Biological Journal of the Linnean Society, 2025, **146(2)**, blaf072
https://doi.org/10.1093/biolinnean/blaf072

Original Article

Phylogenetic and ecological drivers of dietary preferences in lizards: a comparative analysis

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ABSTRACT

Investigating how recent and historical factors can mould species traits is crucial for understanding the evolution of biodiversity. We explored lizard dietary preferences, hypothesizing that phylogenetic divergences are correlated with dietary niches, and we examined how they are correlated with ecological and morphological traits. Using data from 751 populations of 347 lizard species, we identified 59 prey categories. Our analyses revealed significant phylogenetic signals in 12 categories, indicating niche conservatism. Phylogenetic principal component analysis indicated that global structure explained 52.5% of the dietary variation, with key prey categories including plants, Formicidae, and Coleoptera. Furthermore, phylogenetic generalized least squares models indicated significant relationships between dietary preferences and climate, foraging mode, habitat type, and body size. Our findings highlight the significant role of niche conservatism, with specific clades exhibiting distinct dietary adaptations. Iguanians primarily consume plants and ants, whereas non-iguanians focus on diverse prey, such as Orthoptera, Araneae, and Blattodea. These patterns are also influenced by ecological factors, such as habitat and climate, underscoring the complexity of ecological interactions. Our study contributes to a deeper understanding of the interplay between evolutionary history, ecological traits, and environmental factors affecting the dietary niches of lizards, emphasizing the need for robust phylogenies in ecological and evolutionary research.

Keywords: feeding habits; Squamata; phylogenetic signal; phylogenetic principal component analysis; ecological traits

INTRODUCTION

Understanding factors that directly affect the ecological traits of species is crucial for revealing historical events that might have influenced species interactions and how these interactions occur today (Losos 1994, 1996a, Espinoza *et al.* 2004, Crisp and Cook 2012). Interspecific interactions, particularly predation and competition, have been hypothesized to be major determinants of the ecological traits of species (Losos 2008a, b, Wiens 2008, Wiens *et al.* 2010). Many ecological studies support this idea, leading to the development of significant ecological theories, such as the 'competitive exclusion principle', the 'ghost of competition past', and the 'habitat heterogeneity theory' (e.g. Morin 1986, Lenihan *et al.* 2011, Buchmann *et al.* 2013). This framework persisted throughout much of the 20th century and laid the foundation for many ecological studies across different taxa and communities (e.g. Zaret and Rand 1971, Pianka 1973, Cody 1974, Lynch 1979). The rapid development of comparative phylogenetic methods in the 1990s enabled more detailed analyses of similarities and divergences among clades and closely related species (Cadle and Greene 1993, Losos 1996b, Webb 2000). These studies revealed that many observed ecological traits reflect historical phylogenetic effects (Kelt *et al.* 1996, Vitt and Pianka 2005, Helmus *et al.* 2007, Colston *et al.* 2010). Building on this understanding, the concept of 'phylogenetic niche conservatism' emerged, in which closely

Received 13 May 2025; accepted 25 July 2025

related species are expected to have more similar ecological traits than evolutionarily distant ones (e.g. Wiens and Graham 2005, Pyron *et al.* 2015). This concept has significant implications for various evolutionary and ecological processes, further enriching our understanding of the ecological traits and interactions of species (Costa *et al.* 2007, Wiens *et al.* 2011, Brown 2014, Rolland *et al.* 2014).

More than 20 years ago, Vitt *et al.* (2003) found strong phylogenetic conservatism in the ecological traits of species using a multicontinental dataset of lizards. They suggested that significant ecological niche divergences took place during the divergence of the two major basal groups of Squamata (Scleroglossa and Iguania) and that, within Scleroglossa, most ecological divergence was concentrated in the basal split between Autarchoglossa and Gekkota (Vitt *et al.* 2003). These results were based on a traditional morphological phylogenetic hypothesis for squamates (see Estes *et al.* 1988). Dietary shifts in lizards have been linked to the development of an efficient chemosensory system (vomeronasal apparatus in autarchoglossans and olfactory systems in gekkotans) and the transition from lingual prey capture to jaw prehension (Cooper 1995). These adaptations presumably allowed scleroglossans to access cryptic and sedentary prey, enhancing selectivity through chemical discrimination (Cooper 1994, 1995, Vitt *et al.* 2003). The shift to an active foraging mode further increased prey accessibility in autarchoglossans, contrasting with the ancestral traits retained by iguanians, such as lingual prey prehension, sit-and-wait foraging, and visual prey discrimination (Cooper 1994, 1995, Vitt *et al.* 2003). As a result, iguanians typically consume more mobile prey with noxious chemicals, such as coleopterans and hymenopterans (primarily ants), generally avoided by active foragers (Huey and Pianka 1981, Vitt *et al.* 2003, Vitt and Pianka 2005, Cavalcanti *et al.* 2024). The synapomorphies of autarchoglossans are likely to have made them more competitive in terrestrial habitats, possibly driving iguanians to exploit vertical habitats, such as rocky outcrops and trees, to avoid competition (Vitt *et al.* 2003).

The above findings were corroborated by a study using dietary information on 184 lizard species from 12 families from four continents (Vitt and Pianka 2005). Six major divergences explained nearly 80% of the total dietary variation among clades. The divergence explaining the most variation (27%) was Scleroglossa vs. Iguania (based on the morphological phylogenetic hypothesis). Iguanians consumed more beetles, ants, and other hymenopterans compared with scleroglossans. However, recent squamate phylogenies based on molecular data refuted previous morphological reconstructions, in that Iguania is nested within Scleroglossa rather than being its sister clade, prompting a re-examination of the evolution of diets and associated traits in major squamate groups (Townsend *et al.* 2004, Losos *et al.* 2012, Pyron *et al.* 2013, Title *et al.* 2024). One such study, using molecular phylogenies, suggested that the shift to high ant ingestion in Iguania occurred when this clade diverged from other squamate clades (Sites *et al.* 2011).

Other biological traits are also linked to lizard dietary niches. For example, body size and habitat preferences are directly related to prey choice. Larger lizard species tend to ingest larger prey items, probably to acquire energy more efficiently from their food sources (Herrel *et al.* 2004, Herrel 2006, Costa 2008b). Moreover, herbivorous lizards are larger than omnivorous and carnivorous ones (Herrel 2007, Meiri 2008, Iverson 1985, Szarski 1962). Habitat preferences also influence lizard diets. In desert communities, fossorial lizard species often include termites and ant larvae in their diets, because these prey are commonly found in soil (Abensperg-Traun and Steven 1997). Likewise, some Neotropical termite-specialist geckos live inside termitaria, using them as shelter, foraging sites, and for thermoregulation (Colli *et al.* 2003a, Vitt *et al.* 2007b).

In addition to historical and inherent biological impacts, other factors, such as climatic variability, can influence different aspects of lizard ecology. Microscale structural habitat characteristics are good predictors of lizard species occurrence and abundance (Vitt *et al.* 2007a, Garda *et al.* 2013). Climate plays a crucial role in global patterns of lizard life-history traits, with seasonality being associated with reduced clutches per year and increased clutch size (Mesquita and Colli 2010, Mesquita *et al.* 2016). Climate characteristics can also affect lizard diets. For example, in Australia, termite consumption by lizards increases from mesic to xeric environments, where termites are abundant in dry, seasonal areas, such as deserts (Abensperg-Traun 1994). Herbivory is positively associated with arid, seasonal environments, because food scarcity and water requirements drive lizards to exploit new food sources, such as plant material (Cooper and Vitt 2002, Pietczak and Vieira 2017). Additionally, warmer areas might favour herbivory by facilitating plant digestion (Zimmerman and Tracy 1989), except for liolaemids, where herbivory evolved recurrently in small isolated cool-climate regions (Espinoza *et al.* 2004). Finally, islands are often considered drivers of herbivory in lizards (Van Damme 1999, Taverne *et al.* 2019).

In this study, we investigate several hypotheses regarding the dietary preferences of lizards. First, we hypothesize that major divergences among squamate clades are correlated with dietary differences among lizard species, suggesting a phylogenetically dependent dietary niche. Second, we explore the relationship between dietary preferences and various ecological and morphological factors, including foraging mode, habitat, distribution, and body size. We predict that sit-and-wait ambushers will consume more highly mobile prey, fossorial lizards will have higher rates of termite consumption, herbivory is positively associated with arid, seasonal environments, and larger lizard species will ingest larger prey and more plant matter. Finally, we investigate the influence of climatic variables on dietary preferences. We predict that ingestion of termites and plant matter will be greater in seasonal, dry, and warm environments. By testing these hypotheses using a large diet dataset and incorporating newer phylogenies, we aim to deepen our understanding of the complex interactions between evolutionary history, ecological traits, and environmental factors in shaping the dietary niches of lizards.

MATERIALS AND METHODS

Dietary database and data collection

We compiled data from 751 populations of 347 lizard species, sampling 29 families from all continents except Antarctica (Fig. 1). Dietary data were obtained from the authors' long-term collections across these continents over more than five decades (~70% of the dataset). All specimens are housed in scientific collections,

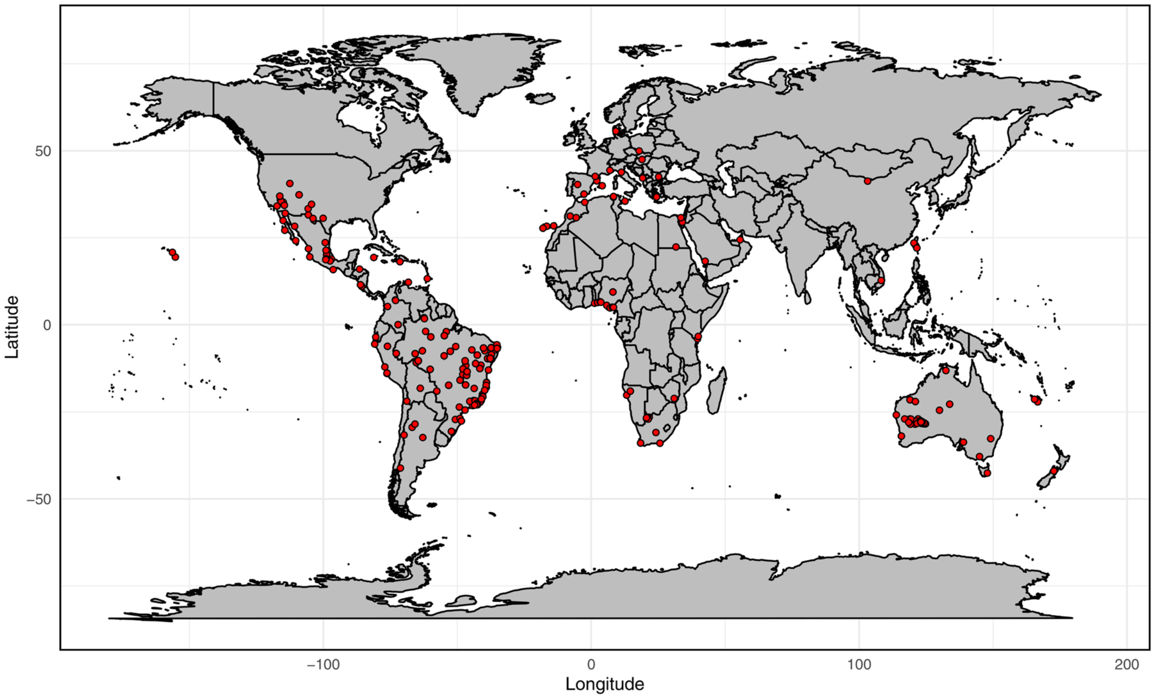

Figure 1. Sampling locations of all 347 lizard species from 721 populations, pooled for dietary database.

including the Herpetological Collection of the University of Brasília (CHUNB), the Federal University of Paraíba (CHUFPB), the Museum of Zoology of the University of São Paulo (MZUSP), the Museu Paraense Emílio Goeldi (MPEG), the University of Texas at Austin (UT), and the Sam Noble Oklahoma Museum of Natural History (SNOMNH). We also complemented the data collection with a bibliographical search of online scientific databases from Google Scholar™ and Zoological Record™. We used the keywords 'lizard', 'diet', 'feeding habits', 'feeding ecology', and 'dietary aspects'. All data collected are available as Supporting Information (Tables S1 and S2). We used data from direct observation of stomach contents (~96% of the data), faecal analysis, and direct observations (~4% of the data for both). We calculated four variables for each population and prey category: occurrence (number of individuals ingesting a given prey category), number, volume, and mass of prey. Whenever data were separated into ontogenetic and sexual categories (e.g. juvenile/adults, males/females), we calculated averages for each prey category weighted by sample sizes. We also recalculated percentages of all categories to remove unidentified prey or to combine prey categories, to standardize our dataset. For data we collected, dietary data came from direct observation of prey items in lizard stomachs. We dissected all specimens and removed stomachs for analysis under a stereomicroscope. We identified and categorized each prey item, calculating their absolute and relative occurrence, number, and volume (in millimetres cubed). To calculate volume (V), we measured the width and length of each intact prey item using electronic callipers (precision of 0.01 mm), then applied the following ellipsoid formula:

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right)\times\left(\frac{w}{2}\right)^2,$$

where l is the prey length, and w is the prey width. After collecting data, we calculated weighted averages for each prey category to combine populations from a given species using sample sizes of each population as weights. In species where we had no data on volumetric percentages but had data on prey frequency, numerical or mass proportions, we used multiple imputation methods implemented in the MISSFOREST R package (Stekhoven and Buehlmann 2012, Stekhoven 2013) to obtain estimated volumetric proportions. Multiple imputation is a robust method for imputing values for missing observations (Rubin 1996, Van Buuren *et al.* 2006), which often results in less bias than completely removing cases with missing values (Penone *et al.* 2014). We found 59 prey categories, mostly arthropods (Fig. 2).

Ecological and climatic variables

We assembled a dataset for the following variables for each sampled population: latitude and longitude (in decimal degrees), foraging mode (active or sit-and-wait), maximum snout–vent length (in millimetres), and habitat (arboreal, semi-arboreal, bromelicolous, terrestrial, fossorial, semi-aquatic, and saxicolous). We extracted data to summarize variables from bibliographical sources that included dietary data or supplemented by databases or species description papers. We obtained 19 climatic variables from WorldClim (Hijmans *et al.* 2005), scaled them, then used the first principal component (PC1) scores to account for highly correlated variables and summarize climatic variables. We extracted the first two canonical axes from temperature and precipitation variables. Together, temperature principal components explained 88% of the total variation in the data. Temperature PC1 was positively correlated with temperature seasonality (BIO4) and negatively correlated with minimum temperatures in the coldest month (BIO6). Temperature PC2 was positively correlated with

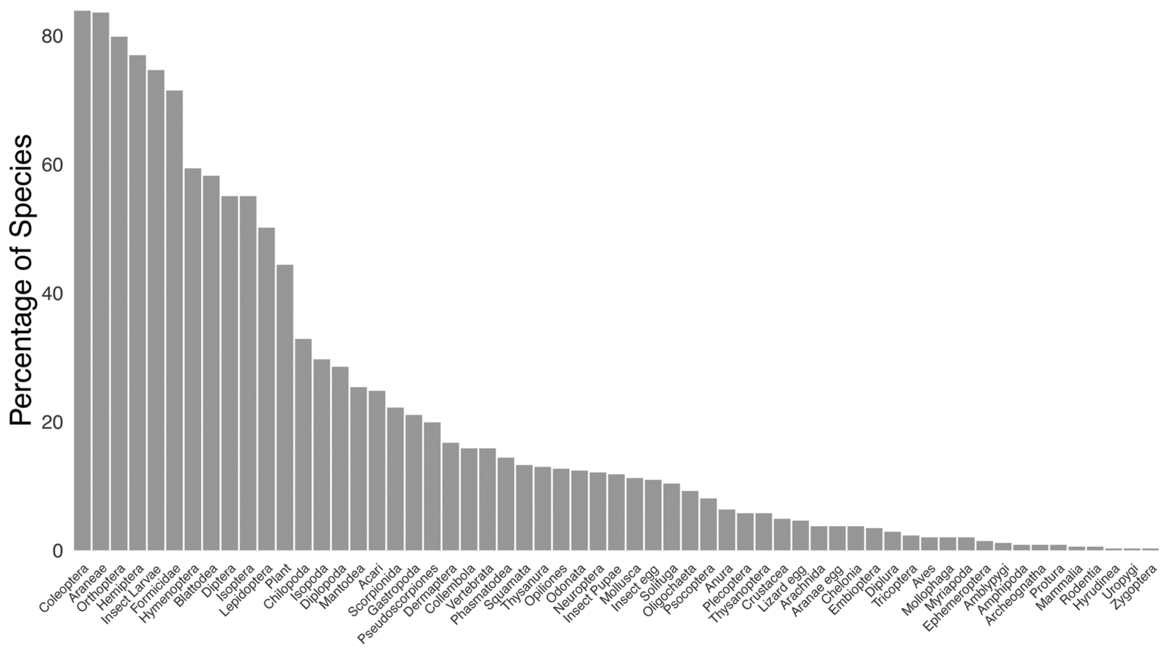

Figure 2. Percentage of all 347 lizard species ingesting each prey category, pooled for dietary database.

isothermality (BIO3) and negatively correlated with maximum temperature of warmest month (BIO5). Precipitation principal components explained 86% of all variation together. Precipitation PC1 was positively correlated with precipitation seasonality (BIO15) and negatively correlated with total precipitation (BIO12). Precipitation second principal component (PC2) was positively correlated with precipitation seasonality (BIO15) and negatively correlated with precipitation of the driest month (BIO14). We then used these four climatic variables to conduct the analysis described below.

Statistical analyses

To test for phylogenetic signal in each prey category, we calculated the Blomberg *K* statistics using the *phytools* package in R (Revell 2012). Values of *K* near zero indicate phylogenetic independence of data, whereas values near 1 indicate that a given character follows a Brownian motion (BM) evolutionary model (Freckleton *et al.* 2002, Blomberg *et al.* 2003, Losos 2008a). A value of $K > 1$ indicates that closely related taxa are more similar than expected in a BM model. Posteriorly, we tested for the significance of phylogenetic signal (null hypothesis $K = 0$) by randomizing species names in the phylogeny and comparing the randomized and the real phylogeny using likelihood ratio tests (Blomberg *et al.* 2003). We used 100 pseudo-posterior sets of molecular phylogenetic trees (Title *et al.* 2024), pruned to our sampled species containing branch lengths and a matrix containing prey type percentages for each species and prey category. Values of *K* and *P* were averaged across the set of trees.

To account for global (phylogenetic) and local (ecological) effects on dietary preferences, we performed a phylogenetic principal component analysis (pPCA) (Jombart *et al.* 2010). The pPCA (Jombart *et al.* 2010) is a multivariate method that correlates a phylogenetic tree containing branch lengths with a set of ecological traits (e.g. dietary) for each species found in a given pool, then tests for phylogenetic autocorrelation (Gittleman and Kot 1990). A positive phylogenetic autocorrelation indicates similarities among closely related taxa for a given trait (global structure), whereas negative phylogenetic autocorrelation indicates divergences among close taxa (local structure). The pPCA summarizes the patterns of phylogenetic autocorrelation, identifying principal components representing the highest phylogenetic correlation (phylogenetic influence, i.e. global structure) and the lowest phylogenetic autocorrelation (ecological influence, local structure). Then, we can access the global and local structure scores to identify which dietary traits and clades are involved. For phylogenetic relationships, we used the consensus phylogenetic tree based on a recently published phylogenetic hypothesis for Squamata (Title *et al.* 2024).

To examine the impact of climatic variables and lizard ecological traits on the type of prey ingested, we built generalized linear models with binomial error structure (GLM). Additionally, we made phylogenetic regression models using phylogenetic generalized least squares (PGLS, Grafen 1989). To build these models, we used covariance matrices based on BM and Ornstein–Uhlenbeck (OU) expectations derived from phylogenetic trees of sampled species obtained from Title *et al.* (2024). In the BM model, trait variance accumulates linearly over time (Cavalli-Sforza and Edwards 1967); in the OU model, trait variance remains relatively constant over time, with extreme trait values tending to fluctuate around a long-term mean (Lande 1976). Consequently, the BM model describes the evolution of continuous traits under random drift or adaptive evolution, with adaptations randomly following shifts in adaptive optima for each lineage. Conversely, the OU model describes trait evolution around an adaptive optimum to which traits are drawn or the evolution of the adaptive optimum itself (O'Meara and Beaulieu 2014). By using these distinct models, we attempted to account for variation in modes of trait evolution, thereby ensuring robustness in our analyses. These models effectively control for the influence of evolutionary history, thereby ensuring data independence. We implemented phylogenetic regressions using the package *caper* (Orme *et al.* 2013) and performed all statistical analyses in R v.4.3.2 (R Development Core Team 2021), with a significance level set at 5% to reject null hypotheses. Throughout the text, we present means ± 1 SD for clarity.

RESULTS

We found 59 prey categories (Fig. 2) in 347 lizard species. The most frequent prey were Coleoptera, Araneae, Orthoptera, Hemiptera, and insect larvae, all being ingested in any amount by ≥75% of all species (Fig. 2).

Phylogenetic signal and historical effects on diet

We found *K* values significantly different from zero in 12 prey categories, demonstrating that the consumption of Acari, Blattodea, Coleoptera, Collembola, Diptera, Formicidae, Hemiptera, insect eggs, Isopoda, Isoptera, plants, and Vertebrata did not evolve randomly in lizard evolutionary history (Table 1). For all other prey categories, *K* values were not significantly different from zero, indicating that the consumption of these categories was independent of the phylogeny (Table 1).

The phylogenetic pPCA indicated that the two highest eigenvalues related to global structure (positive phylogenetic autocorrelation). The eigenvalues for local structure (ecological influence) were very small, with the highest explaining only 1.75% of the variation (Fig. 3B). Conversely, the two global axes explained 52.5% of total variation: the first explained 30%, and the second explained 22.5%. Prey categories determining the first global axis were plants, Formicidae, and Coleoptera with positive scores (Fig. 3; black circles in Fig. 4), and Araneae, Blattodea, Orthoptera, insect larvae, and Squamata with negative scores (Fig. 3; white circles in Fig. 4). Prey categories determining the second global axis were a contrast between Isoptera (major), insect larvae, Coleoptera (lesser) (positive scores in Fig. 3; black circles in Fig. 4); and plant material, Araneae, Orthoptera, Blattodea, Squamata (major), Hymenoptera, and Formicidae (lesser) (negative scores in Fig. 3; white circles in Fig. 4).

The most important relationships contributing to the patterns described above were high plant consumption in Iguanidae, Liolaemidae, Crotaphytidae, Agamidae (*Uromastyx aegyptia* and *Acanthocercus yemensis*), Teiidae (*Dicrodon guttulatum* and *Cnemidophorus murinus*), Scincidae (*Tiliqua multifasciata*), and Gerrhosauridae; and high termite consumption in Diplodactylidae, Scincidae, Teiidae, Gymnophthalmidae, Phrynosomatidae (*Sceloporus jalapae*), Tropiduridae (*Tropidurus jaguaribanus*, *Tropidurus helenae*), and Leiosauridae (*Enyalius leechii*). For details, see Figure 4.

Relationships between diet and climatic variables, foraging mode, habitat, and body size

Results from GLMs showed no significant relationships between lizard diet and climatic variables, foraging mode, habitat, and body size (Supporting Information, Table S3). Results from PGLS showed that some prey categories were significantly related to some of the variables we investigated (Table 2). Insect larvae, plants, Blattodea, Plecoptera, insect pupae, Chelonia, Mallophaga, Pseudoscorpiones, and Amphipoda were negatively related to

Table 1. Phylogenetic signal estimates for each prey category found on sampled lizard species around the globe ($N = 347$).

Prey category	Average *K*	SD *K*	Average *P*-value
Acari	0.253	0.015	**.034**
Amblypygi	0.144	0.008	.281
Amphipoda	0.091	0.010	.678
Anura	0.005	0.000	.969
Arachnida	0.170	0.012	.085
Araneae egg	0.110	0.005	.459
Araneae	0.070	0.002	.313
Archaeognatha	0.228	0.011	.081
Aves	0.105	0.012	.567
Blattodea	0.122	0.004	.043
Chelonia	0.100	0.012	.587
Chilopoda	0.090	0.004	.502
Coleoptera	0.184	0.007	**.001**
Collembola	0.347	0.044	**.011**
Crustacea	0.106	0.005	.501
Dermaptera	0.027	0.001	.857
Diplopoda	0.094	0.005	.515
Diplura	0.060	0.003	.901
Diptera	0.164	0.007	**.009**
Embioptera	0.139	0.006	.396
Ephemeroptera	0.328	0.015	.093
Formicidae	0.136	0.005	**.016**
Gastropoda	0.089	0.003	.607
Hemiptera	0.129	0.004	**.013**
Hymenoptera	0.114	0.005	.128
Hirudinea	0.192	0.013	.276
Insect egg	0.373	0.014	**.010**
Insect larvae	0.027	0.001	.642
Insect pupae	0.101	0.004	.502
Isopoda	0.272	0.013	**.008**
Isoptera	0.155	0.006	**.002**
Lepidoptera	0.045	0.002	.692
Lizard egg	0.121	0.011	.400
Mammalia	0.076	0.004	.775
Mantodea	0.101	0.003	.405
Mallophaga	0.151	0.007	.293
Mollusca	0.016	0.001	.914
Myriapoda	0.091	0.004	.674
Neuroptera	0.113	0.008	.438
Odonata	0.064	0.003	.768
Oligochaeta	0.027	0.001	.928
Opiliones	0.181	0.007	.060
Orthoptera	0.004	0.000	.891
Phasmatodea	0.158	0.008	.152
Plants	0.321	0.011	**.001**
Plecoptera	0.104	0.005	.556
Protura	0.215	0.009	.152
Pseudoscorpiones	0.147	0.006	.082
Psocoptera	0.109	0.004	.466
Rodentia	0.116	0.008	.524
Scorpiones	0.160	0.006	.106
Solifugae	0.108	0.005	.413
Squamata	0.109	0.011	.424
Thysanoptera	0.095	0.004	.622
Thysanura	0.124	0.006	.325
Trichoptera	0.102	0.004	.582
Uropygi	0.106	0.005	.582
Vertebrata	0.274	0.008	**.015**
Zygoptera	0.164	0.008	.372

Bold values represent statistical significance.

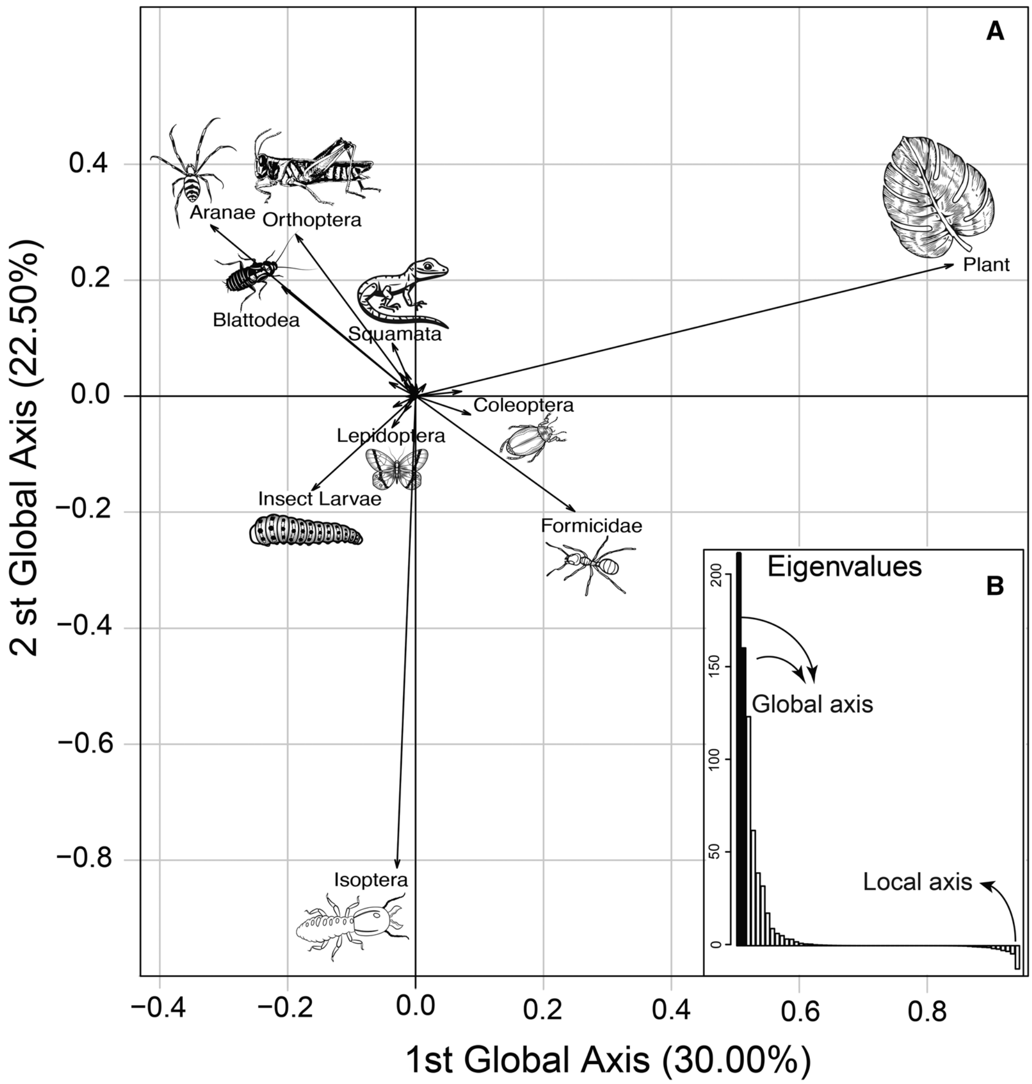

Figure 3. A, canonical axis based on the two global principal components from phylogenetic principal component analysis from dietary aspects of sampled lizard species ($N = 347$). The horizontal axis represents the first global component, and the vertical axis represents the second global component. Prey categories close to zero on both axes were omitted. B, eigenvalue bar plots correspond to global (left) and local (right) principal components.

Temperature PC1 (hot and more seasonal). Diplura, Solifugae, Coleoptera, Hemiptera, Formicidae, and Orthoptera were positively related to Temperature PC1. Formicidae and Isoptera were negatively related to Temperature PC2 (variable and colder temperatures). Amphipoda, Protura, Odonata, Chelonia, Arachnida, Isopoda, Gastropoda, Diplopoda, Diptera, plants, Coleoptera, and insect larvae were positively related to Temperature PC2 (Table 2).

Anura, Blattodea, Hemiptera, Lepidoptera, Oligochaeta, Dermaptera, and Mollusca were negatively related to Precipitation PC1 (drier and more seasonal). Pseudoscorpiones, Mallophaga, Myriapoda, Chelonia, Thysanoptera, Plecoptera, Thysanura, Vertebrata, and plants were positively related to Precipitation PC1. Anura, Thysanura, Plecoptera, Thysanoptera, Mollusca, Aves, Myriapoda, Embioptera, Chelonia, Hemiptera, and Pseudoscorpiones were negatively related to Precipitation PC2 (drier and more seasonal). Crustacea, lizard eggs, Araneae, and Orthoptera were positively related to Precipitation PC2 (Table 2).

In the foraging mode analysis, only three prey items presented significant differences in ingestion: Araneae and Blattodea, both of which were ingested more by actively foraging lizards, and Formicidae, which were ingested more by sit-and-wait foragers (Table 2). The PGLS results revealed diverse habitat-type effects on prey categories, demonstrating positive and negative associations. For instance, the bromelicolous habitat exhibited positive and negative coefficients, indicating its varying impact depending on the prey category. Specifically, using bromeliads positively affected the coefficient for Anura, suggesting an increased likelihood of occurrence in comparison to the reference habitat type (arboreal). In contrast, it negatively affected Neuroptera and Amblypygi, indicating that lizards living in these habitats are less likely to consume these items. Likewise, the fossorial habitat had mixed effects, having positive coefficients for Isoptera and insect larvae and negative coefficients for Orthoptera and Diptera. Saxicolous habitats also showed varied impacts, with positive coefficients for Diptera and

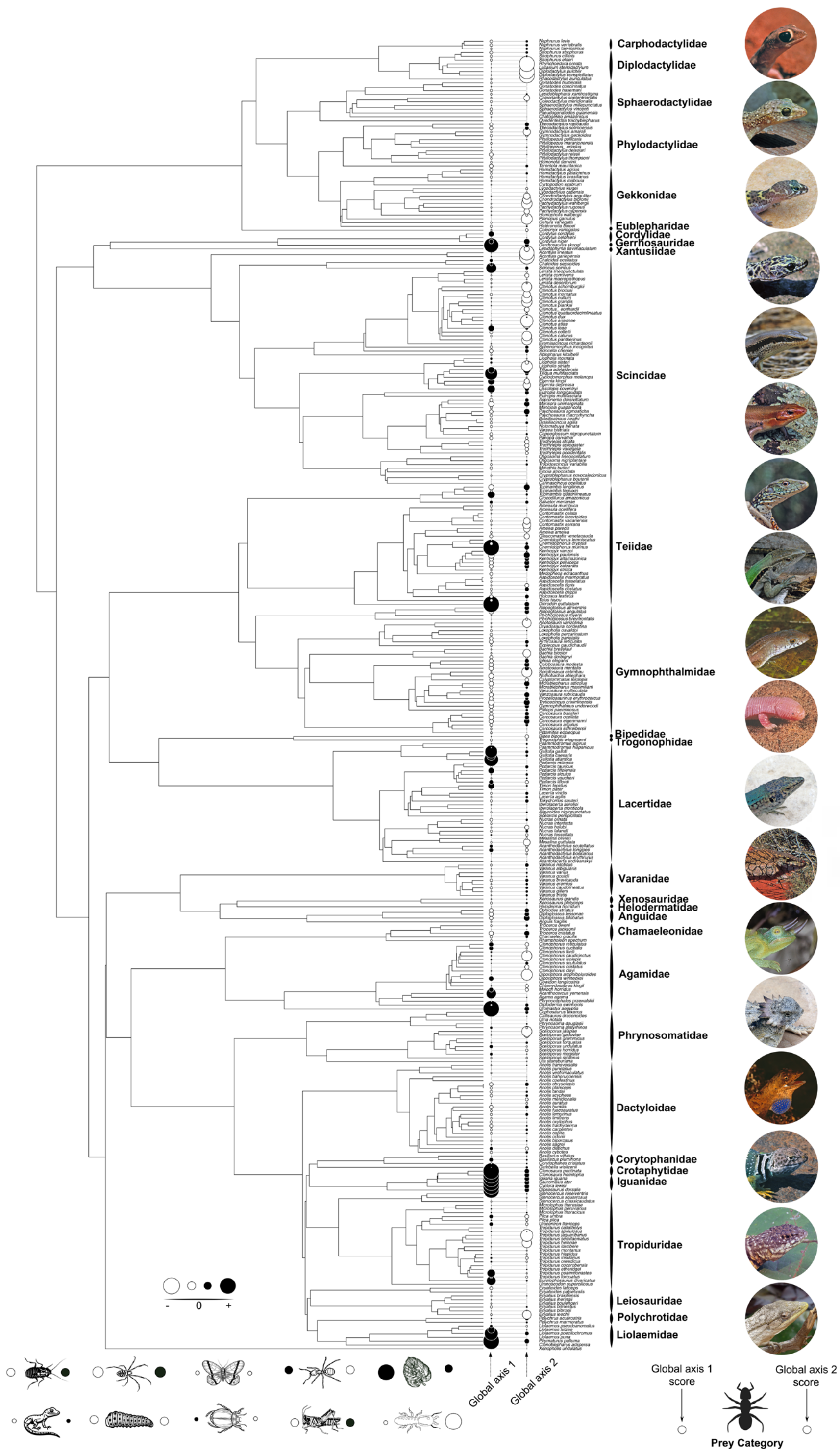

Figure 4. Phylogenetic tree of all sampled lizard species of our data ($N = 347$), containing canonical eigenvalues for global principal components from phylogenetic principal component analysis. White circles represent negative values on the canonical axis, whereas black circles represent positive values. Larger circle sizes indicate a higher association with a given axis from Figure 4. Circle size is proportional to score value. All images by Laurie J. Vitt.

Lepidoptera and negative coefficients for Orthoptera, Blattodea, and Phasmatodea. The semi-aquatic habitat type was predominantly negative for specific prey categories, such as Diplopoda and Phasmatodea, but had positive coefficients for others, such as Anura and Hymenoptera. Semi-arboreal habitats had positive coefficients for Isoptera. Lastly, the terrestrial habitat type also had mixed effects, with positive coefficients for prey categories such as Anura and plants and negative coefficients for Orthoptera and Coleoptera (Table 2). Overall, results indicated that habitat types have varied effects on the presence of different prey categories in

Table 2. Significant results from phylogenetic regressions (phylogenetic generalized least squares) from the relationship between dietary preferences and climatic variables, foraging mode, habitat, and body size for sampled lizard species around the globe ($N = 347$), based on Brownian motion (BM) and Ornstein–Uhlenbeck (OU) evolution models.

Dependent variable	Parameter	BM estimate	BM SE	BM *P*-value	OU value	OU SE	OU *t*-value	*P*-value OU
Acari	Habitat × Terrestrial	4.80×10^{-6}	2.43×10^{-6}	.050	9.46×10^{-6}	4.59×10^{-6}	2.059	**.040**
Amblypygi	Habitat × Bromelicolous	-1.11×10^{-5}	5.57×10^{-6}	**.047**				
Amphipoda	PC1 Temperature	-5.77×10^{-7}	1.62×10^{-7}	**.001**				
	PC2 Temperature	7.19×10^{-7}	2.03×10^{-7}	**.001**				
Anura	Habitat × Bromelicolous	8.27×10^{-4}	3.97×10^{-4}	**.038**				
	Habitat × Semi-aquatic	1.22×10^{-3}	1.94×10^{-4}	**.000**				
	Habitat × Terrestrial	4.04×10^{-4}	5.82×10^{-5}	**.000**				
	PC1 Precipitation	-9.08×10^{-5}	1.70×10^{-5}	**.000**				
	PC2 Precipitation	-5.18×10^{-5}	2.24×10^{-5}	**.022**				
Arachnida	Habitat × Fossorial	7.83×10^{-5}	3.94×10^{-5}	**.049**				
	PC2 Temperature	8.98×10^{-6}	2.96×10^{-6}	**.003**				
Araneae	Foraging mode × Sit and wait	-1.14×10^{-3}	1.68×10^{-3}	.498	-6.95×10^{-4}	1.73×10^{-4}	−4.010	**.000**
	Maximum SVL	-4.71×10^{-6}	1.38×10^{-6}	**.001**	-2.63×10^{-6}	9.22×10^{-7}	−2.848	**.005**
	PC2 Precipitation	1.38×10^{-4}	6.90×10^{-5}	**.047**	4.97×10^{-5}	6.06×10^{-5}	0.820	.413
Aves	Habitat × Saxicolous	-2.94×10^{-5}	1.38×10^{-5}	**.035**				
	Habitat × Semi-aquatic	-6.76×10^{-5}	2.63×10^{-5}	**.012**				
	Habitat × Terrestrial	-2.50×10^{-5}	7.90×10^{-6}	**.002**				
	PC2 Precipitation	-7.39×10^{-6}	3.04×10^{-6}	**.016**				
Blattodea	Foraging mode × Sit and wait	-3.76×10^{-4}	1.05×10^{-3}	.720	-3.31×10^{-4}	1.28×10^{-4}	−2.589	**.010**
	Habitat × Saxicolous	-1.73×10^{-4}	1.95×10^{-4}	.377	-4.16×10^{-4}	1.84×10^{-4}	−2.252	**.025**
	PC1 Precipitation	-8.22×10^{-5}	3.26×10^{-5}	**.012**	-5.48×10^{-5}	3.35×10^{-5}	−1.636	.103
	PC1 Temperature	-5.12×10^{-5}	3.18×10^{-5}	.109	-7.42×10^{-5}	2.70×10^{-5}	−2.743	**.006**
Chelonia	Habitat × Semi-aquatic	-1.18×10^{-4}	1.83×10^{-5}	**.000**	-4.90×10^{-5}	2.00×10^{-5}	−2.451	**.015**
	Maximum SVL	5.28×10^{-7}	4.24×10^{-8}	**.000**	3.20×10^{-7}	2.97×10^{-8}	10.791	**.000**
	PC1 Precipitation	6.42×10^{-6}	1.61×10^{-6}	**.000**	2.65×10^{-6}	1.46×10^{-6}	1.816	.070
	PC1 Temperature	-4.53×10^{-6}	1.57×10^{-6}	**.005**	-3.00×10^{-6}	1.16×10^{-6}	−2.577	**.010**
	PC2 Precipitation	-4.25×10^{-6}	2.12×10^{-6}	**.046**	-5.41×10^{-6}	1.91×10^{-6}	−2.839	**.005**
	PC2 Temperature	7.19×10^{-6}	1.97×10^{-6}	**.000**	3.03×10^{-6}	1.30×10^{-6}	2.328	**.020**
Coleoptera	Habitat × Terrestrial	-2.85×10^{-4}	1.53×10^{-4}	.065	-6.31×10^{-4}	2.29×10^{-4}	−2.757	**.006**
	PC1 Temperature	2.25×10^{-5}	4.36×10^{-5}	.607	1.40×10^{-4}	3.62×10^{-5}	3.877	**.000**
	PC2 Temperature	7.77×10^{-5}	5.46×10^{-5}	.158	9.42×10^{-5}	4.14×10^{-5}	2.273	**.024**
Crustacea	Habitat × Semi-aquatic	3.18×10^{-4}	2.16×10^{-5}	**.000**	2.54×10^{-4}	2.47×10^{-5}	10.285	**.000**
	Habitat × Terrestrial	1.47×10^{-5}	6.48×10^{-6}	**.024**	2.03×10^{-6}	8.86×10^{-6}	0.230	.818
	PC2 Precipitation	8.38×10^{-6}	2.49×10^{-6}	**.001**	3.77×10^{-6}	2.32×10^{-6}	1.622	.106
Dermaptera	Habitat × Semi-aquatic	2.90×10^{-4}	7.44×10^{-5}	**.000**				
	Habitat × Terrestrial	8.66×10^{-5}	2.23×10^{-5}	**.000**				
	PC1 Precipitation	-1.98×10^{-5}	6.54×10^{-6}	**.003**				
Diplopoda	Habitat × Semi-aquatic	-6.76×10^{-4}	1.61×10^{-4}	**.000**				
	Maximum SVL	1.47×10^{-6}	3.72×10^{-7}	**.000**				
	PC2 Temperature	4.09×10^{-5}	1.72×10^{-5}	**.022**				
Diplura	PC1 Temperature	1.18×10^{-6}	4.67×10^{-7}	**.013**				
	Habitat × Fossorial	-6.54×10^{-5}	2.26×10^{-4}	.772	-2.77×10^{-4}	1.38×10^{-4}	−2.004	**.046**
	Habitat × Saxicolous	1.92×10^{-4}	8.28×10^{-5}	**.021**	5.00×10^{-5}	9.06×10^{-5}	0.552	.582
	PC2 Temperature	5.14×10^{-5}	1.69×10^{-5}	**.003**	5.77×10^{-5}	1.46×10^{-5}	3.939	**.000**
Embioptera	Habitat × Saxicolous	-3.01×10^{-5}	1.36×10^{-5}	**.028**				
	Habitat × Semi-aquatic	1.64×10^{-4}	2.59×10^{-5}	**.000**				
	Habitat × Terrestrial	-2.06×10^{-5}	7.79×10^{-6}	**.008**				
	PC2 Precipitation	-6.25×10^{-6}	3.00×10^{-6}	**.038**				
Formicidae	Foraging mode × Sit and wait	2.00×10^{-4}	2.04×10^{-3}	.922	5.79×10^{-4}	2.29×10^{-4}	2.528	**.012**
	PC1 Temperature	1.30×10^{-4}	6.17×10^{-5}	**.037**	3.90×10^{-5}	4.35×10^{-5}	0.895	.371
	PC2 Temperature	-1.93×10^{-4}	7.74×10^{-5}	**.013**	-5.83×10^{-5}	5.32×10^{-5}	−1.097	.274

(Continued)

Table 2. (Continued)

Dependent variable	Parameter	BM estimate	BM SE	BM *P*-value	OU value	OU SE	OU *t*-value	*P*-value OU
Gastropoda	Habitat × Terrestrial	-8.02×10^{-5}	2.79×10^{-5}	**.004**	-4.31×10^{-5}	3.88×10^{-5}	−1.112	.267
	Maximum SVL	2.43×10^{-7}	2.15×10^{-7}	.263	4.65×10^{-7}	1.61×10^{-7}	2.893	**.004**
	PC2 Temperature	2.83×10^{-5}	9.98×10^{-6}	**.005**	1.98×10^{-5}	7.04×10^{-6}	2.817	**.005**
Hemiptera	Maximum SVL	-5.35×10^{-7}	8.44×10^{-7}	.528	-1.97×10^{-6}	6.47×10^{-7}	−3.048	**.002**
	PC1 Precipitation	-7.51×10^{-5}	3.20×10^{-5}	**.020**	-6.01×10^{-5}	3.17×10^{-5}	−1.893	.059
	PC1 Temperature	7.00×10^{-5}	3.12×10^{-5}	**.026**	8.18×10^{-5}	2.52×10^{-5}	3.252	**.001**
	PC2 Precipitation	-4.17×10^{-6}	4.21×10^{-5}	.919	8.09×10^{-5}	4.07×10^{-5}	1.989	**.047**
Hymenoptera	Habitat × Semi-aquatic	6.60×10^{-4}	2.47×10^{-4}	**.008**				
Insect Larvae	Habitat × Fossorial	4.34×10^{-3}	7.98×10^{-4}	**.000**				
	Habitat × Terrestrial	6.42×10^{-4}	1.67×10^{-4}	**.000**				
	PC1 Temperature	-2.96×10^{-4}	4.77×10^{-5}	**.000**				
	PC2 Temperature	2.07×10^{-4}	5.99×10^{-5}	**.001**				
Insect Pupae	Habitat × Semi-aquatic	1.59×10^{-4}	4.31×10^{-5}	**.000**	9.98×10^{-5}	3.21×10^{-5}	3.105	**.002**
	PC1 Temperature	-8.65×10^{-6}	3.69×10^{-6}	**.021**	1.17×10^{-6}	1.74×10^{-6}	0.672	.502
Isopoda	PC2 Temperature	2.51×10^{-5}	1.89×10^{-5}	.185	3.78×10^{-5}	1.88×10^{-5}	2.008	**.045**
Isoptera	Habitat × Fossorial	1.05×10^{-3}	1.14×10^{-3}	.356	1.46×10^{-3}	5.66×10^{-4}	2.579	**.010**
	Habitat × Semi-arboreal	2.27×10^{-3}	9.61×10^{-4}	**.019**	1.82×10^{-3}	1.01×10^{-3}	1.810	.071
	Maximum SVL	-6.75×10^{-7}	1.84×10^{-6}	.714	-4.21×10^{-6}	1.37×10^{-6}	−3.064	**.002**
	PC2 Temperature	-1.71×10^{-4}	8.53×10^{-5}	**.047**	-3.04×10^{-4}	6.01×10^{-5}	−5.053	**.000**
Lepidoptera	Habitat × Saxicolous	2.69×10^{-4}	1.17×10^{-4}	**.022**	9.65×10^{-5}	1.21×10^{-4}	0.799	.425
	Habitat × Terrestrial	1.64×10^{-4}	6.66×10^{-5}	**.015**	5.27×10^{-6}	1.08×10^{-4}	0.049	.961
	PC1 Precipitation	-3.94×10^{-5}	1.95×10^{-5}	**.046**	-3.64×10^{-5}	2.19×10^{-5}	−1.664	.097
Lizard egg	Maximum SVL	1.22×10^{-6}	2.25×10^{-7}	**.000**				
	PC2 Precipitation	2.48×10^{-5}	1.13×10^{-5}	**.030**				
Mammalia	Maximum SVL	1.17×10^{-7}	3.68×10^{-8}	**.002**				
Mallophaga	PC1 Precipitation	2.30×10^{-6}	1.03×10^{-6}	**.027**	1.05×10^{-6}	1.06×10^{-6}	0.998	.319
	PC1 Temperature	-3.08×10^{-6}	1.01×10^{-6}	**.002**	-7.57×10^{-7}	8.04×10^{-7}	−0.942	.347
Mollusca	PC1 Precipitation	-5.60×10^{-6}	1.84×10^{-6}	**.003**	-4.28×10^{-6}	1.68×10^{-6}	−2.552	**.011**
	PC2 Precipitation	-8.29×10^{-6}	2.43×10^{-6}	**.001**	-1.20×10^{-6}	1.91×10^{-6}	−0.631	.528
Myriapoda	Maximum SVL	1.14×10^{-7}	4.17×10^{-8}	**.007**				
	PC1 Precipitation	5.85×10^{-6}	1.58×10^{-6}	**.000**				
	PC2 Precipitation	-6.27×10^{-6}	2.08×10^{-6}	**.003**				
Neuroptera	Habitat × Bromelicolous	-2.21×10^{-4}	1.09×10^{-4}	**.044**				
Odonata	Habitat × Semi-aquatic	9.54×10^{-5}	2.41×10^{-5}	**.000**				
	PC2 Temperature	5.99×10^{-6}	2.58×10^{-6}	**.022**				
Oligochaeta	Habitat × Terrestrial	2.01×10^{-4}	4.09×10^{-5}	**.000**				
	PC1 Precipitation	-3.91×10^{-5}	1.20×10^{-5}	**.001**				
Orthoptera	Habitat × Fossorial	-3.29×10^{-3}	1.13×10^{-3}	**.004**				
	Habitat × Saxicolous	-1.11×10^{-3}	4.15×10^{-4}	**.008**				
	Habitat × Terrestrial	-1.89×10^{-3}	2.37×10^{-4}	**.000**				
	PC1 Temperature	2.33×10^{-4}	6.77×10^{-5}	**.001**				
	PC2 Precipitation	4.44×10^{-4}	9.13×10^{-5}	**.000**				
Phasmatodea	Habitat × Saxicolous	-1.45×10^{-4}	6.19×10^{-5}	**.020**				
	Habitat × Semi-aquatic	-4.35×10^{-4}	1.18×10^{-4}	**.000**				
Plant material	Habitat × Terrestrial	3.23×10^{-4}	1.64×10^{-4}	.051	6.41×10^{-4}	3.23×10^{-4}	1.986	**.048**
	Maximum SVL	3.90×10^{-6}	1.27×10^{-6}	**.003**	9.13×10^{-6}	1.34×10^{-6}	6.829	**.000**
	PC1 Precipitation	2.10×10^{-4}	4.81×10^{-5}	**.000**	3.34×10^{-4}	6.56×10^{-5}	5.089	**.000**
	PC1 Temperature	-1.24×10^{-4}	4.69×10^{-5}	**.009**	-1.42×10^{-4}	5.26×10^{-5}	−2.697	**.007**
	PC2 Temperature	7.73×10^{-5}	5.88×10^{-5}	.192	2.12×10^{-4}	5.85×10^{-5}	3.629	**.000**
Plecoptera	Habitat × Semi-aquatic	3.02×10^{-4}	9.73×10^{-5}	**.002**	1.95×10^{-4}	7.29×10^{-5}	2.671	**.008**
	PC1 Precipitation	2.02×10^{-5}	8.54×10^{-6}	**.019**	2.93×10^{-6}	5.73×10^{-6}	0.506	.615
	PC1 Temperature	-1.75×10^{-5}	8.33×10^{-6}	**.036**	-4.66×10^{-6}	3.96×10^{-6}	−1.172	.245
	PC2 Precipitation	-3.50×10^{-5}	1.12×10^{-5}	**.002**	-3.65×10^{-7}	3.41×10^{-6}	−0.104	.918
Protura	PC2 Temperature	3.10×10^{-6}	1.54×10^{-6}	**.045**				
Pseudoscorpiones	Maximum SVL	-1.17×10^{-8}	2.43×10^{-8}	.633	-3.83×10^{-8}	1.87×10^{-8}	−2.048	**.041**
	PC1 Precipitation	2.11×10^{-6}	9.21×10^{-7}	**.023**	2.39×10^{-6}	9.15×10^{-7}	2.615	**.009**
	PC1 Temperature	-1.25×10^{-6}	8.99×10^{-7}	.167	-2.23×10^{-6}	7.20×10^{-7}	−3.092	**.002**
	PC2 Precipitation	-2.38×10^{-6}	1.21×10^{-6}	.050	-3.01×10^{-6}	1.15×10^{-6}	−2.630	**.009**

(Continued)

Table 2. (Continued)

Dependent variable	Parameter	BM estimate	BM SE	BM *P*-value	OU value	OU SE	OU *t*-value	*P*-value OU
Solifugae	PC1 Temperature	6.83×10^{-6}	3.44×10^{-6}	**.048**				
Squamata	Maximum SVL	2.31×10^{-6}	9.41×10^{-7}	**.015**				
Thysanoptera	PC1 Precipitation	6.46×10^{-6}	2.94×10^{-6}	**.029**				
	PC2 Precipitation	-9.15×10^{-6}	3.87×10^{-6}	**.019**				
Thysanura	Maximum SVL	-1.83×10^{-7}	2.28×10^{-7}	.424	-3.28×10^{-7}	1.62×10^{-7}	−2.025	**.044**
	PC1 Precipitation	2.39×10^{-5}	8.64×10^{-6}	**.006**	1.05×10^{-5}	7.25×10^{-6}	1.452	.148
	PC2 Precipitation	-3.81×10^{-5}	1.14×10^{-5}	**.001**	-5.15×10^{-6}	4.76×10^{-6}	−1.081	.280
Uropygi	Maximum SVL	1.89×10^{-10}	8.15×10^{-11}	**.021**				
Vertebrata	Habitat × Terrestrial	8.33×10^{-5}	4.15×10^{-5}	**.046**				
	PC1 Precipitation	3.99×10^{-5}	$1.21\times10^{-5}\times10^{-5}$	**.001**				

Bold values indicate statistical significance. Results are the average *F* and *P*-values of each PGLS performed with ≤100 pseudo-posterior sets of molecular phylogenetic trees (Title *et al.* 2024). Some PGLS models failed to run owing to singular fit errors; consequently, we could not fit any model for some prey categories of very low importance in the diet of most lizard species. For complete results of all PGLS models, see Supporting Information, Table S3. Abbreviations: BM, Brownian motion; OU, Ornstein–Uhlenbeck; PC, principal component; PGLS, phylogenetic generalized least squares; SVL, snout–vent length.

lizard diets. Positive coefficients suggest a higher likelihood of ingestion of the prey category in the specified habitat in comparison to the reference, whereas negative coefficients indicate a lower likelihood, underscoring the complexity and specificity of ecological interactions within these environments.

Finally, PGLS analysis identified prey groups that presented significant positive relationships with body size, which were Uropygi, Myriapoda, Mammalia, Gastropoda, Chelonia, lizard eggs, Diplopoda, Squamata, and plants; conversely, there was a significant negative relationship between ingestion and body size for Araneae, Isoptera, Hemiptera, Thysanura, and Pseudoscorpiones (Table 2). Overall, these results are consistent with larger lizards ingesting prey categories that are usually larger, in addition to the ingestion of plants.

DISCUSSION

Evolutionary history and diet

Our study revealed that lizards consume a wide variety of prey categories. However, many of these categories are present in the diet of only a few species. Specifically, ~80% of all prey categories occur in <30% of species (Fig. 2). Consequently, we will focus on the top 20% of the most frequent prey categories, which occurred in ~50% of the species. We observed a significant phylogenetic signal for some of these prey categories, notably plants, Isoptera, Diptera, Formicidae, Hemiptera, and Coleoptera. The pPCA indicated that global structure overwhelmingly accounts for dietary variation, with the local structure being negligible. The prey categories strongly influencing the two global axes were plants, Isoptera, Formicidae, insect larvae, Araneae, Orthoptera, and Blattodea. Our findings highlight significant niche conservatism in lizard diets. Additionally, most of the prey categories with significant phylogenetic signal are well known for defining clades (e.g. Iguania) and are correlated with ecological traits such as foraging behaviour.

Our dataset, although comprehensive, is subject to taxonomic and geographical biases, which might influence some of our conclusions. Notably, some well-studied clades, such as Lacertidae, Liolaemidae, and *Anolis*, are underrepresented in our analyses. This is primarily attributable to the availability and format of dietary data in the literature. Many studies on these groups report diet composition qualitatively or in non-standardized metrics (e.g. presence–absence or prey counts without volumetric measures), making integration with our dataset challenging (e.g. Meiri 2008, Cooper *et al.* 2002). The absence of small-bodied lacertids, which are known to include plant material in their diets (Cooper *et al.* 2002, Van Damme 1999), could influence our findings regarding the relationship between body size and herbivory. Likewise, liolaemids, a group with multiple independent herbivorous lineages in cool climates (Espinoza *et al.* 2004), and *Anolis* lizards, which exhibit diverse dietary strategies across habitats (Schoener 1968; Schoener and Gorman 1968; Losos 2009), could provide additional insights into the evolutionary and ecological factors shaping lizard diets. Although we believe that our main conclusions remain robust, because our database has some of them, we acknowledge that the inclusion of more samples from these groups in future studies could refine our understanding of dietary evolution in lizards.

Plant consumption accounted for the highest contribution to the first global axis of the pPCA, with iguanians showing the highest plant ingestion. Within the Iguania clade, several families, such as Iguanidae and Liolaemidae, include many strictly herbivorous species. Moreover, even among species that are not strictly herbivorous, some tend to consume higher proportions of plants (Cooper and Vitt 2002, Espinoza *et al.* 2004, Pietczak and Vieira 2017). Iguanians have evolved morphological and physiological adaptations for herbivory, including specialized intestinal flora and colic valves (Iverson 1982, Cooper and Vitt 2002). Herbivory has also evolved independently in other clades, and it has been hypothesized to be associated with factors such as aridity (Van Leeuwen *et al.* 2011), insularity, and prey availability (Cooper and Vitt 2002). Our findings align with these studies, as we observed that all non-iguanian clades with high plant consumption occur in arid climates (e.g. Teiidae: *Dicrodon guttulatum*, Scincidae: *Tiliqua multifasciata*, and Gerrhosauridae: *Gerrhosaurus skoogi*) or on islands (e.g. Teiidae: *Cnemidophorus murinus*). Additionally, we found that plant consumption is related to low and seasonal precipitation (see PGLS results and discussion below).

High termite consumption evolved independently in several non-iguanians, where typical iguanian dietary components, such as Formicidae, Coleoptera, and non-ant hymenopterans, were replaced by Isoptera, Orthoptera, and Araneae (Vitt *et al.* 2003). Termite consumption accounted for the highest contribution to the second global axis of the pPCA, with notable termite consumption observed in many families (Fig. 4). The importance of termites in the diets of lizards varies significantly across different ecosystems. In the Brazilian Cerrado, many lizard species, including *Gymnodactylus carvalhoi* (Colli *et al.* 2003a, Mesquita *et al.* 2006) and *Ameiva parecis* (Colli *et al.* 2003b, Mesquita and Colli 2003), rely heavily on termites as a primary food source. This trend is even more pronounced in arid regions such as the Kalahari Desert and Australia, where the proportion of termites in lizard diets is substantially higher and with many species, such as those in *Ctenotus* (Scincidae), specializing in them (Pianka 1969, 1986). In contrast, Amazonian lizards exhibit a much lower dependence on termites. This discrepancy is not attributable to differences in termite availability but rather the presence of alternative prey. In Amazonia, an abundance of energetically rewarding prey, such as Orthoptera, Araneae, and Blattodea, reduces the reliance on termites (Costa *et al.* 2008a).

Dietary differences between Iguania and non-iguanian clades stem from variations in foraging strategies, prey capture mechanisms, and prey discrimination abilities (Huey and Pianka 1981, Cooper *et al.* 2002, Vitt *et al.* 2003). Our results show a clear separation between iguanian and non-iguanian diets. Non-iguanian lizards, often active foragers, use chemical cues to locate and discriminate cryptic and sedentary prey, such as Blattodea, Araneae, and Orthoptera, which are energetically rich and more accessible during their active periods (Slobodkin 1962). In contrast, iguanians, which frequently include sit-and-wait predators, tend to consume more conspicuous, mobile, and sometimes noxious prey, such as Coleoptera and Formicidae (Sugiura 2018, Cavalcanti *et al.* 2024). This dietary divergence is associated with evolutionary adaptations, with non-iguanian lizards evolving traits that favour active hunting and efficient prey discrimination, whereas iguanians use strategies suited for capturing highly mobile prey. These differences are further compounded by morphological, physiological, and behavioural variations across clades, leading to distinct dietary preferences that reflect their evolutionary histories (Vitt *et al.* 2003, Vitt and Pianka 2005).

Relationship between diet and climatic variables, foraging mode, habitat, and body size

Our GLMs showed no significant relationships between lizard diet and climatic variables. However, our PGLS analysis reveals nuanced relationships between prey categories and climatic variables, highlighting how different prey types are correlated with temperature and precipitation gradients represented by the pPCA axis (Global axis). Significant relationships in the phylogenetic model but not in the GLM highlight the importance of considering evolutionary history in ecological and evolutionary studies (Brooks and McLennan 1991, Harvey and Pagel 1991, Diniz Filho 2000, Revell *et al.* 2008).

Insect larvae, plants, and Blattodea were frequently consumed in cooler or less seasonal environments. This suggests that Blattodea, which typically inhabit leaf litter, are important for many tropical forest lizards (Bell *et al.* 2016), whereas insect larvae and plant material are less abundant or less consumed in hotter, more seasonal areas (Pough 1973, Cooper and Vitt 2002, Pietczak and Vieira 2017). Conversely, Coleoptera, Hemiptera, Formicidae, and Orthoptera were more associated with hotter, more seasonal environments. Coleopterans have adaptations for surviving in variable temperatures (Sinclair 1999, Kime and Golovatch 2000), and Formicidae are well suited to a wide range of habitats, including deserts and savannas (Hölldobler and Wilson 1990, 1994, Cavalcanti *et al.* 2024). Hemiptera and Orthoptera, common in various climates (Specht 1988, Schuh and Slater 1995, Stamou 1998, González and Seastedt 2000), also show a preference for hotter conditions, aligning with their ecological flexibility and abundance in seasonal environments.

Termite ingestion in lizards has been shown to decrease from arid to mesic zones (Abensperg-Traun 1994, Abensperg-Traun and Steven 1997, Costa *et al.* 2008a). In agreement, we found a lower prevalence of Isoptera (and Formicidae) in colder and more variable climates. Conversely, Diptera, plants, Coleoptera, and insect larvae were more common in colder, more variable climates. Diptera and Coleoptera are known for their broad distributions and adaptability (Sinclair 1999, Kime and Golovatch 2000, Wagner *et al.* 2008), which might explain their presence in colder environments. The positive relationship with plant material and insect larvae suggests that these resources are crucial for lizards in such climates, perhaps owing to the availability of plant material as a water source and larvae as a high-protein food option in challenging conditions (Espinoza *et al.* 2004).

Blattodea, Hemiptera, and Lepidoptera were consumed less by lizards in drier, more seasonal environments. Blattodea and Lepidoptera often thrive in moist environments, supporting their negative association with drier conditions. The negative relationship of Hemiptera might be attributable to their reliance on moisture in various life stages (Schuh and Slater 1995, Polhemus and Polhemus 2008). Plant material was positively related to Precipitation PC1, reinforcing the idea that herbivory in lizards is influenced by dry, seasonal climates where plant material can serve as a crucial resource for water and nutrients, especially when other food sources are scarce (Cooper and Vitt 2002, Espinoza *et al.* 2004, Pietczak and Vieira 2017). The negative relationship of Hemiptera with Precipitation PC2 indicates a preference for moister and less seasonal climates, possibly owing to the specific moisture levels required for their lifecycle (Schuh and Slater 1995, Polhemus and Polhemus 2008). In contrast, Araneae and Orthoptera were positively related to Precipitation PC2, suggesting that these prey types are more abundant or consumed in drier, more seasonal environments. This is consistent with the habitat preferences of many spiders and grasshoppers (Gause 1930, Turnbull 1973, Wise 1984), which often favour moist conditions and the abundance of prey items in such environments.

Foraging mode significantly impacts the trophic niches of species. Generally, sit-and-wait ambush foragers tend to feed on more mobile, active prey (Huey and Pianka 1981, Cooper 1995). In contrast, active foragers that can search for food more efficiently tend to consume more sedentary prey, with higher energetic content and palatability (Cooper 1994, Cooper and Van Wyk 1994, Vitt *et al.* 2003). Despite these general patterns, our study did not find a relationship between most prey categories and foraging mode. This lack of association could be attributed to the pronounced dietary niche conservatism of lizards. When accounting for evolutionary history, the covariation between foraging mode and dietary preferences might leave little variance to be explained (Perry 1999, Pianka and Vitt 2003). However, we did observe differences in the proportion of ingestion between foraging modes for three prey categories. Araneae and Blattodea were more prevalent in the diets of active foragers, whereas Formicidae were more common in the diets of sit-and-wait foragers. Phylogeny alone cannot account for the observed patterns for these prey categories, indicating an ecological relationship between prey ingestion and foraging mode. Araneae, Blattodea, and Formicidae are prominent in lizard diets (Fig. 2) and appear across various species within the phylogeny. Specifically, Araneae and Blattodea are more associated with non-iguanians (mainly in Teiidae, Gymnophthalmidae, and Anguidae; Fig. 4), whereas Formicidae are more associated with iguanians (mainly in Tropiduridae, Phrynosomatidae, and Agamidae; Fig. 4).

Our PGLS models, which control for phylogenetic effects, indicated that microhabitat preferences are significantly related to lizard diets. Several trends emerge when comparing habitat categories with the reference habitat (arboreal) (Table 2). Lizards in fossorial habitats show a distinct dietary preference for Isoptera and insect larvae, probably owing to the abundance of these prey types in subterranean environments (Pianka 1986, Kitivo *et al.* 2015, Jowett *et al.* 2021). Conversely, fossorial lizards consume fewer Orthoptera and Diptera, suggesting a potential scarcity or inaccessibility of these prey items underground (Gause 1930, Grabener *et al.* 2020, Leksono *et al.* 2020). In saxicolous habitats, lizards demonstrate a preference for Diptera and Lepidoptera, which might be more accessible in open, rocky areas, where these insects are prevalent (Grabener *et al.* 2020, Kozlov *et al.* 2022). However, they consume less Orthoptera and Blattodea, which are infrequent in this habitat owing to sparse vegetation (Gause 1930, Bell *et al.* 2016, Grabener *et al.* 2020). Lizards in semi-arboreal habitats show a notable increase in the consumption of Isoptera, suggesting that termites are a significant dietary component in these partly arboreal environments, which might offer a balanced mixture of arboreal and ground-level foraging opportunities (Pianka 1986, Colli *et al.* 2003a, Costa *et al.* 2008a). Terrestrial habitats present a mixed dietary pattern, with lizards consuming more plant material and fewer Orthoptera and Coleoptera. This could indicate an adaptive dietary strategy to maximize the diverse food resources available at ground level, including a variety of plant matter alongside typical insect prey (Dearing 1993, Espinoza *et al.* 2004, Vitt 2004, Pietczak and Vieira 2017). Overall, the PGLS models underscore how habitat type is a strong selective pressure on lizard dietary preferences. Lizards appear to specialize in prey types that are more accessible and abundant within their specific ecological niches. This finding aligns with broader studies on the relationship between diet and habitat in reptiles, demonstrating the crucial role of habitat-specific adaptations in shaping dietary habits (Pianka 1986, Vitt *et al.* 2003, Costa *et al.* 2008a).

Body size and dietary preferences often covary in many taxa (Mittelbach 1981, Fleming 1991, Emmerson and Raffaelli 2004). Among predaceous lizards, larger body size is typically associated with the consumption of larger prey, which maximizes energetic gain from food, potentially leading to a narrower niche breadth for larger species (Costa *et al.* 2008b, Costa 2009). Our study found a positive relationship between lizard body size and the ingestion of several prey types, including Uropygi, Myriapoda, Mammalia, Gastropoda, Chelonia, lizard eggs, Diplopoda, Squamata, and plants. Although we did not directly measure prey size, many of these categories consist of vertebrates and large arthropods, supporting the idea that larger lizards tend to consume larger prey. Interestingly, we also observed that herbivory was associated with increased body size. Previous studies have suggested that larger body size in lizards and reptiles facilitates the physiological requirements of plant digestion (Pough 1973, Cooper *et al.* 2002). Herbivory in lizards is often linked to larger body sizes and warmer climates (Zimmerman and Tracy 1989, Van Damme 1999, Cooper *et al.* 2002). This trend is hypothesized to result from the scarcity of large prey and the difficulty that smaller species face in degrading plant material (Cooper *et al.* 2002, Pietczak and Vieira 2017).

However, some studies contradict these findings, noting that certain herbivorous lizard species are small bodied and inhabit cooler climates (e.g. liolemids; Espinoza *et al.* 2004, Vitt 2004). These discrepancies might arise because many of these studies are regional and rely on qualitative observations rather than a continuum of plant ingestion. Additionally, some did not use phylogenetic comparative analysis. Our results suggest that larger body size in lizards generally facilitates herbivory, although this relationship is not restricted to warmer climates. Other factors, such as body mass, physiological activity, and ontogenetic variation, might also influence plant ingestion. Conversely, we found that Araneae, Isoptera, Hemiptera, Thysanura, and Pseudoscorpiones were negatively correlated with body size. This inverse relationship is likely to reflect the smaller size of these prey categories, indicating that smaller lizards tend to have diets with a higher proportion of these smaller prey items (Costa *et al.* 2008b).

CONCLUSION

Our study underscores the significant influence of evolutionary history on the dietary preferences of lizards, highlighting that dietary habits are highly conserved. Prey categories such as plants, Isoptera, Formicidae, and others exhibit significant phylogenetic signal, aligning with the established dietary patterns of clades such as Iguania. Herbivory, for instance, is particularly prominent in iguanians, which have evolved specialized morphological and physiological adaptations for plant digestion. Conversely, termite consumption is notable among non-iguanian clades, indicating independent dietary specializations. These results are also reflected in foraging modes, with sit-and-wait predators consuming more mobile prey and active foragers targeting more sedentary prey. Habitat type might also act as a strong selective pressure on lizard dietary preferences, because lizards appear to consume prey types that are more accessible and abundant within their specific microhabitats. Finally, body size is correlated with diet, with larger lizards tending to consume larger prey and more plant material. These findings emphasize the importance of evolutionary history and ecological interactions in understanding lizard diets, supporting the idea that dietary preferences are deeply rooted in phylogenetic heritage and ecological adaptations.

ACKNOWLEDGEMENTS

We acknowledge several undergraduate and graduate students, field assistants who have their blood in fieldwork during the last five decades.

AUTHOR CONTRIBUTIONS

Lucas B. Q. Cavalcanti, Gabriel C. Costa, and Daniel O. Mesquita designed the study, analysed and interpreted the data, and wrote the manuscript. All authors provided the data and reviewed the manuscript.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

FUNDING

This work was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—CAPES. D.O.M. thanks CNPq and FAPESQ-PB for financial support. G.R.C. thanks CAPES, Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq and Fundação de Apoio à Pesquisa do Distrito Federal—FAPDF for financial support. L.J.V. was supported by NSF Grants DEB 9200779, DEB 9505518, and DEB 0415430 and the Sam Noble Museum and the Research Council of the University of Oklahoma. Eric Pianka is grateful for the Denton A. Cooley Centennial Professorship in Zoology at The University of Texas at Austin.

DATA AVAILABILITY STATEMENT

The data underlying this article are available in the article and in its online supplementary material.

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