

# Regional Diversity and Diversification in Mammals

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**ABSTRACT:** The effects of regional diversity on diversification remain controversial. The classic hypothesis that diversification decelerates as regional diversity increases has been recently revived. Yet, there is little geographic evidence for slower diversification across regions of high diversity, and diversity is often thought to promote diversification through its effects on ecological divergence and speciation. Here, we use the newest phylogeny for mammals (4,990 species) and two different methods to test the effects of regional diversity on diversification. We find that regions of high diversity are dominated by expanding clades that are far from their estimated carrying capacities. Regions of low diversity host clades that are small and mostly saturated. These results were supported across mammals and their six largest orders. They were corroborated by the two methods when controlling for clade relatedness, clade nestedness, and clade size. Together, these results reject the hypothesis that high geographic concentration of mammals effectively suppresses their further diversification. Instead, highly diverse regions (especially the tropics) seem to act as the engine of mammalian richness.

**Keywords:** biodiversity, equilibrium, niche, conservatism, gradient, richness.

## Introduction

Whether the process of evolutionary diversification is influenced by the diversity it has previously produced is a question that remains controversial (Benton and Emerson 2007; Ricklefs 2007; Erwin 2008; Losos 2010). It has been argued that regional diversity suppresses diversification (Simpson 1953; MacArthur 1965; Rabosky and Hurlbert 2015), but the exact opposite has also been proposed, namely, that high diversity within a region promotes diversification (Erwin 2008; Benton 2009; Schemske et al. 2009). Despite this polarity, the two hypotheses have not been thoroughly evaluated together within one study. Here, we investigate whether

regional diversity suppresses or promotes diversification. We further distinguish the regions whose diversity is expanding from those that are mostly saturated and identify the geographic engines of mammalian richness.

The idea that diversity suppresses diversification was pioneered by Simpson (1953). In his classic model, species diversify after they invade an empty niche space. Niches become gradually filled with species, and diversification decelerates (MacArthur 1965; Rosenzweig 1978; Walker and Valentine 1984; Schluter 2000) until it reaches an equilibrium where speciation and extinction are mutually balanced (MacArthur 1965; Jablonski and Sepkoski 1996; Rabosky 2009a, 2009b), such that diversity stays constant through time. Diversification is, therefore, portrayed as an equilibrium process whereby high richness of a clade within a region suppresses its further growth (Simpson 1953; MacArthur 1965; Rosenzweig 1978; Walker and Valentine 1984; Schluter 2000).

Equilibrium diversification has been supported by several lines of evidence, derived from molecular phylogenies and the fossil record (McPeck 2008; Gavrilets and Losos 2009; Morlon et al. 2010; Rabosky and Glor 2010; Rabosky and Hurlbert 2015). Molecular phylogenies reveal that diversification on a newly colonized island often decelerates as niches become filled with species and competition for resources increases (e.g., Caribbean anoles, Madagascan vangas; Gavrilets and Losos 2009; Rabosky and Glor 2010; Jonsson et al. 2012). But whether these dynamics commonly operate outside the island setting remains contentious (Gavrilets and Losos 2009; Rundell and Price 2009). Decelerating diversification has been detected across hundreds of molecular phylogenies (McPeck 2008; Phillimore and Price 2008; Morlon et al. 2010), and clade age and richness are often decoupled across higher taxa (Rabosky et al. 2012), which suggests that equilibrium dynamics might be common. However, many of the reported slowdowns are likely statistical artifacts (Pennell et al. 2012; Moen and Morlon 2014; Morlon 2014; Harmon and Harrison 2015) that emerged in the absence of competition and niche filling (e.g., in clades whose spe-

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cies cannot compete because they are completely allopatric; Wiens 2011; Machac et al. 2013). Further evidence has been reported from the fossil record, indicating that mass extinctions are typically followed by diversity rebounds (Alroy et al. 2008; Rabosky and Hurlbert 2015). But it has been questioned whether these rebounds are pronounced enough to prove that fossil diversity tends toward an equilibrium (Benton and Emerson 2007; Alroy et al. 2008; Harmon and Harrison 2015).

The alternative hypothesis—namely, that regional diversity promotes diversification (Hutchinson 1959; Whittaker 1972; Farrell 1998; Benton and Emerson 2007; Erwin 2008; Schemske et al. 2009)—postulates that ecological opportunities are more likely to arise in regions of high diversity where different groups of unrelated organisms interact in complex ways, which should precipitate evolutionary novelty and speciation (Ehrlich and Raven 1964; Vermeij 1994; Losos 2010). Niche filling and competition between related species might still slow the diversification process down, but these slowdowns should be negated by biotic interactions with unrelated species that facilitate diversification (e.g., coevolution, escalation, mutualism) and become particularly prominent as regional diversity increases (Hutchinson 1959; Ehrlich and Raven 1964; Vermeij 1994; Schemske et al. 2009). The degree of species relatedness at which these effects might negate the slowdowns has not been properly investigated, such that it remains unclear over which phylogenetic scales species tend to constrain or facilitate the diversification of each other (e.g., within genera, families, orders, classes).

Expansionary diversification seems supported by the fact that taxa often diversify most rapidly in regions that harbor most of their diversity, especially in the tropics (Ricklefs 2006; Wiens 2007; Jansson and Davies 2008). Even though this observation fits the hypothesis that regional diversity facilitates diversification, it may result under some special cases of equilibrial diversification (Rabosky 2009a), especially if diversification rates are evaluated under the rate-constancy assumption (i.e., that they have stayed constant through time; Raup 1985; Magallon and Sanderson 2001; Rabosky 2009a). Consequently, regions saturated at high diversities (e.g., tropical) appear to diversify faster than regions saturated at low diversities (e.g., temperate) even though diversification rates have, in fact, uniformly declined to zero across each of the saturated regions (e.g., in the tropics and in the temperate; Rabosky 2009a). The rate-constancy assumption has been commonly invoked by classic studies (e.g., Raup 1985; Magallon and Sanderson 2001) but also under the recently developed diversification inference (e.g., BiSSE, QuaSSE, GeoSSE; FitzJohn 2010; Rabosky and Goldberg 2015), and its frequent violation invites the revision of previous findings (Machac 2014; Rabosky and Goldberg 2015). Moreover, the assumption inherently precludes any assessment of expansionary/equilibrial dynamics because these dynamics inevitably invoke changes in diversification rates over time. The support for or against these dynamics, therefore, needs to be further evaluated.

Diversification dynamics remain surprisingly contentious even in generally well-studied taxa, such as mammals. Recent studies have reported conflicting results (Weir and Schluter 2007; Purvis et al. 2011; Soria-Carrasco and Castresana 2012; Rolland et al. 2014), suggesting that mammalian diversification decelerates with latitude (Purvis et al. 2011; Rolland et al. 2014), accelerates with latitude (Weir and Schluter 2007), or stays unchanged across latitudes (Soria-Carrasco and Castresana 2012). These results were based on different statistical methods and different schemes of taxonomic and geographic sampling (Weir and Schluter 2007; Soria-Carrasco and Castresana 2012; Rolland et al. 2014), suggesting that methodology can influence diversification inference profoundly. These conflicts currently prevent a clear consensus about the geography of mammalian diversification (Weir and Schluter 2007; Purvis et al. 2011; Soria-Carrasco and Castresana 2012; Rolland et al. 2014) and present an excellent opportunity to evaluate diversification dynamics across geographic regions of different diversities, including the previously hypothesized effects of regional diversity on diversification.

Here, we evaluate whether regional diversity suppresses or promotes diversification, using two different methods. One of the methods assumes that diversification may be unbounded (coalescent inference), while the other assumes that diversification decelerates over time until it reaches an equilibrium (logistic inference). Both methods avoid the rate-constancy assumption, and each of the two evaluated hypotheses (equilibrial diversification and expansionary) receives a fair chance of being supported. To ensure exhaustive taxonomic and geographic sampling, both methods are applied across hundreds of clades that span the entire evolutionary history of mammals and their distributions worldwide. We confirm that the methods converge on similar results and conclude that regional diversity of mammals does not effectively suppress their further diversification. This conclusion yields a number of relevant implications for macroevolutionary theory and global diversity dynamics.

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## Methods

Mammals present an excellent opportunity to study the geography of diversification. They include numerous examples of explosive radiations (rodents and bats) but also very ancient, isolated lineages (platypus, armadillo, or red panda) and have colonized nearly the entire world. Moreover, their phylogeny and geographic distributions are well known.

*Phylogenetic and Distributional Data*

We used the most recent, most inclusive (4,990 species out of a total of 5,488 currently recognized species) and highly resolved phylogeny of mammals (75%; Hedges et al. 2015; accessible at <http://www.biodiversitycenter.org/ttol>). The phylogeny updates previous mammalian trees (Bininda-Emonds et al. 2007; Meredith et al. 2011), integrating molecular and morphological data and using multiple fossil calibration points (Hedges et al. 2015). Species without molecular sequences were grafted onto the phylogeny, based on taxonomy (Hedges et al. 2015). Marine species (Cetacea in Cetartiodactyla, Pinnipedia in Carnivora) were omitted for the purpose of our analyses, given that they never geographically co-occur with the terrestrial species and, therefore, cannot influence their diversification.

Importantly, some parts of the mammalian phylogeny are of higher quality than others, in terms of their topology, divergence times, and the degree of phylogenetic resolution. Carnivora, Artiodactyla (Cetartiodactyla without Cetacea), and Primates are highly resolved; their relationships are strongly supported and consistent with those reported by detailed studies for these three respective taxa (Perelman et al. 2011; Hassanin et al. 2012; Nyakatura and Bininda-Emonds 2012). Eulipotyphla have been traditionally more problematic, but their constituent taxa (Soricidae, Talpidae, Solenodontidae, Tenrecidae) are morphologically well defined (Symonds 2005; Hedges et al. 2015), and their relationships have been recently confirmed by genomics (Douady et al. 2002; Nikaido et al. 2003; He et al. 2014, 2015). Chiroptera consist of families that are similarly well defined, both ecologically and morphologically (e.g., Phyllostomidae, Mormoopidae, Noctilionidae), with phylogenetic relationships largely resolved and supported across studies (Simmons and Geisler 1998; Jones et al. 2002; Agnarsson et al. 2011; Meredith et al. 2011; Hedges et al. 2015), even though some families remain admittedly hard to place (e.g., Emballonuridae; Agnarsson et al. 2011; Hedges et al. 2015). The most problematic part of the present tree are Rodentia (Hedges et al. 2015) that show only limited correspondence with detailed multigene analyses (Blanga-Kanfi et al. 2009; Fabre et al. 2012; Schenk et al. 2013), especially across Murinae and their tribes (Rattini, Arvicanthini; less than 20% of the nodes correspond; Fabre et al. 2012; Schenk et al. 2013). This lack of correspondence pertains to other rodent clades as well, even though it seems less severe in these cases (e.g., Cricetidae and Sciuridae) and indicates that our results for rodents need to be interpreted cautiously and potentially further revised in the future (Blanga-Kanfi et al. 2009; Fabre et al. 2012; Schenk et al. 2013).

To reflect the fact that some parts of the mammalian phylogeny are more resolved and more accurate than others, we repeated our analyses across mammals and their six

largest orders (Carnivora, Artiodactyla, Chiroptera, Eulipotyphla, Primates, Rodentia). If the same results are supported across multiple, well-resolved, and highly accurate segments of the phylogeny (Carnivora, Primates, Artiodactyla), they likely warrant strong conclusions about the geographic patterns of diversification. Errors across the phylogeny should erase these patterns (e.g., randomly resolved phylogeny would not produce any clear pattern because it does not carry any geographic information). But if similar results emerge across orders (including the notoriously problematic Rodentia), the geographic patterns are likely robust, with similar diversification dynamics operating across mammals, taxon-wide, despite their dramatically divergent life history, geographic distributions, and evolutionary strategies (fossorial rodents, arboreal primates, flying bats, etc.).

Geographic distributions of mammals were taken from the International Union for Conservation of Nature database (<http://www.iucnredlist.org>) and projected onto a  $1^\circ \times 1^\circ$  grid to limit false presences in the data (Hurlbert and Jetz 2007). The grid cells, however, do not represent distinct suites of mammals because species distributions typically overlap across many cells. The species are, consequently, expected to influence the diversification of each other across multiple cells simultaneously.

*Expanding and Saturated Clades*

From the range of available methods (e.g., Ricklefs 2007; Rabosky and Lovette 2008; Morlon et al. 2010; Morlon 2014), we chose two that were most suitable and based on conceptually different foundations. The first method allowed for unbounded diversification (coalescent inference; Morlon et al. 2010), while the second assumed that diversification decelerated as clades approached their carrying capacities (logistic inference; Rabosky and Lovette 2008).

The coalescent inference fits nine diversification models, mathematically defined in the appendix (table S1; appendix and table S1 available online), to the phylogeny (Morlon et al. 2010). These models include various combinations of time-constant and time-variable rates of speciation and extinction and time-constant and time-variable diversity. Each of these models was fitted for each mammalian clade, and its support was estimated using Akaike's weights. Following Morlon et al. (2010), we identified the clades that expanded in terms of their diversity and those that were saturated.

The logistic inference, in contrast, assumes only one diversification model. Clades are expected to diversify exponentially at first, but their diversification later decelerates, and the clades eventually reach their equilibrium diversity (i.e., carrying capacity) and saturate (Rabosky and Lovette 2008). We fitted the logistic model for each mammalian clade and estimated its carrying capacity. Clades close to

their carrying capacities have limited potential for further growth, and vice versa.

Each of the two methods has its strengths and limitations (Rabosky and Lovette 2008; Morlon et al. 2010; Morlon 2014). The coalescent inference selects the best-fitting model from a range of candidates, which maximizes model fit, but diversification parameters might not be comparable across clades that conform to different models (Morlon et al. 2010). The logistic inference assumes one model only, which makes model parameters comparable (e.g., how clades differ in terms of their distance from saturation). But the model itself might fit some clades poorly, and its estimates may be associated with a high degree of uncertainty, especially across small-sized clades (Rabosky and Lovette 2008). This motivated us to use the two methods together and remove small-sized clades from our analyses (clades with less than five species; Rabosky and Lovette 2008; Morlon et al. 2010). Importantly, both methods explicitly model branching time distributions under time-varying diversification, which circumvents some of the potentially problematic issues, including the rate-constancy assumption or the pull of the present (see Rabosky and Lovette 2008; Morlon et al. 2010).

We analyzed all clades of mammals (i.e., all nodes of the mammalian phylogeny) to avoid the biases typically associated with clade selection (Phillimore and Price 2008; Pennell et al. 2012; Moen and Morlon 2014). It has been reported that researchers prefer to work with clades that are likely to show equilibrational diversification (Phillimore and Price 2008; Pennell et al. 2012) because these clades underwent an early diversification burst, occupy the same bounded region, possess a conspicuous adaptive trait, or because they consist of species that are likely competition limited (e.g., named taxa; Phillimore and Price 2008; Pennell et al. 2012; Rabosky 2013; Moen and Morlon 2014). The inclusive sampling of clades helped us avoid these issues and examine unbiased, comprehensive results that covered a range of phylogenetic scales. To account for phylogenetic correlations among the analyzed clades and their nestedness, we used phylogenetic corrections (Faith 1992; see below) and confirmed our results across nonnested clades (see below).

### *The Geography of Diversification*

To delimit the geographic distribution for each clade, we overlaid the distributions of its constituent species. Clades may show differential dynamics within the area of their geographic distribution if their subclades show diversification heterogeneity. Had we worked with select clades only, this heterogeneity would not have been captured. But we included all clades of mammals into our analysis, such that geographic regions would be dominated by clades (and their subclades) that occurred immediately within those re-

gions and, therefore, determined the dynamics of regional diversification.

To examine the coalescent results, we compared the number of expanding and saturated clades across the grid cells that covered the entire globe (see Hurlbert and Jetz 2007). Instead of simply counting the clades, we summed up the branch lengths separating the clades occurring in each cell. The sum of branch lengths increases with the number of clades in a cell while penalizing for their relatedness, much like the widely used indexes of phylogenetic diversity (Faith 1992). The percentage of expanding and saturated clades across grid cells identified the regions whose diversity expands and those that are largely saturated in terms of their diversity. To evaluate the geographic pattern, we regressed the percentages against the number of species within each cell, using generalized least squares (GLS) in R (nlme package; Pinheiro et al. 2016; R Core Team 2016), which explicitly account for the spatial autocorrelation in the data by modeling correlations in regression residuals (Pinheiro et al. 2016).

The logistic inference estimated the carrying capacity for each clade. We used these estimates to calculate clade distance from saturation, defined as the log-transformed difference between clade richness and its carrying capacity, which captured how much more diversity a clade can produce over time. We summed and averaged these distances across clades occurring in each grid cell, correcting for clade relatedness (Faith 1992; sums and averages revealed similar trends, so we report only the latter). The average distance from saturation was then mapped, revealing the regions where clades are generally close to their carrying capacities. We again used GLS for spatially correlated data in R (nlme package; Pinheiro et al. 2016; R Core Team 2016) to determine whether clade distance from saturation varied systematically with regional diversity.

To examine the geographic patterns further, we studied them in detail across latitude. Specifically, we calculated the two examined variables (the percentage of expanding/saturated clades and the distance from saturation) across latitudinal bins, which extended from the tropics to the poles, and analyzed the latitudinal trends, using nonparametric correlations for mammals and, separately, for their six largest orders (Carnivora, Artiodactyla, Chiroptera, Eulipotyphla, Primates, Rodentia). We confirmed that different thresholds (1° bins, 5° bins) and different treatments of latitude (latitudinal midpoints, median latitude, mean latitude, mean absolute latitude) produced similar results (see below).

It was our expectation that regions of high diversity would be mostly saturated if regional diversity suppresses diversification. If high-diversity regions tend to further expand in terms of their diversity, regional diversity does not effectively suppress diversification and could even facilitate it. Finally, mixed results would suggest that the connection between regional diversity and diversification is

weak, absent, or too complex to conform to either of the two hypotheses (equilibrial/expansionary diversification). In this case, the hypotheses would prove inadequate and potentially too simplistic to realistically reflect macroevolutionary dynamics.

### Supporting Analyses

We performed a series of post hoc analyses to further confirm our findings. We confirmed that the findings were supported across multiple unrelated taxa, across mutually nonnested clades, and across clades of comparable sizes. We also confirmed that they were robust toward missing species, inferential uncertainty, and different measures of clade latitude.

First, we confirmed that the findings were supported by multiple unrelated taxa, evenly spread across the mammalian tree, rather than concentrated in select lineages (e.g., within rodents and bats). To this end, we divided the analyzed clades into quartiles, based on their estimated distance from saturation, and inspected their position across the tree. We further inspected the position of clades that were particularly far from saturation ( $\log(\text{clade richness} - \text{carrying capacity}) > 10$ ).

Next, we confirmed that our results held for nonnested clades. From the pool of the analyzed clades, we randomly selected 100 clades that were mutually nonnested. We reanalyzed the latitudinal trends for these clades and repeated the procedure 1,000 times for different sets of nonnested clades.

We further confirmed that our results were independent of the differences in clade size across latitudes. Following the common practice in the field, we divided the clades into tropical and temperate, based on the latitudinal position of their distributional midpoints (Cardillo et al. 2005; Wiens et al. 2006; Pyron and Burbrink 2009). The results for the tropics and the temperate areas were then compared across three categories of clade size (less than 40 species, 40–150 species, more than 150 species) to confirm that tropical clades had significantly higher expansionary potential than similarly sized temperate clades.

Next, we confirmed that our results were robust toward missing species and inferential uncertainty. We reran the logistic and the coalescent inference with and without the missing species (i.e., those grafted onto the mammalian tree; Hedges et al. 2015) and confirmed that our findings did not change. Inferential uncertainty was not quantified by the logistic model (Rabosky 2007), but we did reanalyze the coalescent results using clades whose expansion/saturation was unambiguous and determined with a high degree of confidence (Akaike's weight  $> 0.9$ ).

Finally, we confirmed that the results were robust toward different treatments of clade latitude. We confirmed

that the mean latitude of the grid cells where the clades occurred, their median latitude, mean absolute latitude, and the commonly used latitudinal midpoints, placed halfway between the southernmost and the northernmost latitude of clade distributions (Cardillo et al. 2005; Wiens et al. 2006; Pyron and Burbrink 2009), were highly mutually correlated and supported similar latitudinal trends. We also confirmed that clades with the highest expansionary potential ( $\log(\text{clade richness} - \text{carrying capacity}) > 10$ ) covered narrow latitudinal extents and limited geographic areas centered in the tropics.

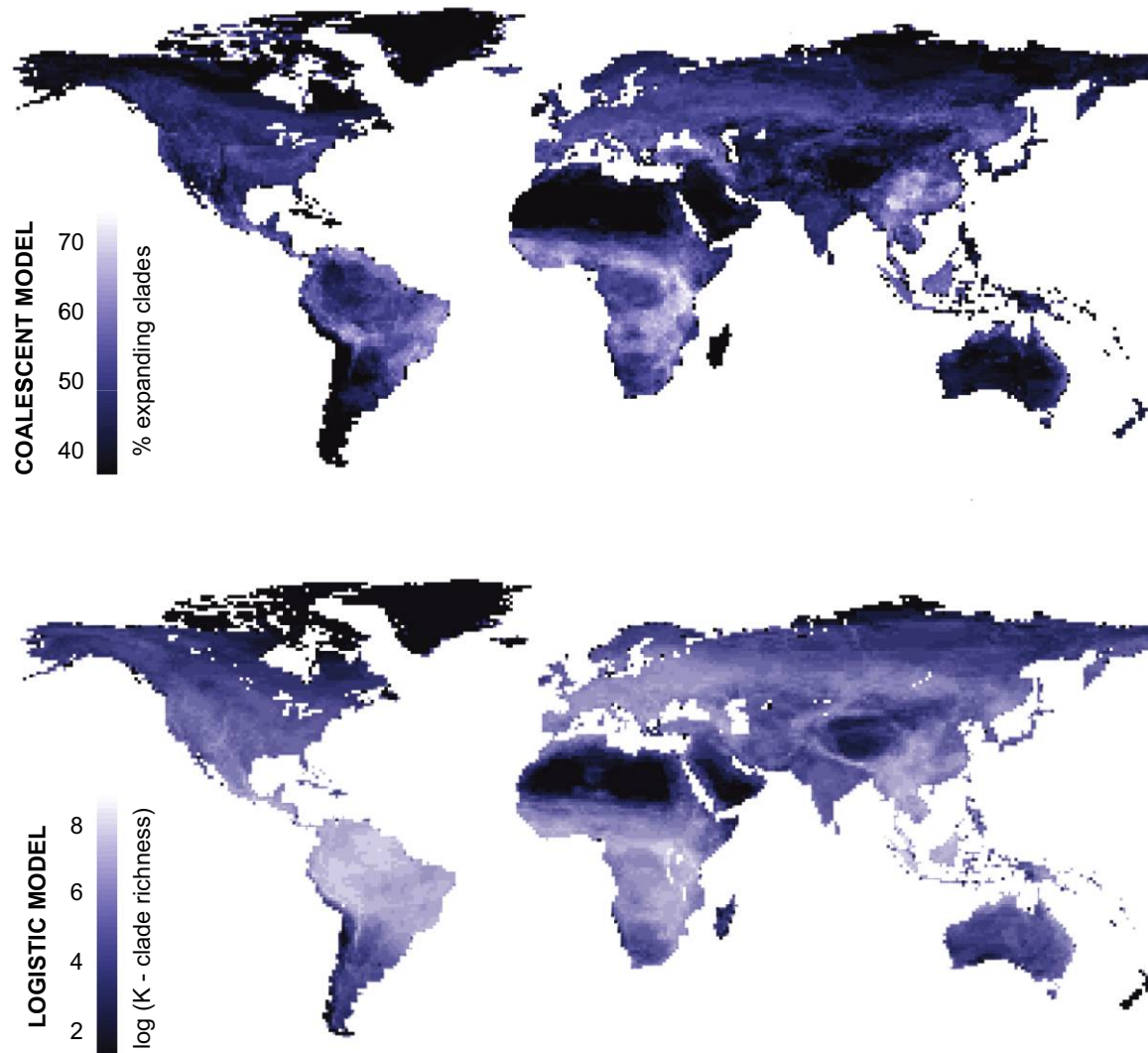
All analyses were performed in the statistical environment R (R Core Team 2016). Clade richness and the estimates of carrying capacities were log transformed to satisfy the statistical assumptions of normality and variance homogeneity and to reflect the fact that these variables are multiplicative rather than additive (Ricklefs 2007).

### Results

The coalescent and the logistic inference returned similar results. The coalescent inference revealed that most clades of mammals expand, at constant, slowing, or accelerating rates (78.4% out of 4,989 clades). In addition, the percentage of expanding clades within a region significantly increases with regional diversity (GLS:  $R^2 = 0.185$ ,  $df = 15,735$ ,  $P < .001$ ; fig. 1) and decreases with latitude ( $\rho = -0.641$ ,  $P = .001$ ; fig. 2). The relationship held for mammals ( $\rho = -0.641$ ,  $P = .001$ ) but also for each of their six orders (Carnivora, Artiodactyla, Eulipotyphla, Primates, Rodentia, Chiroptera; table 1), and even though it varied to some extent across the orders (e.g., it was less pronounced in Eulipotyphla and Carnivora; table 1), it explained much of the variation in the relative prevalence of the expanding/saturated clades across latitudes in most orders ( $R^2 = 0.525 \pm 0.269$ ,  $P < .03$ ).

The logistic inference revealed that the average distance from saturation increased with regional diversity (GLS:  $R^2 = 0.692$ ,  $df = 15,735$ ,  $P = .001$ ; fig. 1), such that tropical regions were dominated by clades that were far from their estimated carrying capacities (fig. 3), while temperate regions hosted clades that were mostly saturated (fig. 3). These results again held for mammals ( $\rho = -0.973$ ,  $P = .001$ ) and each of their six orders (Carnivora, Artiodactyla, Eulipotyphla, Primates, Rodentia, Chiroptera; table 2). Further analyses corroborated that clade richness, the estimated carrying capacities, and the distance from saturation increased toward the tropics (fig. S3; figs. S1–S11 available online), confirming the pattern of tropical expansion (figs. 1–3).

The two methods produced similar results globally but diverged in select regions (fig. 1). Pronounced differences between the Palearctic and the Paleotropics, for example, were uncovered by the coalescent—but not by the logis-



**Figure 1:** Geography of mammalian diversification. Coalescent inference revealed that regions of high diversity are dominated by expanding clades. Regions of low diversity are dominated by saturated clades (*top*). Logistic inference further revealed that clades are generally far from their estimated carrying capacities ( $K$ ) across species-rich regions. Species-poor regions host clades that are close to saturation (*bottom*). Both panels indicate that mammalian diversity expands mostly in the tropics.

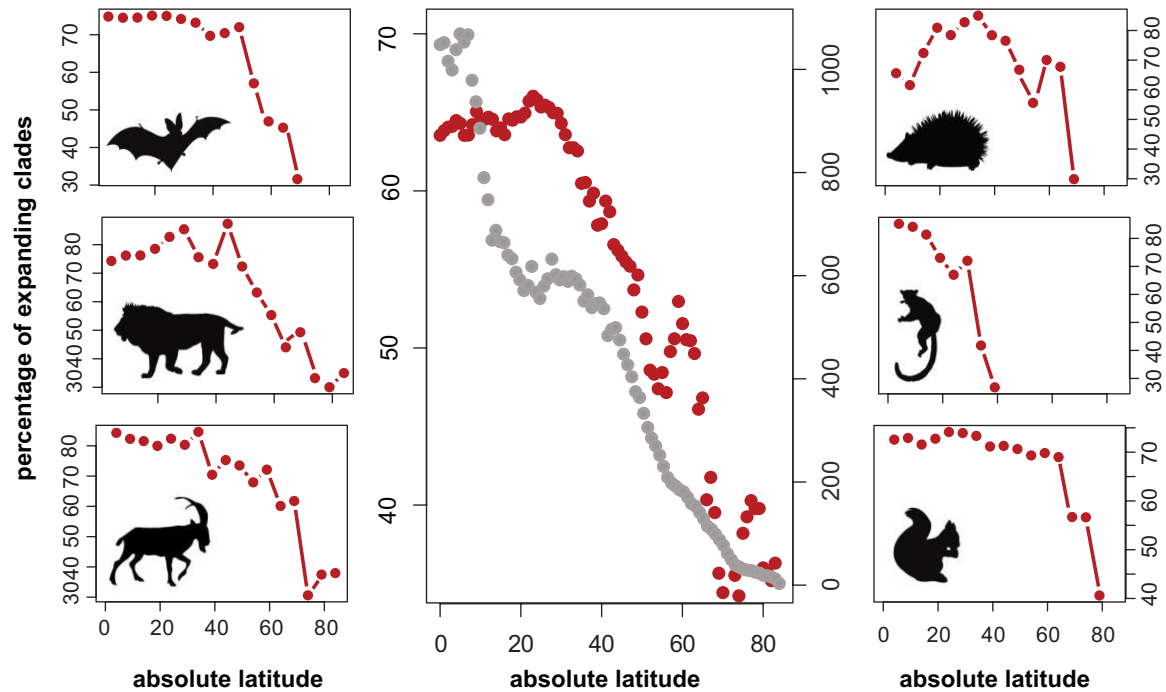
tic—inference (fig. 1). Island systems produced divergent results as well (e.g., the Malay Archipelago, Madagascar, the West Indies, Japan; fig. 1), suggesting that the methods are unevenly sensitive toward the structure of the data (e.g., long branches, polytomies, outliers; Rabosky and Lovette 2008; Morlon et al. 2010; Morlon 2014). These regional differences motivated us to interpret only the well-supported global patterns.

Importantly, similar results were supported across the six examined orders (figs. 2, 3), across multiple unrelated lineages within these orders (e.g., megabats, sloths, cricetid rodents, and ungulates; figs. S1, S2), across similarly sized clades (fig. S4), and across nested and nonnested clades

(figs. S5, S6). The same results were supported under different treatments of latitude (midpoint, median, mean, and mean absolute latitude; fig. S7), across analyses with and without the missing species (fig. S8), and when accounting for inferential uncertainty (fig. S9). Further analyses confirmed that the clades with the highest expansionary potential covered narrow latitudinal extents and limited geographic areas centered in the tropics (fig. S10).

## Discussion

We find that mammal diversity expands differentially across the world. Regions of high diversity (especially the



**Figure 2:** Results of the coalescent inference. Expanding clades dominate at the species-rich latitudes of the tropics and become less prevalent toward the poles. The trend holds for mammals (*center*) and each of their six largest orders (*side panels*: Chiroptera, Carnivora, Artiodactyla, Eulipotyphla, Primates, Rodentia). Mammal diversity across latitudes is indicated in the middle panel (gray circles, with units given on the right-hand axis). The percentages are corrected for clade relatedness.

tropics) host clades that are expanding and far from their estimated carrying capacities. These dynamics wane toward the poles. Temperate clades are mostly saturated and unlikely to enhance the limited diversity of the regions they occupy. The pattern was confirmed by two different methods applied across hundreds of clades that covered a range of phylogenetic scales and taxonomic groups (Artiodactyla, Carnivora, Chiroptera, Eulipotyphla, Primates, Rodentia). These results challenge the view that diversification dynamics are largely equilibrational, given that even the enormous diversity of mammals in the tropics (84% of their total species richness) does not seem to suppress further diversification in the region. Indeed, the diversification process cannot be entirely unbounded, given that the number of living species will never be infinite. But there seems to be much scope for further diversity growth, especially in those regions that are already hyperdiverse.

Even though the expansion of tropical diversity has been reported before (Wiens 2007; Jansson and Davies 2008; Pyron and Wiens 2013; Rolland et al. 2014), it has not been resolved to date whether the expansion is constrained or perpetuated by the previously accumulated diversity (Benton and Emerson 2007; Ricklefs 2007; Erwin 2008; Losos 2010; Wiens 2011; Harmon and Harrison 2015; Rabosky and Hurlbert 2015). Many higher taxa, including angiosperms,

amphibians, and birds, diversify most rapidly toward the tropics (Wiens 2007; Jansson and Davies 2008; Pyron and Wiens 2013; Rolland et al. 2014), but mammals have produced largely conflicting results, dependent on the methodology of the study (Weir and Schluter 2007; Purvis et al. 2011; Soria-Carrasco and Castresana 2012; Rolland et al. 2014; Oliveira et al. 2016). Employing different statistical methods under exhaustive taxonomic and geographic sampling, we find that the diversification process is not measurably constrained across regions that have previously accumulated an extraordinary diversity of mammals. In fact, these regions, especially the tropics, seem to act as the engine of mammalian richness.

Tropical diversity has been hypothesized to foster diversification through several mechanisms (Dobzhansky 1950; Fischer 1960; Ehrlich and Raven 1964; Van Valen 1973; Schluter 2000; Erwin 2008; Schemske et al. 2009) whose empirical relevance is still debated (Erwin 2008; Schemske et al. 2009). The biotic milieu and selection regimes change rapidly across the highly diverse regions, which increases the likelihood of population divergence and speciation (Dobzhansky 1950; Van Valen 1973; Schluter 2000; Schemske et al. 2009). The newly originating species may create ecological opportunities for both related and unrelated species, acting as ecosystem engineers (Jones et al. 1994). Diversification of

**Table 1:** Coalescent results indicating species richness and the percentage of expanding clades for mammals (Mammalia) and their six largest orders (Artiodactyla, Carnivora, Chiroptera, Eulipotyphla, Primates, Rodentia)

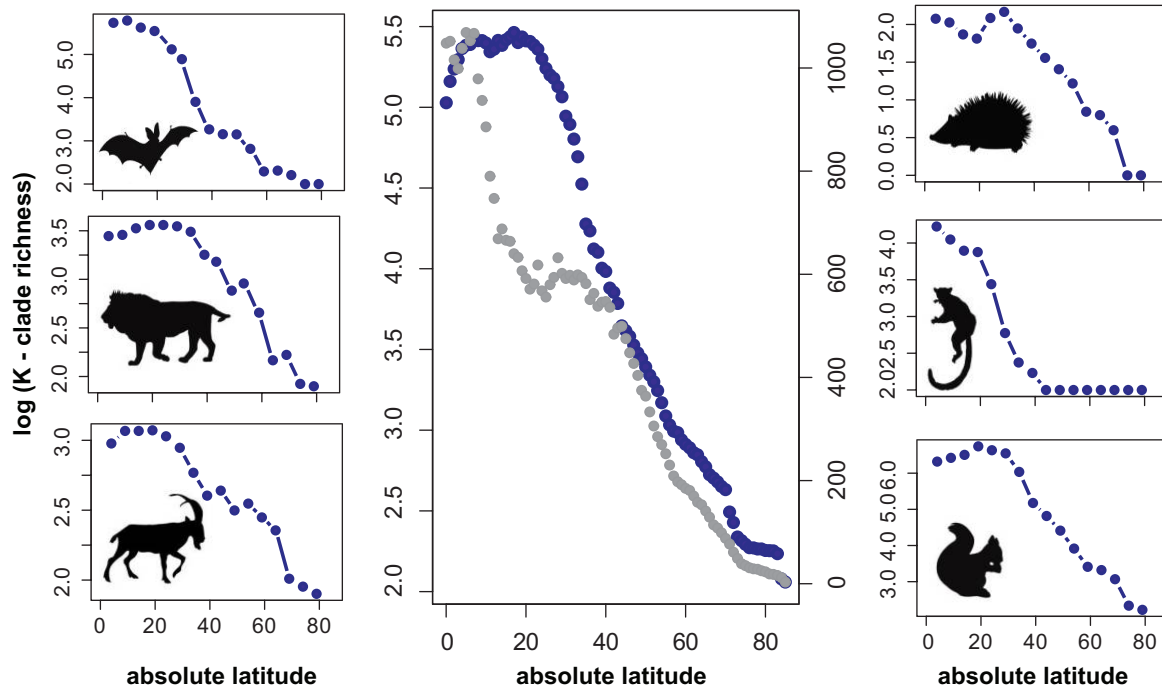
Taxon	Species richness	Expanding clades (%)	Correlation across latitudes	
			$\rho$	$P$
Mammalia	4,990	78.4	-.641	.001
Artiodactyla	309	75.0	-.906	.001
Carnivora	275	83.8	-.583	.001
Chiroptera	1,052	74.9	-.899	.001
Eulipotyphla	401	81.6	-.133	.026
Primates	350	80.6	-.757	.001
Rodentia	2,066	75.9	-.841	.001

Note: Negative correlations between the percentage of expanding clades and latitude were found in all taxa. The correlations were assessed by means of the nonparametric Spearman's rank test.

one taxon may precipitate the diversification of another, resulting in diversification cascades, most commonly reported from the highly diverse tropics (Ehrlich and Raven 1964; Vermeij 1994; Farrell 1998; Moreau et al. 2006). Together with increasing biotic complexity, evolutionary escalation, and niche construction, these effects may perpetuate diversification as regional diversity increases (Jones et al. 1994; Odling-Smee et al. 1996; Erwin 2008).

Regional diversity and diversification might be connected indirectly, through shared controlling factors, as well. Environ-

mental temperature (Allen et al. 2006; Machac et al. 2012), geographic range size (Evans et al. 2005; Weir and Schluter 2007), and niche breadth (Evans et al. 2005) have been reported to influence diversity and diversification independently, strengthening or even producing their statistical correlation (Evans et al. 2005; Allen et al. 2006; Machac et al. 2012). The expansion of tropical diversity might, therefore, result from multiple possible mechanisms and, likely, from some interplay between them, including the direct effects of regional diversity and the indirect effects of shared controlling factors.



**Figure 3:** Results of the logistic inference. High-richness latitudes host clades that are far from their estimated carrying capacities ( $K$ ). Low-richness latitudes host clades that are mostly saturated. The trend holds for mammals (center) and each of their six largest orders (side panels: Chiroptera, Carnivora, Artiodactyla, Eulipotyphla, Primates, Rodentia). Mammal diversity across latitudes is indicated in the middle panel (gray circles, with units given on the right-hand axis). The distances are corrected for clade relatedness.



**Table 2:** Logistic results indicating species richness and the estimated carrying capacities ( $K$ ) for mammals (Mammalia) and their six largest orders (Artiodactyla, Carnivora, Chiroptera, Eulipotyphla, Primates, Rodentia)

Taxon	Species richness	Estimated $K$	Correlation across latitudes	
			$\rho$	$P$
Mammalia	4,990	9,890	-.973	.001
Artiodactyla	309	590	-.961	.001
Carnivora	275	650	-.879	.001
Chiroptera	1,052	2,154	-.996	.001
Eulipotyphla	401	436	-.905	.001
Primates	350	1,024	-.936	.001
Rodentia	2,066	4,172	-.908	.001

Note: Negative correlations between the distance from saturation and latitude were found in all taxa. The correlations were assessed by means of the nonparametric Spearman's rank test.

Regardless of the underlying cause, however, the detected diversification pattern has empirically relevant ramifications. It suggests, for example, that tropical niche conservatism cannot fully explain the latitudinal diversity gradient in mammals (Wiens and Donoghue 2004; Wiens and Graham 2005; Buckley et al. 2010). It has been postulated that the gradient has emerged as tropical clades gradually colonized temperate latitudes and that, given enough time for colonization and diversification, temperate diversity is expected to increase (Wiens and Graham 2005). Our results, however, reveal only limited potential for such an increase, given that most temperate clades are close to saturation (fig. 1). Niche conservatism, therefore, may have contributed to the formation of the gradient, but its effects were likely reinforced by further factors that may have constrained temperate diversity (e.g., environmental resources, productivity, physiological constraints; Mittelbach et al. 2007). We can also speculate that temperate diversity is too low and covering too limited phylogenetic scales (only select and often related lineages) to produce the expansionary dynamics observed in the hyperdiverse tropics.

Importantly, we do not dispute that regional diversity might sometimes suppress diversification. Rather, we submit that these effects might depend on the phylogenetic scale. Diversity might suppress diversification across limited phylogenetic scales where species are closely related, ecologically similar, and potentially competing with each other for resources (Rabosky and Glor 2010; Wiens et al. 2011; Graham et al. 2016). Regional diversity of rodents, for example, does not suppress rodent diversification, but more narrowly defined clades within rodents show such effects (e.g., Schenk et al. 2013). Higher taxa encompass extensive phylogenetic scales and species that are so ecologically divergent that they rarely constrain each other's diversification. In fact, high concentration of a variety of ecologically divergent species can facilitate the diversification process (e.g., through evolutionary escalation, ecosystem engineering, niche construction, mutualisms; Hutchinson 1959; Farrell 1998; Moreau

et al. 2006). It would be interesting to systematically investigate diversification dynamics across phylogenetic scales (sensu Graham et al. 2016). The results reported here illustrate that, across the range of phylogenetic scales within mammals, the expansionary dynamics predominate.

These results are generally consistent with the fossil record, which indicates that the diversity of mammals has been expanding since the Cenozoic (65 Ma–present; Romer 1966; Gingerich 1987), and even though some lineages have declined or went extinct over time (e.g., Creodonta, Plesiadapiformes), the core taxa have been apparently expanding in terms of their diversity (e.g., Rodentia, Artiodactyla, Carnivora; Romer 1966; Alroy 2000). Even though these fossils often fall outside the extant clades and, therefore, may have conformed to different diversification dynamics, they provide relevant validation of the phylogenetic results that, similarly, supplement the fossil evidence.

Regional differences in diversification have often been evaluated under the restrictive rate-constancy assumption (e.g., BiSSE, QuaSSE, GeoSSE; Raup 1985; Magallon and Sanderson 2001; Ricklefs 2006, 2007; Smith et al. 2007; Wiens 2007; Jansson and Davies 2008; FitzJohn 2010; Machac 2014; Rabosky and Goldberg 2015), which largely precludes insights as to whether the diversification process is expansionary or equilibrational (Rabosky 2009a; Morlon et al. 2010). Here, we used two methods that allowed for time-varying diversification and found support for expansionary dynamics. These dynamics held across different schemes of taxonomic sampling, including mammals and their six orders (Artiodactyla, Chiroptera, Eulipotyphla, Primates, Rodentia; figs. 2, 3), nested and nonnested clades (figs. S5, S6), and clades that differed in their potential for further expansion (figs. S1, S2). Previous studies often compared temperate versus tropical clades (Ricklefs 2006; Kozak and Wiens 2007; Ricklefs et al. 2007; Cadena et al. 2011; Salisbury et al. 2012; Jansson et al. 2013; Rolland et al. 2014) or collapsed clade distributions into latitudinal midpoints (Cardillo et al. 2005; Wiens et al. 2006; Weir and Schluter 2007; Pyron and Burbrink

2009) and reported mutually conflicting results (Weir and Schluter 2007; Soria-Carrasco and Castresana 2012; Rolland et al. 2014), which motivated us to evaluate diversification across a grid that covered the entire globe (fig. 1), under different treatments of latitude (fig. S7), and when controlling for the possible effects of clade area and latitudinal extent (fig. S10). These analyses have consistently confirmed expansionary dynamics, in line with some previously reported evidence (e.g., Cardillo et al. 2005; Wiens 2007; Jansson and Davies 2008; Rolland et al. 2014).

We acknowledge several sources of potential errors, including inaccurate estimates of the carrying capacities (Rabosky 2007; Rabosky and Lovette 2008) and incorrectly identified clade expansion and saturation (Morlon et al. 2010). These respective errors, however, pertain to only one of the two methods employed (either the logistic or coalescent inference) and would not produce broadly similar results (figs. 1–3). Errors associated with the mammalian phylogeny may have affected some of our results (especially, Rodentia; Bonga-Kanfi et al. 2009; Fabre et al. 2012; Schenk et al. 2013; Hedges et al. 2015) but seem unlikely to overturn the main results, which held for the phylogenetically well-resolved Carnivora, Artiodactyla, Primates (Bininda-Emonds et al. 2007; Meredith et al. 2011; Perelman et al. 2011; Hassanin et al. 2012; Nyakatura and Bininda-Emonds 2012; Hedges et al. 2015) and for mammals in general (figs. 1–3). Newly discovered species will likely further reinforce our results, given that previously unknown mammals are typically reported from tropical, fast-diversifying clades (especially, Rodentia; IUCN 2016). This indicates that the current phylogeny underestimates, rather than overestimates, the magnitude of tropical expansion. Random addition of species into the phylogeny, which would increase clade richness but also the corresponding estimates of carrying capacities, would not change the main results (see fig. S11). Episodic extinctions, which are generally hard to capture using diversification inference (Romer 1966; Stuart 1991; Alroy 2000; Rabosky and Lovette 2008; Morlon et al. 2010; Fortelius et al. 2014), are unlikely to have introduced any clear bias toward or against either of the two hypotheses (expansionary diversification or equilibrial), given that episodic extinctions temporarily constrain diversification but subsequently produce empty niches that promote diversification (Romer 1966; Stuart 1991; Alroy 2000). In addition, we conducted a series of supplementary analyses to confirm our conclusions across clades whose expansion/saturation was established with a high degree of confidence (fig. S9) and when controlling for the possible effects of missing species (fig. S8). Supported by these measures, our results consolidated the previous evidence for tropical expansion, challenging the empirical relevance of equilibrial diversification.

Taken together, we found that mammalian diversity expands dramatically in the tropics whose high diversity does

not effectively suppress further mammalian diversification. The tropical expansion may result from a host of direct and indirect mechanisms, but its implications remain interesting regardless of the underlying cause. Namely, the latitudinal gradient of mammalian diversity may become even steeper in the future, and regions of high diversity presumably act as the engine of global mammalian richness. Species loss occurring in the tropics, therefore, does not remove only the species themselves but gradually dismantles the engine responsible for their origination.

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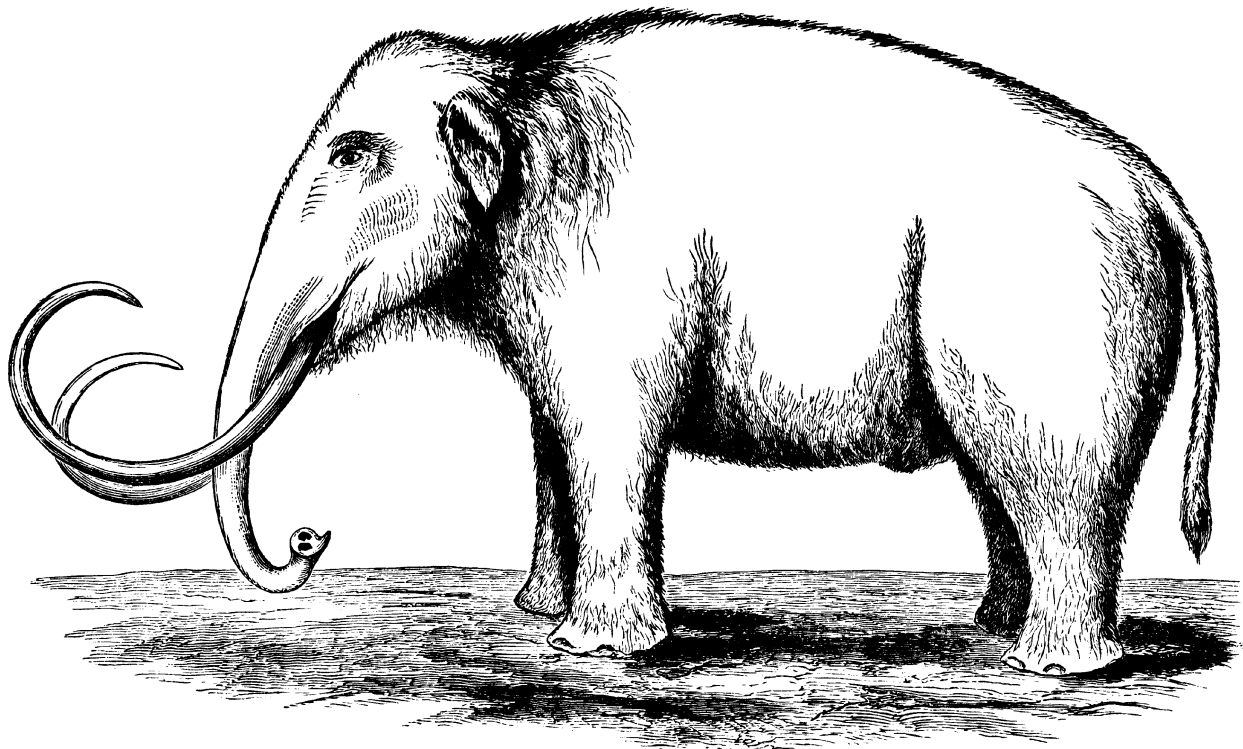
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“It has been objected, despite its hairy coat, fitting it for the rigors of a Siberian winter, that the Mammoth could not have been indigenous to the shores of the Arctic Ocean, since the vegetation was so scanty; but Professor Owen sets aside such objections, observing that ‘forests of hardy trees and shrubs still grow upon the frozen soil of Siberia, and skirt the banks of the Lena, as far north as latitude 60°. In Europe, arboreal vegetation extends ten degrees nearer the pole, and the dental organization of the Mammoth proves that it might have derived subsistence from the leafless branches of trees, in regions covered during a great part of the year with snow.’” From “The Hairy Mammoth” by A. S. Packard Jr. (*The American Naturalist* 1868, 2:23–35).