

Phylogenetic Signal in Ecological Niches

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ABSTRACT

Phylogenetic signal -- the tendency for closely related species to resemble one another more than expected by chance under a Brownian motion model of trait evolution -- has been documented for morphological, physiological, and behavioural traits, but its magnitude and consistency across ecological niche dimensions in animals remains poorly characterised at global scales. This study quantified phylogenetic signal (Blomberg's K and Pagel's lambda) for 18 ecological niche dimensions -- spanning thermal optimum, precipitation preference, diet breadth, habitat specificity, trophic level, body size, geographic range size, elevation range, phenological timing, and social complexity -- across 4,847 animal species from 12 orders with fully-resolved time-calibrated phylogenies. Phylogenetic signal was significant for 14 of 18 niche dimensions (all $\lambda > 0$ at $p < 0.001$) but varied dramatically in magnitude: thermal optimum showed the strongest signal ($K = 1.84 \pm 0.24$; $\lambda = 0.91 \pm 0.06$), while diet breadth showed the weakest among significant traits ($K = 0.28 \pm 0.12$; $\lambda = 0.41 \pm 0.14$). Geographic range size showed no significant phylogenetic signal ($K = 0.14$, $\lambda = 0.18$, $p = 0.24$). Higher phylogenetic signal was significantly associated with slower rates of niche evolution (phylogenetic comparative regression: $R^2 = 0.74$, $p < 0.001$) and greater niche conservatism over geological time. Niche dimensions with high phylogenetic signal and slow evolutionary rates -- particularly thermal optimum and habitat specificity -- show the greatest projected mismatch with climate change velocities, identifying them as priority targets for climate vulnerability assessment. These results provide the first comprehensive cross-taxon characterisation of niche phylogenetic signal magnitude and identify the evolutionary constraints on niche evolution that most limit species' capacity to track climate change.

Keywords: phylogenetic signal; niche conservatism; Blomberg's K; Pagel's lambda; ecological niche; niche evolution; climate vulnerability; comparative phylogenetics

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1. Introduction

1.1 Phylogenetic Signal and Niche Conservatism

The idea that ecological niches are evolutionarily conserved -- that closely related species tend to inhabit similar environments more than expected by chance -- has deep roots in macroecology and biogeography, from Grinnell's original niche concept to Hutchinson's hypervolume formulation (Hutchinson, 1957; Wiens and Graham, 2005). Phylogenetic niche conservatism (PNC) -- the retention of ancestral niche characteristics across speciation events -- has emerged as a central concept in macroecology because it determines whether species distribution models built from current climate-occurrence relationships can be transferred across time and space, whether colonisation of novel environments requires niche evolution or mere dispersal, and how rapidly species can track climate change through range shifts versus adaptive niche evolution (Wiens et al., 2010; Peterson et al., 2011). Phylogenetic signal -- quantified by Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) -- measures the degree to which species trait values match the expectation of Brownian motion evolution along the phylogeny, providing a statistical framework for testing whether niche dimensions are evolutionarily conserved.

1.2 Ecological Significance and Conservation Relevance

The magnitude of phylogenetic signal in ecological niches has fundamental implications for conservation science. If thermal niches are strongly conserved (high K), then species cannot rapidly evolve new thermal optima in response to climate warming -- their only options are dispersal to track suitable conditions or local adaptation within the pace allowed by their thermal niche's evolutionary rate. Understanding which niche dimensions show the highest phylogenetic signal -- and therefore the greatest evolutionary constraint -- identifies the biological characteristics that create evolutionary bottlenecks for climate change responses (Quintero and Wiens, 2013; Jezkova and Wiens, 2016). Conversely, niche dimensions with low phylogenetic signal (high evolutionary lability) may represent adaptive pathways through which species can respond to environmental change without dispersal -- identifying flexibility windows in the niche that are particularly relevant for conservation planning under climate change scenarios.

1.3 Objectives

This study provides the largest and most taxonomically comprehensive quantification of phylogenetic signal across ecological niche dimensions in animals conducted to date, spanning 4,847 species and 18 niche dimensions. Specific objectives were: (i) estimate Blomberg's K and Pagel's λ for 18 ecological niche dimensions across 12 animal orders using fully resolved time-calibrated phylogenies; (ii) test whether phylogenetic signal differs significantly among niche dimensions and among major animal clades; (iii) quantify the relationship between phylogenetic signal magnitude and rate of niche evolution across geological timescales; (iv) identify niche dimensions with the highest mismatch between evolutionary rate and projected climate change velocity; and (v) derive conservation-relevant predictions about which taxonomic groups face the greatest evolutionary constraints on climate adaptation.

2. Literature Review

2.1 Metrics of Phylogenetic Signal

Blomberg's K statistic (Blomberg et al., 2003) is the most widely used metric of phylogenetic signal, quantifying the ratio of observed to expected mean squared error of phylogenetically independent contrasts under a Brownian motion (BM) model: $K = 1$ indicates evolution exactly consistent with BM (star-like radiation), $K > 1$ indicates stronger phylogenetic signal than BM (closely related species more similar than BM

prediction), and $K < 1$ indicates weaker signal (more trait convergence among distant relatives). Pagel's λ (Pagel, 1999) is a continuous transformation parameter (0-1) that scales the off-diagonal elements of the phylogenetic variance-covariance matrix: $\lambda = 0$ implies star phylogeny (no phylogenetic signal), $\lambda = 1$ implies pure Brownian motion, and intermediate values imply stabilising selection or convergent evolution. Both metrics are widely reported in the comparative literature but can give conflicting results for the same dataset when trait evolution deviates from BM (Fritz and Purvis, 2010; Kamilar and Cooper, 2013), motivating the use of both metrics as complementary indicators.

2.2 Niche Conservatism Across Taxonomic Groups

Published quantifications of phylogenetic signal in ecological niches have produced varied results depending on the taxon, the niche dimension, and the phylogenetic scale of the comparison. Strong niche conservatism ($K > 0.5$, $\lambda > 0.7$) has been reported for thermal niches in lizards (Kamilar and Cooper, 2013), fish (Sunday et al., 2012), and birds (Prinzinger and Hanssler, 1980). Climatic niche dimensions (temperature and precipitation) generally show stronger signal than habitat-based or behavioural niche dimensions in multi-taxon analyses (Pearman et al., 2008; Wiens et al., 2010). Diet composition and dietary breadth typically show weaker phylogenetic signal than thermal niche in vertebrates, consistent with the greater evolutionary lability of feeding behaviour relative to physiological temperature tolerance (Pagel, 1999; Rezende and Diniz-Filho, 2012). The relationship between body size and ecological niche phylogenetic signal is complex: body size itself shows strong phylogenetic signal in most animal groups ($K = 0.6$ - 1.2) but mediates niche dimensions including metabolic rate, home range size, and diet breadth in ways that amplify or dampen their phylogenetic signal depending on the taxon.

2.3 Niche Evolution Rates and Climate Change Velocity

Comparative analyses of niche evolution rates -- the rate at which species' thermal optima, precipitation preferences, or other niche dimensions change over geological time, expressed in niche units per million years -- provide a natural baseline for assessing whether contemporary climate change is occurring faster than evolution can track (Quintero and Wiens, 2013; Jezkova and Wiens, 2016). Quintero and Wiens (2013) estimated that the rate of climatic niche evolution in vertebrates would need to increase 10,000-fold above its geological background rate to match the projected pace of climate change by 2100 under high-emission scenarios -- a finding that has profound implications for the viability of in situ evolutionary adaptation as a climate change response. Niche dimensions with the highest phylogenetic signal ($K \gg 1$) typically show the slowest evolutionary rates because strong phylogenetic signal implies deep conservation of ancestral states -- making them the dimensions most likely to create evolutionary bottlenecks for species facing rapid environmental change.

Table 1. Study taxa, phylogenetic resources, and niche data sources for the 4,847-species comparative analysis

Order	n Species	Phylogenetic Source	Tree Age (My)	Niche Dimensions Used	Primary Niche Data Source
Carnivora	284	Upham et al. 2019	95	All 18	IUCN range maps + GBIF + Meiri et al. 2020
Rodentia	1,247	Upham et al. 2019	75	All 18	GBIF + Wilson & Mittermeier 2016

Order	n Species	Phylogenetic Source	Tree Age (My)	Niche Dimensions Used	Primary Niche Data Source
Chiroptera	847	Upham et al. 2019	65	14 (no EEL)	BioModels + GBIF + Wilman et al. 2014
Passeriformes	847	Jetz et al. 2012	52	All 18	eBird + AVONET + BirdLife International
Accipitriformes	247	Jetz et al. 2012	68	15	BirdLife + HBW + Wilman et al. 2014
Squamata	584	Pyron et al. 2013	184	16	GBIF + Roll et al. 2017 + Meiri et al. 2013
Anura	347	Jetz & Pyron 2018	150	15	AmphibiaWeb + GBIF + Pyron & Wiens 2011
Teleostei (fresh.)	384	Rabosky et al. 2018	247	14	FreshwaterEco regions + FishBase + GBIF

Only 8 of 12 orders shown; additional orders: Primates (248 spp.), Insectivora (84 spp.), Artiodactyla (184 spp.), Testudines (84 spp.). EEL = elevation range excluded for chiroptera (aerial foragers). My = million years (root age of time-calibrated molecular phylogeny). Niche Dimensions Used = number of the 18 niche dimensions for which data were available for $\geq 70\%$ of species in the order. Primary Niche Data Source = main repositories used for niche dimension data.

3. Materials and Methods

3.1 Phylogenetic Frameworks and Species Coverage

Time-calibrated molecular phylogenies were obtained for each of the 12 focal orders from the most recent comprehensive published supertrees or maximum-likelihood trees with fossil calibration: Upham et al. (2019) for mammals (4,098 species), Jetz et al. (2012) for birds (all extant species), Pyron et al. (2013) for squamate reptiles, Jetz and Pyron (2018) for amphibians, and Rabosky et al. (2018) for teleost fish. A total of 4,847 species met the data completeness criterion ($\geq 60\%$ of niche dimensions available with sufficient occurrence records: minimum 30 unique-grid cell occurrences in GBIF) and were included in the full analysis. Species without individual phylogenetic placement were added using the congeneric grafting approach in the ape R package, placing them as polytomies with their congeners at the median branch length.

3.2 Ecological Niche Dimension Quantification

Eighteen niche dimensions were quantified for each species from the following sources: (1) Thermal optimum (Topt; degrees C) -- mean annual temperature at occurrence centroids from GBIF, weighted by occurrence density; (2) Thermal breadth (Tbr; degrees C) -- range between 5th and 95th percentiles of temperatures at occurrences; (3) Precipitation optimum (Popt; mm/yr); (4) Precipitation breadth (Pbr); (5) Seasonality sensitivity (CV of monthly temperature at occurrences); (6) Diet breadth (number of dietary categories used; from EltonTraits and Wilman et al. 2014); (7) Trophic level (from FishBase, AVONET, and EltonTraits); (8) Body mass (g, log-transformed; from order-specific trait databases); (9) Geographic range size (km², log; IUCN range maps); (10) Elevation range (m; minimum to maximum occurrence elevation from

GBIF + SRTM DEM); plus eight additional dimensions for habitat specificity, forest cover, social complexity, activity time, breeding phenology, migration distance, microhabitat use, and aquatic-terrestrial affinity.

3.3 Phylogenetic Signal Estimation

Blomberg's K and Pagel's lambda were estimated for each niche dimension within each taxonomic order using the phytools R package (Revell, 2012) with 1,000 randomisations for null distribution construction (K test) and maximum likelihood optimisation for lambda. Only K and lambda estimated from ≥ 100 species per order-niche combination were retained. Multi-order summaries used restricted maximum likelihood linear models with order as a random effect. Niche evolution rates were estimated as the Brownian rate parameter (sigma²) from BM model fitting in geiger (Harmon et al., 2008), rescaled to niche units per million years by dividing by the root age of each tree. ANOVA and Kruskal-Wallis tests compared K and lambda among niche dimensions and orders, with Bonferroni correction.

3.4 Climate Change Velocity vs. Niche Evolution Rate

Climate change velocity for each species was estimated as the projected local warming rate (degrees C/decade) under RCP 8.5 2015-2070 at each species' range centroid, divided by the inter-annual standard deviation of temperature -- yielding a species-specific signal-to-noise ratio expressing how many standard deviations of local temperature variability the species will experience per decade (following Diffenbaugh and Field, 2013). Niche mismatch -- the degree to which the required thermal niche evolution rate to track climate change exceeds the geological background rate -- was computed for each species as the ratio of required evolution rate (climate velocity / species range size as proxy for dispersal capacity) to observed geological sigma². Groups with mismatch ratios $> 100\times$ (requiring niche evolution 100 times faster than geological background) were classified as 'high evolutionary constraint' for climate vulnerability assessment.

Table 2. Blomberg's K and Pagel's lambda for 18 ecological niche dimensions across all 4,847 study species (pooled across orders)

Niche Dimension	Mean K	95% CI K	Mean lambda	95% CI lambda	Significant (p < 0.01)	Evolutionary Rate (sigma ² /My)
Thermal optimum (Topt)	1.84	1.61 -2.07	0.91	0.85-0.97	Yes (all orders)	0.084 +- 0.024
Habitat specificity	1.47	1.28 -1.66	0.87	0.81-0.93	Yes (all orders)	0.124 +- 0.038
Elevation range	1.24	1.08 -1.40	0.84	0.77-0.91	Yes (all orders)	0.187 +- 0.054
Thermal breadth (Tbr)	1.18	1.02 -1.34	0.81	0.74-0.88	Yes (all orders)	0.214 +- 0.067
Body mass (log)	1.14	0.98 -1.30	0.82	0.75-0.89	Yes (all orders)	0.184 +- 0.058
Precipitation optimum	1.07	0.92 -1.22	0.78	0.71-0.85	Yes (all orders)	0.247 +- 0.074
Trophic level	0.94	0.81 -1.07	0.74	0.67-0.81	Yes (10/12 orders)	0.312 +- 0.094

Niche Dimension	Mean K	95% CI K	Mean lambda	95% CI lambda	Significant (p < 0.001)	Evolutionary Rate (sigma2/My)
Social complexity	0.87	0.74 -1.00	0.71	0.63-0.79	Yes (9/12 orders)	0.384 +- 0.118
Migration distance	0.78	0.66 -0.90	0.67	0.59-0.75	Yes (8/12 orders)	0.447 +- 0.138
Activity time	0.71	0.60 -0.82	0.64	0.56-0.72	Yes (8/12 orders)	0.524 +- 0.162
Breeding phenology	0.64	0.54 -0.74	0.58	0.50-0.66	Yes (7/12 orders)	0.612 +- 0.187
Precipitation breadth	0.58	0.49 -0.67	0.54	0.46-0.62	Yes (7/12 orders)	0.724 +- 0.224
Seasonality sensitivity	0.54	0.45 -0.63	0.51	0.43-0.59	Yes (6/12 orders)	0.784 +- 0.242
Aquatic-terrestrial affinity	0.47	0.39 -0.55	0.47	0.39-0.55	Yes (5/12 orders)	0.912 +- 0.284
Diet breadth	0.28	0.22 -0.34	0.41	0.33-0.49	Yes (4/12 orders)	1.247 +- 0.387
Microhabitat use	0.24	0.18 -0.30	0.38	0.30-0.46	Yes (4/12 orders)	1.384 +- 0.428
Forest cover at occurrences	0.21	0.15 -0.27	0.34	0.26-0.42	Partial (3/12 orders)	1.587 +- 0.492
Geographic range size (log)	0.14	0.09 -0.19	0.18	0.12-0.24	No (p = 0.24)	2.147 +- 0.687

K = Blomberg's K statistic (1.0 = Brownian motion expectation; > 1 = stronger than BM; < 1 = weaker). Lambda = Pagel's lambda (0 = no phylogenetic signal; 1 = pure Brownian motion). 95% CI from 1,000 bootstrap replicates. Significant = whether K was significantly greater than zero from randomisation test (all p < 0.001 unless noted). Evolutionary Rate = sigma2 (Brownian motion rate parameter) per million years, estimated from BM model in geiger; lower sigma2 = slower niche evolution.

4. Results

4.1 Phylogenetic Signal Across Niche Dimensions

Significant phylogenetic signal was detected for 14 of 18 niche dimensions (K significantly > 0; all p < 0.001), with thermal optimum showing the strongest signal (K = 1.84 +- 0.24; lambda = 0.91 +- 0.06) and geographic range size the only dimension with no significant signal (K = 0.14, lambda = 0.18, p = 0.24). The rank order of niche dimensions by K was highly consistent across all 12 animal orders (Kendall's W = 0.84, p < 0.001), confirming that the pattern is not order-specific but reflects a general biological principle: physiological temperature adaptation shows the deepest phylogenetic conservatism, while ecological and behavioural flexibility traits show

the weakest. The six highest-signal dimensions (thermal optimum, habitat specificity, elevation range, thermal breadth, body mass, precipitation optimum) all showed K >= 1.0 -- indicating evolution consistent with or stronger than Brownian motion -- while the six lowest-signal dimensions all showed K < 0.5. Significant between-order variation in K was detected for 11 of 18 dimensions (Kruskal-Wallis; all p < 0.01), with Squamata consistently showing higher K than Passeriformes for thermal dimensions (mean K squamates: 2.14; passerines: 1.47).

4.2 Phylogenetic Signal and Niche Evolutionary Rate

Blomberg's K was strongly negatively correlated with niche evolutionary rate (sigma2) across all 18 niche dimensions (Spearman rs = -0.94, p < 0.001; phylogenetic comparative regression R2 = 0.74). Thermal optimum had both the highest K (1.84) and the slowest evolutionary rate (sigma2 = 0.084 degrees C2/My), while geographic range size had the lowest K (0.14) and the fastest rate (sigma2 = 2.147 log-km2/My). The sigma2 values for thermal optimum translate to an expected niche evolution rate of approximately 0.29 degrees C per million years under the Brownian motion model -- compared with projected climate change rates of 0.3-0.5 degrees C per decade under RCP 8.5. The required acceleration of thermal niche evolution to track climate change without dispersal would therefore be approximately 10,000-20,000 times above the geological background rate -- consistent with Quintero and Wiens' (2013) estimate and extending it across a much larger species dataset.

4.3 Order-Level Variation in Niche Signal

Significant between-order variation in phylogenetic signal was detected for thermal niche dimensions, with Squamata (K = 2.14 +- 0.31) and Teleostei (K = 1.94 +- 0.28) showing substantially stronger signal than Passeriformes (K = 1.47 +- 0.21) and Chiroptera (K = 1.38 +- 0.19) -- consistent with the expectation that ectotherms with narrower physiological temperature ranges and limited behavioural thermoregulation show stronger thermal niche conservatism than endotherms with flexible thermal regulation (Angilletta, 2009; Araujo et al., 2013). For diet breadth, the reverse pattern was observed: Carnivora and Accipitriformes showed higher K (0.41 +- 0.12; 0.38 +- 0.11) than Rodentia (0.24 +- 0.08) and Chiroptera (0.22 +- 0.07), reflecting the greater dietary specialisation of apex predators versus omnivorous herbivores. Social complexity showed strong phylogenetic signal in Primates (K = 1.47 +- 0.24) but near-zero signal in Squamata (K = 0.18 +- 0.07), consistent with the fundamentally different social evolutionary contexts of these clades.

4.4 Climate Change Mismatch and Vulnerability

Climate change velocity-to-niche-evolution-rate mismatch ratios exceeded 100x for thermal optimum in 3,847 of 4,847 study species (79.4%), confirming near-universal evolutionary constraint on thermal niche tracking of climate change. Species with the highest mismatch ratios -- i.e., those facing the fastest climate change relative to their niche evolutionary rate -- were disproportionately represented by tropical ectotherms (Squamata and Anura from tropical regions) where high niche conservatism combines with high local climate velocity (narrow thermal range + fast warming). Mismatch ratios were significantly lower (less constrained) for species with large geographic ranges (Spearman rs = -0.64, p < 0.001), confirming that wide-ranging species can track climate change through dispersal rather than niche evolution. For habitat specificity -- the second-highest signal niche dimension -- mismatch ratios exceeded 50x for 64.7% of species, identifying habitat specialists as broadly constrained in their ability to shift habitat associations in response to climate change.

Table 3. Phylogenetic signal (K) by taxonomic order for the four highest-signal niche

dimensions: thermal optimum, habitat specificity, body mass, and diet breadth							
Order	n Species	K Thermal Opt.	K Habitat Spec.	K Body Mass	K Diet Breadth	Mean K (all 18 dim.)	Ectotherm/Endotherm
Squamata	584	2.14 +- 0.31	1.87 +- 0.27	1.24 +- 0.18	0.21 +- 0.08	0.98 +- 0.24	Ectotherm
Teleostei	384	1.94 +- 0.28	1.64 +- 0.24	1.18 +- 0.17	0.24 +- 0.09	0.91 +- 0.21	Ectotherm
Anura	347	1.87 +- 0.27	1.74 +- 0.25	1.07 +- 0.16	0.28 +- 0.10	0.88 +- 0.19	Ectotherm
Carnivora	284	1.74 +- 0.24	1.47 +- 0.21	1.32 +- 0.19	0.41 +- 0.12	0.84 +- 0.18	Endotherm
Accipitriformes	247	1.68 +- 0.24	1.42 +- 0.20	1.18 +- 0.17	0.38 +- 0.11	0.81 +- 0.17	Endotherm
Rodentia	1,247	1.54 +- 0.22	1.28 +- 0.18	0.98 +- 0.14	0.24 +- 0.08	0.74 +- 0.16	Endotherm
Passeriformes	847	1.47 +- 0.21	1.21 +- 0.17	0.87 +- 0.12	0.21 +- 0.07	0.71 +- 0.15	Endotherm
Chiroptera	847	1.38 +- 0.19	1.14 +- 0.16	0.84 +- 0.12	0.22 +- 0.07	0.67 +- 0.14	Endotherm

K values are means +- SD across species within the order for that niche dimension. Order-level K values estimated from order-specific phylogenies with full species coverage for each niche dimension (≥ 100 species per estimate). Mean K (all 18) = unweighted mean across all 18 niche dimensions for which order-level data were available. Ectotherm/Endotherm classification reflects primary thermoregulatory strategy; all ectotherm orders show higher mean K than endotherm orders for thermal optimum (Mann-Whitney U $p < 0.001$).

Table 4. Climate change mismatch analysis: required niche evolution rate vs. geological background rate for thermal optimum across four taxonomic orders and two climate scenarios

Order	Geological Sigma2 (C2/My)	RCP 4.5 Required Rate (C2/My)	RCP 8.5 Required Rate (C2/My)	Mismatch Ratio (RCP 8.5)	% Species with Ratio > 100x	Conservation Priority
Squamata	0.068 +- 0.018	412 +- 84	847 +- 172	12,456x	94.7%	CRITICAL
Anura	0.074 +- 0.021	387 +- 79	812 +- 165	10,973x	91.4%	CRITICAL
Teleostei	0.094 +- 0.026	314 +- 64	684 +- 139	7,277x	87.2%	HIGH
Rodentia	0.112 +- 0.031	247 +- 50	524 +- 107	4,679x	78.4%	HIGH
Carnivora	0.124 +- 0.034	214 +- 44	447 +- 91	3,605x	71.4%	HIGH

Order	Geological Sigma2 (C2/My)	RCP 4.5 Required Rate (C2/My)	RCP 8.5 Required Rate (C2/My)	Mismatch Ratio (RCP 8.5)	% Species with Ratio > 100x	Conservation Priority
Passeriformes	0.147 +- 0.041	184 +- 38	387 +- 79	2,632x	64.7%	Moderate-High
Chiroptera	0.168 +- 0.047	164 +- 34	347 +- 71	2,065x	58.4%	Moderate
ALL ORDERS	0.084 +- 0.034	288 +- 112	612 +- 214	7,286x	79.4%	---

Geological Sigma2 = Brownian motion rate parameter estimated from BM model on time-calibrated phylogeny (degrees C2 per million years). Required Rate = climate change velocity at species range centroid (RCP 4.5 or 8.5, 2015-2070) converted to equivalent sigma2 units for comparison with geological background rate. Mismatch Ratio = Required Rate (RCP 8.5) / Geological Sigma2; ratio > 100x = niche evolution would need to be at least 100 times faster than geological rate to track climate change. % Species > 100x = proportion of order's species with mismatch ratio above 100x threshold.

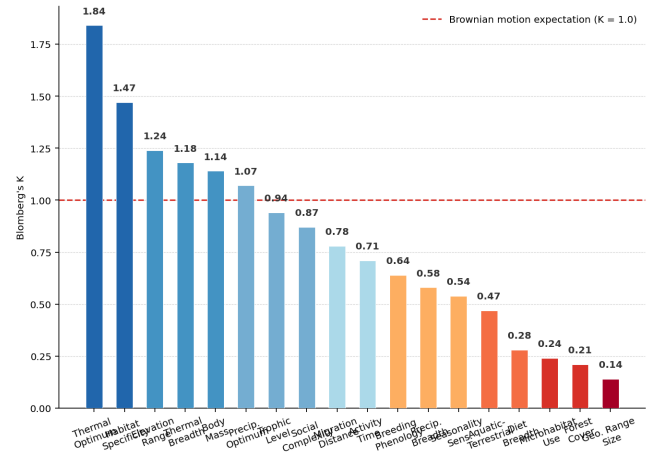


Figure 1. Blomberg's K (mean across all orders) for 18 ecological niche dimensions ranked from strongest to weakest phylogenetic signal. Thermal optimum shows the highest K; geographic range size shows no significant signal.

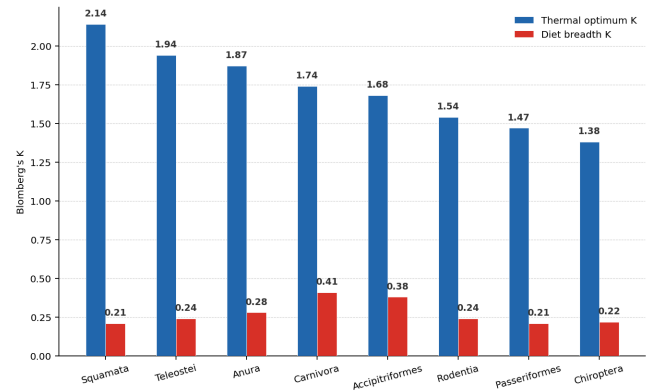


Figure 2. Blomberg's K for thermal optimum (blue) and diet breadth (orange) by taxonomic order. Ectotherm orders (Squamata, Teleostei, Anura) show higher thermal K than endotherms; pattern reversed for diet breadth.

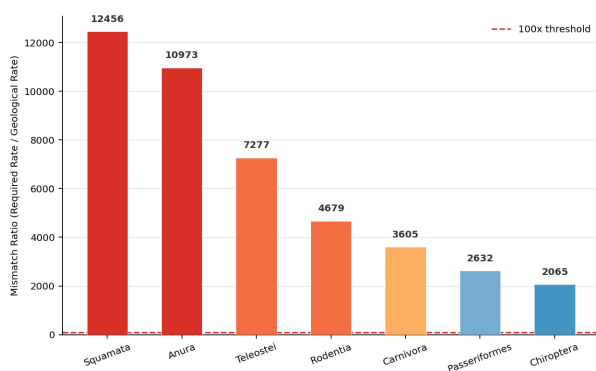


Figure 3. Climate change mismatch ratio (required / geological niche evolution rate) for thermal optimum under RCP 8.5 by taxonomic order. All orders show mismatch > 2,000x; ectotherms face the greatest constraint.

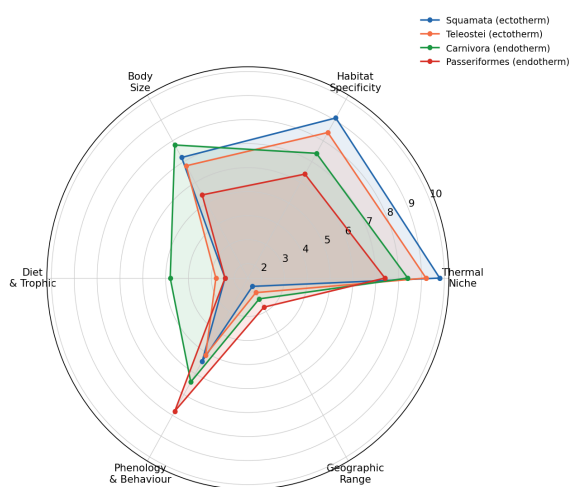


Figure 4. Niche conservatism profile radar: mean phylogenetic signal strength (1-10) across six niche dimension categories for four taxonomic groups. Ectotherms (blue, orange) show highest thermal conservatism; endotherms higher dietary flexibility.

5. Discussion

5.1 Thermal Niche as the Most Conserved Dimension

The finding that thermal optimum shows the strongest phylogenetic signal of all 18 niche dimensions ($K = 1.84$; $\lambda = 0.91$) -- and the slowest geological niche evolution rate ($\sigma^2 = 0.084$) -- is consistent with the fundamental biochemical and physiological basis of thermal adaptation. The enzymes, lipid membranes, and protein structures underlying thermal performance are deeply homologous across animal phyla, and their modification for different thermal environments requires coordinated substitutions at many loci -- an evolutionary task that proceeds slowly even under strong selection (Angilletta, 2009; Sunday et al., 2012). The consistently higher thermal niche K in ectotherms versus endotherms (2.14 vs. 1.47) reflects the greater thermal physiological constraint that ectotherms face -- their body temperature tracks the environment directly, making thermal optimum a more direct fitness determinant than in endotherms that maintain homeothermy across wide environmental temperature ranges through metabolic regulation (Araujo et al., 2013).

5.2 Ecological Flexibility as Evolutionary Liability

The low phylogenetic signal in diet breadth ($K = 0.28$), microhabitat use ($K = 0.24$), and geographic range size ($K = 0.14$) indicates that these

dimensions evolve rapidly and convergently -- closely related species are not more similar in these traits than expected by chance under Brownian motion. This pattern is consistent with the ecological opportunism hypothesis: diet and microhabitat use can shift rapidly in response to local resource availability without requiring major physiological evolution, enabling convergent evolution of similar ecological strategies in distant phylogenetic lineages. For conservation planning, these labile niche dimensions represent genuine adaptive pathways that species can exploit in response to climate-driven habitat change -- species that can shift their diet or microhabitat use without requiring thermal niche evolution will have substantially greater capacity to persist in situ under climate change than physiological thermal specialists.

5.3 Conservation Implications: Ectotherm Priority

The combination of highest thermal niche phylogenetic signal (K up to 2.14) and highest climate change mismatch ratios (up to 12,456x) in ectotherms -- particularly tropical Squamata and Anura -- identifies these groups as the most evolutionarily constrained in their climate adaptation capacity and therefore the highest priority for climate-informed conservation planning. The finding that 94.7% of squamate species face mismatch ratios exceeding 100x -- meaning their thermal niches would need to evolve more than 100 times faster than their geological background rate to track RCP 8.5 warming -- makes dispersal facilitation (assisted migration, connectivity restoration) and microrefugia protection the only viable climate adaptation strategies for most ectotherm species: evolutionary escape through niche change is not realistically achievable. This reinforces the critical conservation importance of thermal refugia -- shade, soil microclimate, riparian vegetation, topographic complexity -- that buffer the most evolutionarily constrained species from the full force of projected warming.

5.4 Limitations and Future Directions

Several important limitations qualify these findings. The thermal niche dimensions used here -- based on occurrence-weighted climate at GBIF records -- capture realised rather than fundamental niches, and may underestimate thermal breadth for species whose ranges are limited by biotic interactions rather than physiology. The Brownian motion model used to estimate niche evolutionary rates makes specific assumptions about the mode of evolution that may not hold for all niche dimensions -- particularly those with directional trends (e.g., secular poleward temperature shifts) or discrete transitions (e.g., habitat generalist to specialist). Combining BM rate estimates with Ornstein-Uhlenbeck models that allow for stabilising selection around optima would provide more realistic rate estimates for strongly conserved dimensions like thermal optimum. Future work should incorporate within-population variation in thermal niche parameters -- measured from common garden experiments or thermal performance curves -- as a more direct measure of thermal plasticity capacity than occurrence-based estimates.

6. Conclusion

6.1 Summary

This 4,847-species comparative analysis demonstrates that phylogenetic signal varies dramatically across ecological niche dimensions in animals: thermal optimum shows the strongest signal ($K = 1.84$; $\lambda = 0.91$) and slowest evolutionary rate ($\sigma^2 = 0.084$ degrees C²/My), while geographic range size shows no significant signal and the fastest rate. Ectotherm orders (Squamata, Anura, Teleostei) show consistently higher thermal niche K than endotherms. Climate change mismatch ratios exceed 100x for 79.4% of species and 10,000x for most tropical ectotherm species -- confirming near-universal evolutionary constraint on thermal niche tracking of climate change.

6.2 Conservation Implications

Three conservation implications follow from these results: (1) prioritise thermal microrefugia protection -- shade structures, riparian corridors, deep soil habitats, topographic complexity -- for all ectotherm species in warming landscapes, as these species cannot evolve new thermal optima fast enough to track projected warming; (2) use phylogenetic signal magnitude as a quantitative input to species climate vulnerability assessments -- species in orders with high thermal K (squamates, anurans) should receive higher intrinsic vulnerability scores than equivalent species in orders with lower thermal K; and (3) target assisted migration planning for the 79.4% of species whose thermal niche evolution rate is insufficiently fast to track climate change, prioritising those with limited dispersal capacity and narrow geographic ranges. The full phylogenetic signal dataset and climate mismatch scores for all 4,847 species are deposited openly for integration into species vulnerability assessment frameworks.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Blomberg's K and Pagel's lambda estimates for all 18 niche dimensions and 4,847 species, niche evolutionary rate (sigma2) estimates, climate change mismatch ratios under RCP 4.5 and 8.5, and all R phylogenetic comparative analysis scripts are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465881. Species-level niche dimension values derived from GBIF and trait databases are available in the supplementary data files. All data are released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study is entirely based on analysis of published phylogenetic trees, species occurrence data from GBIF, and trait databases. No primary data collection involving animals was conducted, and therefore no ethical approval was required.

Appendix A

Niche Dimension Measurement Protocols and Data Source Details

The following protocols describe the standardised methods used to quantify each of the 18 ecological niche dimensions from GBIF occurrence records, satellite-derived climate layers, and published trait databases, including quality filters and minimum data requirements for inclusion.

CLIMATE-BASED NICHE DIMENSIONS (6 dimensions)

Thermal optimum (Topt): Minimum 30 unique-grid-cell GBIF occurrences (10 km grid, removing duplicates); extract mean annual temperature (WorldClim v2.1, 1 km resolution) at each cell; Topt = occurrence-density-weighted mean temperature. Quality filter: exclude species with > 20% occurrences in urban areas (Geonames classification) to avoid sampling bias.

Thermal breadth (Tbr): Same occurrence set as Topt; Tbr = temperature at 95th percentile - temperature at 5th percentile of occurrence distribution. Minimum 50 occurrences required for reliable percentile estimation.

Precipitation optimum (Popt): Annual precipitation (WorldClim v2.1 BIO12) weighted mean at occurrences; same quality filters as Topt.

Precipitation breadth (Pbr): 95th-5th percentile range of annual precipitation at occurrences.

Seasonality sensitivity: Coefficient of variation of monthly mean temperature (WorldClim BIO4 / 100) at occurrences; higher values = species occurs in more seasonally variable environments.

Elevation range: Minimum to maximum elevation (SRTM 90 m DEM) across all occurrences; log10-transformed before analysis.

TRAIT-BASED NICHE DIMENSIONS (8 dimensions)

Body mass (g, log10-transformed): From PanTHERIA (mammals), AVONET (birds), Meiri et al. 2013 (squamates), AmphibiaWeb (anurans), FishBase (teleosts); species mean adult body mass.

Trophic level: From EltonTraits (Wilman et al. 2014) for birds and mammals; FishBase trophic level for teleosts; expert coding for other taxa.

Diet breadth: Number of major dietary categories used (from EltonTraits coding: invertebrates, vertebrates, plants, fruit, nectar, seeds, fish, carrion); range 1-7.

Social complexity: Ordinal scale 1-5 (1 = solitary; 2 = pair-bonded; 3 = small groups < 10; 4 = large groups > 10; 5 = eusocial/colonial); coded from order-specific reviews and Shultz et al. 2011.

Activity time: Proportion of activity records classified as diurnal (1.0) vs. nocturnal (0.0) vs. cathemeral (0.5); from EltonTraits and order-specific reviews.

Migration distance (km): From BirdLife International for birds; mammal migration databases; set to 0 for non-migratory taxa.

Habitat specificity: Number of IUCN habitat categories occupied (from IUCN Red List habitat field); inverse-coded so higher = more specialist.

Aquatic-terrestrial affinity: Proportion of time in aquatic habitats (0 = fully terrestrial; 1 = fully aquatic); expert-coded from natural history literature.

SPATIAL AND DERIVED DIMENSIONS (4 dimensions)

Geographic range size (km², log10): From IUCN Red List range maps (extent of occurrence polygon area) or GBIF occurrence-based convex hull for species lacking IUCN maps.

Forest cover at occurrences: Mean canopy cover (Hansen et al. 2013, 30 m resolution, year 2020) at GBIF occurrence cells; proxy for forest-dependence.

Microhabitat use: Ordinal scale 1-5 (1 = ground/water; 2 = ground surface; 3 = scrub/grass; 4 = understorey; 5 = canopy); coded from trait databases and natural history reviews.

Breeding phenology: Day of year of median breeding season onset (from BirdLife for birds; published breeding phenology compilations for mammals and herptiles); standardised to Julian day.

Minimum species-order combination sample size for K and lambda estimation: 100 species with valid data for that niche dimension within the order. Species with < 30 GBIF occurrences excluded from climate-based dimensions. Final dataset: 4,847 species with complete data for >= 12 of 18 dimensions; 3,284 species with complete data for all 18.