Angiosperm speciation speeds up near the poles

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Abstract

Recent evidence has questioned whether the Latitudinal Diversity Gradient (LDG), whereby species richness increases towards the Equator, results from higher rates of speciation in the tropics. Allowing for time heterogeneity in speciation rate estimates for over 28,000 angiosperm species, we found that the LDG does not arise from variation in speciation rates because lineages speciated faster outside the tropics. These results were consistently retrieved using two other methods to test the association between occupancy of tropical habitats and speciation rates. Our speciation rate estimates were robust to the effects of both undescribed species and missing taxa. Overall, our results show that speciation rates follow an opposite pattern to global variation in species richness. Greater ecological opportunity in the temperate zones, stemming from less saturated communities and greater environmental change, may ultimately explain these results.

Keywords: latitudinal diversity gradient, speciation, angiosperms, macroevolution, biogeography, biodiversity
Introduction

Biodiversity on Earth is very unevenly distributed. The Latitudinal Diversity Gradient (LDG), whereby species richness increases towards the Equator, is the most prominent example of this unevenness. This pervasive pattern has fascinated biologists for more than two centuries, but its underlying causes remain largely unknown.

A major class of explanations proposes that elevated rates of speciation generate the higher diversity in the tropics and so primarily create the LDG. This increase in speciation is generally attributed to higher environmental energy in the tropics, which in turn can hasten evolution, such as through shorter generation times, higher mutation rates and foster more complex biotic interactions (e.g., faster coevolution or the ‘Red Queen running faster when she is hot’). All these factors make reproductive isolation more likely and favour speciation. However, while some studies on mammals, amphibians and butterflies have shown that tropical lineages speciate faster, other studies have found no latitudinal differences or higher rates of speciation in temperate areas, particularly when focusing on recent rates of speciation. Recent speciation rates should be less affected by extinction and more accurate than deep-time estimates, even in the absence of paleontological evidence. They should also reflect any variable that historically influenced speciation and also varied latitudinally, such as environmental energy.

Flowering plants are one of the largest eukaryotic radiations (roughly 350,000 species) and show a marked LDG. Despite this pattern, latitudinal differences in
macroevolutionary rates in angiosperms have received comparatively little attention at
a species-level. Previous efforts have shown that angiosperm diversification is faster
in tropical families\textsuperscript{22} and in tropical lineages within a limited number of clades\textsuperscript{23,24}.
The only species-level analysis found no differences in speciation, but did so by
assuming all rate differences in the angiosperm Tree of Life (ToL) were due to
geographic distribution alone\textsuperscript{25}. One reason for the lack of attention to angiosperms is
that their vast diversity makes it difficult to obtain well-sampled phylogenetic and
distributional data at a species-level, which is required to estimate speciation rates
accurately.

Results and discussion

Here we use species-level data from the whole angiosperm ToL to assess the
latitudinal variation of speciation rates in plants. We first estimated species-specific
(i.e., tip-based) speciation rates for 29,703 species of flowering plants\textsuperscript{26} using
Bayesian Analysis of Macroevolutionary Mixtures (BAMM\textsuperscript{27}). BAMM allows for
rate heterogeneity through time and across lineages and accommodates non-random
incomplete taxon sampling. We then obtained latitudinal data for 236,894 angiosperm
species from a previous study\textsuperscript{28} and classified species as tropical or temperate using
their median latitude estimated from the Global Biodiversity Information Database
(GBIF, see Methods for details). We collated the BAMM and GBIF datasets to obtain
a dataset (herein ‘full’) of 28,057 species.

We found that speciation rates consistently increased towards the poles using several
ways of delimiting tropical and temperate species. Using correlation tests that control
for phylogenetic pseudoreplication [24], we found that tropical species had smaller
mean speciation rates ($\lambda$) than temperate species (Fig 1a; $\lambda_{\text{temperate}} = 1.24$ species/myr, $\lambda_{\text{tropical}} = 0.81$ species/myr, p-value = 0.024). Angiosperms in all 10° latitudinal bands outside the tropics (i.e. absolute median latitude $>$23.5°) speciated at faster rates than in any tropical latitudinal band (Fig. 1b). The absolute median latitude occupied by individual species was also positively correlated with their speciation rate (Fig. 1c; Spearman’s $\rho = 0.128$, p-value = 0.013). These results were maintained when we: i) analysed only those species that were densely sampled in GBIF; ii) compared strictly tropical and strictly temperate species (i.e., discarding broadly ranging species that occurred both inside and outside the tropics); and iii) discarded the highest latitudinal bands ($>$50° N and S), which contained very few species (Table S1).
Figure 1. Temperate species have higher speciation rates ($\lambda$) than tropical species. a) Rank ordered distribution and boxplot (inset) of $\lambda$ inferred with BAMM for tropical (red) and temperate (blue) species. * indicates significant difference (p-value = 0.024) between the two groups, assessed with a Mann-Whitney test implemented in STRAPP. b) $\lambda$ grouped by latitudinal band of each species. Notches in boxplots indicate 95% confidence intervals around median, denoted by thick vertical lines and boxes span the interquartile ranges. c) Spearman’s ρ correlation between species absolute median latitude and $\lambda$ as estimated with STRAPP. Grey lines are correlations across 1000 samples of the posterior distribution estimated with BAMM. Inset shows the difference between the empirical and null correlations estimated with 1000 permutations of evolutionary rates across the phylogeny.

Our full dataset contained a disproportionate amount of temperate species but this did not explain the consistent association between latitude and speciation rates. The initial GBIF dataset was consistent with the LDG, containing 42.5% and 57.5% temperate and tropical species, respectively (Fig S1a-c). However, the data were disproportionately represented by temperate species (61.7%) after merging GBIF distributions with the macroevolutionary rates (Fig. S1d-f). We assessed if this latitudinal bias could affect our results in two ways. First, we generated 100 random samples of our full dataset (herein ‘unbiased’ datasets), each with 10,000 species that maintained the proportion of tropical (57.5%) and temperate (42.5%) species present in GBIF. Second, we generated another set of 100 random samples (herein ‘extreme tropical’ datasets), where the proportions of temperate and tropical species were 29.1% and 70.9% respectively. These were calculated assuming that all species absent from GBIF were tropical and therefore represent the most extreme scenario of
latitudinal bias. We then assessed whether the λ estimates were affected by the poorer sampling for tropical species, which may result in average longer branches and lower λ. We reran BAMM for 10 of the 100 unbiased and extreme tropical datasets and compared the resulting estimates with the ones from the full dataset (n = 28,057 species). We found that the λ estimates from the full and the subsampled datasets were very positively correlated (median ρ = 0.82, median p-value < 0.001 and median ρ = 0.83, median p-value < 0.001 for the unbiased and the extreme tropical datasets, respectively), and that this association did not differ between tropical and temperate species (Figs S2, S3). We also confirmed that the association of λ and latitude was not a result of the excessive proportion of temperate species in the full dataset by repeating the STRAPP analyses subsetted to the species present in each of the 100 unbiased and extreme tropical datasets. Our conclusions were identical between the full and both the unbiased (Fig S4) and extreme tropical datasets (Fig S5). Finally, we confirmed that our results could not be explained by different levels of sampling for BAMM between temperate and tropical species. We found that the relationship of median latitude and BAMM sampling fraction was positive but small (Fig S6).

Moreover, densely sampled clades, which occurred at higher latitudes, tended to have smaller estimates of λ (Fig. S7), contrary to what we might expect if our results were a sampling artefact. These analyses collectively exclude the conclusion that our results stem from lower estimates of speciation rates in more sparsely sampled tropical clades.

We also confirmed that the speciation rate estimates were robust despite the low levels of sampling of the angiosperm ToL. Our full dataset contained 8% of the angiosperm species described in The Plant List. To assess the effect of missing taxa,
we randomly sampled 8% of the species (n = 2,273 species) in our full dataset ten
times and reran BAMM on these ‘small’ datasets. As above, the λ estimates from the
full and the small datasets were positively correlated (median ρ = 0.66, median p-
value < 0.001), and this association did not differ between tropical and temperate
species (Fig. S8).

The positive association between speciation rates and latitude was consistently
retrieved using two alternative methods for estimating macroevolutionary rates. First,
we used FiSSE (Fast, intuitive State-dependent Speciation-Extinction analysis31), a
non-parametric test that determines the effect of a binary trait on speciation rates. We
found a positive association of speciation rate estimated with FiSSE (DR) and
whether species were temperate with our full dataset (median DRtemperate = 0.29
species/myr, median DRTropical = 0.18 species/myr, p-value = 0.001). To test whether
the excess of temperate species influenced this result, we repeated the analyses in the
100 unbiased datasets of 10,000 species and found no significant differences
(DRtemperate = 0.15 species/myr, DRTropical = 0.13 species/myr, p-value = 0.168).
However, simulations suggested that this non-significant result may stem from a lack
of power with FiSSE for our given phylogenetic and trait data (Fig S9, see Methods).
FiSSE, unlike BAMM, also does not account for incomplete sampling in the
speciation rate estimates, so we caution against strong interpretations of the results
obtained with this method with the present levels of missing taxa. Second, we
analysed the association between latitude and speciation rate across clades of different
ages in the angiosperm ToL. Following ref. 26, we defined six 4 million-year-wide
time slices, from 0 to 24 million years (myr), which were used to select clades where
speciation rates could confidently be estimated (i.e., probability of recovering the
crown age of lineages was > 70% following ref. 30) and GBIF coverage was > 50%.

We then fitted models that implemented time-variable and time-constant functions for speciation and extinction\textsuperscript{32}, and selected the best fitting model to obtain clade-based estimates of speciation rates. Mirroring the BAMM results, we found that clades with a larger proportion of temperate species had higher rates of speciation (Fig S10).

Overall, our findings do not support the long-standing notion that the greater species diversity of the tropics can be explained by higher rates of speciation. We instead found higher rates of recent speciation closer to the poles. As temperate biotas have fewer species, their niche space may be less saturated, thereby increasing opportunities for lineage divergence\textsuperscript{15,33}. Similarly, reproductive isolation may be elevated at higher latitudes by the greater ecological opportunity generated from recurrent environmental change and climate instability\textsuperscript{34}. Other explanations may be related to the ecological and life history traits of temperate species. For example, faster speciation rates at higher latitudes could stem from the higher frequency of small-seeded species\textsuperscript{35}. Small seed size is positively correlated with angiosperm diversification\textsuperscript{26}, and temperate species did have smaller seeds in our full dataset (see Methods, phylANOVA: p value = 0.001, significance assessed with 1,000 random simulations with phytools\textsuperscript{36}). Therefore, our results suggest that latitudinal differences in speciation rate do not shape the LDG but are shaped by differences in species diversity and traits\textsuperscript{16,37}.

Rejecting the role of speciation rate as the cause of the LDG calls for alternative explanations\textsuperscript{25}. From a macroevolutionary perspective, greater tropical species diversity may arise for at least three reasons\textsuperscript{38}: i) higher rates of diversification (i.e.,
speciation minus extinction), ii) higher rates of net migration, and iii) greater potential for historical colonisation. First, the elevated speciation near the poles could be coupled with higher extinction rates to produce a scenario where temperate zones act as both a “cradle” and “grave” of biodiversity. Net diversification might therefore still be higher in tropical areas despite the absolute rates of speciation and extinction each being smaller than closer to the poles. However, the lack of reliable extinction rate estimates from molecular phylogenies in the absence of fossil data complicates a direct test of this hypothesis. Second, the tropical conservatism hypothesis proposes that lower net migration from the tropics to temperate zones contributes to the LDG: most lineages originated in the tropics and have been unable to disperse into harsher environments. Third, if rates of diversification and migration have no latitudinal variation, the greater diversity of the tropics may stem from their larger area through time (age-and-area hypothesis).

An alternative to these ideas is that the LDG may simply have nothing to do with macroevolution. A whole class of hypotheses posits that there are ecological limits to the number of species that a region can hold, and that these limits vary with latitude. For example, the larger diversity in the tropics could be explained by expanded niche spaces and greater niche packing.

Recent findings have suggested that rates of species origination are highest in species-poor areas. Our results are consistent with these findings and therefore suggest that latitudinal variation in speciation rates is not a major engine of global diversity patterns in one of the largest eukaryotic radiations. Using time-heterogeneous estimates of speciation, we were able to exclude faster rates of evolution, such as...
arising from more favourable environmental conditions or more intense biotic 
interactions, as responsible for shaping the angiosperm LDG. Future work must now 
resolve whether recent rapid speciation nearer the poles is widespread across the ToL 
and its underlying causes.

**Methods**

*Latitudinal and phylogenetic datasets*

We obtained latitudinal data for 236,894 angiosperms that included the median, 
maximum and minimum latitude for each species\textsuperscript{28}. We then intersected these data 
with speciation rates estimated with BAMM v.2.5.0\textsuperscript{27} for 29,703 angiosperms\textsuperscript{26}. The 
input phylogeny was obtained from a time-calibrated phylogenetic tree for 31,389 
land plant species\textsuperscript{45,46}. BAMM detects heterogeneity in speciation and extinction rates 
through time and across lineages. Non-random incomplete taxon sampling was 
incorporated into the estimation process by calculating the number of species sampled 
in each family.

The species names in the GBIF and BAMM datasets were standardised with The 
Plant List (TPL) using the *Taxonstand*\textsuperscript{47} and *Taxonlookup*\textsuperscript{48} packages before collation, 
resulting in 28,057 species in our full dataset. Tropical and temperate species were 
defined as those where the absolute median latitude was below and above 23.5°, 
respectively. Species were also grouped into 10° bins according to their median 
latitude to define latitudinal bands (starting from a band centered in the Equator from 
-5° to 5°, then from 5° to 15, etc). We repeated the analyses using only densely 
sampled species (i.e., with five or more data points in the GBIF dataset). Strictly
tropical and temperate species were defined as species with median, maximum and minimum latitude occurring inside and outside the tropics, respectively. We discarded widespread species (i.e., neither strictly tropical nor strictly temperate) for analyses comparing strict tropical and temperate taxa (retaining 20,766 species). Finally, we discarded data with median latitudes in the highest latitudinal bands (>50° and <-50°), which contained very few species with extreme estimates of λ (retaining 25,189 species).

**BAMM-based analyses**

We correlated BAMM speciation rates and latitudinal data using Structured Rate Permutations on Phylogenies (STRAPP)\(^9\). STRAPP assesses the significance of the empirical association of macroevolutionary rates and phenotypic traits by comparing it to a null distribution generated by permuting the speciation rates across the phylogeny while maintaining the position of the rate shifts in the phylogenetic tree. We performed all STRAPP two-tailed tests using the `traitdependentBAMM` function of the BAMMtools package\(^9\) with 1000 replicates and logging the rates. We assessed whether i) tropical and temperate species had different speciation rates using a Mann Whitney U test; ii) speciation rates for each of the latitudinal bands were different using the Kruskal-Wallis rank sum statistic; and iii) species absolute median latitude was correlated with its speciation rate using Spearman’s rank correlation coefficient.

We analysed the potential effect of the disproportionate amount of temperate species in our full dataset using BAMM. Subsampled datasets were consistent with the LDG and either i) maintained the proportions of tropical (57.5%) and temperate (42.5%) taxa observed in the GBIF dataset (‘unbiased’); or ii) assumed that the species absent
from the GBIF dataset from ref. 28 were all tropical (‘extreme tropical’) (n = 109,461 species; obtained from subtracting the number of species in The Plant List according to TaxonLookup 48 minus the species in the GBIF dataset). Both subsampled datasets were generated to assess the effect of the excess of temperate species in our full dataset, but the extreme tropical dataset represented the most extreme scenario of the effect of undescribed biodiversity in our analyses. The size of these datasets was fixed at 10,000 species so that the tropical species present in each subsample, which were obtained by random draws of 5,750 and 7,091 species for the unbiased and extreme tropical respectively from a total pool of 10,749 species, were not excessively redundant. We selected 10 random replicates of the 10,000-species subsampled datasets and reran the BAMM analyses as detailed in ref. 26. We then assessed whether the relationship of the full (n=28,057 species) and both the unbiased and extreme tropical λ estimates was different for tropical and temperate species. To do this, we predicted the full λ estimates using the subsampled λ estimates, ‘tropicality’ (i.e. a binary variable indicating if a species was tropical based on our aforementioned definition) and the interaction of the λ estimates and tropicality in each of the 10 replicates for the unbiased and extreme tropical datasets. We incorporated the effect of the phylogeny using the phylolm package 50. We found that the effect size of the interaction of tropicality and the λ estimates was not different from zero across all the 10 replicates for the unbiased (mean = 0.0009, standard deviation = 0.0015) and the extreme tropical (mean = 0.0004, standard deviation = 0.0016) datasets. This result shows that there is no difference in the correlation between λ of the full and subsampled datasets between temperate and tropical lineages.
We also confirmed that our results could not be explained by latitudinal variation in the clade sampling fractions of our BAMM analysis. We found a positive relationship (slope = 0.059, p-value < 0.0001) between the species median latitude and its sampling fraction (i.e. the percentage of species in the same family present in our 28,057 species phylogenetic tree). This result meant that a 10° increase in median latitude corresponded with an average of 0.59% increase in sampling fraction.

Furthermore, we found that there was a negative relationship between sampling fraction and the log-transformed estimated speciation rate (slope = -0.055, p-value < 0.0001). Again, this effect size was small. For example, an increase in sampling fraction from 20% to 30% corresponded with an average decrease of 0.33 lineages/myr in the estimated speciation rate.

Our full dataset contained \( \lambda \) estimates for 28,057 species, which represent 8% of described angiosperm species (total \( n = 346,365 \) calculated with Taxonlookup). To assess the reliability of \( \lambda \) estimates given the large number of missing taxa, we randomly generated 10 subsamples (‘small’ datasets) with 8% of the species in our full dataset (\( n = 2,273 \)). As above, we ran BAMM for each of the 10 subsamples and predicted the full \( \lambda \) estimates using the small \( \lambda \) estimates. Similar to the unbiased and extreme tropical datasets, we found that the effect size of the interaction of tropicality and \( \lambda \) was not different from zero across all the 10 replicates (mean = -0.0033, standard deviation = 0.0189).

Although the reliability of BAMM estimates has recently been questioned\(^{51}\), simulations have shown that accurate estimates of speciation can be obtained even in the absence of fossil data\(^{39,52}\). Tip-based estimates of speciation like the ones we use...
here should also be robust to the effect of extinction and are increasingly used when analysing the effect of traits on lineage diversification\textsuperscript{20}. Extinction estimates are thought to be more unreliable\textsuperscript{19,53,54} so we do not discuss them here.

*FiSSE-based analyses*

*FiSSE* analyses the correlation of a binary trait and diversification and has shown to have a lower type I error than similar trait-dependent diversification methods\textsuperscript{31}. It calculates the speciation rate associated with each trait state and is based on the diversification rate metric (DR\textsuperscript{55}), which was originally proposed to estimate net diversification but has since been shown to approximate speciation rates better\textsuperscript{20}. The distributions of DR for each trait value (i.e. tropical and temperate) had long right-tails and the means were much larger than the medians, so the latter measure better described the central tendency of the DR distributions. Therefore, following ref. \textsuperscript{56} we modified the FiSSE function provided in ref. \textsuperscript{31} to compare the median diversification rate for each trait value instead of the mean.

We also assessed whether the lack of significant differences between tropical and temperate speciation rates that we found with the 100 unbiased datasets could be explained by their sample size (n=10,000 species). We generated 100 replicates of the full dataset of 2,000; 4,000; 6,000; 8,000; 10,000; and 12,000 species and reran FiSSE for each of them. We then ran an exponential regression with the size of a dataset as a predictor and the logged p-value of the association of speciation and tropicality as a response.

*Clade-based analyses*
We estimated clade-level measures of speciation across the angiosperm phylogenetic tree. We used a set of 4 million-year-wide time intervals from 0 to 24 myr to define the ages of the clades. Clades were delimited as the largest non-overlapping monophyletic groups of four or more species where the sampling was larger than 30%. This criterion ensures that the probability of retrieving the correct crown age of the clade is above 70%\(^{30}\). At least 50% of the species in the clades also had to have latitudinal data. We used RPANDA (R: Phylogenetic ANalyses of DiversificAtion\(^{32}\)) to fit six different models of diversification: i) constant speciation (\(\lambda\)) and extinction (\(\mu\)) fixed at 0; ii) constant \(\lambda\) and \(\mu\); iii) exponential \(\lambda\) and \(\mu\) fixed at 0; iv) exponential \(\lambda\) and constant \(\mu\); v) constant \(\lambda\) and exponential \(\mu\); and vi) exponential \(\lambda\) and \(\mu\).

Incomplete sampling within clades was incorporated into the estimates by calculating the proportion of sampled species within the genera in each clade. Speciation rates were estimated using model averaging with AIC weights. The correlation of the clade-level estimates of speciation and the proportion of temperate and tropical species in each clade was assessed using phylogenetic least squares regression as implemented in the R package \textit{nlme}\(^{57}\). The lambda parameter was optimised using a maximum likelihood approach. We weighted the regressions by the proportion of GBIF data points in each clade to account for the effect of different sampling levels of distribution data. We then confirmed that potential latitudinal differences in sampling proportions could not explain our results. To do that, we analysed if the sampling proportions of largely tropical and largely temperate clades (defined as clades where >50% of the species were tropical and temperate, respectively) across the 6 time intervals were different using Pearson’s chi-squared test. We found that temperate clades had significantly denser average sampling only in the 16-20 (sampling...
proportion_{tropical} = 0.65, sampling proportion_{temperate} = 0.56) and 20-24 (sampling
proportion_{tropical} = 0.69, sampling proportion_{temperate} = 0.57) myr intervals.

Latitudinal variation of seed size

Smaller seeded species have been shown to speciate faster than large seeded species\textsuperscript{26}.

We assessed whether seed size differed between temperate and tropical lineages as it
has previously been shown to do so\textsuperscript{35}, and so latitudinal variation in seed size could
explain the differences in speciation between tropical and temperate species. We
obtained seed size measurements for 13,127 species in our full dataset from a
previous study\textsuperscript{26}. The resulting dataset was disproportionately temperate (76.04% of
the species were temperate). Average seed sizes were larger in tropical than in
temperate species (mean seed size_{tropical} = 0.149 g; mean seed size_{temperate} = 0.065 g; t =
-298.7; df = 4189.2; p-value < 0.001). This difference remained when phylogeny was
considered (phylANOVA: t = 35.293; p value = 0.001; significance assessed with
1,000 random simulations).

Data availability

Scripts to reproduce the analyses will be deposited upon acceptance in figshare

Author contributions

J.I. conceived the study and performed the analysis; J.I. and A.J.T interpreted the
analysis and wrote the manuscript.
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Declaration of interests

The authors declare no competing interests.

Supplementary Figures and Tables

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Table S1. Temperate species have mean higher speciation rates ($\lambda$, estimated with STRAPP) than tropical species across different datasets: “more.GBIF.data” excludes species with less than five GBIF data points; “no.widespread” excludes species occurring both in and outside the tropics; “no.high.latitude” excludes species from poorly sampled latitudinal bands with absolute median latitude $\geq 50^\circ$. Units for $\lambda$ and dataset size are lineages/myr and species, respectively.
Figure S1. The full dataset had a disproportionate number of temperate species. a) Proportion of tropical and temperate species in the GBIF dataset (n = 236,894); b) proportion of species in each latitudinal band in the GBIF dataset; c) number of species in each latitudinal band in the GBIF dataset; d) proportion of tropical and temperate species in the full dataset (n = 28,057); e) proportion of species in each latitudinal band in the full dataset; f) number of species in each latitudinal band in the full dataset; in b), c), e) and f), the dotted vertical line denotes the 23.5° threshold between tropical and temperate zones.
**Figure S2.** BAMM $\lambda$ estimates were positively correlated in the full and 10 unbiased datasets with no effect of tropicality on this correlation. a) - j) Solid lines are phylogenetic linear regressions predicting $\lambda$ in the full tree (n = 28,057 species) with $\lambda$ in the unbiased tree (n = 10,000 species) in temperate (shown in blue) and tropical (shown in red) species. Shaded areas indicate the 95% confidence intervals.

**Figure S3.** BAMM $\lambda$ estimates were positively correlated in the full and 10 extreme tropical datasets with no effect of tropicality on this correlation. a) - j) Solid lines are phylogenetic linear regressions predicting $\lambda$ in the full tree (n = 28,057 species) with $\lambda$. 
in the extreme tropical tree ($n = 10,000$ species) in temperate (shown in blue) and tropical (shown in red) species. Shaded areas indicate the 95% confidence intervals.

**Figure S4.** Temperate species have higher speciation rates ($\lambda$) than tropical species for 100 subsampled “unbiased” datasets with 42.5% of temperate and 57.5% of tropical species. a) Rank ordered distribution of $\lambda$ inferred with BAMM for tropical (red) and temperate (blue) species. b) $\lambda$ grouped by latitudinal band of each species. Boxes show the average interquartile range across the 100 subsampled datasets, and lines show the average medians. c) Spearman’s $\rho$ correlation of species absolute median latitude and $\lambda$ as estimated with STRAPP. Solid black line indicates median correlation $\pm$ 95% confidence interval across the posterior distribution. The inset shows the median (black line) $\pm$ 95% confidence interval for the difference between
the empirical and null correlations estimated with 1000 permutations of evolutionary rates across the phylogeny in each of 100 subsampled datasets.

**Figure S5.** Temperate species have higher speciation rates ($\lambda$) than tropical species for 100 subsampled “extreme tropical” datasets with 29.1% temperate and 70.9% tropical species. 

- **a)** Rank ordered distribution of $\lambda$ inferred with BAMM for tropical (red) and temperate (blue) species. 
- **b)** $\lambda$ grouped by latitudinal band of each species. 
- **c)** Spearman’s $\rho$ correlation of species absolute median latitude and $\lambda$ as estimated with STRAPP. Lines and inset shown as in Fig. S4.
Figure S6. Relationship between the species absolute median latitude and the family-level sampling fraction used in the BAMM analyses. The red line is the slope of the linear regression (slope = 0.059, p-value < 0.0001).
Figure S7. More densely sampled clades have smaller estimates of speciation rate ($\lambda$).

The dotted line is the slope of the linear regression of the log($\lambda$) and the BAMM sampling fraction (slope = -0.055, p-value < 0.0001).
Figure S8. BAMM \( \lambda \) estimates are positively correlated in the full and 10 small datasets and tropicality has no effect on this correlation. a) - j) Solid lines are phylogenetic linear regressions predicting \( \lambda \) in the full tree (n = 28,057 species) with \( \lambda \) in the small tree (n = 2,273 species) in temperate (shown in blue) and tropical (shown in red) species. Shaded areas indicate the 95% confidence intervals.
Figure S9. FiSSE power analysis. Each boxplot shows the p-values for the difference of DR\textsubscript{temperate} and DR\textsubscript{tropical} for 100 subsamples of varying size taken from the full dataset (n = 28,057 species) whilst retaining proportions of tropical and temperate species observed in the GBIF dataset. Notches in boxplots indicate 95% confidence intervals around the median, denoted by thick vertical lines. Boxes indicate the interquartile range (IQR) and whiskers extend to the most extreme data points that are not further away than ±1.5×IQR. The solid line is an exponential model predicting the logged mean p-value ± 95% confidence interval (shaded area) from the size of the dataset. The dotted line indicates p-value = 0.05.
Figure S10. Temperate clades have higher speciation rates in the clade-based analysis. Correlation of a) the proportion of tropical and b) temperate species in each clade with the corresponding speciation rate ($\lambda$) estimated with RPANDA. The correlation coefficient is the phylogenetic generalised least squares (PGLS) slope. The size of the points is scaled to the number of clades in each time interval and their colours show the statistical significance of the slope.
References


