also possible, such as multiple separate derivations of extratropical species from bridge species, or a monophyletic radiation drawn directly from tropical endemics. The sparse phylogenetic data for marine species are mixed, supporting (65) or rejecting (66) monophyly out of the tropics and within climate zones, and have yet to be integrated with fossil data.

Although bridge species are phylogenetically pervasive—nearly every genus has at least one, despite widespread interspecific heritability of geographic range end points (47)—they appear to be temporally scarce, judging by the lags between the origins of most genera and their spread to higher latitudes, where the well-studied and rich fossil record is most likely to capture them soon after arrival. When and how this niche expansion occurs in these species is unclear. The necessary high-resolution species-level data are unavailable, but the prolonged genus-level lags suggest that the

OTT process is not strongly linked to short-term oceanographic fluctuations such as the El Niño/La Niña–Southern Oscillation and North Atlantic Oscillation that can ameliorate extratropical conditions for years to decades. We hypothesize that longer Milankovitch-scale oscillations (100,000 y, 400,000 y, etc.) and more protracted events such as the mid-Pliocene Climatic Optimum are more effective drivers of the OTT process. Such climate excursions can position populations in relatively warm but more seasonal refugia at higher latitudes, promoting the evolutionary expansion of thermal ranges under less severe conditions than the surrounding shelf, enabling them to establish in new climate zones (20, 67). Milankovitch oscillations are especially marked during ice ages but leave an imprint on marine systems at other times as well (68). They might also increase the proportion of bridge species by cooling tropical margins and thus promoting in situ lowering of minima on temperature ranges.

We have probably underestimated the fraction of bridge species that originated in the tropics because we only analyzed the present day position of the oldest species of each genus; such species that did not expand OTT might have given rise to bridge species that carried the genus to higher latitudes. Fossil data further suggest that bridge species often originated in the tropical core. The Miocene and Pliocene core tropics enjoyed SSTs at least as warm as today through most or all of our study interval (69, 70), implying that the initial species of OTT genera expanded their temperature ranges and became bridge species. Even if the fossil occurrences are imprecisely identified and instead represent close relatives of extant bridge species, the transition to bridge species capability can evidently occur as readily during a species' history or between related species as among higher-level clades. More intensive sampling of the tropical fossil record is also required to determine whether the lag between a genus' origin and its invasion of higher latitudes involved a prolonged interval in the tropical-temperate transition zone; adaptation to the broader temperature variation there might have enabled bridge species to expand to higher latitudes more readily than for species coming directly from the tropical core.

OTT Selectivity and Speciation Pressure. Many factors probably determine which clades expand out of the tropics; body size may be important, perhaps via positive correlations with fecundity (71–73), and we suspect that differential expansion also occurs among functional groups. Greater competitive or colonizing ability among the range-expanding clades (74) also cannot be ruled out and needs testing. However, a higher-level dynamic also operates: OTT genera tend to be drawn from the most prolific diversifiers (Fig. S4), and the number of bridge species in a genus is also a positive function of species richness in that genus (Fig. S8). OTT expansions at both genus and species level might thus simply derive from “speciation pressure”—more speciation in the tropics yields more potential populations to carry the clade poleward by analogy to propagule pressure in invasion biology (75). Alternatively, OTT clades might have unexceptional speciation rates but are rich in geographically widespread and thus extinction-resistant species, simply because they happened to produce such range-expanding species. More detailed phylogenetic and paleontological data are needed to test these alternatives, which are not mutually exclusive.

Geographic Ranges, Climate Zones, and Extinction. Despite the apparent gradient of increasing thermal range with latitude, latitudinal ranges are broadest in the tropics rather than in high latitudes. This trend, opposite to the pattern termed Rapoport's rule, emerges because tropical waters vary so little in temperature over such great latitudinal distances. Many widespread species apparently achieve their large geographic ranges not because they have broad tolerances but because they are adapted to some of the most widespread temperatures in the oceans. Ironically then, our data directly contradict Rapoport's rule but support the much

older idea that was the explanation for the postulated Rapoport pattern: that tropical species tend to have narrower environmental tolerances and niche dimensions than extratropical species (76–78).

This decoupling of thermal range and geographic range size may explain hierarchical patterns of extinction selectivity observed in the fossil record. For the bulk of geological time, broad geographic range at both species and clade levels correlates with lower extinction rates (79, 80). The analyses above suggest that widespread species are not necessarily extinction resistant through broad environmental tolerances, but because they spread their extinction risk by occurring in regions that normally have semi-independent environmental histories. Thus, a hurricane or a prograding delta is more likely to eliminate a localized species than one with a 10^6 -km² range. However, major perturbations, such as disruptions to entire climate zones or to the thermal structure of the ocean, will overcome extinction buffers that rely on species range size per se, leaving the emergent property of clade range size on a multiprovincial scale as the chief promoter of clade survivorship, largely independent of species-level ranges (81, 82).

Bivalve genus-level extinction rates may also be lower in the tropics (5), as in planktic foraminiferal species (83), but sampling biases and the spatial dynamics of clades again render analysis difficult. Per-taxon origination and extinction rates of macrobenthic genera are reportedly higher in tropical reef systems (84), but sampling and relatively coarse time bins (~10 My) make these observations difficult to generalize beyond reef builders (and presumably obligate reef dwellers), long thought to be more extinction prone than taxa in other marine environments (85). This last point is supported by observations that reef builders have significantly higher extinction rates than taxa with a “reef affinity” [a category defined by a significant excess of reef occurrences rather than by reef-only distributions (86)].

Extinction is also important in the dynamics of the LDG by opening opportunities in recipient regions. Such extinction-mediated range expansions are a common theme for modern and ancient biodiversity at many scales, from mass extinctions (59, 78, 82) through smaller-scale natural perturbations (72, 87) to present-day invasions mediated by anthropogenic disturbance (88, 89), although counterexamples and alternative models exist (90, 91). The very noisy diversity-area relationship for the 20+ temperate-zone marine provinces [statistically insignificant for the most prominent biogeographic schemes (92,93)] suggests that extinction keeps the temperate zones far from saturation, thus promoting entry of taxa from the tropics (87), presumably with some amount of temperate zone origination and biotic interchange, e.g., along the Aleutians in the North Pacific (34), over the Arctic (34), and across the temperate Southern Hemisphere (94). The anomalously low diversity along the coast of Chile, apparently produced by a late-Cenozoic extinction pulse, might seem to contradict this argument, but the Chilean extinction may be related to the intensification of upwelling and thus represents a sustained change in conditions (21, 95). Similarly, extinction near the poles has accompanied high-latitude refrigeration (22) but has evidently left a residue of extinction-resistant taxa in a biota resistant to the entry of clades from lower latitudes (87), a state that may change dramatically as polar climates warm (96, 97). Such warming could place Antarctic species at high extinction risk, as they generally lack the broad thermal ranges to persist in situ and will be unable to track preferred temperatures to cooler latitudes (unlike tropical and temperate species, assuming access to suitable habitats).

The tropics present an intriguing problem on the role of extinction, incumbency, and diversity dependence at large spatial scales. Entry of temperate taxa into the tropics appears to be uncommon, suggesting saturation. However, exceptions to the unidirectional OTT flow exist for marine (55) and terrestrial (56) situations, and more importantly, the tropics are the origination site of plentiful species, genera, and evolutionary novelties (13, 98–

101), contradicting a saturation view. Unless these originations can be closely tied to local opportunities created by extinction, the general resistance of the tropics to extratropical invaders requires a nonequilibrium mechanism, related perhaps to niche dimensions (77) or biotic interactions (74).

Conclusions

The exceptional fossil record and well-sampled modern fauna of marine bivalves affords a valuable model system for understanding the dynamics of a major group that appears to be representative of the temporal and spatial patterns of most post-Paleozoic marine taxa. Our data suggest that most marine clades originate in the tropics and spread poleward, at least initially via bridge species that straddle the tropical-temperate boundary. Despite the apparent role of such bridge species in the OTT dynamic, many more species evidently attain wide latitudinal ranges (and even wider longitudinal ranges) not through broad tolerances but by exploiting a narrow set of widespread spatially uniform temperatures. Expansions out of the tropics are relatively rare, with significant lags between clade origins and their entry into the temperate zone, and clades with greater diversification within the tropics are more likely to export species out of the tropics and across the LDG than clades of similar age but lower diversification rates.

The patterns reported here are statistical in nature, with exceptions, and are blurred by extinction and later range shifts. However, they are pervasive in our model system, repeated temporally for successive cohorts of clades and in the overall fauna, and repeated spatially on multiple coastlines that share relatively few genera and almost no species. These analyses demonstrate the value, and we would argue the necessity, of combining paleontological and neontological data; we have highlighted several emerging opportunities in *Discussion*.

The strength and pervasiveness of the LDG in both marine and terrestrial systems probably stems from the alignment of multiple factors—“favorability,” long-term stability, large habitat areas in the tropics, and the opposite conditions at higher latitudes—all combining to produce higher speciation and lower extinction rates in the tropics and thus more prolific net diversification, which in turn feeds significant poleward expansion of taxa. In the oceans, the complex habitats associated with coral reefs may also be important for tropical originations, although the diversity peak and OTT dynamic in the East Pacific, which has virtually no coral reefs, indicates that reefs are not the primary drivers of tropical diversification. The relative importance of these different factors may vary among clades or between land and sea. High-latitude extinction, although also seen in marine benthos, may be more important for terrestrial systems, where glaciations repeatedly reduced habitable areas during the latest Cenozoic. Extensive dispersal may be more important for marine systems, with pelagic larvae often mediating gene flow and range shifts, although the intensity and constancy of that dispersal remains poorly understood and clearly varies among taxa. Moreover, the relative roles of mean and seasonal variation in solar energy and primary productivity in marine vs. terrestrial systems have yet to be clarified. Nevertheless, evidence is accumulating that geographic range shifts, and not just in situ diversification rate differences, are important for terrestrial and marine LDGs (9, 24, 28, 51, 102). For all of these issues, and many more, an approach integrating paleontological and neontological data will be the most fruitful way forward.

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Supporting Information

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Materials and Methods

Bivalve Database. We compiled and taxonomically standardized spatially explicit data on 5,726 extant marine bivalve species recorded from intertidal and subtidal shelf depths (≤ 200 m), in $\sim 54,000$ occurrences [20 April 2013 download of database; regional latitudinal diversity gradients (LDGs) shown in Fig. S1], based on the literature, museum specimens, and advice from taxonomic experts (see Acknowledgments). To reduce sampling effects, we omit two groups of species: (i) those restricted to the deep sea, a system largely decoupled from the dynamics of the continental shelf and so outside our study (1); and (ii) several poorly known families of minute bivalves (the galeommatoidae and cyamioidean families, Gaimardiidae, and Neoleptonidae). Both categories demonstrably have a poor fossil record, measured as the proportion of extant genera known fossil (2). We focus on paleontological analyses on what we term well-preserved families, in which $\geq 75\%$ of their extant genera are known as fossils (2). The twofold difference between tropical and extratropical first occurrences reported here is not sensitive to that criterion: for families with 75% of their genera known as fossils, 70% first appear in the tropics during our study interval (total $n = 146$ genera); at 60% known, 68% first appear in the tropics ($n = 167$); and at 90% known, 70% first appear in the tropics ($n = 79$).

The identity, location, and geologic age of the oldest known species of each extant genus were compiled from the primary literature and museum collections following taxonomic standardization. Our revisions raise the total number of fossil bivalve genera from 2,861 (3) to 3,207, with 1,589 additions, deletions, alterations, and refinements of stratigraphic ranges. Some errors must remain, owing to incorrect placement of fossil species and poor paleontological sampling of the tropics relative to northern and southern midlatitudes, but our results should be conservative with respect to these biases. Tropical and extratropical occurrences in the fossil record were assigned by reference to the distribution of coral reefs in the geologic past (4, 5). Fig. 1 was generated by intersecting all 1° grid cells that contained seafloor depths < 200 m with the geographic range polygons for each bivalve species in the database. The spatial resolution of individual occurrence records varies among data sources and ocean regions because of imprecise records and incomplete sampling, but the median latitudinal reso-

lution of occurrences is 1.2° . Intersections were done in ArcMap 10. For diversity calculations, a species was considered present in each 1° grid cell that intersected its geographic range polygon.

Thermal Ranges. We approximate the realized thermal range of a species as the interquartile range of mean sea surface temperature (SST) values for each 1° latitude and longitude grid cell occupied by a species. Measures of environmental breadth such as thermal range inevitably correlate with geographic range size or the number of occurrences, but the interquartile range (IQR) is less affected by this effect than total range and is less determined by outliers. This variable inevitably encompasses multiple factors, from competitive exclusion and dispersal failure to source-sink dynamics, and thus represents realized thermal ranges rather than potential thermal tolerance. However, if used cautiously in large data arrays, it can provide insights into temperature regimes broadly accessible to species (6–8).

We use raw occurrences to estimate thermal ranges rather than a range-through assumption that spatially, and thus thermally, interpolates between known occurrences; results are similar using either method. SST data were obtained from the HadISST 1.1 database (UK Meteorological Office, Hadley Centre), averaged over 10 y (1998–2008). Despite temperature changes with depth, thermal ranges of species measured at 50 and 100 m (obtained from the World Ocean Atlas 2005 at 1° resolution) are highly correlated with their sea surface thermal ranges (9).

To evaluate whether the correlation between latitudinal range sizes and thermal range sizes is smaller or larger than expected if range position and size limits are not determined by climatic gradients, we use a null model with a spatially explicit random and independent placement of 2D geographic ranges with respect to latitude (10). In this null model, 2D geographic ranges (approximated by a rectangle defined by latitudinal and longitudinal range) were randomly drawn (without replacement) from the frequency distribution of observed species latitudinal ranges, i.e., the range-shuffling algorithm in ref. 11) and randomly placed on the Earth sea surface (using the range-rejection algorithm in ref. 12). We repeated this procedure 1,000 times and then computed the expected thermal range for each species.

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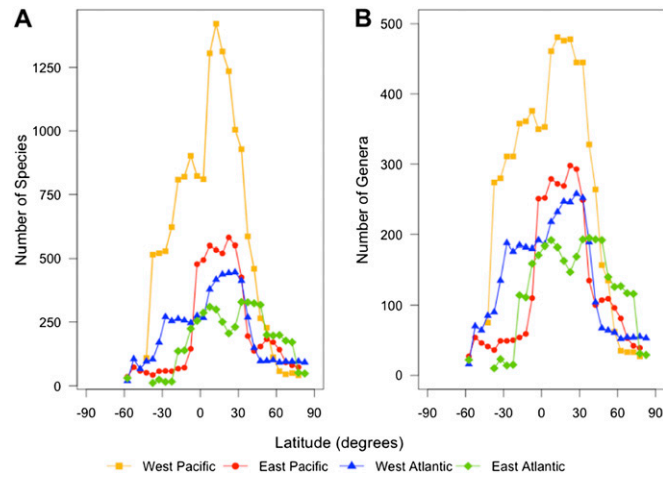


Fig. 51. Present-day bivalve latitudinal diversity gradients at (A) species and (B) genus levels at shelf depths (<200 m) along four major north-south coastlines.

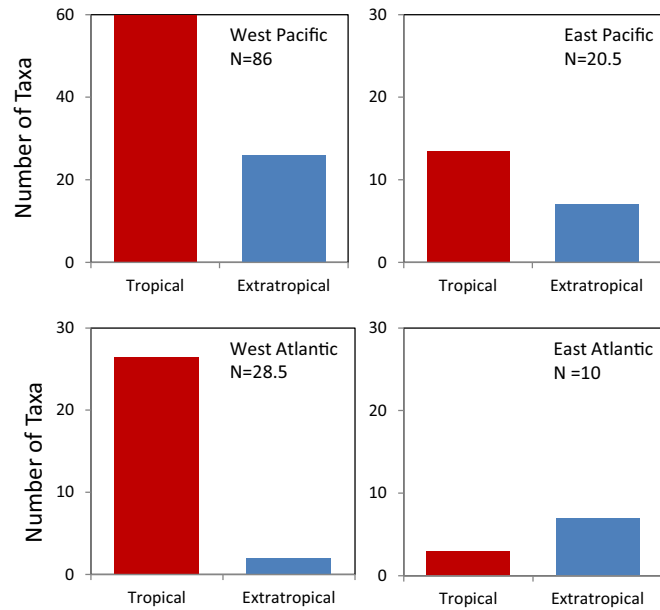


Fig. 52. Climate zones of first occurrences of Late Miocene-Pleistocene bivalve genera by major coastlines. The fractional occurrence involves *Lyratellina*, which has species of similar ages in both the Caribbean and the tropical Eastern Pacific.

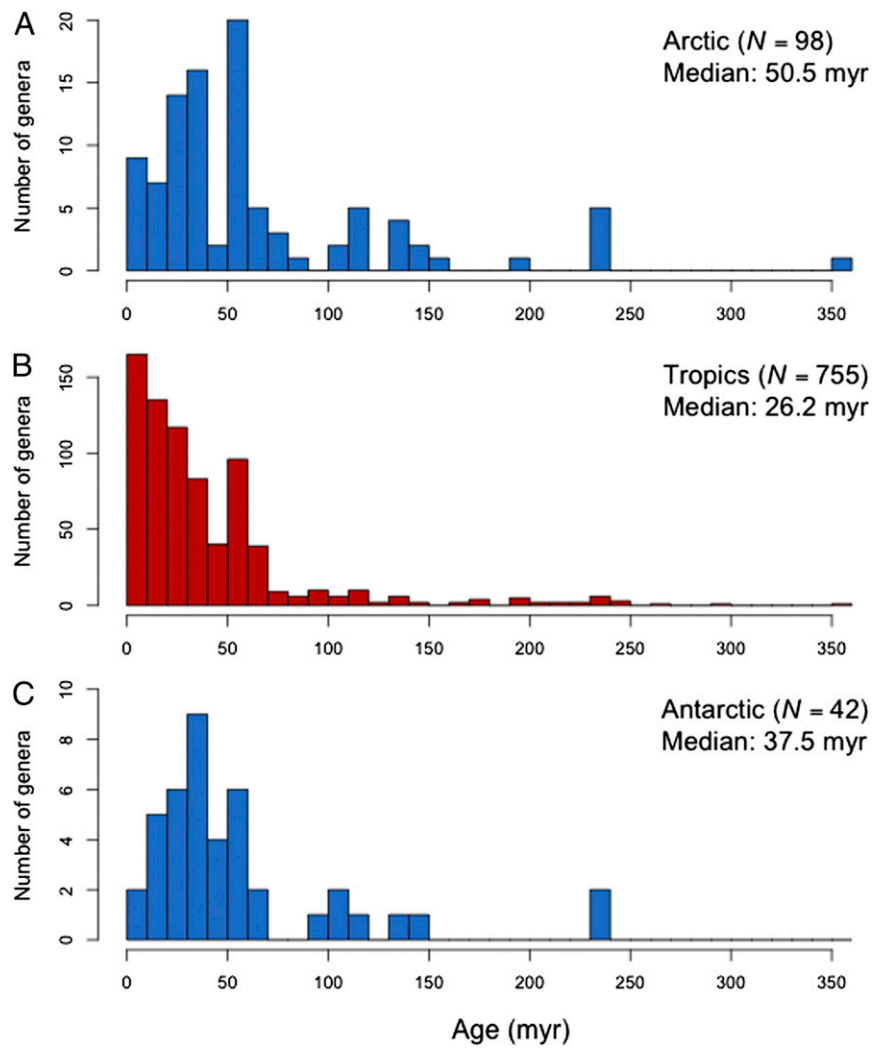


Fig. 53. Age-frequency distributions of geologic ages of bivalve genera currently living in (A and C) polar and (B) tropical climate zones.

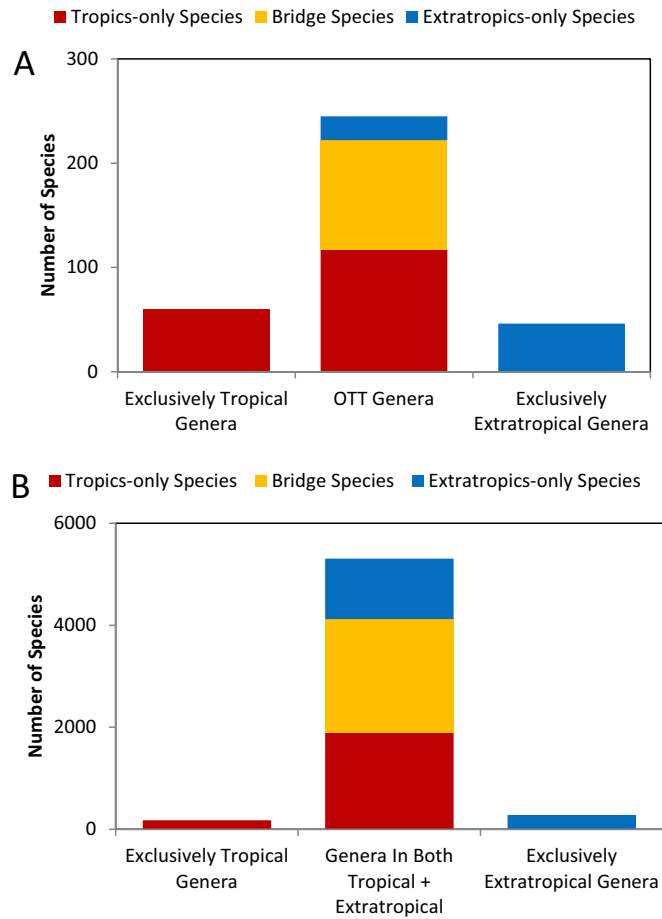


Fig. S4. (A) Relative diversification of bivalve genera originating in Late Miocene-Pleistocene and now in different biogeographic categories. (B) Diversity differences among all extant marine bivalve genera in different biogeographic categories, showing patterns similar to A, suggesting that the process documented for the Late Miocene-Pleistocene operated throughout the Cenozoic. Extant genera in both tropical and extratropical regions probably include many out-of-the-tropics (OTT) genera, but this is not yet documented for genera that originated before the Late Miocene.

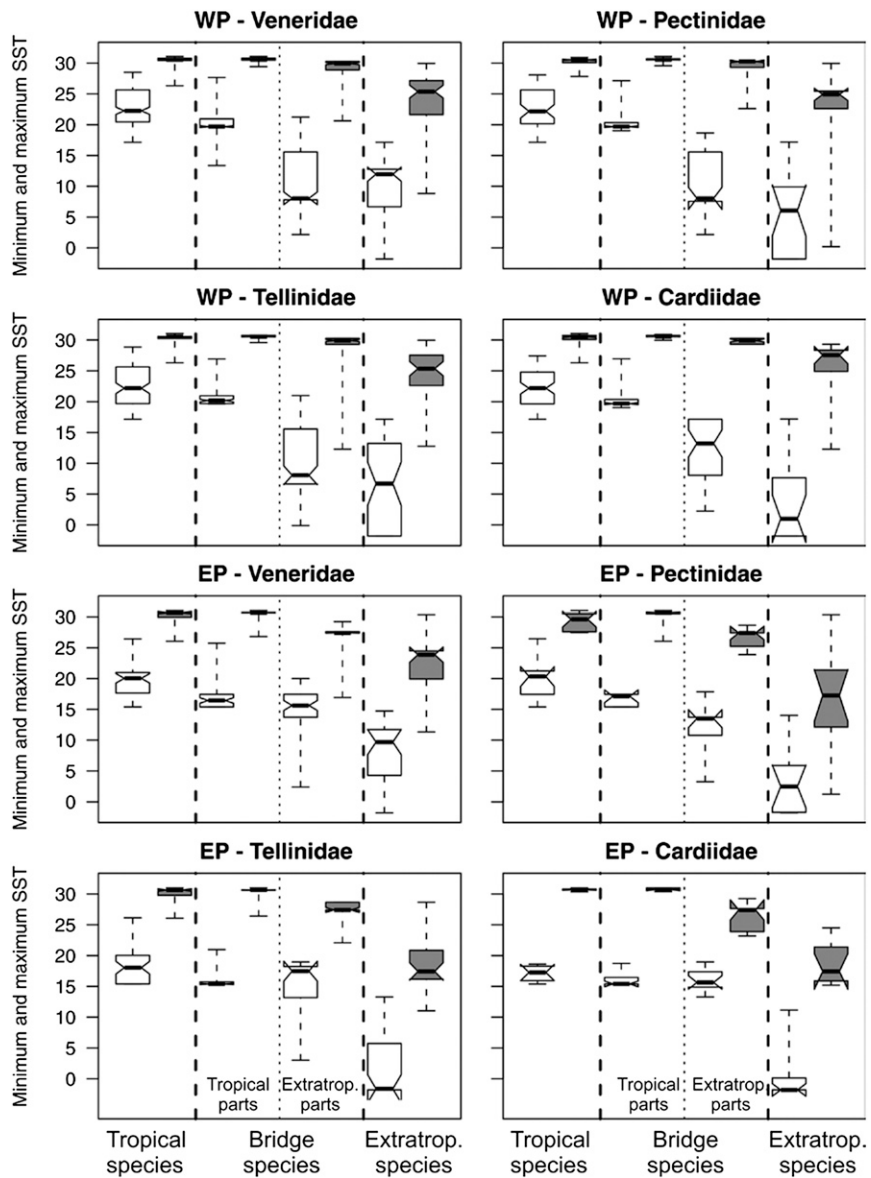


Fig. S5. Minimum (white) and maximum (shaded) SSTs occupied today by tropics-only and extratropics-only species compared with the tropical and extratropical parts of bridge species ranges in four of the most diverse bivalve clades in two oceanographically disparate regions [West Pacific (WP) and East Pacific (EP)].

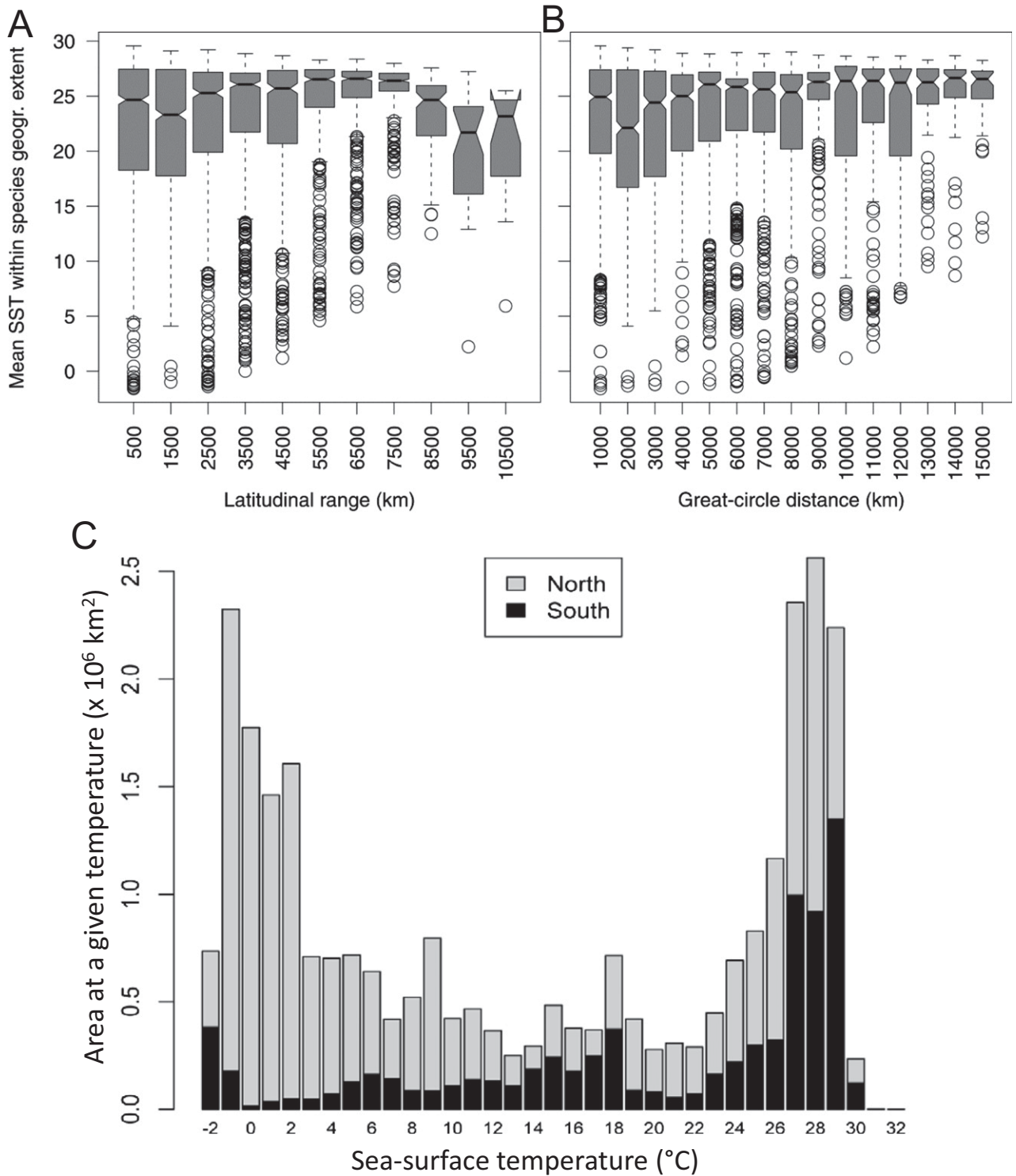


Fig. 56. Widespread species tend to occupy warm waters, as measured by the mean SST of the shelf area they occupy, in terms of both (A) latitudinal range and (B) the great-circle distance between their most distant points (a metric strongly influenced by the longitudinal extent of the tropical Indo-West Pacific); bar in each box = median; range-size classes having <10 species omitted. Not all SSTs are equally widespread, as shown in C, the spatial extent (areal coverage in square kilometers) of mean annual SST in 1° latitude-longitude cells that intersect the continental shelf; black, Southern Hemisphere, gray, Northern Hemisphere. Temperature ranges in A and B suggest that most widespread species are tracking the most widespread warm temperatures, which occupy the right mode in C.

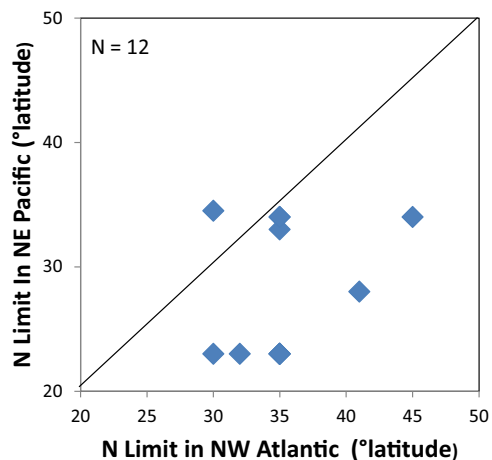


Fig. S7. Genera that first appeared in the Middle Miocene-Pleistocene tropics of the New World tend to expand further north in the northwest Atlantic than in the northeast Pacific; Diagonal = 1:1 line.

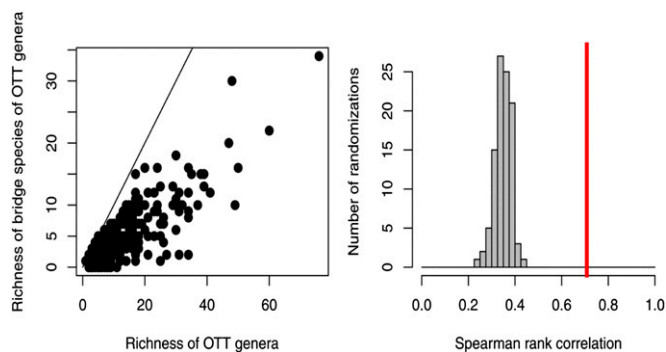


Fig. S8. (Left) Number of bridge species is significantly related to the total number of species in the genus; genera falling on the 1:1 line consist entirely of bridge species. (Right) Spearman rank correlation of data (red) relative to results from 1,000 bootstrapped randomizations.

Other Supporting Information Files

[Dataset S1 \(XLS\)](#)