

Current Biology

Limited ecological opportunity influences the tempo of morphological evolution in birds

Highlights

- The availability of open niches is thought to accelerate evolution
- Models of trait evolution often fail to find evidence in support of this idea
- A new approach uncovers abundant support for the influence of ecological opportunity
- Ecological constraints are not more pronounced in the tropics

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In brief

Drury et al. improve upon existing models of trait evolution and find abundant evidence that trait evolution responds to changes in ecological opportunity in birds—a prediction of theory which has not been consistently supported previously.



Report

Limited ecological opportunity influences the tempo of morphological evolution in birds

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SUMMARY

According to classic models of lineage diversification and adaptive radiation, phenotypic evolution should accelerate in the context of ecological opportunity and slow down when niches become saturated.^{1,2} However, only weak support for these ideas has been found in nature, perhaps because most analyses make the biologically unrealistic assumption that clade members contribute equally to reducing ecological opportunity, even when they occur in different continents or specialize on different habitats and diets. To view this problem through a different lens, we adapted a new phylogenetic modeling approach that accounts for the fact that competition for ecological opportunity only occurs between species that coexist and share similar habitats and diets. Applying this method to trait data for nearly all extant species of landbirds,³ we find a widespread signature of decelerating trait evolution in lineages adapted to similar habitats or diets. The strength of this pattern was consistent across latitudes when comparing tropical and temperate assemblages. Our results provide little support for the idea that increased diversity and tighter packing of niches accentuates evolutionary slowdowns in the tropics and instead suggest that limited ecological opportunity can be an important factor determining the rate of morphological diversification at a global scale.

RESULTS AND DISCUSSION

A central goal of modern ecology and evolutionary biology is to understand the mechanisms shaping patterns of biodiversity across space and time. Many theoretical frameworks posit that ecological opportunity (“the availability of ecologically accessible resources that may be evolutionarily exploited”⁴) is a key driver of rates of both lineage and phenotypic diversification, in which case macroecological patterns of variation in diversity can be explained by variation in limits to these ecological opportunities.^{1,2} Ecological opportunity is also a central factor in macroevolutionary frameworks that aim to explain bursts of morphological disparity in the fossil record^{5,6} and the phenotypic diversification typical of adaptive radiations.⁷

Some of the key tools for quantifying evolutionary responses to changes in ecological opportunity are models of time and diversity dependence. These models aim to identify whether changes in rates of lineage diversification (i.e., speciation minus extinction)^{8–10} or trait evolution^{11–15} decline through time or covary with the changes in the number of lineages in a clade. The reasoning is that ecological opportunity is reduced as clades diversify and species fill an increasingly packed niche space,

resulting in an “early-burst” (EB) pattern where fast evolution at the origin of clades is followed by slowdowns. Slowdowns may occur in the absence of diversity dependence, and diversity dependence may occur in the absence of limiting ecological opportunity.¹⁶ However, if evolutionary rates are indeed constrained by limited ecological opportunity, we expect to find evidence of declining evolutionary rates over time or in correlation with the number of lineages in a clade. Hereafter, we refer to time-dependent and diversity-dependent (DD) models with declining rates as “models of limited ecological opportunity.” Contrary to studies of lineage diversification, where models of limited ecological opportunity are often well supported,^{8,9} empirical tests of time or diversity dependence in trait evolution often fail to find widespread statistical support.^{15,17}

Several factors might explain why studies of trait evolution have failed to recover evidence for slowdowns. First, the taxonomic scale at which these studies are conducted matters, such that evolutionary changes in morphology associated with transitions between different “adaptive zones” are the likeliest to drive bursts in disparity.¹⁸ Indeed, studies conducted at taxonomic scales higher than the family seem to be more likely to uncover evidence of time/diversity dependence in phenotypic



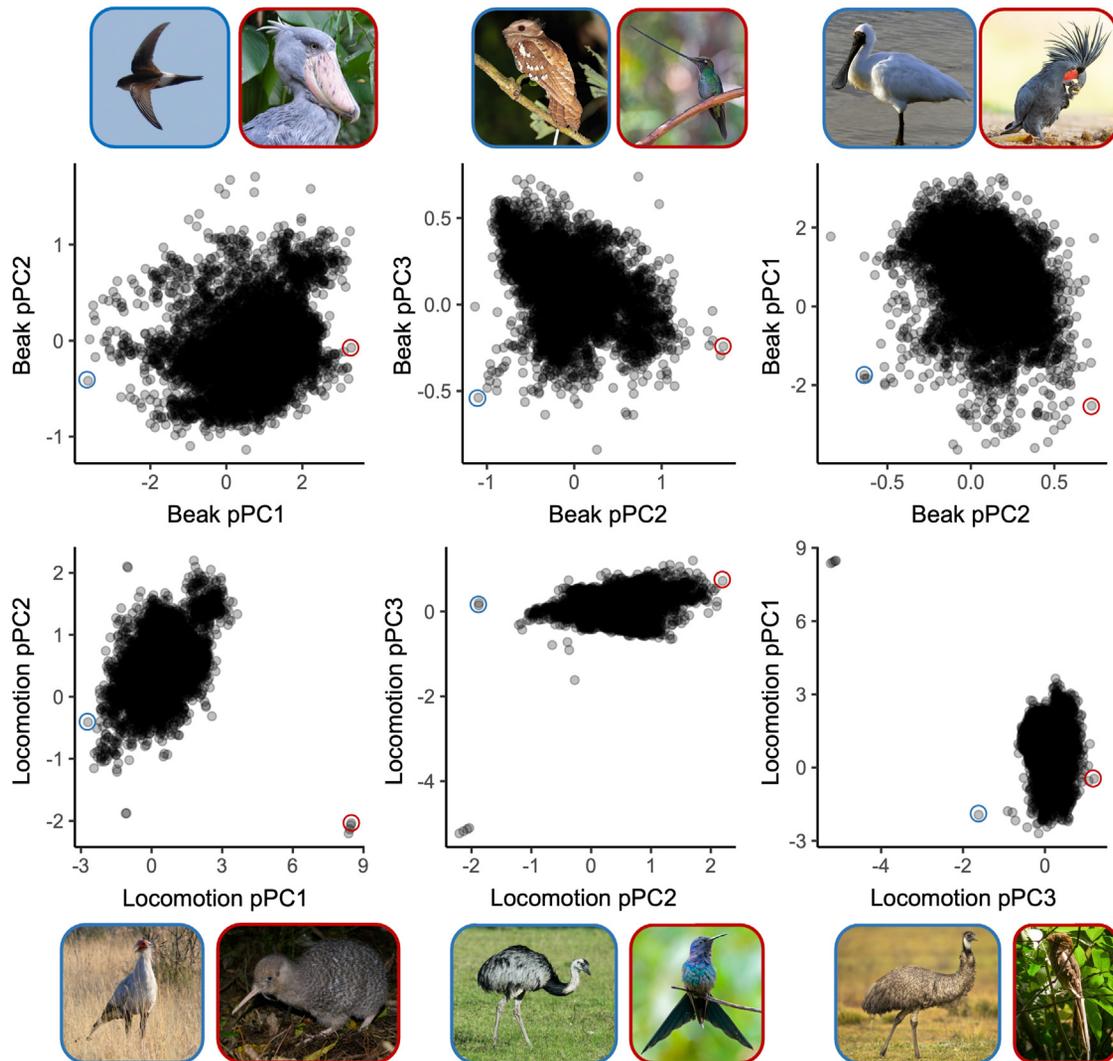


Figure 1. pPC axes describe morphological variation across all birds

Axes were constructed on (top row) beak ($n = 9631$ species) and (bottom row) locomotory ($n = 9636$ species) trait measurements. Phylogenetic principal component (pPC) axes constructed with only species analyzed in the paper are indistinguishable (regression R^2 all >0.997). Photos of representative birds (clockwise from top left): *Tachornis phoenicobia* [Dave Curtis, CC BY-NC-ND 2.0], *Balaeniceps rex* [Michael Gwyther-Jones, CC BY 2.0], *Batrachostomus harterti* [JJ Harrison, CC BY-SA 3.0], *Ensisifera ensifera* [Doug Greenberg, CC BY-NC 2.0], *Platalea regia* [Bernard Spragg, CC0 1.0], *Probosciger aterrimus* [JJ Harrison, CC BY-SA 3.0], *Sagittarius serpentarius* [photo by J.P. Drury], *Apteryx owenii* [Kimberley Collins, CC BY-SA 4.0], *Rhea americana* [Nick Athanas, CC BY-NC-SA 2.0], *Eupetomena macroura* [Dario Sanches, CC BY-SA 2.0], *Dromaius novaehollandiae* [JJ Harrison, CC BY-SA 4.0], and *Nyctibius aethereus* [Nick Athanas, CC BY-NC-SA 2.0].

evolution.^{19–21} Second, bursts of morphological disparity need not be followed by monotonically declining rates of phenotypic evolution,^{19,20} particularly if radiations proceed in a hierarchical fashion, such that diversification within adaptive “subzones”¹⁸ occurs after diversification between larger zones, with different traits being influenced at different scales.^{20,22–24} Existing models of trait evolution may not be able to detect such complex radiation patterns.

A third reason why evidence for evolutionary responses to fluctuations in ecological opportunity remains scarce may be that models of trait evolution typically lump together species that do not interact with one another—because they have different ecologies, live on different continents, and/or inhabit

different habitats—and therefore do not contribute to relevant dynamics in ecological opportunity. Finally, not accounting for intraspecific trait variation and/or measurement error can artificially boost support for Ornstein-Uhlenbeck (OU) processes,²⁵ whose likelihood is equivalent to that of accelerating rates models,²⁶ and may thus hide the signal of limiting ecological opportunities. We recently developed time-dependent, DD, and matching competition models of trait evolution that more accurately account for these factors.^{17,27} Briefly, these phylogenetic models allow trait evolution to vary according to ancestral reconstructions of ecologies and/or biogeographies while accounting for measurement error. In addition, “two-regime” versions of these models enable the estimation of distinct parameter values

on parts of the tree that correspond to distinct categories (e.g., “tropical” versus “temperate”).¹⁷ We previously applied these models to bird trait data, at or below the level of taxonomic families, to assess how competition-driven trait divergence varies across traits²⁸ and latitudes.¹⁷ Here, our focus shifts to the significance of ecological opportunity, which has been hypothesized to be stronger at taxonomic scales beyond the family.¹⁸ We focus on the time-dependent and DD models, as the matching competition model^{13,29} represents a character-displacement-like process rather than the macroevolutionary consequences of reduced ecological opportunities; in addition, classical character displacement theory generally applies to taxa with relatively recent common ancestors (e.g., confamilials).³⁰ We refer to the time-dependent model with declining rate as the EB model, and we consider two versions of the DD model: one with an exponential dependency (DD_{exp}) and another with a linear dependency (DD_{lin}). These models all assume anagenetic trait evolution, such that the distribution of branching nodes in the phylogeny (e.g., whether they are concentrated towards the root or the tips) does not influence results of model fits. Previous work supporting a decorelation between phenotypic change and speciation events in birds suggests that phenotypic evolution is indeed mostly anagenetic.³¹

We speed up these methods such that they can be applied at larger taxonomic scales than was previously possible (see “model-fitting” in STAR Methods), and we deploy them at the scale of the entire bird phylogeny on a global dataset of seven functional trait measurements (Figure 1).³ These traits describe functional variation in beak morphology and locomotion, which are highly predictive of the diet and foraging niches occupied by birds.³² This allows us to gather new insights about the key processes influencing rates of evolution in traits that we expect to be constrained by limited ecological opportunity.

We first fitted trait evolution models to data from lineages sharing the same diet or habitat (referred to as “guilds”) and from the same continent (Figures 2 and S2). Importantly, the results of these fits provide information on phenotypic evolution in these species assemblages and not on the composition of the assemblages themselves (e.g., whether assemblages are made of distantly or closely related lineages). Using this approach, we found ample support for models of limited ecological opportunity (Figures 2 and S2A): EB models outperformed other models in 38.3% of fits, and DD models with negative slope parameters (consistent with evolutionary slowdowns in response to niche filling; Table S1) in 29.9% of fits. While this signature is not universal, as a stochastic “diffusion” model of evolution (Brownian motion [BM]) is commonly favored (31.2% of fits), these levels of support (in total, >68% of fits favor models with limited ecological opportunity) contrast with much lower support recovered for these models in most studies conducted at lower (e.g., family-level; Table S2) taxonomic scales, lumping together all species within clades regardless of ecology or biogeography and/or not accounting for measurement error (but see Landis and Schraiber³³,^{15,17,20,23,34}

Model adequacy tests showed that rate heterogeneity is often higher in the data than accounted for by our rate-homogeneous models (Figure S3). This is consistent with previous large-scale analyses of birds,¹⁹ even if subsetting the data by guild membership builds in more rate heterogeneity than has been possible

previously with such models. However, heterogeneity did not affect inference of temporal patterns, as empirical disparity-through-time (DTT) plots fell within simulated ones in 83.3% of the cases. Removing these cases of model misspecification did not affect the relative proportions of datasets supporting models of limited ecological opportunity (66.5% when removing cases falling outside of DTT plots). In addition, adequacy tests focusing on temporal rate variation found more cases where rate declines in the data were more pronounced than accounted for in the models. Together, these results confirm previous findings that rate heterogeneity does not bias model selection toward models with rate slowdowns^{35,36} and corroborate our finding that limited ecological opportunity commonly impacts trait evolution in birds.

Examining each case separately (Figure S2), some stood out as having consistent support for slowdowns across several trait axes. For instance, many diet and habitat guilds in Africa revealed high support for EB models, consistent with observations of lower spatial turnover of habitats and, consequently, lower opportunities for niche divergence, limiting ecological opportunity in Africa compared to other tropical regions.^{37,38} Similarly, DD models were best-fit models across several trait axes for invertivores in both the Palearctic and Nearctic, perhaps because prey availability is reduced in these regions by higher climatic seasonality,³⁹ which leads to shorter growing seasons and lower vegetation complexity,⁴⁰ thereby substantially reducing habitat heterogeneity and insect diversity compared with tropical ecosystems.⁴¹ Additionally, there was elevated support for EB models in the second phylogenetic principal component (pPC) axes for both beak and locomotory traits (Figure S2), suggesting that beak and body shape experience slowdowns in response to limiting ecological opportunity more than size. This presumably reflects the greater information content of beak and body shape, which are both three to four times more predictive of avian dietary niches than body size.³² Overall, however, no trait axis (i.e., mass, beak, or locomotion traits), continent, or guild was consistently predictive of support for all models of limited ecological opportunity (Figures 2 and S2; Table S3). The only explanatory variable that was consistently present in the pool of best-performing regression fits was sample size, with more support for an effect of limited ecological opportunity on trait evolution in larger species groups. This pattern is consistent with the expectation that the significance of ecological opportunity is stronger at higher taxonomic scales,¹⁸ although it could also simply result from increasing statistical power with increased sample sizes.¹⁵

Support for declining rate models might occur in the absence of changing ecological opportunity if the pace of phenotypic evolution depends on some other factor that itself varies over geological timescales.¹⁶ For instance, global cooling has occurred over the time frame of bird diversification, and this could in part explain declines in diversification rates.¹⁰ Yet, for body size at least, evolutionary rates seem to increase rather than decrease with decreasing temperatures.³⁶ To further assess the role of limited ecological opportunity per se, we performed randomization tests where we fitted the same models as above to species groups randomly sampled across the bird phylogeny (i.e., with no account of continent-guild membership). Statistical support for declining rate models was overall higher

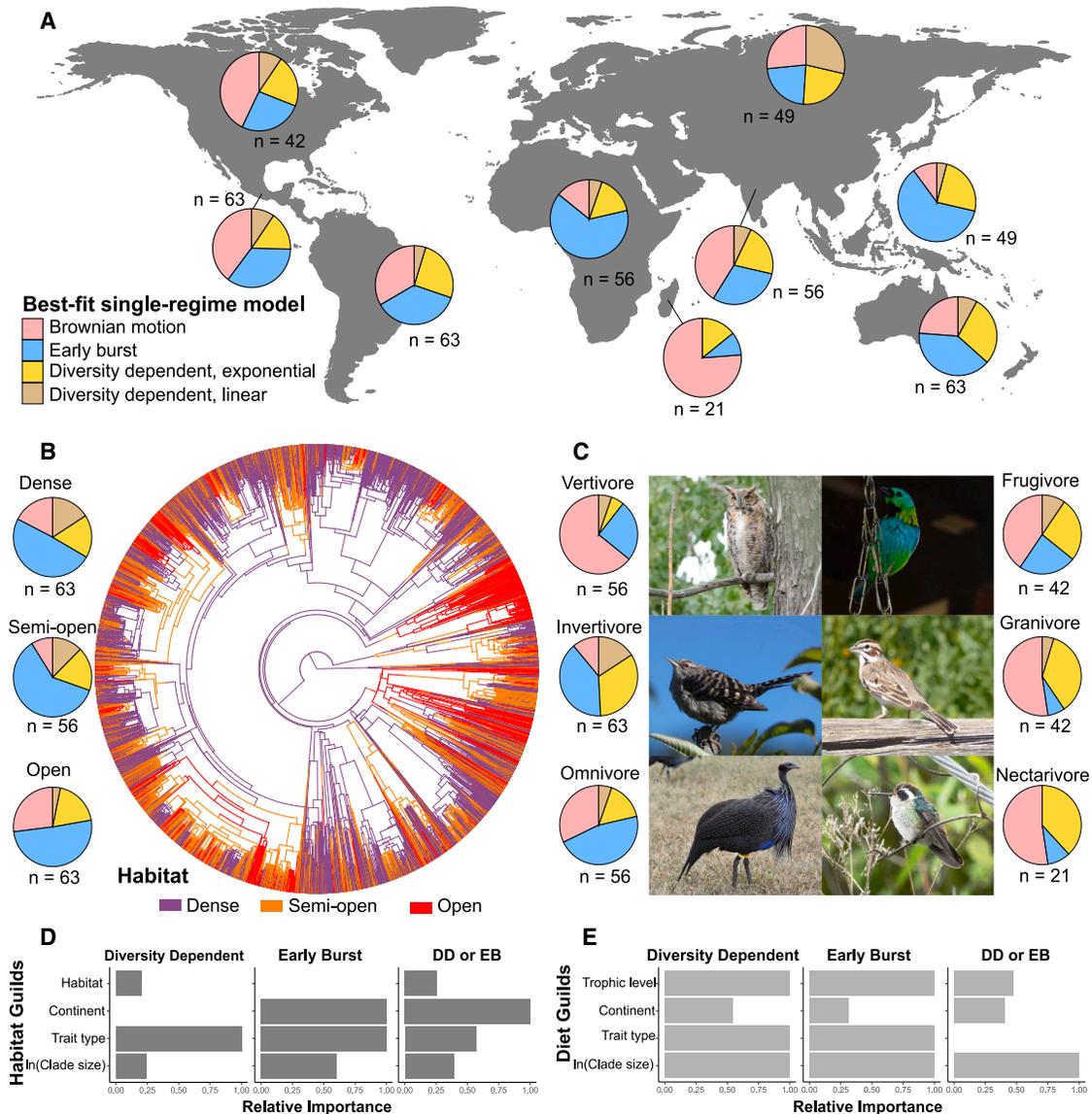


Figure 2. Trait evolution inferred from morphological data for nearly all extant bird species provides widespread support for models of limited ecological opportunity

(A–C) Pie charts depict the best-fitting single-regime models ($n = 462$ total fits) (A) within each continent (combining results from fits to all guild-trait combinations for those continents) and (B) across habitat guilds (combining results from fits to all continent-trait combinations for those habitats) with a stochastic map of habitat plotted across the avian phylogeny used in analyses and (C) across diets (combining results from fits to all continent-trait combinations within those diet categories). For best-fit models for each continent-guild-trait combination, see Figure S2. Sample sizes indicate the number of (A) guild-trait combinations or (B–C) continent-trait combinations included within each category. In no case was an Ornstein-Uhlenbeck (OU) model the best-fitting model. In panel (C), photos are of (clockwise from top left) *Bubo virginianus*, *Tangara seledon*, *Chondestes grammacus*, *Basilinna leucotis*, *Acryllium vulturinum*, and *Campylorhynchus megalopterus* (all photos by J.P. Drury).

(D and E) generalized linear models (GLMs) of support for models with ecological opportunity show that multiple factors impact the support for diversity-dependent (DD) models, a time-dependent (“early-burst” [EB]) model, and any model where rates of trait evolution vary with time or diversity for (D) habitat guilds and (E) diet guilds (Table S3). Log-transformed clade size is the only factor consistently and largely positively predictive of model support across different models.

when the species included were limited to guild members (Figure 3), which would be unexpected if rate declines were indicative of something other than limited ecological opportunity. Although lower than in empirical datasets, the statistical support for declining rate models in randomized datasets was still high (reaching >0.75 relative support in the largest datasets) and likely

explained, in part, by the presence of species that interact with one another in the randomized sets.

Ecological opportunity is often invoked as a driver of latitudinal variation in biodiversity. The ecological limits hypothesis for the latitudinal biodiversity gradient, for instance, argues that species richness declines towards the poles because of lower carrying

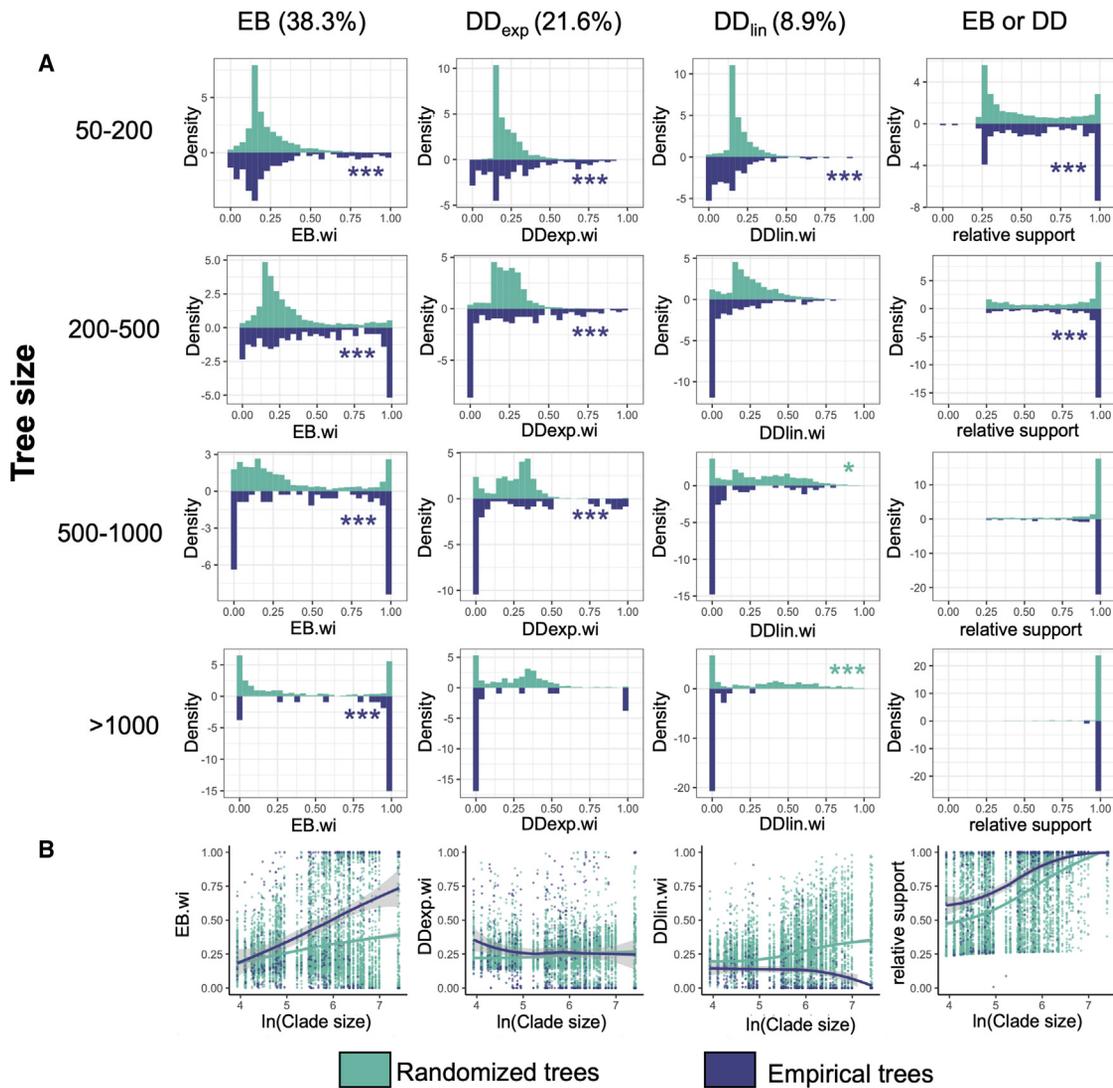


Figure 3. Results from randomization analyses demonstrate that the inclusion of ecological traits and biogeography into models improves the performance of EB and DD models of trait evolution

(A) Decisive model support (Akaike weight > 0.50) for models incorporating ecological opportunity (i.e., EB and DD models) is more likely in empirical trees (i.e., those with actually interacting species) than in random trees, except for the DD_{lin} model in large trees (>200 tips). The percentages of continent-trait-guild combinations for which each model was identified as the best model are indicated in parentheses; the DD_{lin} model was the best in <10% of the combinations. Asterisks indicate statistical significance (**p* < 0.05, ****p* < 0.001) in χ^2 contingency tables testing for differences between observed and expected numbers of trees with Akaike weight > 0.50.

(B) For EB, DD_{exp}, and the index of relative support for a model with limiting ecological opportunity, empirical trees receive higher model support than randomized trees across all sample sizes. The error around the lines (plotted in gray) represents the standard error of the loess-smoothed trendline.

capacities (resulting, e.g., from fewer resources, shorter growing seasons) in temperate regions.^{1,42,43} We might therefore expect the strength of diversity or time dependence to be higher at higher latitudes. In analyses where we fit two-regime models in which the strength of diversity or time dependence could vary according to latitudinal regions (i.e., tropical and temperate) within continents, model selection generally favored simpler models without a latitudinal effect (79% of fits; Figure S2B). This is not likely an effect of low sample sizes, as in the majority of the fits (85%), the tropical and temperate categories are sufficiently diverse (>20 species) to detect effects.¹⁷ When a two-

regime model of limited ecological opportunity was favored, it was more likely to be the DD_{exp} model than either EB or DD_{lin}.

Although latitudinal models had relatively poor fit, they revealed latitudinal trends in diversity and time dependence. For instance, we found steeper (i.e., more negative) slopes in temperate regions in low trophic levels (i.e., granivores, frugivores, and nectarivores)—as expected based on lower carrying capacities—but the opposite pattern in high trophic levels (i.e., invertivores, omnivores, and vertivores) and open habitats (Figures 4 and S4; Table S4). On average, the effect of limited ecological opportunity between lineages living in open habitats

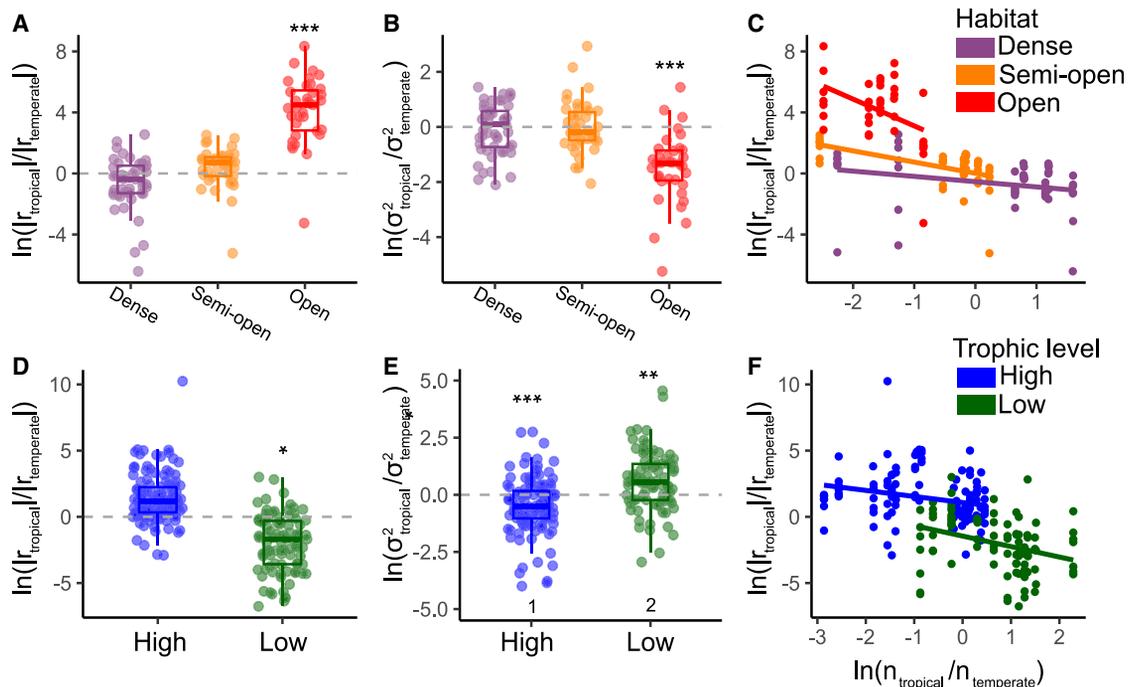


Figure 4. The ecologies of interacting species influence the relationships between latitude and the pace at which phenotypic evolution decelerates, results of two-regime models of DD_{exp}

(A–C) Lineages inhabiting open environments experience a more pronounced effect of diversity dependence (i.e., the slope parameter ‘ r ’) in open habitats is higher in tropical regions ($p < 0.001$). Each point represents the mean parameter estimates across 25 fits for each continent-habitat-trait combination ($n = 126$, see STAR Methods). (B) Consequently, present-day rates of trait evolution (i.e., σ^2) in open habitats are lower in tropical regions ($p < 0.001$). (C) The ratio of maximum likelihood estimates of slope in exclusively tropical lineages versus other lineages is negatively correlated with the ratio of the number of lineages, though the impact of competition in open habitats remains higher in tropical taxa even after controlling for this (Table S4).

(D–F) High and low trophic levels experience contrasting responses to diversity dependence in tropical and temperate areas ($n = 217$ continent-trophic-trait combinations). (D) The estimated per-lineage impact of competition between high-trophic level (vertivores, invertivores, and omnivores) lineages is higher in tropical regions ($p < 0.001$); contrastingly, the impact of competition on low-trophic levels (frugivores, granivores, and nectarivores) is reduced in tropical regions ($p < 0.001$). (E) Consequently, present-day rates of trait evolution in the tropics are lower for higher trophic levels ($p < 0.001$) and higher for lower trophic levels ($p < 0.001$). Numbers below data points indicate outliers removed for plotting. (F) The ratio of maximum likelihood estimates of slope in exclusively tropical lineages versus other lineages is negatively correlated with the ratio of the number of lineages, though the impact of competition in high trophic levels remains higher in tropical taxa even after controlling for this (Table S4). Results were similar for parameters estimated under latitudinal (two-regime) versions of linear density-dependent and time-dependent models (Figure S4; Table S4). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (term differs from 0).

is more pronounced in tropical regions (Figures 4A–4C; Table S4). Open habitats may have relatively few niches regardless of latitude,⁴⁴ and the ecological limits this imposes may be accentuated in the tropics because of lower extinction rates⁴⁵ and higher rates of colonization from adjacent forest or woodland habitats (owing to the higher species richness of regional species pools). Similarly, the effect of limited ecological opportunity on high trophic lineages was stronger in the tropics. This might indicate that high trophic lineages are closer to the saturation of niche space in tropical environments. In lower trophic levels, the effect of limited ecological opportunity is more impactful between temperate lineages, as expected if the saturation of niche space constrains morphological evolution for low trophic levels in temperate regions (Figures 4D–4F).

Evolutionary biologists have long sought a general signature of the effect of limited ecological opportunity on the dynamics of trait evolution in comparative data, but thus far this signature has been detected in a handful of cases rather than as a general

phenomenon.^{19–21} By modeling how trait evolution responds to dynamics of ecological opportunity for species that co-occur and are ecologically similar at a large taxonomic scale, we find support for ecologically mediated slowdowns in about two-thirds of our analyses. These evolutionary responses to diminishing ecological opportunity appear to have consistent effects across latitude, suggesting that ecological constraints are no more prevalent in hyper-diverse tropical systems than in temperate systems. Our results instead suggest that the degree of ecological opportunity is a key factor regulating the dynamics of trait evolution at a global scale.

STAR METHODS

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Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2023.12.055>.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.P.D., H.M., and J.A.T.; data curation, C.S., J.A.T., and J.R.; formal analysis, J.P.D.; funding acquisition, J.P.D., H.M., J.C., and J.A.T.; investigation, J.P.D., C.S., J.A.T., and J.R.; methodology, J.P.D., H.M., and J.C.; project administration, J.P.D.; resources, J.P.D. and H.M.; software, J.P.D. and J.C.; supervision, H.M.; validation, J.P.D.; visualization, J.P.D.; writing – original draft, J.P.D. and H.M.; writing – review & editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Body mass data	EltonTraits ⁴⁶	N/A
Linear measurements of bill length, width, height, and wing length, tarsus length, and tail length	AVONET ³	N/A
Diet data	EltonTraits ⁴⁶	N/A
Habitat data	Tobias et al. ⁴⁷	N/A
Avian phylogeny	Jetz et al. ⁴⁸ (birdtree.org)	N/A
Distribution data	Drury et al. ¹⁷	N/A
Software and algorithms		
RPANDA	Morlon et al. ⁴⁹ ; This paper	N/A
mvMORPH	Clavel et al. ⁵⁰	N/A
spptest	Myllymäki et al. ⁵¹	N/A
data.table	Dowle & Srinivasan ⁵²	N/A
geiger	Pennell et al. ⁵³	N/A
rank_dtt.R	Murrell ⁵⁴	N/A
phytools	Revell ⁵⁵	N/A
MuMIn	Barton ⁵⁶	N/A
lme4	Bates et al. ⁵⁷	N/A
lmerTest	Kuznetsova et al. ⁵⁸	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and code should be directed to and will be fulfilled by the lead contact, Jonathan Drury (jonathan.p.drury@durham.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

All data are available on Mendeley Data.⁵⁹ All code for fitting models is available in the R-package RPANDA⁴⁹ (<https://github.com/hmorlon/PANDA>).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Phylogeny and trait data

We created a maximum clade credibility tree²⁸ using 1000 samples from the posterior distribution from birdtree.org.⁴⁸ To maintain as wide a taxonomic breadth as possible and to limit the underestimation of the number of species in the past used in diversity-dependent models (see below), we included all species in this tree, including those that were included based on taxonomic information rather than molecular sequence data. Ideally, to account for phylogenetic uncertainty, we would have conducted our analyses across many trees from this posterior distribution and alternative avian phylogenies. However, this would have been too computationally intensive given the scale of our analyses, which already accounted for uncertainty in guild membership through time (see “Subsetting likely interactions”, below). Previous analyses of morphological evolution in birds using the same phylogeny have found results that are consistent across alternative trees and the removal of species without molecular data.⁶⁰

Mass data

Mass data were compiled from EltonTraits⁴⁶ ($n = 9442$).

Other morphological measurements

Beak length (culmen length), width, and depth ($n = 9388$, mean = 4.5 individuals per species), as well as wing, tarsus, and tail length ($n = 9393$, mean = 5.0 individuals per species) were collected as described in ref. ^{61,62}. To generate variables that describe functional variation in beak morphology and locomotion, we constructed two sets of phylogenetic principal component (pPC) axes⁶³ (Figure 1): one on the mean of individually log-transformed values for beak length, height, and width data (beak pPCs 1–3), and another on the mean of individually log-transformed values for wing, tarsus, and tail length (locomotion pPCs 1–3). Though these seven traits may not capture all possible niche dimensions, phylogenetic PC axes broadly similar to these have been shown to be highly predictive of ecological function in birds at this scale.³² We also calculated intraspecific variability (i.e., known measurement error) for each observation.¹⁷

Habitat data

For the habitat guild, we classified each species as occurring in dense ($n = 4432$), semi-open ($n = 3177$), or open ($n = 1796$) habitats from ref. ⁴⁷, excluding lineages without data ($n = 37$).

Diet data

We assigned species to feeding guilds based on diet from EltonTraits,⁴⁶ focusing on the six most common diet categories: invertivory ($\geq 60\%$ invertebrate, $n = 4845$), granivory ($\geq 60\%$ seed, $n = 586$), frugivory ($\geq 60\%$ fruit, $n = 902$), vertivory ($\geq 60\%$ vertebrate, $n = 447$), nectarivory ($\geq 60\%$ nectar, $n = 441$), and omnivory ($< 60\%$ of any category, $n = 2028$), excluding species that eat plants (except fruits or seeds) and scavengers ($n = 193$).

Distribution data

We compiled distribution data (i.e., information on which continent each species inhabits) from ref. ¹⁷.

METHOD DETAILS

Model-fitting

We fit^{49,50} several models of trait evolution to the seven trait values described above (mass and the 6 PC axes), while accounting for likely interactions by fitting the models to subsets of the global bird phylogeny trimmed to retain lineages with the same diet or habitat guild, and from the same continent (see details below). This trimming procedure does not bias model support, regardless of the shape of the trimmed phylogeny (e.g., if the phylogeny has long terminal branches if guilds or continents comprise distantly related lineages). Indeed, likelihoods associated with models of trait evolution account for phylogenetic structure through the phylogenetic variance-covariance matrix.⁶⁴ The phylogenetic variance-covariance matrix is fixed when comparing statistical model support and estimating parameters. Accordingly, simulations have shown that both model selection and parameter estimation of BM processes are robust to large proportions of 'missing taxa' under a variety of sampling schemes.⁶⁵ A corollary is that results of these model fits are not informative about the shape of phylogenies (or the composition of assemblages), they are only informative about modes of phenotypic evolution in these assemblages.

The set of models fit comprised two models in which trait evolution is independent of species richness and the age of a clade, Brownian motion (BM) & Ornstein-Uhlenbeck (OU) models, and three models in which rates of trait evolution respond to changing ecological opportunity: a model with time-dependent rates (the 'early burst' [EB] model) often used as a proxy for declining ecological opportunity through time,^{11,12} and two models with diversity-dependent rates (exponential diversity-dependent [DD_{exp}], linear diversity-dependent [DD_{lin}]) in which rates of trait evolution vary through time according to the number of lineages present in the reconstructed phylogeny. This number of lineages underestimates the true number of species in the past due to extinctions, but simulations¹³ have shown that DD models are robust to levels of extinction even higher than those estimated to have occurred in the avian radiation.⁶⁶ We refer to these models as 'single-regime' models, as the key parameters are estimated on all lineages in the (trimmed) phylogeny. In all models, we also incorporated observation error in two ways¹⁷: as known measurement error, to account for the inherent variability of trait measurements, and unknown 'nuisance' error, estimated as a model parameter, to account for error not accounted for by the model itself.^{67–69}

To test whether ecological opportunity impacts trait evolution differently at different latitudes, we fit a second version of each of these models where the parameters were estimated separately for lineages with exclusively tropical breeding distributions and lineages with ranges that include the temperate region.¹⁷ We refer to these models as 'two-regime' models.

Previously, computational limits prohibited DD models to particularly large (i.e., >500 tip) trees. Thus, we developed model fitting tools using a fast branch transformation algorithm⁵⁰ to enable fitting DD models in larger clades than was previously feasible (e.g., the largest tree in our analyses has 1674 species). As an example, an exponential diversity dependent model fit to body mass data on the family Strigidae ($n = 188$ species), including both biogeography and measurement error, using the previously existing method took 2928.5 s to fit on an iMac computer with a 3.1 GHz 6-Core Intel Core i5 processor, while, with our new approach, this reduced to 12.3 s (> 200x faster). For the family Tyrannidae ($n = 420$ species), the previous method took 13574.1 s, while the new approach took 37.5 s (> 360x faster). To our knowledge, diversity dependent models of trait evolution have never been fit to phylogenetic datasets as large as the ones analysed here.

We note that, while our focus is on the temporal dynamics of phenotypic evolution, other dynamic processes (e.g., guild evolution, range evolution, and community assembly) interact to influence the composition of clades in our analyses. Nevertheless, as outlined above, our approach of applying trait evolution models to lineages within the same guild and continent is not influenced by (nor does it provide insights into) the lineage diversification or assembly processes. Whether phenotypic change is associated with lineage diversification, whether guilds comprise distantly related or closely related lineages, and which processes, including those related to the exploitation of ecological opportunities, shape the composition of assemblages are equally interesting questions. Some of these questions have been explored from a community phylogenetics perspective,^{70,71} and new phylogenetic comparative frameworks that jointly model range dynamics, lineage diversification and (cladogenetic as well as anagenetic) trait evolution should provide further insights.^{31,72} Our framework, however, aims only to test whether trait evolution has slowed down over time in these assemblages. It does so by using models that are an oversimplification of reality; for example, we expect major events in Earth history to generate different timings of divergences along different niche dimensions. Nonetheless, these simplified models enable testing for general trends in temporal dynamics of phenotypic evolution across the entire avian radiation.

Subsetting likely interactions

From the perspective of any given lineage, the effect of other lineages on ecological opportunity depends on their ecology. For instance, the impact of a seed-eating species is likely to be greatest on other granivorous lineages but negligible on invertivores. We therefore defined two sets of ‘guilds’—one based on habitat, and another based on diet—comprising sets of ecologically similar species and fit models separately for each guild. We note that omnivores could be considered to interact across multiple guilds, but here we follow other large-scale morphological analyses of birds^{32,73} and treat them separately. Future analyses could examine the extent to which different items comprising omnivores’ diets influence levels of competition. Similarly, future developments could enable finer scale reconstructions of diet and/or habitat, thereby further increasing the biological realism of this approach.

We further restricted analyses to lineages found in the same global regions⁷⁴ (Australia, Southeast Asia, India, Central America, South America, Africa, Madagascar, Nearctic, and Palearctic; for more information on how we assigned species to each region, see ref. 17). For simplicity, and to differentiate these biogeographical regions from latitudinal regions (see below), we refer to these regions as ‘continents’. We acknowledge that continental scale overlap is a relatively crude way of incorporating the potential for species to interact. However, the computational limits of existing tools for reconstructing ancestral ranges currently preclude finer scale reconstructions on the scale of all birds. Moreover, we have shown previously (at the family level) that species ranges overlap with the ranges of approximately ~50% of the species present on each continent (with 34% to 74% range overlap across all continents).¹⁷ We therefore argue that limiting analyses to the continental scale is a meaningful step toward incorporating biological realism into analyses of ecological opportunity.

For each model fit, we computed likelihoods associated to the trait data of the members of each continent-guild combination in turn. For instance, all birds inhabiting dense (i.e., forest) habitats in Central America comprised one set of analyses, all nectarivores in Central America comprised another, etc. As mentioned (see Model-fitting), these groups of species do not correspond to monophyletic clades, but monophyly is not a requirement for accurate use of models of phenotypic evolution.⁶⁴ Indeed, the phylogenetic distances between pairs of species used in the computation of the likelihood are not affected by missing species in the phylogeny. We excluded trees with < 50 species due to low statistical power of the models on small trees¹⁷ (mean number of tips for habitat-by-continent analyses = 481, range = 81 – 1674; mean number of tips for diet-by-continent analyses = 300, range = 51 – 1636). For BM, OU, and EB models, we simply trimmed the global phylogeny of birds to retain only members of the continent-guild combination analyzed. For diversity-dependent models, we first constructed stochastic maps representing the estimated ancestral states of each guild, then trimmed the global phylogeny of birds to retain only members of the focal continent, and computed the likelihood corresponding to a model where traits evolve as a BM process on non-focal lineages, and as a DD process on focal lineages, with diversity of the continent-guild combination computed from the stochastic maps (Figure S1). In doing so, lineages that are reconstructed as belonging to a particular guild in the past are included in ancestral estimates of diversity, even if those lineages do not belong to the trimmed phylogeny of that guild in the present day. Ideally, we would also have used stochastic maps of ancestral biogeographies, rather than a phylogeny trimmed to retain only members of the focal continent, as in ref. 17, but ancestral biogeographic reconstructions at the scale of the entire avian radiations are too computationally intensive to fit. For DD models, we allowed the maximum likelihood optimisation to search both positive and negative slope parameters (Table S1).

For two-regime models, in addition to subsetting to continental guilds as above, we also combined stochastic maps of guild membership and latitudinal ranges, such that diversity dependence was modeled as occurring only between continent-guild member lineages in the same latitudinal region (see details in ref. 17). In two-regime fits, in addition to excluding trees with < 50 tips, we also excluded any cases where any regime had fewer than 10 tips.

To account for uncertainty in the ancestral reconstructions of guild membership and latitude, we fit the models to each continent-guild-trait combination across a sample of 25 stochastic maps of guild membership (for all DD models), and across 25 stochastic maps of breeding region (for all latitudinal models). For each fit, we conducted model selection by identifying the model with the lowest small-sample corrected Akaike information criterion (AICc) value, unless a simpler model was within 2 AICc units,⁷⁵ in which case we considered the simpler model with the next lowest AICc value to be the best-fitting model. Across fits, we identified the modal best-fit model for each continent-guild-trait combination (i.e., the most common best-fit model across fits conducted on a

bank of stochastic maps of guild membership and latitudinal region ranges). To compare our model fits at the continental scale to those at a shallower, family-level, we conducted model selection for family-level fits from ref. 17, excluding the results from the matching competition model in that manuscript (Table S2).

Model adequacy

To examine model adequacy, we simulated 2,500 datasets under maximum likelihood parameter estimates for the best-fitting single-regime models. We then examined how closely our empirical datasets matched simulated datasets in three ways. First, we used the rank envelope test of ref. 54 to determine whether the empirical ‘disparity through time’ (DTT) plots fall within the 95% confidence interval of DTTs calculated on datasets simulated under the best-fitting model. The second approach we used was to calculate C_{VAR} ,⁷⁶ which is the coefficient of variation of the absolute value of the (phylogenetic independent) contrasts. If this value is more extreme in the observed dataset than in the simulated datasets, this suggests that rate heterogeneity is higher than accounted for in the models. Finally, we calculated S_{HGT} ,⁷⁶ or the slope of a linear model fitted to the log-transformed absolute value of the contrasts against node depth. This captures rate variation through time—when S_{HGT} in empirical datasets is more negative than that calculated on simulated datasets, this suggests stronger temporal decline in rates than accounted for by the model. Model adequacy results are depicted according to best-fit models in Figure S3.

Randomization tests

To examine whether the improved fit of models with ecological opportunity relates to the inclusion of relevant ecological variables (i.e., habitat or diet) *per se*, rather than the sampling of deeper nodes in the bird phylogeny, we conducted a randomization analysis. Specifically, we randomly sampled a dataset from the pool of empirical fits, recorded its clade age (y) and tree size (n), and then randomly sampled n lineages from the largest bird clade younger than age y , fit all models to all seven morphological traits (i.e., ln-transformed body mass, three pPC axes describing beak shape, and three pPC axes describing locomotory traits) and the randomized tree, and repeated this 1,000 times. We then compared the Akaike weights (w_i) obtained with empirical versus randomized trees for the EB, DD_{exp} , and DD_{lin} models, as well as an index of relative support for a model of limited ecological opportunity (i.e., $\max(EB.w_i, DD_{exp}.w_i, DD_{lin}.w_i) / (\max(BM.w_i, OU.w_i) + \max(EB.w_i, DD_{exp}.w_i, DD_{lin}.w_i))$). We found that by incorporating biological realism into our models, support for models with ecological opportunity is increased (Figure 3). Specifically, we found that EB and DD_{exp} (across tree sizes) and DD_{lin} (in trees < 200 tips) were better supported on empirical trees than random trees. Note that DD_{lin} were better supported on random trees than empirical trees for large trees (>1000 tips), but that DD_{lin} models were rarely supported in empirical data (in less than 4% of continent-trait-guild combinations, see Figures 2 and S2). Relative support for models of limited ecological opportunity increased with sample size, and empirical trees outperformed randomized trees across all tree sizes.

QUANTIFICATION AND STATISTICAL ANALYSES

Statistical analyses

To identify predictors of statistical support for single-regime models of limited ecological opportunity (i.e., EB or DD models), we fit generalised linear models (GLMs) to binary variables identifying support for models (i.e., if a particular model was the modal best-fit model for that continent-guild-trait combination in fits across stochastic maps of guild memberships). For each response variable, we fit all linear combinations of several explanatory variables. We measured the Akaike weight of each of these regression fits, and for each explanatory variable, we measured the probability that this variable explains model support as the ratio of the sum of Akaike weights of regression fits that include this variable to the sum of Akaike weights of all models⁷⁷ (Figures 2D and 2E). As explanatory variables, we use trait (grouped according to trait type, i.e., body mass, beak, or locomotory trait), continent, habitat, diet (grouped into “low” [granivores, frugivores, and nectarivores] and “high” [vertivores, invertivores, and omnivores] trophic levels, and log(clade size). Analyses were qualitatively similar when we excluded omnivorous species from the “high” trophic level category (Tables S3 and S4).

We also tested for an effect of latitudinal region on the impact of diversity and time dependence with mixed-effect linear models. Specifically, we modelled the log-transformed ratio of tropical to temperate slopes, as well as the log-transformed ratio of tropical to temperate evolutionary rates at the tips (both calculated as the mean maximum likelihood estimates across all stochastic maps of guild category and latitudinal region), estimated from our two-regime DD and EB model fits. In these models, we used zero-intercept models to directly examine the effect of latitudinal region (tropical versus temperate) on the slope estimates, since 0 values correspond to equal values in temperate and tropical lineages. We included guild categories and an index of the bias in species richness in tropical regions as fixed effect variables and continent and trait as random effect variables.