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

David Jablonski,[1]* Kaustuv Roy,[2] James W. Valentine[3]

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 (*1*), 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.

[1]Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, IL 60637, USA. [2]Section of Ecology, Behavior and Evolution, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093–0116, USA. [3]Department of Integrative Biology, University of California, Berkeley, Berkeley, CA 94720, USA.

*To whom correspondence should be addressed. E-mail: djablons@uchicago.edu

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 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
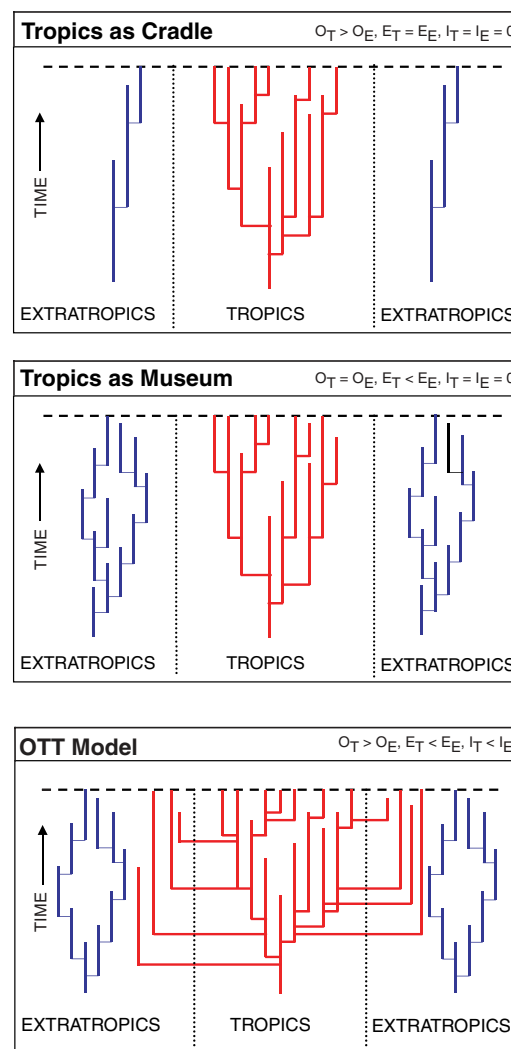

Fig. 1. Simple hypothetical scenarios illustrating the cradle, museum, and OTT models. Red denotes lineages that originated in the tropics; blue denotes lineages that originated outside the tropics. The horizontal lines connecting sister lineages also represent geographic distributions; those extending 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.
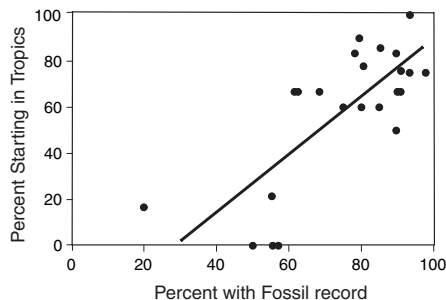

Fig. 2. Sampling quality versus tropical originations in marine bivalve families since the start of the late Miocene (11 million years ago) for families having three or more first occurrences within that interval. Families having more complete fossil records [measured as the proportion of living genera 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 ≥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
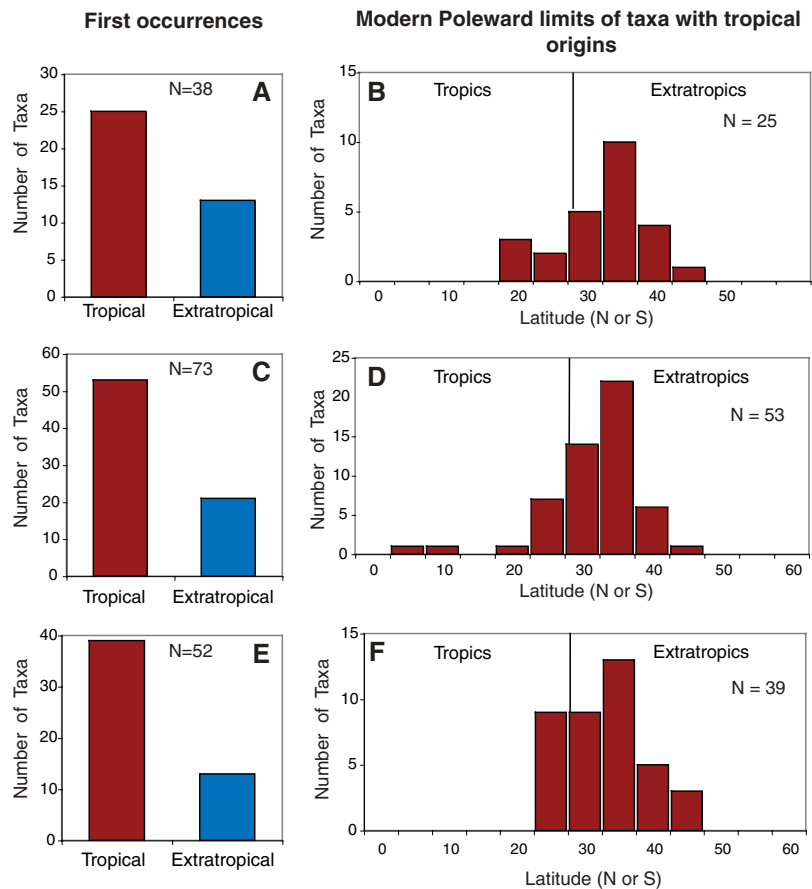
Fig. 3. Latitudinal differences in originations (left) and present-day range limits of marine bivalve genera first occurring in the tropics (right), using only families with ≥75% of their living taxa known as fossils. (**A** and **B**) Genera first appearing in the Pleistocene. (**C** and **D**) Genera 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 hetero-conch 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, ≥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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REPORTS

Molecular Loops in the Galactic Center: Evidence for Magnetic Flotation

Yasuo Fukui,[1]* Hiroaki Yamamoto,[1] Motosuji Fujishita,[1] Natsuko Kudo,[1] Kazufumi Torii,[1] Satoshi Nozawa,[2] Kunio Takahashi,[3,4] Ryoji Matsumoto,[5] Mami Machida,[3] Akiko Kawamura,[1] Yoshinori Yonekura,[6] Norikazu Mizuno,[1] Toshikazu Onishi,[1] Akira Mizuno[7]

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 ^{12}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 electrons spiraling along magnetic field lines. The magnetic field of these electrons is estimated to be typically a milligauss (*1*, *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 looplike shape with a length of several hundred parsecs and width of ~30 pc within ~1 kpc

[1]Department of Astrophysics, Nagoya University, Chikusa-ku, Nagoya 464-8602, Japan. [2]Department of Science, Ibaraki University, 2-1-1 Bunkyo, Mito, Ibaraki 310-8512, Japan. [3]National Astronomical Observatory of Japan, 2-21-1 Osawa, Mitaka, Tokyo 181-8588, Japan. [4]The Graduate University for Advanced Studies, Hayama, Miura, Kanagawa, 240-0193, Japan. [5]Department of Physics, Faculty of Science, Chiba University, 1-33, Yayoi-cho, Inage-ku, Chiba 263-8522, Japan. [6]Department of Physical Science, Osaka Prefecture University, 1-1 Gakuen-cho, Sakai, Osaka 599-8531, Japan. [7]Solar-Terrestrial Environment Laboratory, Nagoya University, Chikusa-ku, Nagoya, 464-8601, Japan.

*To whom correspondence should be addressed. E-mail: fukui@a.phys.nagoya-u.ac.jp