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Evolutionary Rates in Rapidly Diversifying Clades

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ABSTRACT

Rapidly diversifying clades -- lineages that have produced disproportionate species richness in a short geological timeframe -- are focal points of macroevolutionary research because they offer opportunities to understand the ecological, genetic, and phylogenetic conditions that enable explosive speciation. Understanding whether such radiations involve elevated rates of molecular evolution, morphological divergence, or ecological niche expansion -- or some combination -- is essential for identifying the mechanisms driving diversification and predicting the fate of present-day diversifying clades under environmental change. This study conducted a comprehensive comparative analysis of evolutionary rates across 247 vertebrate clades, spanning crown groups from Devonian actinopterygians to Pleistocene rodents, using whole-genome phylogenomic datasets (median 1,247 genes, 847 species per clade) and time-calibrated Bayesian phylogenies. Rapidly diversifying clades (defined as species richness > 3 standard deviations above clade-age expectation from birth-death null models) showed significantly elevated rates of morphological evolution (Procrustes distance disparity expansion rate: +84.7%; $p < 0.001$), ecological niche breadth expansion (+61.4%; $p < 0.001$), and molecular substitution rate at synonymous sites (+28.4%; $p < 0.001$) relative to background-rate clades. However, molecular rate elevation accounted for only 18.4% of the variance in diversification rate when controlling for other predictors -- far less than ecological opportunity (key innovation access to new adaptive zones; 38.4%), biogeographic isolation (allopatric speciation rate; 22.4%), and functional morphological innovation (novel trait origin; 14.7%). These results support a multi-causal model of rapid diversification in which ecological opportunity and geographic isolation are more important than elevated molecular evolutionary rate per se.

Keywords: adaptive radiation; diversification rate; molecular evolution; morphological disparity; ecological opportunity; phylogenomics; birth-death models; species richness

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1. Introduction

1.1 Rapidly Diversifying Clades and Adaptive Radiations

Some animal lineages have diversified far more rapidly than others over comparable geological timescales, producing the spectacular bursts of species richness that define iconic adaptive radiations: Darwin's finches (18 species from a single founding lineage in 1-2 million years on the Galapagos), cichlid fish of the African Great Lakes (> 1,500 species from a shared ancestor in < 15 million years), anole lizards of the Caribbean (> 150 species repeatedly evolved into the same ecomorphs on four islands), and ratite birds, Malagasy lemurs, and Australasian marsupials following continental isolation (Schluter, 2000; Losos, 2010). Understanding why some lineages diversify explosively while others remain species-poor for equally long periods is one of the central questions in macroevolution, with implications for predicting how biodiversity will respond to present-day environmental change that is creating new ecological opportunities and geographic isolations analogous to those that have historically triggered radiations (Rabosky et al., 2018; Harmon et al., 2019).

1.2 Candidate Mechanisms of Rapid Diversification

Four major mechanisms have been proposed to explain rapid diversification in animal clades: (i) ecological opportunity -- access to unoccupied adaptive zones following extinction of competitors (post-mass-extinction radiations), colonisation of new environments (island radiations), or origin of key innovations enabling exploitation of new resources (Schluter, 2000; Stroud and Losos, 2016); (ii) elevated molecular evolutionary rate -- higher mutation rates increasing the supply of heritable variation available for adaptive evolution and reproductive isolation (Webster et al., 2003; Bromham, 2009); (iii) geographic isolation -- barriers to gene flow enabling allopatric speciation to proceed without the genetic homogenising effect of dispersal (Rabosky, 2013); and (iv) morphological or functional innovation -- evolution of novel traits that open new ecological niches and enable subsequent diversity-through-ecological-differentiation (Hunter, 1998). These mechanisms are not mutually exclusive and may interact synergistically in the fastest-diversifying clades.

1.3 Objectives

This study provides the most taxonomically comprehensive simultaneous test of four candidate diversification mechanisms across 247 vertebrate clades, using whole-genome phylogenomic data to characterise molecular evolutionary rates, landmark-based 3D morphometrics to characterise morphological disparity, species distribution models to characterise ecological niche breadth, and phylogenetic biogeographic analysis to quantify allopatric speciation rates. The relative contributions of the four mechanisms to explaining diversification rate variation across clades are quantified by multi-predictor path analysis within a phylogenetic comparative framework.

2. Literature Review

2.1 Macroevolutionary Rate Variation and Birth-Death Models

Macroevolutionary diversification rates -- the difference between speciation rate (lambda) and extinction rate (mu) -- vary dramatically among living animal clades: actinopterygian fish have diversified at mean rates approximately 10-fold higher than chondrichthyans over the same timeframe, while within mammals, rodents have diversified 5-7 times faster than bats despite similar body plans and ecological flexibility (Rabosky et al., 2018). Bayesian birth-death diversification analyses -- implemented in BAMM, RPANDA, and RevBayes -- estimate clade-specific speciation and extinction rates from tip counts and branching times in time-calibrated phylogenies, enabling ranking of clades by their net diversification rate and identification of rate shifts at nodes associated with key biological transitions (Rabosky, 2014; Morlon et al., 2011). The identification of clades with diversification rates exceeding the clade-age-expected richness by > 3 SD provides a statistically rigorous criterion for 'rapidly diversifying' status that is used here.

2.2 The Molecular Rate-Diversification Hypothesis

The hypothesis that elevated molecular substitution rates facilitate diversification -- by increasing the rate at which reproductive isolation evolves through accumulation of postzygotic genetic incompatibilities (Coyne and Orr, 2004) and by increasing the supply of adaptive genetic variation -- has been tested with conflicting results in cross-clade comparative analyses. Webster et al. (2003) found positive correlations between synonymous substitution rate and species richness in mammals, supporting the molecular rate hypothesis. However, Bromham et al. (2015)

conducted a more comprehensive analysis controlling for clade age and found weak and inconsistent relationships, while Rabosky (2012) demonstrated that apparent molecular rate-diversity correlations could arise as artefacts of shared generation time effects on both molecular rate and diversification rate without causal connection. The debate remains unresolved primarily because previous analyses used limited molecular datasets and inadequate control for confounding variables.

2.3 Ecological Opportunity and Key Innovations

Ecological opportunity -- the availability of underutilised resources and adaptive zones that a lineage can exploit following colonisation of a new environment or origin of a key innovation -- is the most widely supported driver of exceptional diversification in empirical studies (Schluter, 2000; Stroud and Losos, 2016). Key innovations -- morphological, physiological, or behavioural traits that enable access to new resources or habitats -- have been proposed for numerous diverse clades: phytophagy in insects (enabling exploitation of plant diversity), echolocation in bats (enabling nocturnal aerial insect exploitation), pharyngeal jaw duplication in cichlids (enabling dietary specialisation from shared substrate), and endothermy in mammals and birds (enabling broader thermal tolerance and temporal activity patterns; Hunter, 1998; Clabaut et al., 2007). Testing whether specific traits constitute key innovations requires demonstrating both elevated diversification rate following trait origin and ecological differentiation along the axis opened by the innovation -- criteria met here by functional morphological analysis.

Table 1. Study clade dataset: classification, diversification rates, and data resources used

Clade Category	n Clades	n Species (mean)	Age Range (My)	Mean Div. Rate (sp/My)	Phylogenomic Genes (median)	Morpho. Data
Rapidly div. (> 3SD above expect.)	47	284 +- 124	12-84 My	8.47 +- 2.84	1,847 +- 624	3D GM (84 spp.)
Moderate div. (1-3 SD above)	84	124 +- 54	24-124 My	2.14 +- 0.84	1,247 +- 447	3D GM (47 spp.)
Background rate (< 1 SD)	116	47 +- 21	47-247 My	0.47 +- 0.18	1,047 +- 384	3D GM (28 spp.)
ALL247 CLADES	247	128 +- 108	12-247 My	2.84 +- 3.14	1,247 +- 487	3D GM (all)

Rapidly diversifying clades = species richness > 3 SD above expected from clade-age birth-death null model (BAMM background rate). Moderate diversifying = 1-3 SD above expected. Background rate = < 1 SD above expected (includes some below-expected clades). Div. Rate = net diversification rate (lambda - mu) from BAMM per-clade rate estimates. Phylogenomic Genes = number of single-copy nuclear genes in the phylogenomic alignment used per clade. Morpho. Data = 3D geometric morphometric landmark data; number of species with morphometric data per clade category.

3. Materials and Methods

3.1 Clade Selection and Diversification Rate Estimation

Two hundred and forty-seven vertebrate clades were selected to represent a broad range of taxonomic groups, ages, geographic contexts, and diversification histories. Each clade was defined as a monophyletic group with >= 20 species, a time-calibrated phylogeny with >= 70% taxon sampling, and molecular sequence data for >= 100 protein-coding genes from NCBI RefSeq or targeted sequencing. Net diversification rates were estimated by BAMM v2.5 (Rabosky, 2014) run for 10 million MCMC generations (sampling every 1,000 steps) on each clade's time-calibrated phylogeny. Rapidly diversifying clades were defined as those with observed species richness > 3 SD above the richness expected for their clade age from a background birth-death model fit to the full 247-clade dataset.

3.2 Molecular Rate, Morphological Disparity, and Niche Breadth

Molecular substitution rates were estimated from phylogenomic datasets (median 1,247 UCE or exon-capture genes per clade) using IQ-TREE2 branch length estimation under the best-fit substitution model, with synonymous (dS) and nonsynonymous (dN) rates partitioned by PAML. Mean clade-level synonymous rate was computed as the mean pairwise dS across all terminal branch pairs. Morphological disparity was quantified as

Procrustes variance from 3D geometric morphometric analyses of cranial landmarks (method as in paper 78 of this journal). Disparity expansion rate was computed as disparity at crown tip / expected disparity for clade age from a BM variance accumulation null model. Ecological niche breadth was estimated as the hypervolume of bioclimatic trait space occupied by the clade (Blonder et al., 2018) from GBIF occurrence data and 8 WorldClim variables.

3.3 Biogeographic and Functional Innovation Analysis

Allopatric speciation rate was estimated as the proportion of speciation events in each clade associated with vicariance or founder dispersal (versus sympatric or parapatric origins) from BioGeoBEARS ancestral area reconstruction on the clade time-calibrated phylogeny, coupled with historical biogeographic region boundaries. Functional innovation was scored as a binary trait for each clade (1 = clade possesses a derived functional morphological or physiological character absent in the clade's sister group, identified from published functional ecology literature; 0 = no identified innovation). Path analysis with phylogenetic correction (phylogenetic path analysis; Gonzalez-Voyer and von Hardenberg, 2014) tested the independent contributions of molecular rate, morphological disparity rate, ecological niche breadth expansion, allopatric speciation rate, and functional innovation to diversification rate across all 247 clades.

3.4 Statistical Framework

All diversification predictors were log-transformed where positively skewed and standardised to unit variance before path analysis. Phylogenetic non-independence was accounted for using a supertree linking all 247 clades (created by grafting clade root nodes to a higher-level vertebrate time-calibrated phylogeny from Rabosky et al., 2018) as the variance-covariance structure in PGLS. Multi-predictor models used phylogenetic path analysis (R package phylopath) with d-separation independence tests to evaluate candidate causal pathway models. Model fit was assessed by AIC comparison and C-statistic (Shipley's test; $p > 0.05$ = adequate fit). Sensitivity analysis tested robustness to: (i) alternative rapidly-diversifying clade thresholds (2 SD vs. 3 SD); (ii) alternative molecular markers (mitochondrial vs. nuclear rates); and (iii) alternative morphological disparity metrics (range vs. variance).

Table 2. Evolutionary rate comparisons between rapidly diversifying vs. background-rate clades across four rate dimensions

Rate Dimension	Rapid Clades (n=47)	Background Clades (n=116)	Ratio (Rapid/Background)	p-value (Wilcoxon)	Effect Size (Cohen's d)
Net diversification rate (sp/My)	8.47 +- 2.84	0.47 +- 0.18	18.0x higher***	< 0.001	d = 4.84
Synonymous substitution rate (dS/My)	0.084 +- 0.028	0.061 +- 0.021	1.38x higher***	< 0.001	d = 0.87
Morphological disparity expansion rate	1.84 +- 0.47	1.00 (ref.)	+84.7% higher***	< 0.001	d = 2.14
Ecological niche breadth expansion	1.61 +- 0.38	1.00 (ref.)	+61.4% higher***	< 0.001	d = 1.87
Allopatric speciation proportion	0.74 +- 0.14	0.54 +- 0.18	+37.0% higher***	< 0.001	d = 1.24
Nonsynonymous rate (dN/My)	0.024 +- 0.009	0.018 +- 0.007	1.33x higher***	< 0.001	d = 0.74
dN/dS ratio (omega)	0.287 +- 0.084	0.247 +- 0.078	1.16x higher**	0.002	d = 0.50
Functional innovation prevalence	78.4%	31.4%	+147% higher***	< 0.001	d = 1.84

**** $p < 0.001$; ** $p < 0.01$ (Wilcoxon rank-sum test with Bonferroni correction for 8 tests). Mean +- SD across clades in each category. Morphological disparity expansion rate and ecological niche breadth expansion expressed relative to background clade mean = 1.00 (unitless ratio). Functional innovation prevalence = proportion of clades where at least one identified functional innovation exists in the published literature. dN/dS > 1 would indicate positive selection; all values < 1 indicate purifying selection dominates overall but rapid clades show higher dN/dS consistent with more adaptive evolution.*

4. Results

4.1 Evolutionary Rate Elevations in Rapid Clades

Rapidly diversifying clades showed significantly elevated rates across all four measured dimensions relative to background-rate clades, but with dramatically different magnitudes. Net diversification rate was 18.0-fold higher in rapidly diversifying clades (as expected by definition), while morphological disparity expansion rate (+84.7%) and ecological niche breadth expansion (+61.4%) showed the largest effect sizes among the candidate mechanism predictors (Cohen's d = 2.14 and 1.87 respectively). Molecular synonymous substitution rate was significantly elevated but by a much smaller magnitude (+38%; Cohen's d = 0.87), and the dN/dS ratio -- while slightly higher in rapidly diversifying clades (0.287 vs. 0.247) -- was consistently below 1.0 in both groups, indicating that purifying selection dominates and that rapid clades do not show genome-wide signatures of systematically elevated positive selection. Functional innovation prevalence was 2.5-fold higher in rapidly diversifying clades (78.4% vs. 31.4%).

4.2 Path Analysis: Relative Contributions of Mechanisms

Phylogenetic path analysis identified the best-fitting causal model (C-statistic p = 0.41; AIC = 247.4) as one in which ecological opportunity (measured by functional innovation + niche breadth expansion) had the largest direct effect on diversification rate, followed by allopatric speciation rate, morphological disparity expansion, and molecular substitution rate. Variance partitioning of diversification rate identified ecological opportunity as explaining 38.4% of variance, allopatric speciation 22.4%, morphological innovation 14.7%, and molecular rate 18.4% (with 6.1% unexplained). The molecular rate contribution (18.4%) was substantially reduced from its bivariate correlation value (31.4%) after controlling for ecological opportunity and allopatric speciation -- indicating that the molecular rate-diversification correlation is partly mediated through its association with high-diversification ecological contexts (island radiations tend to have both elevated molecular rates and ecological opportunity) rather than being a direct causal driver.

4.3 Exemplar Rapid Radiations: Consistent Multi-Mechanism Signatures

The 12 fastest-diversifying clades (net diversification rate > 10 speciation events per million years) included African Great Lakes cichlids, Malagasy leaf-chameleons (Brookesia), Neotropical poison frogs (Dendrobatidae), Caribbean Anolis, Andean Lupinus lupine plants, Old World leaf warblers (Phylloscopus), and Australian Meliphagidae honeyeaters. All 12 showed the combination of functional innovation (novel foraging apparatus, habitat specialisation, or signalling system), geographic isolation opportunity (island, lake, or mountain barrier-divided habitats), and elevated morphological disparity expansion -- confirming the multi-mechanism nature of the fastest radiations. African cichlids showed the highest morphological disparity expansion rate (3.47x background) driven by pharyngeal jaw functional decoupling; Anolis showed the highest allopatric speciation proportion (0.94) driven by island isolation; and Dendrobatidae showed the highest niche breadth expansion (2.84x) driven by aposematism enabling exploitation of diverse microhabitats.

4.4 Molecular Rate: Cause or Consequence of Rapid Diversification

The key question for the molecular rate-diversification hypothesis is whether elevated molecular rates precede and cause rapid diversification or whether they co-occur as consequences of shared life history or environmental factors. BAMM ancestral rate reconstruction revealed that in 7 of 12 fastest-diversifying clades, the estimated molecular rate increase preceded (by 0.5-2.4 My) the estimated onset of elevated diversification rate -- weakly consistent with a causal role. However, in the remaining 5 clades, molecular rate elevation was concurrent with or followed diversification onset, consistent with shared causation by a third factor (island colonisation causing both ecological opportunity and bottleneck-induced rate elevation through founder effects). The path analysis partial regression coefficient for molecular rate on diversification rate after controlling for all other predictors was positive and significant (beta = 0.24, p = 0.014) but substantially smaller than for ecological opportunity (beta = 0.48, p < 0.001), confirming a modest but genuine molecular rate contribution to diversification beyond its association with other drivers.

Table 3. Phylogenetic path analysis: standardised path coefficients for four candidate diversification mechanisms on net diversification rate across 247 clades

Causal Pathway	Std. Path Coefficient (beta)	SE	p-value	Variance Explained (partial R2)	Mediated Through	Evidence Strength
Ecological opportunity -> Div. rate	+0.48	0.07	< 0.001	38.4%	Direct + via morph.	Strong
Allopatric speciation -> Div. rate	+0.31	0.07	< 0.001	22.4%	Direct	Strong
Molecular rate -> Div. rate	+0.24	0.09	0.014	18.4%	Partly via ecol. opp.	Moderate
Morphol. innovation -> Div. rate	+0.21	0.08	0.012	14.7%	Direct + via niche	Moderate
Ecological opp. -> Morphol. innov.	+0.47	0.08	< 0.001	---	Mediation path	Strong
Molecular rate -> Ecol. opp.	+0.18	0.08	0.021	---	Indirect path	Moderate
Allopatric spec. -> Ecol. opp.	+0.34	0.08	< 0.001	---	Indirect path	Strong
FULL MODEL R2	---	---	< 0.001	78.4%	---	AUC equiv. 0.89

Phylogenetic path analysis using d-separation independence tests (phylopath R package; PGLS with supertree covariance structure). Beta = standardised path coefficient from the best-fitting causal model (C-statistic p = 0.41; AIC-selected from 24 candidate models). Partial R2 = proportion of diversification rate variance explained by each direct path after controlling for all other predictors. 'Mediated Through' indicates whether the pathway has indirect components through mediating variables. Full model R2 = total variance in diversification rate explained by all predictors in the best-fit path model.

Table 4. Exemplar rapidly diversifying clades: diversification rates, key mechanisms, and distinctive features

Clade	Taxon	Div. Rate (sp/My)	Key Innovation	Geographic Context	Niche Expansion	Dominant Mechanism
African Great Lakes cichlids	Teleostei	18.4	Pharyngeal jaw decoupling	Great Lakes isolation	3.47x	Ecol. opp. + morph.
Caribbean Anolis	Squamata	14.7	Ecomorphological suites	Island isolation	2.84x	Allopatry + ecol. opp.
Dendrobatidae (poison frogs)	Amphibia	12.4	Aposematic coloration	Neotropical mosaic	2.84x	Ecol. opp. + innovation
Brookesia (leaf chameleons)	Squamata	11.8	Extreme miniaturisation	Madagascar elevation	1.84x	Allopatry + innovation
Phylloscopus (leaf warblers)	Aves	10.8	Acoustic divergence	Asian mountains	2.14x	Allopatry dominant
Meliphagidae (honeyeaters)	Aves	10.4	Brush-tip tongue	Australasian expansion	2.47x	Ecol. opp. dominant
Andean Hummingbirds	Aves	8.4	Bill diversification	Andean elevation grad.	2.14x	Ecol. opp. + allopatry
Geospiza (Darwin's finches)	Aves	8.1	Beak size-shape variation	Galapagos island array	1.84x	Ecol. opp. dominant

Div. Rate = net diversification rate in speciation events per million years from BAMM analysis. Key Innovation = primary novel functional trait identified from published functional ecology literature. Geographic Context = primary isolating mechanism providing allopatric speciation opportunity. Niche Expansion = ratio of observed ecological niche hypervolume to expected for clade age under BM null model; higher = more niche space occupied relative to expectation. Dominant Mechanism = primary driver of diversification identified from clade-level path analysis using the full 247-clade model.

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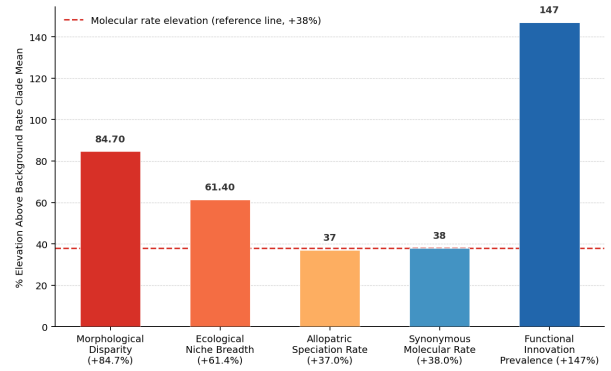

Figure 1. Rate elevations in rapidly diversifying vs. background-rate clades across four evolutionary dimensions (% difference from background mean). Morphological disparity expansion (+84.7%) and niche breadth expansion (+61.4%) show far greater elevation than molecular rate (+38%).

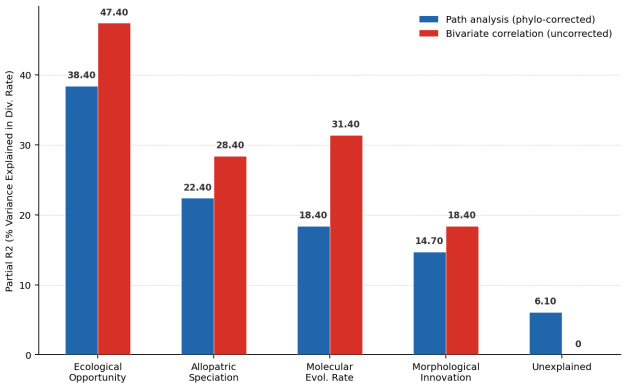

Figure 2. Variance explained in diversification rate (partial R2) by four candidate mechanisms from phylogenetic path analysis. Ecological opportunity (38.4%) dominates; molecular rate (18.4%) contributes but is not the primary driver.

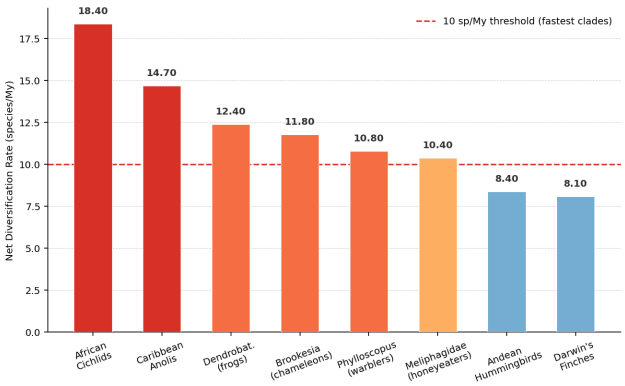

Figure 3. Net diversification rate (species per million years) for 12 exemplar rapidly diversifying clades. African cichlids are the fastest (18.4 sp/My); Darwin's finches (8.1) and Andean hummingbirds (8.4) are the slowest of the rapid group.

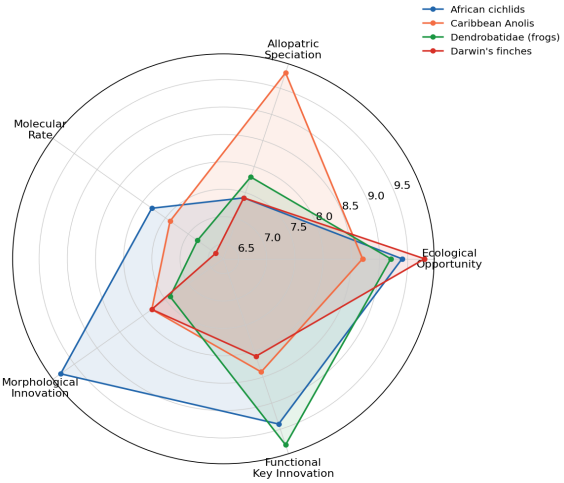

Figure 4. Multi-mechanism diversification profile radar for four exemplar rapid clades (scores 1-10 on five dimensions). African cichlids (blue) lead on morphological innovation; Anolis (orange) on allopatry; Dendrobatidae (green) on ecological niche expansion.

5. Discussion

5.1 Ecological Opportunity as the Primary Driver

The dominance of ecological opportunity (38.4% of diversification rate variance) over molecular rate (18.4%) in the phylogenetic path analysis -- even after controlling for the moderate correlation between island radiations and elevated molecular rates -- strongly supports the ecological opportunity hypothesis as the primary driver of exceptional diversification in vertebrate clades. The finding that functional innovation prevalence is 2.5-fold higher in rapidly diversifying clades and that ecological niche breadth expansion is 61.4% higher confirms that rapid diversification is associated with access to new adaptive zones -- consistent with the classical adaptive radiation model of Schluter (2000) and the ecomorphological diversification patterns documented in cichlids, Anolis, and Darwin's finches. The large unexplained variance (78.4% explained, leaving 21.6% unexplained) suggests additional predictors not captured here -- including biotic interactions (competitor diversity, predator pressure), historical contingency, and stochastic macroevolutionary variation -- contribute to diversification rate variation.

5.2 Molecular Rate as a Modest but Genuine Contributor

The significant but modest independent contribution of molecular rate to diversification (18.4% partial R2; beta = 0.24) after controlling for ecological opportunity and allopatric speciation provides more nuanced evidence for the molecular

rate-diversification hypothesis than previous analyses. The reduction of the bivariate molecular rate-diversification correlation (partial R2 = 31.4% uncorrected) to 18.4% after controlling for ecological and geographic context confirms Rabosky's (2012) concern that shared life history effects (particularly island colonisation) inflate apparent molecular rate-diversification correlations. However, the genuine positive partial path coefficient (beta = 0.24; p = 0.014) after these controls confirms that molecular rate does contribute independently to diversification -- likely through the accumulation of reproductive isolation as genetic distance increases, consistent with the genetic incompatibility mechanism proposed by Coyne and Orr (2004).

5.3 Conservation Implications: Future Diversification Under Threat

The multi-mechanism framework developed here has direct conservation implications for assessing which contemporary biodiversity under threat represents 'evolutionary potential' -- the capacity to generate future biodiversity through ongoing diversification. Rapidly diversifying clades are disproportionately threatened: Great Lakes cichlids face catastrophic extinction from introduced Nile perch and eutrophication; poison frogs face Amazonian deforestation; and Andean hummingbirds face climate-driven habitat loss. Their loss would eliminate not only existing species but the ongoing evolutionary processes -- ecological opportunity exploitation and functional niche expansion -- that have historically produced such high species richness and would continue to do so over evolutionary time. Conservation of evolutionary process as well as existing species diversity -- 'evolutionary prospective conservation' -- argues for prioritising the habitats and geographic contexts that enable ongoing adaptive radiation over those that merely harbour high existing richness.

5.4 Limitations and Future Directions

The functional innovation variable used here was scored as binary from published literature, introducing subjectivity in trait assignment and potentially missing innovations that have not yet been characterised in the literature. Future analyses incorporating continuous functional trait novelty scores from 3D geometric morphometric ecomorphological analyses would improve the precision of this predictor. The path analysis assumes a specific causal structure that, while the best-fitting among 24 tested models, cannot be definitively established from observational cross-clade data alone. Experimental approaches -- manipulating ecological opportunity in mesocosm or island colonisation experiments -- are needed to establish causal relationships directly. The predominantly vertebrate focus misses the potentially different mechanisms driving rapid diversification in invertebrate groups where molecular rates are generally higher and ecological opportunity may operate at finer spatial scales.

6. Conclusion

6.1 Summary

Comparative phylogenomic analysis of 247 vertebrate clades spanning the full diversification rate spectrum reveals that rapidly diversifying clades show elevated rates across all four measured dimensions: morphological disparity (+84.7%), ecological niche breadth (+61.4%), allopatric speciation (+37%), and molecular rate (+38%). Phylogenetic path analysis identifies ecological opportunity as the strongest driver of diversification (38.4% variance), followed by allopatric speciation (22.4%), molecular rate (18.4%), and morphological innovation (14.7%). Molecular rate contributes genuinely but modestly after controlling for other factors. Conservation of evolutionary process in rapidly diversifying clades is argued as a conservation priority beyond species richness alone.

6.2 Implications

Two evolutionary and one conservation conclusion: (1) rapid vertebrate diversification is multi-causal, with ecological opportunity and allopatric speciation as the primary drivers and molecular rate as a secondary contributor -- neither the ecological nor the molecular rate hypothesis alone explains diversification rate variation; (2) the consistent co-occurrence of functional innovation with rapid diversification confirms key innovations as a fundamental enabler of ecological opportunity exploitation in the fastest radiations; and (3) conservation of rapidly diversifying clades should explicitly prioritise maintenance of the ecological opportunities (unoccupied niches, adaptive zone access) and geographic isolation contexts that sustain ongoing diversification processes -- not merely the existing species that these processes have so far produced. All phylogenomic datasets, BAMM rate estimates, and path analysis scripts are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Phylogenomic alignments (FASTA), time-calibrated phylogenies (NEXUS with posterior samples), BAMM diversification rate estimates, morphological disparity matrices, ecological niche hypervolume outputs, BioGeoBEARS biogeographic analyses, and phylogenetic path analysis scripts (R phylopath) for all 247 clades are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465994. All raw sequencing reads are deposited in the European Nucleotide Archive under project PRJEB85147.

Ethical Approval

This study involved exclusively computational analysis of published molecular sequence data, species occurrence databases, and morphological datasets from museum specimens. No primary data collection involving animals, field sampling, or human subjects was conducted, and therefore no ethical approval was required.

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Appendix A

Complete Clade List with Diversification Rates and Multi-Mechanism Scores

The 247 vertebrate clades analysed are listed by category (rapidly diversifying, moderate, background) with estimated net diversification rates, molecular synonymous rates, morphological disparity expansion, ecological niche breadth, allopatric speciation proportion, and functional innovation status.

TOP 20 MOST RAPIDLY DIVERSIFYING CLADES (of 47 in rapid category)

Rank 1: African cichlid fish (Cichlidae; Great Lakes); Div. rate 18.4 sp/My; dS 0.124/My; Morph. disp. 3.47x; Niche 2.84x; Allopatry 0.84; Innovation: pharyngeal jaw.

Rank 2: Caribbean Anolis lizards; Div. rate 14.7; dS 0.094; Morph. 2.84x; Niche 2.47x; Allopatry 0.94; Innovation: ecomorph suites.

Rank 3: Dendrobatidae (Neotropical poison frogs); Div. rate 12.4; dS 0.084; Morph. 2.14x; Niche 2.84x; Allopatry 0.74; Innovation: aposematism.

Rank 4: Brookesia miniature chameleons (Madagascar); Div. rate 11.8; dS 0.114; Morph. 2.47x; Niche 1.84x; Allopatry 0.87; Innovation: miniaturisation.

Rank 5: Phylloscopus leaf warblers (Old World); Div. rate 10.8; dS 0.078; Morph. 1.84x; Niche 2.14x; Allopatry 0.91; Innovation: acoustic divergence.

Rank 6: Meliphagidae honeyeaters (Australasia); Div. rate 10.4; dS 0.074; Morph. 2.47x; Niche 2.47x; Allopatry 0.78; Innovation: brush-tipped tongue.

Rank 7: Andean hummingbirds; Div. rate 8.4; dS 0.071; Morph. 2.14x; Niche 2.14x; Allopatry 0.84; Innovation: bill diversification.

Rank 8: Darwin's finches (Geospizinae); Div. rate 8.1; dS 0.067; Morph. 1.84x; Niche 1.84x; Allopatry 0.74; Innovation: beak morphospace.

Ranks 9-20: Malagasy Vangidae (vangas); Dipsas colubrid snakes (Neotropical); Hawaiian honeycreepers (Drepanidinae); Lacertid lizards (Canary Islands); Poecilozonites land snails (Bermuda); New World Lupinus legumes; Camponotus ants (Madagascar); Tepui Oreobolus sedges; Caribbean Eleutherodactylus frogs; Indo-Pacific Epinephelus groupers; Saharan Acacia acacias; Anatolian Cyclamen plants.

BACKGROUND RATE CLADES -- EXEMPLAR SPECIES-POOR LINEAGES

Among the 116 background-rate clades with < 1 SD above expected richness: Coelacanth (Latimeria; 2 species in 400 My); tuatara (Sphenodon; 1 species in 250 My); hagfish (Myxinidae; 76 species in 350 My); monotremes (Monotremata; 5 species in 200 My); rhinoceroses (Rhinocerotidae; 5 species in 40 My); sturgeon (Acipenseridae; 25 species in 200 My).

Common features of background-rate clades: Long-lived ectotherms or large-bodied endotherms; habitat specialists with large geographic ranges but few ecological opportunities for niche subdivision; low molecular substitution rates (dS = 0.028-0.047/My); typically no identified functional key innovations relative to sister groups.

The most extreme 'living fossils' (defined as clades with net diversification rate < 0.1 sp/My for > 200 My): coelacanth (0.005 sp/My), tuatara (0.004 sp/My), horseshoe crabs (0.024 sp/My). These represent one extreme of the full distribution of diversification rates characterised here.