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# Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient

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The evolutionary dynamics underlying the latitudinal gradient in biodiversity have been controversial for over a century. Using a spatially explicit approach that incorporates not only origination and extinction but immigration, a global analysis of genera and subgenera of marine bivalves over the past 11 million years supports an “out of the tropics” model, in which taxa preferentially originate in the tropics and expand toward the poles without losing their tropical presence. The tropics are thus both a cradle and a museum of biodiversity, contrary to the conceptual dichotomy dominant since 1974; a tropical diversity crisis would thus have profound evolutionary effects at all latitudes.

The most striking large-scale pattern in biological diversity is the dramatic increase in the number of species and higher taxa from the poles to the tropics. This taxonomic trend, commonly called the latitudinal diversity gradient (LDG), has been documented in the multicellular biotas of forests, grasslands, wetlands, continental shelves, the open ocean, and even the deep sea; it characterizes plants, fungi, marine and freshwater invertebrates, and all of the vertebrate classes (1). The history of the LDG extends back through the Mesozoic into the Paleozoic (2–7), although the slope of the gradient has varied over time and the trend might even have disappeared for a time if any of the mass extinctions were disproportionately severe in the tropics (8).

Although the existence of the LDG has been known for more than a century (9, 10) and has

been quantified hundreds of times (11), it remains the “major, unexplained pattern of natural history” [Ricklefs in (11)], with “an astonishing lack of consensus about the mechanisms leading to this variation in diversity” (1). Recent work has focused primarily on ecological explanations for the LDG (9, 12–15), and although these analyses have found interesting correlations between diversity and environmental variables, they reveal little about the evolutionary dynamics of the species and lineages that established and maintain the LDG (16, 17). Because virtually all possible combinations of the key evolutionary parameters have been proposed to shape the LDG (table S1), progress in this area depends on empirical data that can falsify alternatives. Here we (i) outline a framework for evaluating the spatial and temporal dynamics that underlie the present-day LDG, (ii) synthesize previous work from this perspective, and (iii) present paleontological analyses that falsify the classic portrayal of the tropics as either a cradle or a museum of biodiversity (18).

#### Cradles and Museums

From an evolutionary perspective, large-scale spatial patterns of biodiversity depend on three

variables: origination rates ( $O$ ), extinction rates ( $E$ ), and changes in geographic distributions (expressed here as  $I$ , for immigration into a latitudinal bin) of taxa. For a simple two-box model, with the tropics and extratropics denoted as subscripts, diversity in the tropics ( $D_T$ ) is determined by  $O_T - E_T + I_T$ , and diversity in the extratropics ( $D_E$ ) by  $O_E - E_E + I_E$  (Fig. 1). With this notation, it can easily be seen that a latitudinal gradient in richness, with  $D_T > D_E$ , can result from many different combinations of these variables. Theoretically, the extinction terms could represent either true global extinction of taxa, local extinction for a particular spatial bin, or a combination of the two. Estimating local extinction rates using paleontological data is generally difficult owing to incomplete spatial sampling, and even more difficult using phylogenetic information. In addition, our empirical results suggest that the effect of local extinction is much smaller than that of range expansion, at least for marine bivalves. Thus, as in most previous studies (table S1), our discussion of the role of extinction in shaping the LDG focuses primarily on global processes.

The simplest evolutionary models for the LDG assume that taxa are static in their geographic distributions ( $I_T = I_E = 0$ ) and treat the greater number of species and higher taxa in the tropics as the result of either a higher rate of origination of species and lineages ( $O_T > O_E$ ) or lower extinction rates as compared to extratropical regions ( $E_T < E_E$ ). For example, Wallace (19) attributed high tropical diversity to a more stable climatic history, which allowed more time to accumulate taxa ( $E_T < E_E$ ), and this view has found proponents ever since (20) (table S1). Others have argued that extinction rates are high in the tropics but are outstripped by even higher origination rates ( $E_T > E_E$ ,  $O_T \gg O_E$ ) (21). The importance of origination and extinction in generating the LDG was highlighted in Stebbins' (18) famous metaphor of the tropics as a cradle or a museum, and this memorable dichotomy has been the dominant paradigm ever since.

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Distinguishing evolutionary cradles from museums requires separate estimates of origination and extinction rates. Such estimates are currently unavailable even for most large groups with a good fossil record and may not be feasible for groups lacking a fossil record without assuming stochastically constant extinction rates (22), an assumption often violated over the past 15 million years of Cenozoic history (23, 24). Consequently, attempts to quantify the evolutionary underpinnings of the LDG have focused mainly on latitudinal differences in net diversification rates of living taxa [the composite value ( $O - E$ )], a parameter more readily estimated from phylogenies of extant organisms (table S1) (25, 26). Such differences in net diversification rates are valuable for investigating many questions (26), but their application to the cradle/museum problem is again limited by the many combinations of  $O$  and  $E$  that can produce a given net value. Realistically, areas with high net diversification rates are more likely to be evolutionary cradles, but those where such rates are low could have experienced either high or low extinction rates.

### Rate Differences and Range Shifts

The cradle/museum dichotomy, and the more general hypothesis that attributes high tropical diversity to higher net diversification rates, implicitly assume that the LDG derives largely from differences in *situ* origination and extinction (16, 25, 26). However, this simplifying assumption is contradicted by biogeographic data showing that (i) many taxa shift their geographic range limits substantially in response to climatic changes [they have moved across latitudes to track changing climates (27, 28)], and (ii) many taxa have geographic distributions that encompass both tropical and extratropical regions [assuming origination in a single climate zone, they have expanded across latitudes in the face of climate differences (9, 29)]. Thus, the dynamics underlying the LDG must involve not only latitudinal differences in origination and/or extinction rates but also extensive changes in spatial distributions of taxa over time.

Although most analyses of the LDG based on present-day biogeography have ignored the role of past distributional changes, the notion that shifts in latitudinal distributions of taxa play an important role in shaping the LDG is not new (20, 30–33). Scenarios in which taxa preferentially originate in tropical regions and spread out from there ( $I_T < I_E$ ) or the reverse ( $I_T > I_E$ ) have both been advocated (33), but attempts to separate the contributions of  $O$ ,  $E$ , and  $I$  to the shape of the LDG have been undermined by a lack of basic information on the time and place of origin for the vast majority of living taxa. Instead, taxa occurring in both tropical and extratropical regions are generally handled either by (i) including each taxon in rate calculations for all latitudinal bins within its geographic range (34) or (ii) including each taxon only in the bin corresponding to the center of its latitudinal

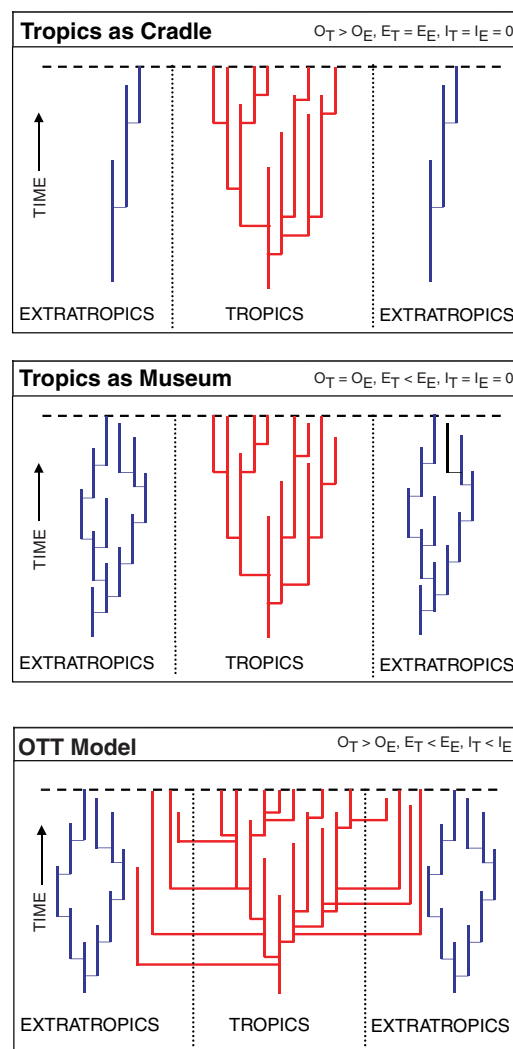
range (25, 26). Neither approach can separate the effects of past distributional shifts from those due to changes in diversification rates with latitude, however. Protocol (i) is analytically problematic (owing to the autocorrelation imposed by counting each taxon in multiple bins) and allows a widespread taxon to influence the age distributions of more latitudinal bins than a restricted taxon does, even though each should contribute only to its latitude of origin. In contrast, protocol (ii) makes the unrealistic assumption that taxa originate near the midpoint of their present-day geographic ranges. The asymmetry of range expansion from the true place of origin is likely to increase with the geographic range of a taxon (26), and even narrow-ranging taxa may abandon ancestral distributions in response to large climatic changes such as occurred during the Pleistocene (27). Some progress has been made recently in estimating origination, extinction, and immigration rates from the shapes of taxon age distributions, but such models also make a number of important simplifying assumptions about the underlying dynamics (35). Thus, direct tests of

the role of large-scale range expansion in shaping the LDG are needed, and the fossil record remains the best source of data for such tests.

### Out of the Tropics: A Dynamic Model

One potential reason why published studies have failed to produce a consensus on whether the tropics are a biological cradle or museum (table S1) is that this dichotomy is misleading. The tropics could be a cradle, a museum, or both; theoretically, so could the polar regions; and taxa could predominantly remain in place or either expand or contract their distributions (Fig. 1). We suggest that the available data are most consistent with an “out of the tropics” (OTT) model, in which the tropics are both a cradle and a museum, with taxa preferentially originating in the tropics and expanding over time into high latitudes without losing their initial tropical distributions. Thus  $O_T > O_E$ ,  $E_T \leq E_E$ , and  $I_T < I_E$ .

Until now, direct empirical tests of this model have been lacking, although one biogeographic model suggests that such a dynamic could explain the age-frequency distributions of bivalve genera found in polar oceans today (35), and some



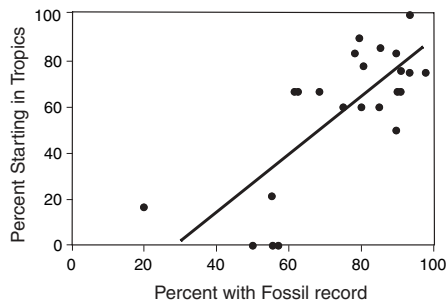
**Fig. 1.** Simple hypothetical scenarios illustrating the cradle, museum, and OTT models. Red denotes lineages that originated in the tropics; blue denotes lineages that originated outside the tropics. The horizontal lines connecting sister lineages also represent geographic distributions; those extending from tropics to extratropics denote clades that originated in the tropics but have subsequently extended their ranges into extratropical regions while retaining a tropical presence. Many other combinations of these parameters are possible. The dashed horizontal line indicates the present day.

phylogenetic analyses find extratropical taxa to be derived from tropical lineages (29, 36). Here we test the OTT model using paleontological and present-day distributions, and frame testable predictions for groups lacking a good fossil record.

### Testing the OTT Model

The marine Bivalvia currently provide one of the few systems that can address each of the OTT predictions directly. As a group, bivalves exhibit a strong LDG, not only for species but also at the level of genera and subgenera (henceforth simply termed genera) (37, 38), which have been the preferred units for large-scale paleontological analyses owing to their taxonomic stability and the robustness of the patterns to sampling artifacts relative to species-level data. The fossil record of marine bivalve genera is rich and densely sampled, with a “pull of the Recent” (the artifact that can arise via strong differences in the sampling of present-day and geologic time intervals) of less than 5% (39). Remaining preservational effects are increasingly well understood (39–42), so that artifacts can be avoided or minimized. Bivalves occur at all latitudes in the modern oceans, and sampling of their fossil record is almost as widespread, although it is not unbiased spatially (43).

Taxonomic standardization, a prerequisite for rigorous analysis of the spatial and temporal patterns of biodiversity, although not fully complete, has been undertaken for many late Cenozoic occurrences (39, 40). Accordingly, marine bivalves are becoming a model system for macroecological and macroevolutionary analysis (40, 44, 45), allowing us to test the predictions of the OTT model with data on the modern latitudinal distributions of bivalve genera, the geologic ages of those taxa relative to their present-day distributions, the spatial pattern of the first occurrences of those taxa, and post-origination changes in their latitudinal range limits.



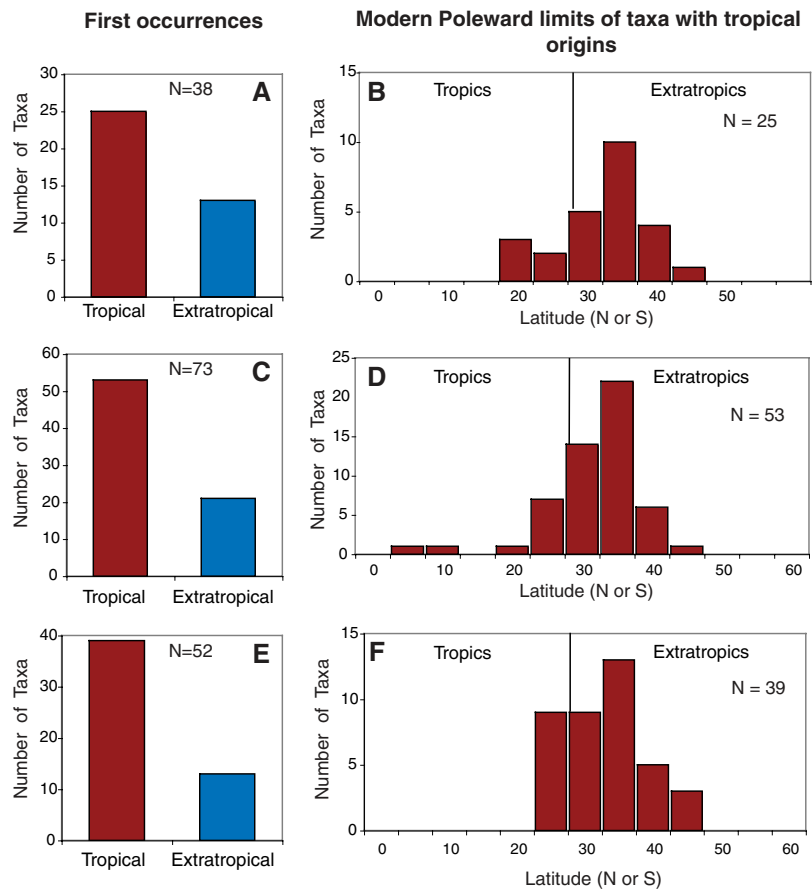
**Fig. 2.** Sampling quality versus tropical originations in marine bivalve families since the start of the late Miocene (11 million years ago) for families having three or more first occurrences within that interval. Families having more complete fossil records [measured as the proportion of living genera known as fossils (40)] tend to show a significantly greater proportion of first occurrences of their constituent taxa in the tropics (simple linear regression,  $R^2 = 0.560$ ,  $P = 0.0001$ ).

$O_T > O_E$ . Testing this prediction for genera requires spatially explicit data on their first occurrences in the geologic record, which must be treated cautiously because of biases toward heavier sampling in temperate latitudes (40, 43, 46–48).

One approach to this problem is to use the proportion of living genera known from the fossil record within each bivalve family as a sampling gauge (49). For the past 11 million years (from the beginning of the late Miocene to the Recent), the proportion of living taxa that first occur in tropical deposits is positively related to the proportion of taxa known from the fossil record: The better the fossil record of a family, the higher the proportion of its genera that first occurs in the tropics (Fig. 2).

We can also tie a more detailed analysis of the geography of origination to the quality of each

family’s fossil record (49). Restricting analyses to families having  $\geq 75\%$  of their genera known as fossils, tropical first occurrences of those bivalve taxa significantly exceed extratropical ones in each of three successive geologic time intervals leading up to the present day (late Miocene, Pliocene, and Pleistocene; Fig. 3, A, C, and E). Summing over the entire 11-million-year interval, we record 117 tropical and 46 extratropical first occurrences (a significant difference,  $P = 2.543 \times 10^{-8}$ ), indicating that the overall pattern will be robust to any error in the assignment of individual stratigraphic units to our three time bins. And because sampling is strongly biased in the opposite direction (so that some genera originating in the tropics will not be recorded paleontologically until they expand into the better-sampled extratropical zones), these data are



**Fig. 3.** Latitudinal differences in originations (left) and present-day range limits of marine bivalve genera first occurring in the tropics (right), using only families with  $\geq 75\%$  of their living taxa known as fossils. (A and B) Genera first appearing in the Pleistocene. (C and D) Genera first appearing in the Pliocene. (E and F) Genera first appearing in the late Miocene.  $N$  indicates the total number of genera in each analysis. For (C) and (E), tropical first occurrences are significantly more frequent than extratropical ones and marginally so for (A), despite the sampling bias favoring extratropical occurrences [(A),  $P = 0.07$ ; (C),  $P = 0.0001$ ; (E),  $P = 0.0004$ ; exact binomial test]. These results are not sensitive to the cutoff value: For example, for the Pliocene, if we use 80% having a fossil record, we find 39 tropical versus 18 extratropical first appearances (FAs); using 70% having a fossil record, we find 52 tropical versus 22 extratropical FAs. Similarly, for the late Miocene, if we use 80% having a fossil record, we find 26 tropical versus 8 extratropical FAs; using 70% having a fossil record, we find 35 tropical versus 9 extratropical FAs. If we treat the data in Fig. 2 as two discrete populations and thus set a 60% cutoff value, we find 38 tropical versus 11 extratropical late Miocene FAs and 56 tropical versus 25 extratropical Pliocene FAs.

almost certainly underestimates of the tropical predominance of first occurrences. The latitudinal difference in originations extends across the Bivalvia and is not just restricted to the heteroconch clade (table S2), which has been the most prolific diversifier through the Cenozoic (50).

$E_T \leq E_E$ . How extinction rates vary with latitude remains poorly known. Taken at face value, the bivalve data show substantially higher extinctions at high latitudes over the past 11 million years; only 30 exclusively tropical genera go extinct as compared to 107 extratropical and cosmopolitan ones. Factoring in the much greater taxon richness in the tropics suggests an even higher differential in per-taxon rates. These data must again be treated cautiously, owing to the severe undersampling of the tropics, but the presence of so many last occurrences at high latitudes constrains potential patterns and suggests that tropical extinction rates are unlikely to be substantially higher than extratropical ones. These results are also qualitatively consistent with previous studies that have found either little variation in species extinction rates with latitude (51) or higher extinction rates of genera and subgenera in polar oceans relative to lower latitudes (35). Further analyses of latitudinal trends in extinction rates are needed.

$I_T < I_E$ . The bivalve data indicate that genera originating in the tropics tend to extend their ranges to higher latitudes over time, as predicted by the OTT model (49). For each of the time bins in Fig. 3, assuming the tropics to be between 25°N and 25°S latitude,  $\geq 75\%$  of the taxa that occur first in the tropics also occur extratropically today; only 2 of those taxa have left the tropics entirely (Fig. 3, B, D, and F; the proportions are  $>80\%$  if 23° is taken as the edge of the tropics). Again, because the number of taxa known to start in the tropics is undersampled, these values of  $I_E$  are almost certainly underestimates.

### Insights from Modern Biogeography

The direct tests listed above require temporal and spatial data on ancient distributions that are not available for many important groups of organisms. In such cases, biogeographic data from living taxa can be tested for consistency with the OTT model, although they will not be definitive tests of the model for the reasons outlined above.

*Endemism versus latitude*. If genera primarily originate in the tropics and expand into extratropical regions, then the simplest biogeographic prediction is that endemism today should decrease with latitude. This prediction is clearly supported for present-day marine bivalves (49), in which the LDG persists if we simply exclude all genera restricted to extratropical latitudes: Most of the diversity of extratropical regions comes from taxa shared with the tropics [(49) and fig. S1]. However, this is strictly a consistency test, evaluating the tendency of taxa to expand outside of their initial geographic distributions (assuming that each taxon starts with a single species within a single climate zone), without establishing the direction of those expansions.

*Age versus latitude*. If living genera preferentially originated in the tropics and subsequently expanded into higher latitudes, their average ages should increase with latitude, with the tropics harboring both old and young taxa and higher latitudes progressively lacking in younger taxa. For marine bivalves, both mean and median geologic ages of genera occurring in 10° latitudinal bins increase from the equator to the poles (49) (fig. S2), and the age-frequency distributions of tropical and polar assemblages differ significantly (fig. S3). However, such trends suffer from the problem of spatial autocorrelation (the right tails of the histograms in fig. S3 share many taxa) and cannot separate the OTT model from the more traditional “tropics as cradle” hypothesis. A better approach is to test for spatial differences in the shapes of taxon age distributions, derived paleontologically or from well-calibrated molecular phylogenies, against predictions of models that incorporate originations, extinctions, and range expansions of taxa (35). Alternatively, reconstructing ancestral geographic ranges of individual taxa from well-supported phylogenies of living species (52), in conjunction with biogeographic data, should permit indirect tests. Finally, the finding that the steepest latitudinal gradients occur in the geologically youngest clades of bivalves (50, 53) is also consistent with a dynamic involving preferential origination at low latitudes and poleward expansion over time.

### Conclusion

Our goal here has not been to formulate yet another hypothesis about the evolutionary dynamics underlying the LDG; most possible combinations of origination, extinction, and spatial shifts have already been proposed. Instead, we suggest that the long-standing “tropics as cradle or museum” paradigm is not supported by paleontological data or present-day biogeographic patterns [also see (29)]. The OTT alternative posits that lineages not only preferentially originate in the tropics but also persist there as they expand poleward; it does not preclude extratropical speciation, of which there are many examples (54), but predicts that most extratropical species belong to lineages that originated in the tropics. Thus, the OTT dynamic is likely to be strongest at the level of lineages (for example, genera and families), and we view this model as providing a framework for understanding latitudinal patterns of speciation. Preferential origination of taxa in the tropics followed by range expansion into high latitudes has been proposed on biogeographic and phylogenetic grounds (34, 36, 55, 56), and the dynamic is consistent with previous paleontological analyses (46). The OTT model is similar to the niche conservatism model (29) in that both view the tropics as a cradle and a museum of diversity [see also (57, 58)], but our model differs in emphasizing the expansion of geographic distributions over time; we see “niches” of taxa expanding over time, perhaps as species proliferate within and among climate zones. The

general scarcity of robust spatial data on where individual taxa originate has hindered direct tests of these dynamics.

The OTT dynamic documented here suggests that the LDG is shaped by the interaction of two different kinds of processes: those that drive the higher origination rates in the tropics and those that determine the geographic range limits of individual taxa, which makes it difficult to untangle causal mechanisms. We still know little about why taxa preferentially originate at lower latitudes; of the many proposed hypotheses (46, 59–61), empirical tests have yielded mixed results for some (61–66) whereas others remain untested. Similarly, the controls on the geographic range limits of taxa are poorly understood, although theoretical and empirical studies are beginning to address this issue (67, 68). Progress is clearly needed on both fronts, particularly if the source-sink macroevolutionary and biogeographic dynamic outlined here is a general feature of diversity gradients (for example, along bathymetric, elevational, and longitudinal gradients) (56, 57).

The OTT model also has implications for present-day biodiversity, beyond providing a framework for modeling biotic responses to future climate changes. If the tropics are the engine of global biodiversity, as suggested by our analyses (see also table S1), then major losses of tropical taxa will have a global effect by suppressing the primary source of evolutionary novelty for all latitudes. A tropical diversity crisis would thus not only affect tropical biotas but also have profound long-term evolutionary consequences for biotas at higher latitudes.

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#### Supporting Online Material

www.sciencemag.org/cgi/content/full/314/5796/102/DC1

Materials and Methods

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References

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## REPORTS

# Molecular Loops in the Galactic Center: Evidence for Magnetic Flotation

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The central few hundred parsecs of the Milky Way host a massive black hole and exhibit very violent gas motion and high temperatures in molecular gas. The origin of these properties has been a mystery for the past four decades. Wide-field imaging of the <sup>12</sup>CO (rotational quantum number  $J = 1$  to 0) 2.6-millimeter spectrum has revealed huge loops of dense molecular gas with strong velocity dispersions in the galactic center. We present a magnetic flotation model to explain that the formation of the loops is due to magnetic buoyancy caused by the Parker instability. The model has the potential to offer a coherent explanation for the origin of the violent motion and extensive heating of the molecular gas in the galactic center.

The magnetic field in the central hundred parsecs of the Milky Way is substantially stronger than elsewhere in the Galaxy, at least in the prominent nonthermal features emitted from high-energy elec-

trons spiraling along magnetic field lines. The magnetic field of these electrons is estimated to be typically a milligauss ( $I$ , 2), although some recent works suggest a weaker global magnetic field in the galactic center (3). Magnetic fields

have the potential to affect the dynamics of molecular gas and may control star formation on a small scale and govern the motion of molecular clouds on a large scale. An observational link between the molecular gas and the magnetic field in the galactic center has been obtained through polarization measurements of magnetically aligned dust grains at mid- to far-infrared to submillimeter wavelengths (4, 5).

Here, we report millimeter-wave observations of two molecular features that have a loop-like shape with a length of several hundred parsecs and width of  $\sim 30$  pc within  $\sim 1$  kpc

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Supporting Online Material for  
**Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity  
Gradient**

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**This PDF file includes:**

Materials and Methods  
Figs. S1 to S3  
Tables S1 and S2  
References

Supporting online material for

## Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient

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### **This PDF file includes:**

SOM Text

Figs. S1 to S3

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### **Materials and methods**

**Paleontological data and analyses:** We used an updated version of Sepkoski's Compendium (*S1*) to identify all living genera and subgenera of bivalves that originated in the last 11 million years (i.e., from the start of the Late Miocene to the present day). Our revision of Sepkoski's data, using an extensive literature search and museum collections that permitted taxonomic standardization, allowed us to specify the oldest known species for each taxon (*S1*, *S2*). We then determined the place of the first occurrence of each taxon using museum collections and an extensive literature search; all occurrences within a stratigraphic substage (e.g., late Tortonian) were treated as contemporaneous, yielding a temporal resolution of 1 m.y. or less, except within the Tortonian stage where resolution was ~ 2 m.y. Finally, the locality or localities of first occurrence were assigned to tropical or extratropical categories depending on their position relative to the contemporary edge of the zone of massive coral reefs and other tropical indicators (as in *S3*). Uncertainties about past environments doubtless remain, but as discussed in the text, the more intensive sampling of extratropical regions makes erroneous attribution of first occurrences to extratropical regions more likely than erroneous attribution to the tropics, biasing the data against the OTT model.

In order to estimate the effects of among-clade differences in preservation potential on patterns of first occurrences, we calculated the proportion of genera and subgenera within individual families that have a fossil record using a recently compiled database (*S1*). For each taxon with a tropical first occurrence during the time interval covered in this study we determined its current maximum pole-ward range limit (either in the northern or in the southern hemisphere) using either (i) the biogeographic data described below or (ii), for taxa not covered by that database, distributional data from the primary literature. The age distributions of Northern Hemisphere taxa shown in Fig. S2 and S3 were derived from the updated version of the Compendium described above. For estimating tropical versus extratropical extinctions, we followed the same general procedure as for estimating patterns of origination, using the stratigraphic range endpoints from the revised version of the Compendium.

**Modern biogeography:** We compiled a database of geographic distributions of 3599 species and 621 genera and subgenera of living marine bivalves using an extensive search of the primary literature, supplemented by data from major museum collections in Europe and North America. We restricted our bathymetric coverage to shelf depths (0 - 200 meters water depth, i.e., from the intertidal to the edge of the continental shelf) since deeper parts of the world oceans are poorly represented in the fossil record (*S1*). These data represent an expanded version of those used by Flessa and Jablonski (*S4*) and include the following superfamilies: Arcoidea, Limopsoidea, Mytiloidea, Pectinoidea, Pterioidea, Pinnoidea, Trigonioidea, Carditoidea, Cardioidea, Solenoidea, Tellinoidea, Arcticoidea, Veneroidea. This represents roughly half of present-day marine bivalve diversity (which totals 1292 genera and subgenera, including exclusively deep-sea taxa, according to *S1*). Only taxa present in the northern hemisphere were used to calculate the LDG shown in Fig. S1, because at present sampling of these taxa is much more complete there; for these calculations we assumed that an individual taxon is present throughout the range demarcated by its range endpoints, an assumption commonly used in macroecological analyses (e.g., *S5- S7*). Of the 503 genera in the Flessa-Jablonski database known as fossils, for figures S3 and S3 we excluded 38 genera belonging to poorly preserved families (< 75% of living genera known as fossils, see Fig. 2), and only plotted data for the Northern Hemisphere, where sampling is most complete; this left 431 genera for analysis.

#### **Previous studies that have examined evolutionary dynamics along latitude**

We searched the primary literature for individual studies that have attempted to quantify differences in evolutionary rates between tropical and extratropical taxa. The resulting list of studies shown in Table S1 reveal the diversity of approaches taken to address the issue and the relatively few taxonomic groups for which such analyses are available. The majority of these studies involve marine invertebrates and these in turn are dominated by mollusks. Among terrestrial groups, invertebrates in general and insects in particular are seriously underrepresented, despite their tremendously high tropical species richness, and freshwater organisms are absent from the list. Data from the fossil record are used by the majority of these studies to test for differences in evolutionary rates between tropical and extratropical regions, while the rest use various phylogenetic methods. Although roughly half of the studies provide species-level analysis, the spatial and taxonomic coverage of species-level analyses are much smaller compared to those at higher taxonomic levels.



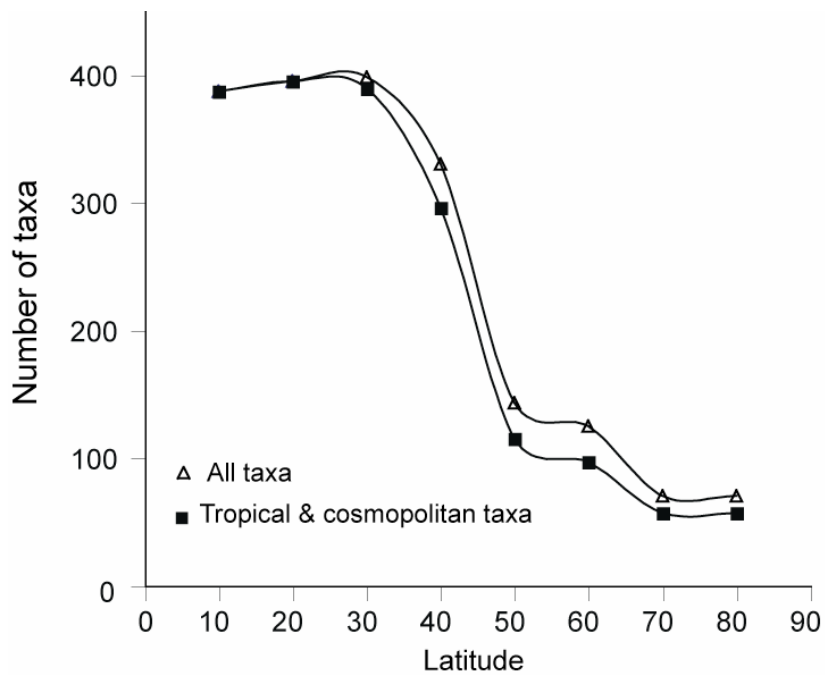


Fig. S1. The latitudinal diversity gradient of living bivalve genera and subgenera in the Flessa-Jablonski database (*S4*; see Methods for taxonomic coverage) that occur in the Northern Hemisphere. The overall trend (open triangles) changes very little when based only on taxa that range into the tropics (solid squares), consistent with the hypothesis that taxa primarily originate in the tropics and expand into extratropical regions (see text for details).

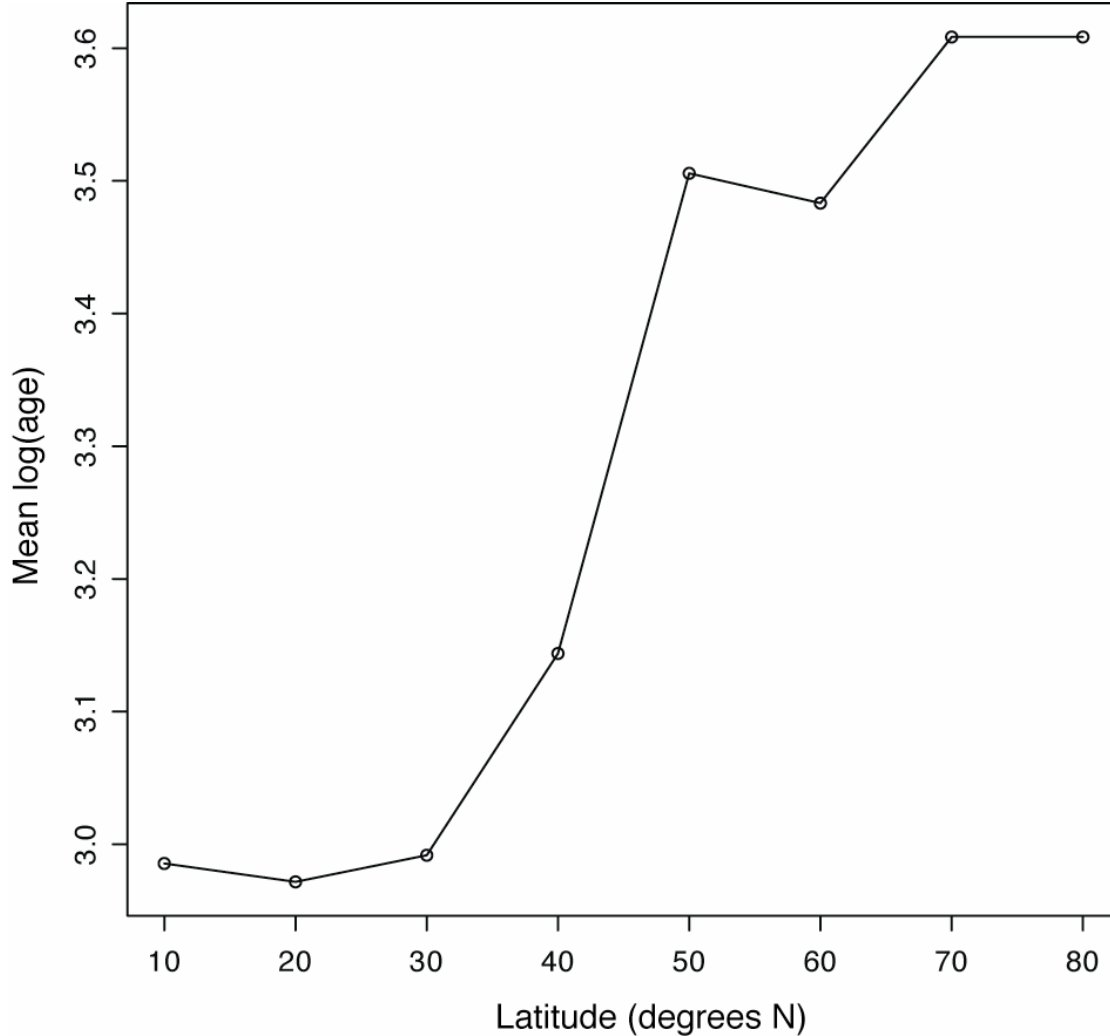


Fig. S2. The average geologic age (log-transformed) of living bivalve genera and subgenera in the Flessa-Jablonski database (S2, S4; see Methods for taxonomic coverage) occurring in 10-degree latitudinal bins in the Northern Hemisphere. Average age of assemblages increases from the equator to the Arctic Ocean; a similar trend is seen if median geologic ages are used instead. This difference is unlikely to be due to the less complete sampling of the tropical fossil record, as the vast majority of living tropical genera also occur in the extratropics (see main text); qualitative results are unchanged if 38 additional genera in this database belonging to poorly preserved families (i.e. <75% of living genera known as fossils, see Fig. 2) are also included.

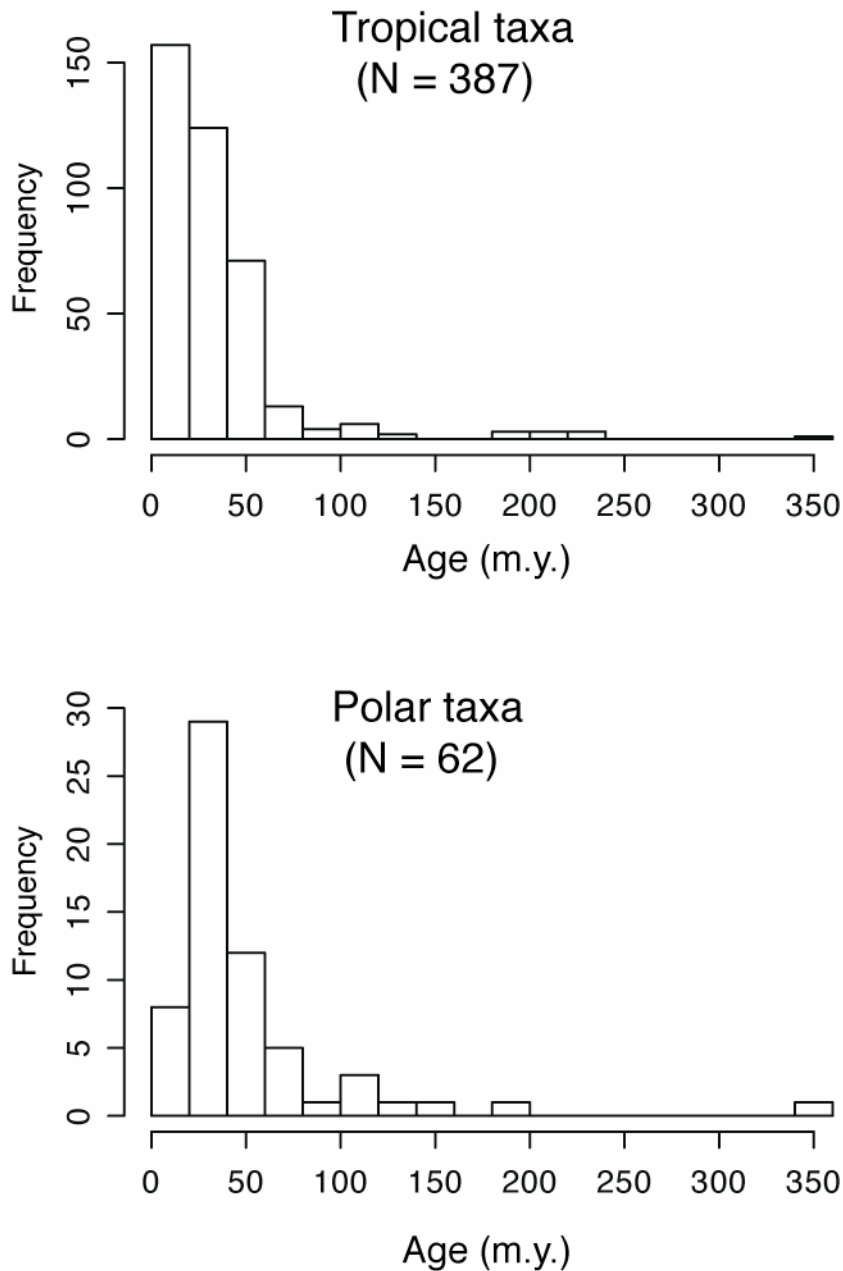


Fig. S3. Comparisons of the age-frequency distributions of living bivalve genera and subgenera at the latitudinal extremes of the LDG in the Northern Hemisphere. Taxonomic coverage restricted to those in the Flessa-Jablonski database. Age distributions of the tropical ( $0^{\circ}$ - $23^{\circ}$ N) and polar ( $>60^{\circ}$ N) assemblages differ significantly ( $p = 0.0002$ , Kolmogorov-Smirnov test; as many genera are shared by the two faunas the p-value is conservative); the greater average ages of the polar taxa are consistent with the prediction of the OTT model (see main text for details). Qualitative results are unchanged if 38 additional genera in this database belonging to poorly preserved families (i.e.  $<75\%$  of living genera known as fossils, see Fig. 2) are also included.

Table S1. Result of a literature search for studies that have empirically tested for differences in evolutionary rates between tropical and extra-tropical assemblages. We only included studies that undertook quantitative comparisons.

<b>Taxon</b>	<b>Taxonomic level</b>	<b>Method</b>	<b>Conclusion</b>	<b>Comments</b>	<b>Source</b>
Angiosperms	Genus, species	Species-genus ratios and other evidence	Extinctions lower in the tropics	One of the few studies to argue that the LDG is primarily shaped by low extinctions in the tropics; however the data used to support this argument do not provide direct estimates of extinction rates	(S8)
Angiosperms (Dicotyledonous taxa)	Family	Character states	Low tropical extinction	Archaic characters persist in tropical rain forests	(S9)
Angiosperms (selected groups)	Family	Morphological phylogenies	Tropical taxa older (basal); implies major groups tend to originate in tropics	Does not quantify how diversification rates vary with latitude or the effects of distributional changes	(S10)
Birds (New World endemic clades)	Genus	Regressions of diversification rates and latitude and other environmental variables	Higher net diversification rates in low latitude clades	Effects of extinction unknown; assumes taxa originated at the mid point of their present geographic distribution	(S11)

Birds (New World)	Tribes	Ages of tribes based on DNA hybridization data	Tropical tribes older	Effects of extinction unknown; does not take into account distributional changes	(S12)
Birds (New World)	Species	Basal vs derived position of families based on DNA hybridization (non-passerines) and nuclear genes (passerines)	Higher extratropical extinction rates, no support for speciation role	Extinction rates inferred by steepness of gradient of basal vs derived families: basal clades are species-poor in north temperate zone relative to derived clades	(S13)
Birds (passerine)	Species	Sister-group comparison	Higher net diversification rate towards equator	Effects of extinction unknown; assumes taxa originated at the mid point of their present latitudinal range	(S14)
Birds (passerine)	Higher taxa (Tribe, Family)	Tropical-temperate comparisons of diversification rates within clades	Net diversification rates higher in tropical regions; diversification rates decrease with clade age	Consistent with higher rate of diversification in lower latitudes; does not separate effects of speciation, extinction and changes in distributions	(S15)
Corals (Hermatypic)	Genus	Time of first appearance, from fossil record	Average age decreases as diversity increases	Effects of extinction unknown; does not take into account distributional changes	(S16)

Foraminifera (benthic)	Genus	Time of first appearance, from fossil record	Average age declines with latitude	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S17)
Foraminifera (benthic; Cenozoic)	Species	Comparison of within habitat diversities in temperate and tropical latitudes through the Cenozoic	Higher net diversification in tropics, higher origination and extinction rates in tropics	Tropical diversity may result from greater accumulation of long-lived species	(S18)
Foraminifera (planktonic)	Species	Paleontological data on region of first occurrence	Higher origination in the warmer waters	Suggests that speciation rates are higher in warmer waters	(S19)
Foraminifera (planktonic; Cretaceous)	Genus	Time of first appearance, from fossil record	Average age younger for tropical assemblage	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S20)
Foraminifera (planktonic; Neogene)	Species and subspecies	Taxonomic survivorship curves	No difference in taxon durations and extinction rates between tropics and extratropics	Origination rates not quantified; high latitude assemblage has shorter mean duration and higher extinction rates than tropics, but not statistically significant	(S21)

Foraminifera (planktonic; Neogene)	Species	Taxon ages, from fossil record	Extinction higher in the tropics, low at the poles but no difference in mean species durations between tropics and extratropics	Data and results could be consistent with a model of higher tropical originations followed by range expansions.	(S22)
Insects (phytophagous)	Species (five sister group pairs)	Sister-group comparison	No difference in net diversification between tropical and temperate taxa	Small sample size; effects of extinction unknown	(S23)
Swallowtail butterflies	Species	Sister-group comparison	Higher net diversification rate towards equator	Effects of extinction unknown; assumes taxa originated at the mid point of their present latitudinal range	(S14)
Mammals	Family	Time of first appearance, from fossil record	Average age younger for tropical assemblage	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S20)
Mammals	Family	Time of first appearance, from fossil record	No difference in average age between tropical and temperate assemblages and taxa	Reanalysis of Stehli et al. (20) data; does not take into account distributional changes	(S24)

Marine bivalves	Family	Species richness versus family ages (from fossil record)	Younger families contribute more species in the tropics	Implies higher net diversification in tropics; effects of extinction unknown; does not take into account distributional changes	(S25)
Marine bivalves	Family	Time of first appearance, from fossil record	Average age younger for "warm-water" groups	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S20)
Marine bivalves	Genus	Age of genera, from fossil record	Tropical genera younger	Effects of extinction unknown; does not take into account distributional changes	(S4)
Marine bivalves	Genus	Time of first appearance, from fossil record	Average age decreases as diversity increases	Whether the trend is statistically significant is not known; effects of extinction unknown; does not take into account distributional changes	(S26)
Marine bivalves	Species, Genus	Comparison of Late Jurassic and Recent regional faunas	Tropical richness increased at a higher rate resulting in a steepening of the LDG over time	Consistent with higher rate of diversification in lower latitudes; does not take into account distributional changes	(S27)



Marine invertebrates (Post-Paleozoic)	Orders	Paleontological data on region of first occurrence	Tropics: significantly more first appearances	Major groups originate in the tropics, and persist there while expanding polewards; does not quantify rates of diversification	(S3, S28)
Marine mollusks	Genus Subfamily, Family	Net diversification rate using geological age of group and its current species richness	No difference in net diversification rates between tropics and extratropics	Effects of extinction unknown; does not take into account distributional changes	(S29)
Marine mollusks (Japan & western N. America)	Species	Lyellian percentages from fossil faunas	No difference in extinctions rates of tropical vs. temperate faunas	Implies higher tropical diversity is driven by higher origination	(S30)
Primates (Cercopithecoid)	Species	Regression model to test for associations between latitude and diversification rate; also used nested sister-taxon comparisons	Regression results suggest negative relation between latitude and net diversification rates, but nested sister group comparisons do not support an association between latitude and diversification rates	Overall favors the hypothesis of higher diversification in lower latitudes; reconstructions of ancestral ranges suggest that lower latitudes are "sources regions" for species	(S31)

Table S2, Percentage of tropical first occurrences among living genera and subgenera in the major clades of marine Bivalvia, for families with  $\geq 75\%$  genera known as fossils (*S1*). The high proportion of taxonomic origination in the tropics is not restricted to the heteroconch clade; note also that the proportion of tropical originations is strongly correlated ( $r^2 = 0.82$ ,  $p = 0.002$ , simple linear regression) with the proportion of taxa known fossil for the entire order (including families with  $<75\%$  of their genera and subgenera known), corroborating family-level results in Fig. 2. Classification follows (*S25*), but with unguinids and thyasirids moved from Lucinoidea to Heteroconchia following (*S32*); lucinoids and anomalodesmatans may be monophyletic groups nested within the heteroconchs (*S33*). The low number of anomalodesmatan first occurrences is consistent with previous studies (*S1*).

Clade	Total number of genera and subgenera occurring in Late Miocene-Pleistocene fossil record	Number with unknown 1 <sup>st</sup> species or unresolved to region	Percent resolved first occurrences that are tropical	Percent genera and subgenera known fossil for entire order ( <i>S1</i> )
Anomalodesmata	5	1	0	55
Arcoida	14	1	69	85
Heteroconchia	111	9	71	75
Lucinoidea	7	1	83	94
Mytiloidea	11	2	78	80
Protobranchia	8	1	57	76
Pteriomorpha	18	1	94	85

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