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From head to tail: Does habitat use drive morphological variation in snakes?

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Abstract

Convergence, defined as lineages evolving to be more similar to one another than their ancestors due to selective pressures is a hallmark of adaptive evolution. Yet, the extent of convergent evolution across different taxa and in different ecological contexts remains unclear. Snakes, with over 4,100 species worldwide, provide a unique model to explore how habitat use influences morphology in a group with an at first sight uniform body plan. We quantified body, head, and tail shape in over 400 species (∼10% of the global snake diversity) to assess the role of habitat use in shaping morphological variation. Our results reveal significant differences across habitats. Terrestrial species display the highest morphological diversity in contrast to other habitats which appear morphologically more specialized. For example, whereas arboreal and semi-arboreal species exhibit elongated heads and slender necks, aquatic and semi-aquatic snakes share streamlined bodies and narrow heads. Fossorial and semi-fossorial species, on the other hand, have compact bodies. Surprisingly, morphological similarity remains limited to arboreal, semi-arboreal, and terrestrial habitat use. Thus, despite strong functional constraints, evolutionary similarity in fossorial and aquatic species is weak, indicating multiple adaptive solutions rather than a single morphological trajectory, possibly due to the relatively homogenous body plan of snakes. Morphological disparity patterns show that non-specialist ecologies generally exhibit greater disparity than highly specialized ones, in accordance with the need of these species to move in different habitats. Our findings underscore the role of ecological constraints in shaping snake morphology and highlight the complexity of adaptation beyond strict convergent evolution.

Keywords morphometric, functional morphology, microhabitat use, evolution, snake

Introduction

Animals must adapt in order to survive and reproduce successfully in continuously changing environments. Indeed, the environment in which an animal lives exerts selective pressures on the performance and behaviour of an animal, driving selection on underlying morphological traits (Arnold, 1983). Thus, traits that promote escape behaviour, feeding efficiency, and reproduction may promote individual fitness and are likely under strong selection. Often, animals subjected to similar selective pressures will exhibit convergent phenotypes as morphological solutions to maximize performance in a given environment may be limited (Deepak et al., 2023; Herrel et al., 2008). Here, we define convergence broadly as the tendency of distantly related species to evolve similar phenotypes when occupying similar habitats, irrespective of whether these phenotypes arose from distinct ancestral morphologies. Although convergence is sometimes more strictly defined as the independent evolution of similar traits from different ancestral states (Bolnick et al., 2018), we here adhere to a broader definition of convergent evolution. This approach allows us to test for consistent ecomorphological associations across macroevolutionary timescales, identifying whether specific morphological configurations are repeatedly associated with particular habitat types. Morphological similarity can arise through convergent evolution, when distantly related lineages independently evolve similar traits from different ancestral states, or through parallel evolution, when closely related species evolve similar traits from a shared ancestral condition under comparable selective regimes (Grossnickle et al., 2024). It is important to distinguish between these two processes, as similar phenotypic traits observed in organisms facing comparable selective pressures may arise through different mechanisms: in the case of parallel evolution, these traits develop independently but follow similar evolutionary trajectories. For example, sea snakes hunting burrowing eels exhibit similar body shapes (Sherratt et al., 2018) and aquatic snakes have evolved similar head morphologies minimizing drag in response

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to hydrodynamic constraints (Herrel et al., 2008; Segall et al., 2016).

Snakes are an excellent model for studying morphological convergence due to their ecological diversity (O'Shea, 2018). They have evolved to thrive in nearly all environments except polar regions. Foraging mode and dietary specialization have been suggested to be the main drivers of the evolutionary success of snakes (Title et al., 2024). This dietary diversity surged after the Cretaceous mass extinction (Grundler & Rabosky, 2021), with ecological opportunism and behavioural flexibility driving adaptive radiations to different diets. For example, distantly related snail-eating snakes, such as those in the genera *Dipsas*, *Sibon*, and *Pareas*, have converged on similar skull shapes (Pandelis et al., 2023). Similarly, habitat-driven similarity in head shape occurs in Boidae and Pythonidae (Esquerré & Keogh, 2016) and in snakes more generally (Hudry & Herrel, 2025), and selective pressures associated with foraging drive morphological evolution in sea snakes (Sherratt et al., 2018) and homalopsid snakes (Fabre et al., 2016). Furthermore, snakes exhibit different activity patterns, with species being diurnal, crepuscular, or nocturnal, driven by prey availability and thermoregulatory needs (Huey & Kingsolver, 1989; Lettoof et al., 2023). This array of adaptations has made snakes one of the most species-rich groups of reptiles, with over 4,000 currently described species (Pyron & Burbrink, 2012).

Previous studies on snakes have also explored morphological associations with habitat use. For example, arboreal snakes tend to have slender bodies and long tails for balance and movement in trees (Alencar et al., 2017; Lillywhite & Seymour et al., 2011), while aquatic snakes have more streamlined heads to reduce drag and capture prey efficiently (Segall, 2017). Fossorial snakes are adapted for burrowing, with reinforced heads, cylindrical bodies, and reduced ventral scales to minimize friction (Strong et al., 2021). Similarly, sand-dwelling snakes show streamlined heads with countersunk jaws, cylindrical bodies, and reduced ventral scales helping them move through sand (Sharpe et al., 2015). Finally, terrestrial species of snakes display long bodies and enlarged ventral scales to crawl efficiently on land (Brischoux & Shine, 2011). Unfortunately, most studies investigating ecomorphological patterns in snakes have primarily focused on specific families, such as Natricinae (Deepak et al., 2023), Boidae (Esquerré & Keogh, 2016), Dipsadinae (Pandelis et al., 2023), and Hydrophiidae (Sherratt et al., 2018). These works have identified consistent associations between phenotype and habitat use, providing evidence for the repeated evolution of similar forms in response to ecological factors. Yet, whether morphological convergence can be observed across snakes more generally, and to what degree remains largely unexplored. This is particularly interesting because the body plan, which at first glance appears rather uniform, may limit the evolution of morphological differences in response to selection imposed by habitat use.

Our study aims to address this by analyzing a phylogenetically and ecologically diverse, yet comprehensive data set composing roughly 10% of the overall species diversity of snakes. We predict that snakes occupying similar habitats will exhibit similar morphologies irrespective of their phylogenetic affinity along functional axes. Based on previous mostly clade-specific studies, we predict that arboreal species will have slender bodies and narrow heads, that aquatic snakes will have more robust bodies and heads with dorsally positioned nostrils, and that fossorial species will show adaptations for burrowing with dorsally positioned nostrils and eyes and short cylindrical bodies. Sand-dwelling snakes are expected to show partial similarity with fossorial species, while semi-aquatic, semi-fossorial, and semi-arboreal species will likely exhibit intermediate traits between specialist categories. We also predict that species using multiple habitats will show greater morphological disparity, reflecting the diversity of habitats they occupy. Habitat specialists such as fossorial snakes, on the other hand, are expected to show lower morphological disparity due to the strong physical constraints imposed by their locomotor environment. In this study, we investigate whether some habitat use are more similar to each other and do so by quantifying morphological differences between groups. In addition, we quantify the morphological disparity within each habitat use to test the idea that specialists should show lower disparity than generalists.

However, interpreting habitat-associated morphological patterns requires careful consideration of body size and allometric relationships, as size variation can fundamentally impact both form and function. Allometry describes how trait proportions change with size, capturing biologically meaningful variation rather than simple scaling effects (Klingenberg, 2016). In snakes, body size is tightly linked to performance, prey size, and energetic constraints, and is often subject to stabilizing selection towards ecological optima (Boback & Guyer, 2003; Feldman et al., 2016). Changes in size following positive allometric trajectories can lead to disproportionate growth of functionally important traits such as jaw length, head dimensions, and body robustness, thereby enabling access to novel prey types or locomotor strategies without requiring changes in size-independent shape (Klingenberg, 2016; Vincent et al., 2007). Although widely used, residual-based size correction can remove biologically meaningful allometric variation (Price et al., 2019). On the other hand, approaches such as the use of log-shape ratios (LSRs) or Procrustes superimposition remove absolute size while preserving allometric structure (Claude, 2013). It is important to note that macroevolutionary interpretations can vary considerably depending on whether residual-based or shape-based approaches are used, particularly when ecological diversification occurs through changes in allometric trajectories rather than through changes in shape independent of size (Lee et al., 2016; Price et al., 2019). Throughout this study, we distinguish *size-corrected* data—where variation associated with body size is removed using regression residuals—from *allometry-corrected* or *shape-based* data, where absolute size is removed but biologically meaningful size–shape covariation is retained (Price et al., 2019).

Materials and Methods

Sample and Ecological Classification

We collected data for a total of 939 specimens of 432 species of snakes, housed in three European natural history museums: the National Natural History Museum of Paris (172 specimens), the Alexander Koenig Museum of Bonn (578 specimens), and the Museum of Natural Sciences of Brussels (189 specimens). All measurements were taken on adult specimens where possible. For some species, only young adult or juvenile individuals were available, and for others, subadults were measured mostly due to a lack of adult specimens in fluid collections (e.g., large species of boas and pythons; see Table S1). Our sampling aimed to cover the phylogenetic and ecological diversity across snakes (Figure 1)

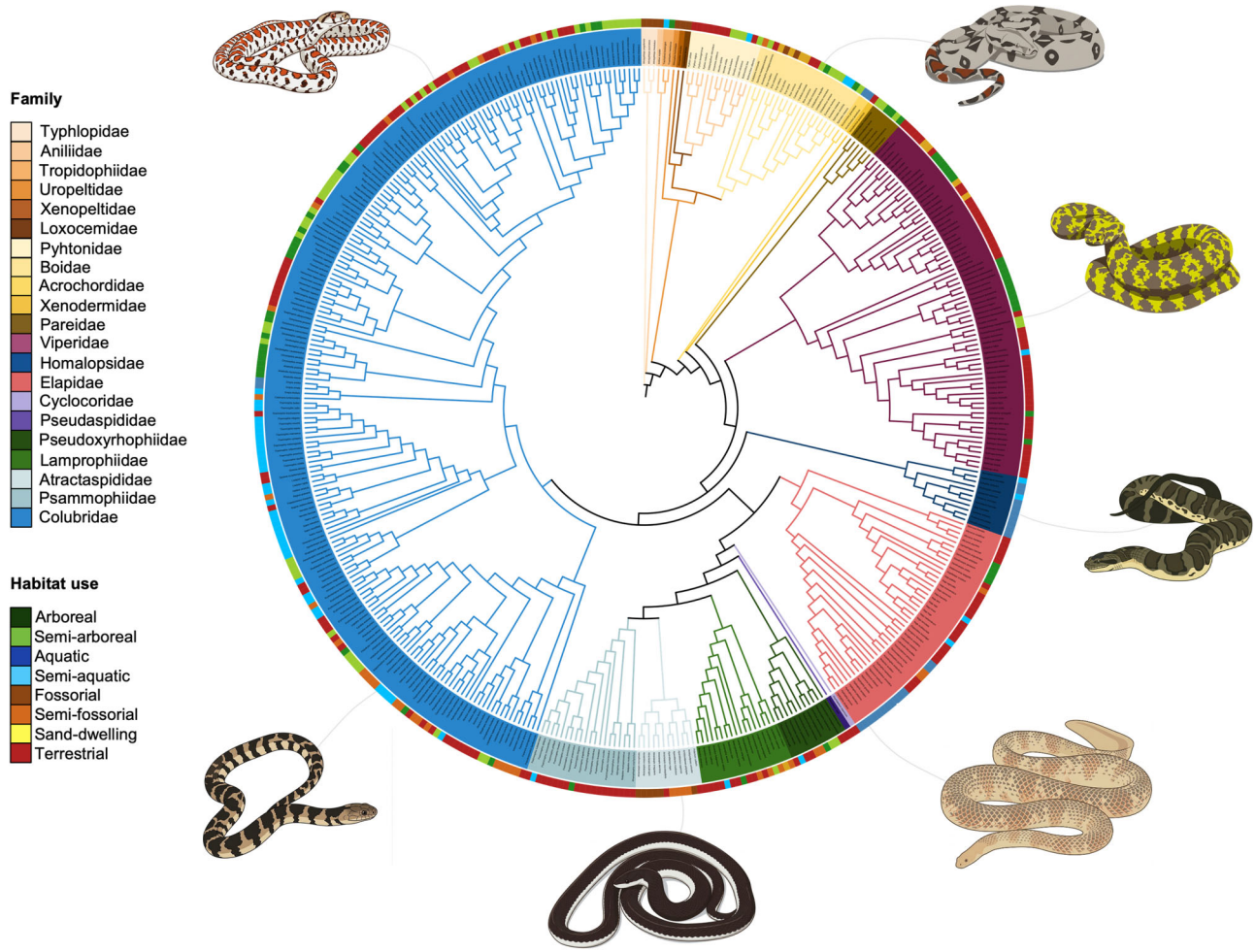

Figure 1. Pruned phylogenetic tree including the 432 snake species analysed in this study, visualized using the iTOL web platform. Branches are coloured according to family-level taxonomy, while coloured boxes at the tips indicate species habitat use (arboreal, semi-arboreal, aquatic, semi-aquatic, fossorial, semi-fossorial, sand-dwelling, and terrestrial). Species labels are coloured by family to facilitate visualization of taxonomic structure across the tree.

while being constrained by the availability of specimens in these collections. Specimens were selected with well-preserved bodies and heads allowing us to quantify trait variation. The sex of specimens was not analysed due to higher inter-specific variation compared to the variation between sexes (Adams et al., 2013; Sidlauskas, 2008). Moreover, sex was often absent from museum records and difficult to assign in many species without invasivebr procedures.

Habitat classifications were defined based on the literature (Allen, 2019; Bartlett & Bartlett, 2009; Campbell & Lamar, 2004; Chippaux, 2019; Das, 2010; Das, 2023; Egan, 2022; Glaw & Vences, 2007; Marais, 2004; O'Shea, 2005; O'Shea, 2018; Pietersen et al., 2021; Spawls et al., 2002; Vogel, 2006; Whitaker & Captain, 2004). We created eight habitat use categories that included 178 terrestrial, 9 sand-dwelling, 56 arboreal, 26 aquatic, 16 fossorial, 65 semi-arboreal, 48 semi-aquatic, and 40 semi-fossorial species (Figure 1). These categories were based on the physical demands imposed by the environment on the snake's body and head (Table S2). For example, the same hydrodynamic constraints apply to snakes living in the ocean or in fresh water, causing us to group these together. We faced some limitations throughout our sampling methodology. First, sand-dwelling species were by default less numerous than others because they are less common (How & Shine, 1999; Šmíd et al., 2023; Mochales-Riaño et al., 2024). Second, despite the fact that Scolecophidia comprises more than 400 described species (Marin et al. 2013), not all morphological measurements could be collected for this clade because their highly modified head and jaws make conventional morphometrics tools such as calipers largely unsuitable. Their cranial and to some degree post-cranial morphology differs profoundly from that of modern alethinophidian snakes, preventing direct comparison within the same analytical framework (Tiatragul et al., 2024).

Morphometric Data

Morphometric data were collected by measuring 13 morphological traits (Table S3). The traits were selected based on the literature on morphometric studies in snakes (Alencar & Quental, 2022; Burbrink & Myers, 2015; Cavalheri et al., 2015; Esquerré & Keogh, 2016; França et al., 2008; Grundler & Rabosky, 2014; Hibbitts & Fitzgerald, 2005; Manjarrez et al., 2017; Pyron & Burbrink, 2009; Reynolds et al., 2016). Snout–vent length (SVL) and total length were measured using a measuring tape ($\pm$1 cm). The remaining

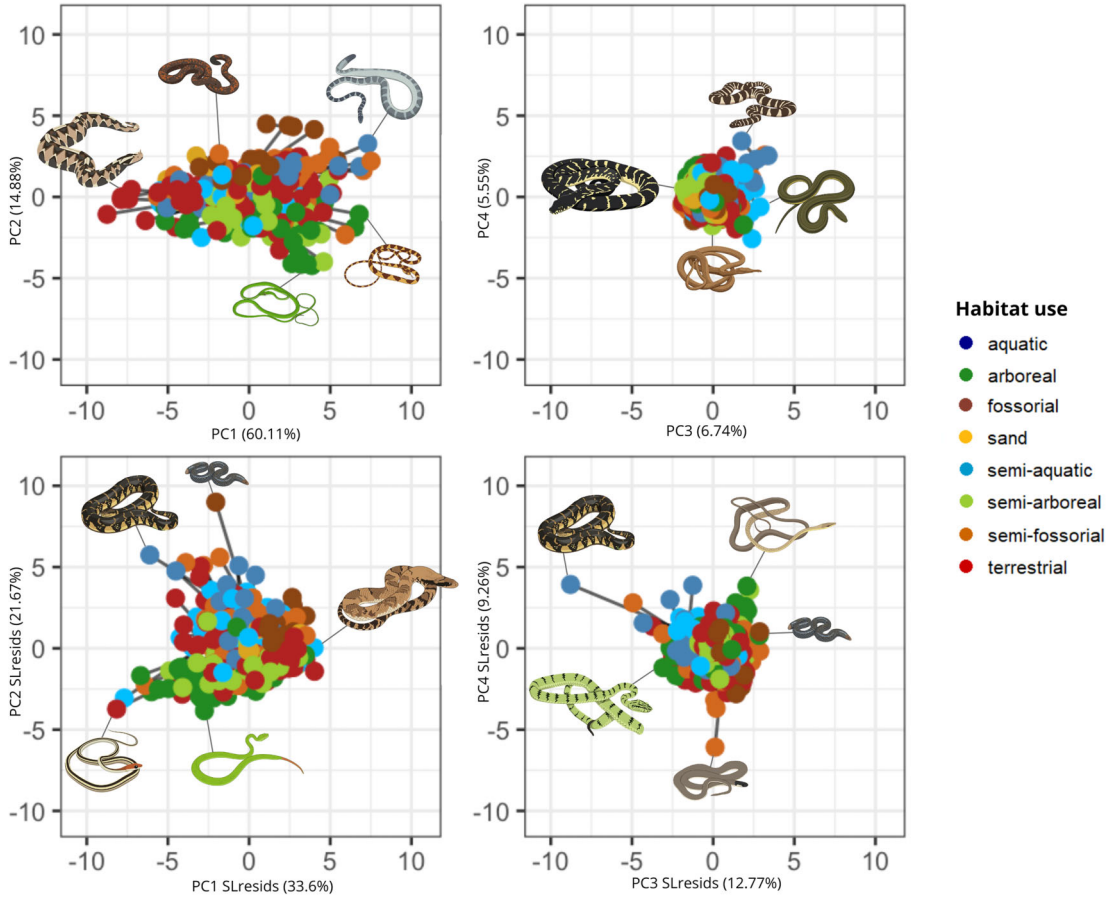

Figure 2. Phylomorphospace illustrating body and head shape variation across 432 snake species. The phylogeny is projected onto the first four principal component axes (PC1 vs. PC2 and PC3 vs. PC4). Nodes are coloured according to ancestral habitat reconstructions using symmetric rates estimation. Results are presented for both size-corrected (A) and allometry-corrected residuals (B).

Table 1. Phylogenetic MANCOVA Results, Including Degrees of Freedom (d.f.), Wilks' Lambda, the *F*-value, and the *P*-value

Model	*df*	Wilks' Lambda	*F*	*P*
Snout–vent length	1	0.02	1967.52	$P < 0.01$
Habitat use	7	0.53	3.22	$P < 0.01$
Interaction	7	0.67	1.98	$P < 0.01$

traits were measured with a digital caliper (Mitutoyo© 150 mm 500–181-30; ±0.02 mm). Before starting data collection, a repeatability test was performed with juveniles of the species *Trimeresurus albolabris*. We measured 10 randomly selected individuals 10 times and performed a principal component analysis (PCA) to explore whether the measurement error was high or not. Our PCA results showed that measurement error is relatively low and that each individual occupies a distinct position in the morphospace (Figure S1). Thus, despite the small size of the specimens used, measurement error is low and repeatability high.

Phylogenetic Comparative Analyses

For each snake species, mean morphological values were calculated as comparative analyses are conducted at the species level. A Log_{10}-transformation was applied to render the data normal and homoscedastic. To perform phylogenetic comparative analyses, we used the phylogenetic tree of Title et al. (2024; Dryad repository: https://datadryad.org/dataset/doi:10.5061/dryad.p5hqbzkvb) imported as a newick file. This phylogenetic tree was inferred from a concatenated molecular dataset combining mitochondrial and nuclear loci, and estimated using Bayesian inference and calibrated with fossil constraints following the methods described in their study. The tree was pruned to include only species present in our dataset using the *drop.tip* function from the *ape* package v5.8–1 (Paradis & Schliep, 2019). In total, 432 species were included in the morphometric analysis. Some species were missing from the original tree (14 in total) and were coded as a closely related taxon present in the phylogenetic tree of Title et al. (2024; Table S4). Three species that were measured were ultimately not included

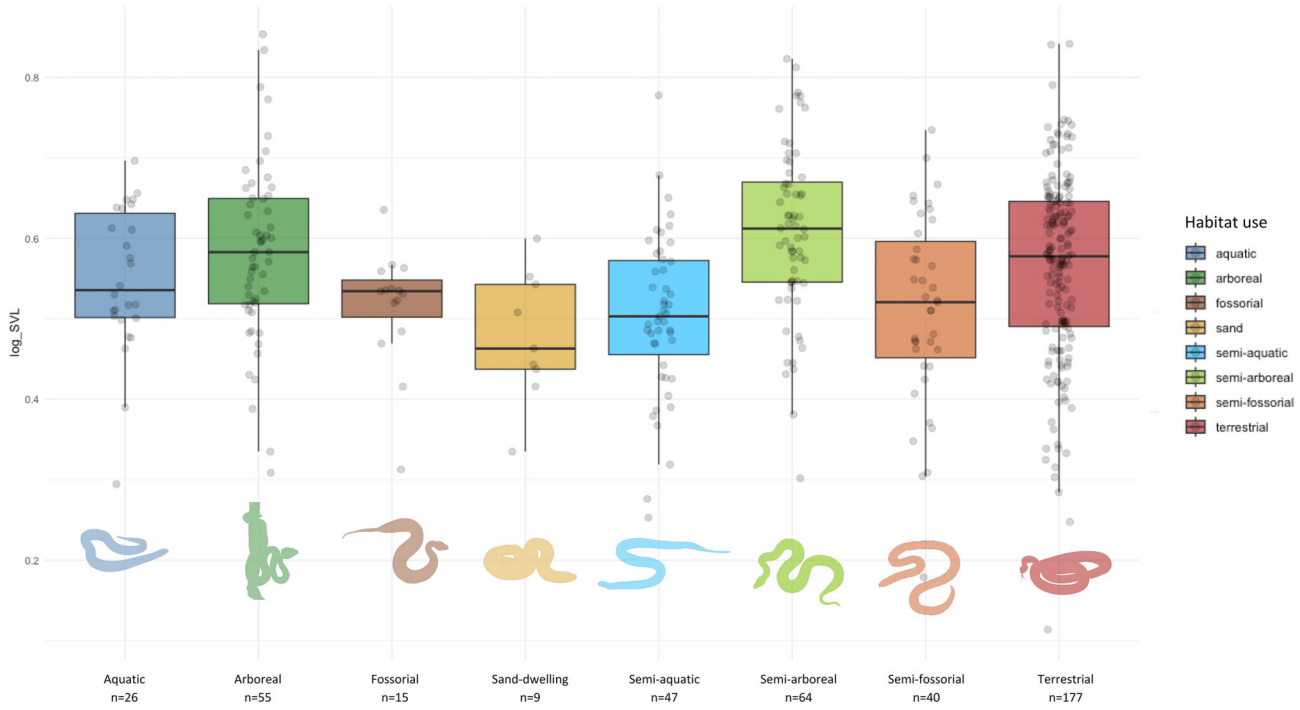

Figure 3. Box plot illustrating the variation in snout–vent length (log-transformed SVL) among the eight habitat use categories.

in the analysis as they were not included in any phylogeny: *Hydraethiops melanogaster*, *Hydraethiops laevis,* and *Hypoptophis wilsoni*.

Size, Shape, and Allometry

To analyse shape variation while retaining allometric structure, we computed LSRs for all linear measurements. This approach removes absolute scale while preserving multivariate size–shape covariation, allowing biologically meaningful allometric relationships to be retained (Claude, 2013; Price et al., 2019). LSRs therefore represent size-standardized shape, including allometric variation, in contrast to residual-based approaches that represent allometry-corrected shape by explicitly removing size-related variation.

In addition, to explicitly investigate evolutionary allometry while accounting for phylogenetic relationships, we performed a phylogenetic multivariate regression of morphological traits on log-transformed SVL and habitat use using the *procD.pgls* function in the *geomorph* R package. Log(SVL) was entered before the categorical niche factor in the model ($Y \sim \log(\text{SVL}) \times \text{habitat}$), following standard practice, allowing assessment of how shape changes with size prior to considering ecological differences. This approach evaluates (i) the general relationship between size and morphology across species, (ii) mean morphological differences among habitats, and (iii) whether allometric trajectories differ among habitat use through the interaction term. Significance of model terms was assessed with 999 phylogenetic permutations. Because a significant size × habitat interaction indicates differing allometric slopes among ecological groups, pairwise comparisons of multivariate slopes were performed to examine group-specific evolutionary allometries. Multivariate regression scores were visualized using the *plotAllometry* function, providing a morphospace representation of each habitat use group's allometric trajectory and allowing explicit interpretation of how ecological divergence is mediated by variation in allometric trajectory rather than by allometry-corrected shape alone (Claude, 2013; Klingenberg, 2016; Price et al., 2019).

To account for phylogenetic non-independence and to explicitly remove variation attributable to body size, we performed phylogenetic generalized least squares (PGLS) regressions of each log-transformed morphological trait on log-transformed SVL. Thus, residuals represent allometry-corrected traits, in which variation associated with SVL is removed, but residuals do not retain the allometric scaling relationships among traits. This analysis was implemented in the *caper* package v1.0.3 (Orme et al., 2013). Phylogenetically size-corrected residuals were extracted from each model and combined into a single dataset containing only residual variation independent of variation in SVL. Conventional PCA was then computed on this residual matrix using the function *prcomp* in R. Loadings correspond to PCA axes derived from phylogenetically size-corrected residuals, representing variation in body and head shape (Supplementary data 2). Next, a phylomorphospace was created using the *ggphylomorpho* package v0.2 (Barr, 2017), integrating the phylogenetic tree with morphological data.

We then performed a phylogenetic multivariate analysis of covariance (Phylo-MANCOVA) using the *mvMORPH* package v1.2.1 (Clavel et al., 2015) to test for differences in morphological traits among habitat use while accounting for phylogenetic relationships, with SVL included as a covariate. First, we performed a multivariate evolutionary model-fitting analysis using the *mvMORPH* package. Phylogenetic residuals of the morphological traits, allometry-corrected using phylogenetic regression, were summarized using a principal component analysis (PC1–PC2) and used as input. Only PC1 and PC2 were retained because they capture the major axes of shape variation (74% of total variance) while

Table 2. Results of the Similarities Test

Habitat use	State	*P*	Time	*P*
Arboreal	56.66	$P < 0.01$	298.21	0.04
Semi-arboreal	57.54	$P < 0.01$	323.02	0.28
Aquatic	72.89	0.64	664.68	1
Semi-aquatic	68.98	0.30	620.05	1
Fossorial	89.54	1	408.66	0.97
Semi-fossorial	79.33	0.997	461.97	1
Sand	77.66	0.75	434.39	0.95
Terrestrial	66.36	$P < 0.01$	331.62	0.42

Note. The mean angles of phenotypic distance are reported using ang.state (state) and the test of convergence with timing of diversification using ang.state.time (time), with the corresponding *P*-values.

Table 3. Results of Morphological Convergence Tests Across Habitat Use Using Stayton's Distance-based Metrics

Habitat use	C1	C2	C3	C4
Arboreal	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Semi-arboreal	$P < 0.01$	$P < 0.01$	0.11	0.76
Aquatic	$P < 0.05$	$P < 0.01$	0.14	0.77
Semi-aquatic	0.33	$P < 0.01$	0.38	0.06
Fossorial	0.17	$P < 0.01$	0.36	0.32
Semi-fossorial	0.43	$P < 0.05$	0.78	0.79
Sand	0.34	0.06	0.41	0.37
Terrestrial	0.37	0.16	0.45	0.32

Note. Values represent the calculated C-metrics (C1–C4) and their corresponding *P*-values derived from 1,000 simulations.

limiting the inclusion of higher-order PCs dominated by low variance and potential noise. Preliminary analyses including additional PCs yielded similar model rankings, indicating that results were robust to PC dimensionality (Table S9).

For multi-rate (BMM) and multi-optimum (OUM) evolutionary models, ecological regimes were incorporated into the phylogenetic framework using stochastic character mapping. Discrete habitat categories were treated as a multistate character and mapped onto the phylogeny under a continuous-time Markov process. To identify the most appropriate transition model, we compared Equal Rates (ER), Symmetric (SYM), and All-Rates-Different (ARD) models using the Akaike information criterion corrected for small sample sizes (AICc). The Symmetric (SYM) model provided the best fit to our data, significantly outperforming the ER and ARD models. Consequently, the SYM model was used for all subsequent reconstructions. Uncertainty in ancestral state reconstruction was explicitly accounted for by generating multiple stochastic maps conditional on the observed tip states 1000 times using the *make.simmap* function in the *phytools* package, resulting in a set of phylogenies with branches probabilistically "painted" according to inferred ecological regimes.

We fitted a single-rate Brownian motion (BM1), multiple-rate Brownian motion (BMM), single-optimum Ornstein–Uhlenbeck (OU1), and multiple-optimum Ornstein–Uhlenbeck (OUM) models, where multiple-rate or multiple-optimum models account for variation among habitat use. Model comparisons using AIC values indicated that the multi-rate Brownian motion model (BMM) had the strongest support, while the multi-optimum OU model (OUM) was also better supported than single-optimum models (Table S5). Subsequent analyses were run with BMM models of evolution in *mvMORPH*. Significance was assessed using a Wilks' Lambda test on the residuals of a PGLS model under a multi-rate Brownian motion model of trait evolution. To identify which traits contributed to these differences, size-corrected residuals from PGLS regressions of each trait against SVL were subsequently analysed with univariate analysis of variance (ANOVA) (fitted using stats:: aov()), followed by Tukey's post-hoc tests using the *emmeans* package v1.10.5 (Lenth & Piaskowski et al., 2025), allowing detection of trait-specific differences among habitats.

Phylogenetic Signal

Blomberg's K statistic (Blomberg et al., 2003) was calculated in R using the *phytools* package v2.3–0 (Revell, 2012) to evaluate the phylogenetic signal present in the morphological traits. This statistic measures the extent to which traits exhibit a phylogenetic signal, quantifying the degree of trait similarity among closely related species compared to what would be expected under a null model of trait evolution. A *K* value close to 1 indicates a strong phylogenetic signal, meaning that closely related species have more similar traits than would be expected by chance. Conversely, values significantly less than 1 indicate a weaker phylogenetic signal, suggesting that trait variation is less influenced by phylogenetic

relationships. We also calculated a multivariate phylogenetic signal using the *physignal()* function in the *geomorph* package v4.0.9 (Adams et al., 2025) to assess the signal across all morphological traits simultaneously.

Similarities Among Habitat Use

The occurrence of morphological similarity among species within the same habitat was examined using the *search.conv* function from the *RRphylo* package (Castiglione et al., 2021) with the state-based approach. To isolate shape variation independent of body size, morphometric traits were allometry-corrected using phylogenetic residuals calculated with the *phyl.resid* function (Revell, 2012). This approach accounts for the relationship between size and shape, ensuring that morphological similarities are not simply a byproduct of shared body size. For each unique ecological state, species were assigned to that "state" and all other species were assigned "nostate." Similarity was then tested for each state individually. The "declust" option was not used, and the number of randomizations "nsim" was set to 1000. This method evaluates whether branches associated with similar ecological states display greater phenotypic similarity than expected under a Brownian motion model of evolution.

In addition to the state-based approach, we also quantified convergent evolution using the distance-based metrics (C1–C4) developed by Stayton (2015). While the *search.conv* function identifies general phenotypic similarity, Stayton's metrics allow for a formal test of whether lineages have evolved to be more similar than their respective ancestors. Specifically, C1 measures the proportion of the maximum ancestral distance that has been closed by subsequent evolution, while C2 quantifies the absolute magnitude of this convergence. C3 and C4 assess whether lineages have converged into a restricted and densely occupied region of the morphospace. To determine the significance of these metrics, we compared the observed values against a null distribution generated from 1,000 simulations under a Brownian Motion model using the R package *convevol* (Stayton, 2018). Each habitat was tested independently to identify specific habitat-driven evolutionary patterns

Disparity Among and Between Groups

Morphological disparity across habitat use categories was assessed to determine whether certain habitat use exhibit higher or lower phenotypic variability. Disparity was quantified as the sum of variances across a set of morphological traits. To test for differences in morphological disparity among habitat use categories, we used the *dispRity* package v1.9 (Guillerme, 2018). First, species were grouped according to their habitat use, and bootstrap resampling (1000 iterations) was applied to estimate disparity distributions. Statistical comparisons were conducted using pairwise Wilcoxon tests with Bonferroni correction to account for multiple comparisons. Additionally, disparity was calculated by summing trait variances for each species, allowing for a finer-scale visualization of disparity patterns across habitat use. These results were visualized using violin plots, where each point represents an individual species, and the distribution of disparity within each habitat use is displayed. We used R version 4.4.2 for all analyses (R Core Team, 2022).

Results

Variation in Body and Head Shape

In our principal component analysis performed on phylogenetically size-corrected residuals (PCA), 74% of the variation in body and head shape is explained by the first two principal components (PC1: 59.98%; PC2: 14.22%; Figure 2). PC1 mainly summarizes the variation in overall head shape (Table S5), with the strongest loadings observed for head width (−0.349), head height (−0.333), jaw length (−0.331), and head length (−0.320). This indicates that PC1 captures variation in relative head length, width, and height. Negative values on PC1 indicate individuals with a wider, taller head and a longer lower jaw, while positive values reflect a more slender head shape. PC2, on the other hand, captures variation in body proportions (Table S5). The greatest loadings were observed for total length (−0.494), midbody width (0.349), cloaca region width (0.419), and neck width (0.424). Snakes with low PC2 scores tend to have longer tails relative to their body width, whereas those with high PC2 scores show a thicker body profile with a shorter tail. This axis thus contrasts elongate versus robust body forms. PC3 (6.99%; Figure S2) explains additional variation linked to specific proportions of the head (Table S5). The highest positive loading is found for tail length (0.636), while inter-nostril width (−0.431) and inter-ocular distance (−0.317) contribute negatively. Individuals with high PC3 scores tend to have relatively longer tails combined with a narrower snout and reduced orbital spacing, while lower scores correspond to broader snouts and wider inter-ocular spacing. This component therefore reflects coordinated changes in tail proportion and snout/orbital morphology. Interestingly, most habitat use categories occupy a large part of the morphospace, especially terrestrial species (Figures S4-S6). PC scores of each species and traits loadings can be found in the Supporting Information (Supplementary data 2).

The PCA performed on LSRs, which retain allometric structure while removing absolute scale, revealed that the first principal component (PC1) primarily captures variation in overall head dimensions, with strong negative loadings for head length, head width, head height, and jaw length. Species with negative PC1 scores therefore exhibit allometrically larger and more robust heads relative to body size, whereas positive scores correspond to more slender head morphologies. The second principal component (PC2) mainly reflects variation in body proportions, with high positive loadings for midbody width, cloacal width, neck width, and total length. This axis contrasts elongate, slender-bodied species with more robust forms characterized by a thicker trunk and neck. Higher-order PCs capture additional, more localized aspects of head morphology, including snout width, orbital spacing, and quadrate length, indicating that fine-scale head proportions vary independently of allometric head and body robustness. PC scores and trait loadings for the LSR PCA are provided in the Supporting Information (Supplementary Data 2).

Phylogenetic Signal

Blomberg's K test revealed that the phylogenetic signal was low for all traits ($K < 0.26$; Table 5), indicating that morphological traits among closely related species are less similar than expected under a pure Brownian Motion model. However, all K values were statistically significant ($P < 0.01$) demonstrating that trait evolution is not

Table 4. Results of the Morphological Disparity Using the Sum of Variances

Habitat use	*N*	obs	bs.median
Arboreal	55	0.401	0.390
Semi-arboreal	64	0.448	0.434
Aquatic	26	0.351	0.333
Semi-aquatic	47	0.386	0.357
Fossorial	15	0.277	0.261
Semi-fossorial	40	0.516	0.499
Sand	9	0.291	0.255
Terrestrial	177	0.499	0.499

Note. The table reports the number of species in each habitat use categories (*N*), the observed disparity (obs), and the median value from bootstrap resampling (bs.median).

independent of phylogenetic history. While the relatively low *K* values may suggest high levels of within-clade variance or potential adaptive divergence, the significance of the multivariate phylogenetic signal (K mult $= 0.171$; $Z = 23.55$; $P < 0.01$) confirms that phylogenetic relatedness continues to exert a measurable influence on the overall phenotype. Phylogenetic signal in the LSR dataset was moderate but significant ($K = 0.356$), confirming that closely related species tend to share similar shapes.

Differences between Habitat Use

Morphological traits were different between habitat use when taking into account variation in SVL (Table 1). The effect of SVL and the interaction between SVL and habitat use was also significant suggesting different allometric patterns in species using different habitats (Table 1; Figure 3). Moreover, Tukey's post-hoc tests revealed significant size differences between snakes utilizing different habitats (Figure 5). Arboreal and semi-arboreal species were significantly longer than all other habitat use categories, except semi-aquatic species. Semi-aquatic species were also longer than aquatic, fossorial, and sand-dwelling snakes. Terrestrial species exhibit medium values in SVL as do semi-fossorial and aquatic species. However, terrestrial species had narrower bodies than their fossorial counterparts (e.g., including mid-body width, neck width, and cloacal width). Sand-dwelling species show the lowest values in body length. Body and head shape (i.e., log transformed traits regressed against log SVL) also differed significantly among habitat use. Sand-dwelling and fossorial species had the widest bodies relative to their SVL (e.g., including midbody width, cloaca width, and neck width). Aquatic and semi-aquatic species exhibit the second widest bodies and were different from terrestrial, semi-fossorial, arboreal, and semi-arboreal species. Arboreal and semi-arboreal species were significantly more slender compared to all other habitat use categories.

Significant differences were also observed in head dimensions (Figure 5). Sand-dwelling species had relatively longer, wider, and taller heads compared to fossorial and semi-fossorial species. In contrast, fossorial species exhibit the lowest values in head traits, along with semi-fossorial snakes. They show the smallest head dimensions compared to all other habitat use categories, especially for head length, head height, jaw length, and rostro-ocular distance (i.e., snout-length). However, fossorial and semi-fossorial snakes further differ in some specific head features from other groups, showing the lowest values in jaw and quadrate length, and rostro-ocular distance, respectively. Aquatic species tend to show an increased head height, while exhibiting the lowest inter-nostril distance. On the other hand, semi-aquatic species show high values in head and jaw length. Moreover, fossorial, and semi-fossorial species had shorter lower jaws and quadrates compared to all other species. Arboreal and semi-arboreal snakes share similar morphological features. Meanwhile, terrestrial species had wider heads and were generally more robust body than arboreal ones (e.g., greater head width, inter-nostril distance, mid-body width, neck width, and cloacal width). The detailed post-hoc results can be found in the supporting information (Supplementary data 4).

Similarities Among and Between Habitat Use

Results from the *search.conv* function show an overall tendency for species that occupy a given habitat to resemble each other more than random (*ang.state*). This was significant for arboreal, semi-arboreal, and terrestrial groups only, however ($P < 0.05$; Table 2). In contrast, for the timing of convergence (*ang.state.time*) the result was significant only for arboreal species (Table 2). This suggests that, in most cases, the evolution of habitat use was not synchronous with species arriving at their respective morphology at different time points.

We then applied Stayton's distance-based metrics (Table 3). These analyses provide complementary evidence for convergent evolution. Specifically, the arboreal group exhibited highly significant convergence across all four metrics (C1–C4), confirming that these taxa have evolved to be significantly more similar to one another than were their ancestors. Significant convergence was also detected for terrestrial (C1–C2) and semi-arboreal species (C1–C2). Other groups, such as aquatic, semi-aquatic, and semi-fossorial, showed significant values for the C2 metric, indicating a reduction in absolute distance in morphospace, although they did not reach significance for C1, C3, or C4. In contrast, the fossorial and sand-dwelling groups showed no significant signs of convergence across any metric.

Disparity Among and Between Habitat Use

Semi-fossorial species showed the highest disparity (0.516), followed by terrestrial (0.499) and semi-arboreal (0.448) species

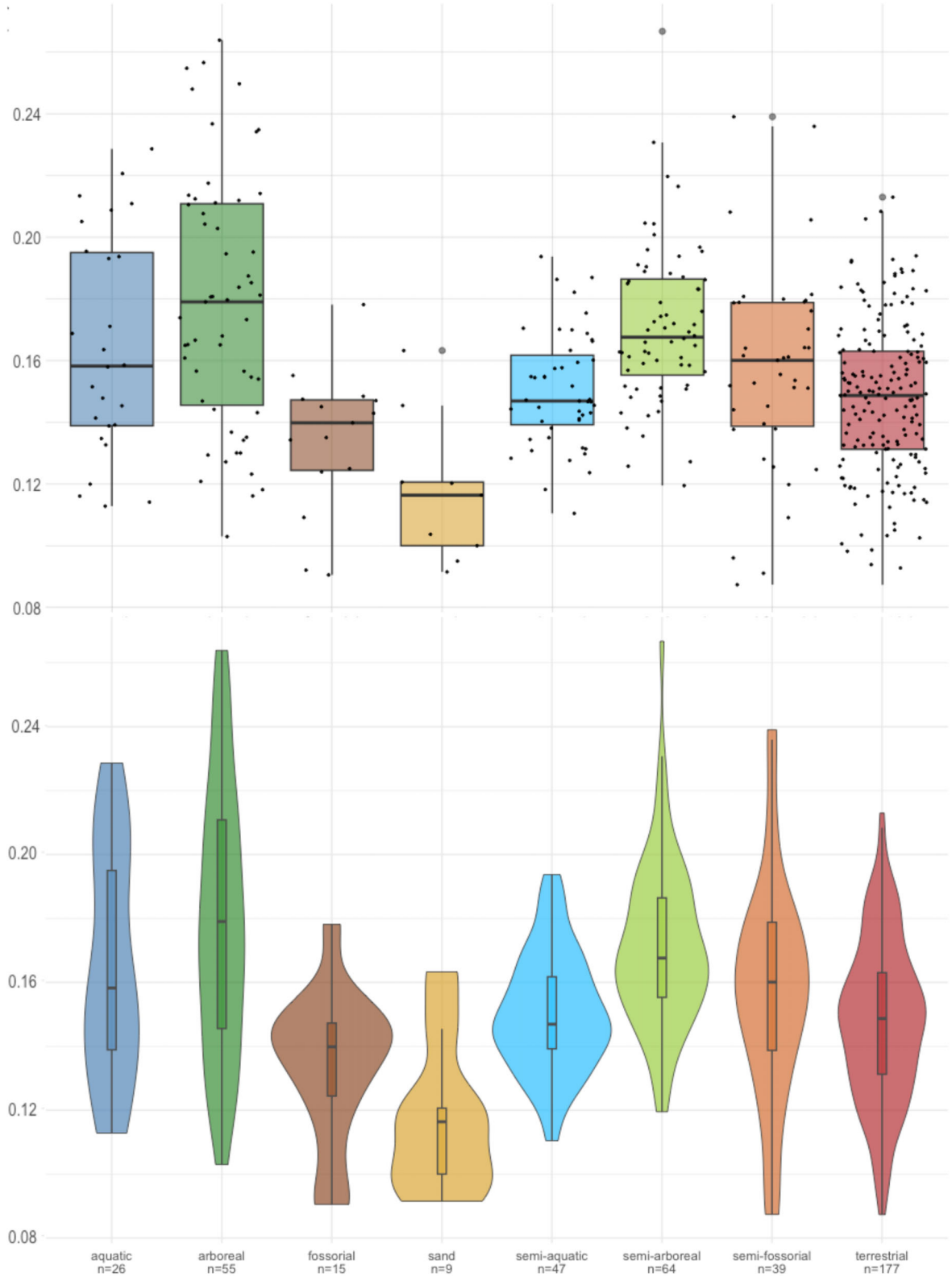

Figure 4. Box plot and Violin plot illustrating the distribution of morphological disparity for the eight habitat use categories.

(Table 4; Figure 4). The lowest disparity was exhibited by fossorial (0.277) and sand-dwelling (0.291) species. Arboreal, aquatic, and semi-aquatic species exhibit intermediates scores (0.401, 0.351, and 0.386 respectively). Pairwise comparisons indicate significant differences in disparity among nearly all habitat use categories (all $P < 0.01$; Figure 4). Morphological disparity also differed between habitat use when using LSR data (Table S8). Aquatic species showed the highest disparity (0.405), followed by fossorial (0.271) and semi-fossorial species (0.287), whereas sand-dwelling (0.094) and semi-arboreal species (0.091) exhibited the lowest dispar-

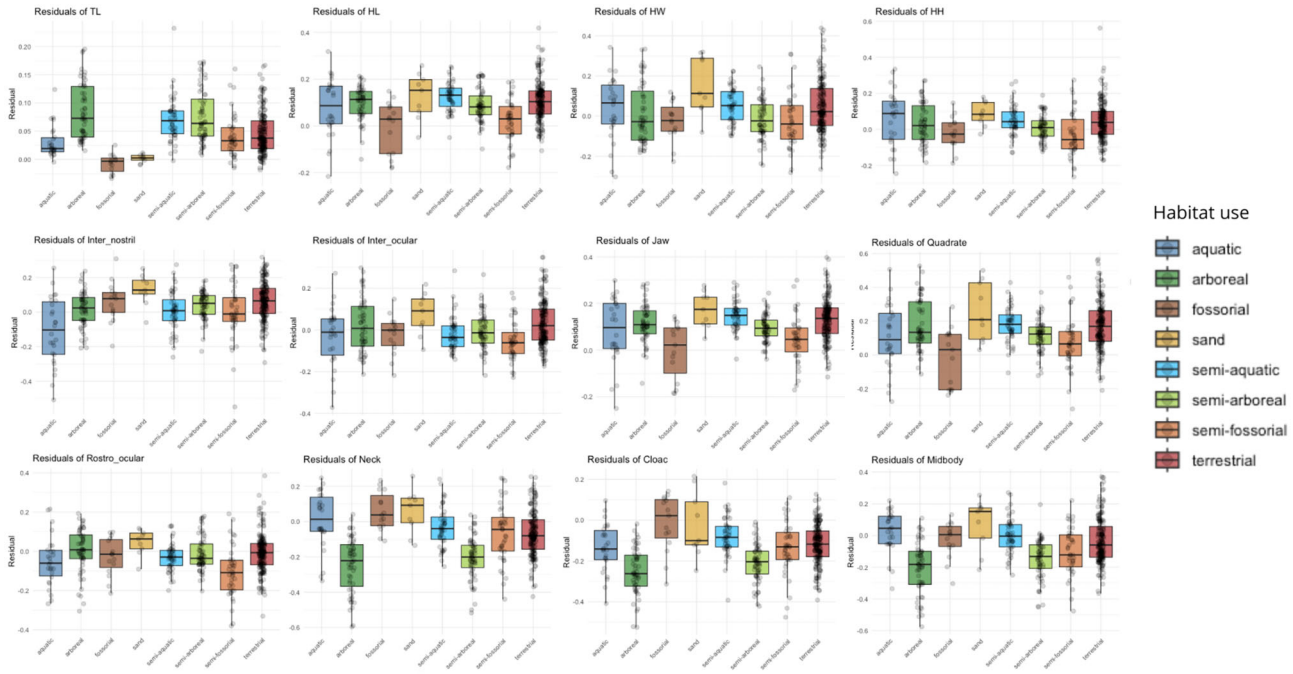

Figure 5. Box plots depict size-corrected residuals of morphological traits across habitat type. Points represent individual species, and colours indicate habitat use categories.

Table 5. Blomberg's *K* Values and Significance

Multivariate model	Blomberg's *K*	*P*
Trait matrix	**0.17**	***P* < 0.01**
Trait		
Snout-vent length	0.14	$P < 0.01$
Tail length	0.18	$P < 0.01$
Head length	0.25	$P < 0.01$
Head width	0.17	$P < 0.01$
Head height	0.17	$P < 0.01$
Jaw length	0.26	$P < 0.01$
Quadrate length	0.25	$P < 0.01$
Inter-nostril distance	0.16	$P < 0.01$
Inter-ocular distance	0.18	$P < 0.01$
Rostro-ocular distance	0.16	$P < 0.01$
Mid-body width	0.14	$P < 0.01$
Body width at the cloaca	0.12	$P < 0.01$
Body width at the neck	0.13	$P < 0.01$

ity. Pairwise Wilcoxon tests revealed significant differences in disparity between most ecological categories ($P < 0.01$), suggesting that habitat specialization may constrain morphological variability, while generalist or high-mobility species occupy a broader morphospace.

Effect of Allometry on Shape

Phylogenetic multivariate regression of morphological traits on log-transformed SVL and habitat use revealed strong allometric effects across snake species (Table S6). Body size accounted for the majority of multivariate variation in head and body traits ($P < 0.01$), while habitat use also significantly influenced morphology ($P < 0.01$). Importantly, the interaction between SVL and habitat use was significant ($P < 0.01$, Table S6), indicating that allometric trajectories differ among habitat use categories. Pairwise comparisons of multivariate slopes confirmed that several groups showed significantly different allometric trajectories (Table S7), particularly in comparisons involving aquatic species (e.g., aquatic vs. arboreal, $P < 0.05$; aquatic vs. terrestrial, $P < 0.05$), while other habitat use showed similar trajectories (e.g., fossorial vs. semi-fossorial, $P = 0.787$). Visualization of regression scores in

morphospace highlighted partial ecological partitioning of size-dependent shape change, with arboreal, aquatic, and fossorial species following distinct allometric trajectories (Figure S7).

Discussion

Our results reveal clear associations between head and body shape variation and habitat use, supporting the idea that morphological diversification in snakes is strongly associated with habitat use, with different ecotypes promoting different rates of character evolution. Terrestrial and semi-fossorial species occupy a broad region of the morphospace, reflecting extensive morphological variation likely shaped by both phylogenetic history and environmental heterogeneity (Burbrink & Myers, 2015; França et al., 2008). In contrast, arboreal species, although spanning the full range of PC1, tend to cluster at low values of PC2 and PC3. This distribution indicates shared morphological tendencies such as elongated and slender bodies, narrow tails, and moderately broad heads with relatively wide inter-ocular distances. These features likely enhance balance, grip, and depth perception when moving through complex three-dimensional habitats. Such patterns align with previous findings suggesting that arboreal snakes often evolve elongated, agile morphologies optimized for branch navigation and stability (Alencar et al., 2017; Esquerré & Keogh, 2016). These results illustrate how ecological pressures can channel morphological diversification along specific adaptive axes, a concept broadly applicable to other elongate vertebrates and taxa with similar homogenous body plans. Similar trends in body elongation and limb reduction have been documented in arboreal lizards and frogs, where elongated forms appear to facilitate locomotion in structurally complex environments (Gans, 1970; Moen et al., 2016).

Aquatic and semi-aquatic species occupy the middle to upper regions of PC1 and PC3, with intermediate values along PC2, reflecting a relatively small and compact head, an elongated trunk and tail, and balanced body proportions. These features likely enhance swimming efficiency and maneuverability in aquatic environments (Brischoux & Shine, 2011; Segall et al., 2016). Fossorial species, in contrast, cluster in the middle of PC1 and PC3 and the upper region of PC2, exhibiting balanced head and body proportions with a slightly more robust trunk and tail, adaptations that facilitate burrowing and movement through substrates (Strong et al., 2021). Together, these patterns highlight not only snake-specific adaptations but also general principles whereby habitat-imposed biomechanical constraints shape morphology, suggesting predictable evolutionary responses across lineages. Comparable functional trends have been observed in other elongate vertebrates, such as limbless lizards and caecilians, suggesting that similar ecological pressures often drive convergent evolution towards streamlined or compact body plans across diverse lineages (Greer, 1991; Wiens et al., 2006).

Our analysis revealed significant differences in body size and shape across habitat use (Figure 4). Arboreal, semi-arboreal, and semi-aquatic species tend to be longer than aquatic, fossorial, semi-fossorial, and sand-dwelling species, with arboreal and semi-arboreal snakes exhibiting the greatest total length, whereas fossorial and sand-dwelling species are shorter, likely facilitating burrowing and reducing friction with the substrate. In terms of body shape, sand-dwelling and fossorial species were allometrically wider, probably optimizing space for the epaxial muscles powering forward movement during burrowing (Gans, 1970; Newman & Jayne, 2018). Aquatic and semi-aquatic species were also relatively wide, enhancing surface area for efficient swimming, while arboreal and semi-arboreal species were the most slender, likely improving maneuverability and gap-bridging in complex three-dimensional habitats (Jayne, 2020).

Sand-dwelling, terrestrial, arboreal, semi-arboreal and semi-aquatic species had significantly longer heads compared to fossorial and semi-fossorial species (Figure 4). Sand-dwelling species also exhibited wider and taller heads than fossorial and semi-fossorial species. Overall, sand-dwelling species displayed the most robust heads, exhibiting allometrically longer, wider, and taller dimensions. Aquatic and semi-aquatic species had a similar head width and height, with semi-aquatic species displaying relatively taller heads than aquatic snakes. We found similar patterns as Fabre et al. (2016), where aquatic and semi-aquatic species were shown to have comparable head widths. However, semi-aquatic snakes tend to have relatively taller heads, possibly reflecting adaptations to their dual-environment lifestyle. In addition, aquatic species had the shortest inter-nostril distance among all groups, due to the dorsal placement of their nostrils, which allows breathing while the body remains submerged, an adaptation to aquatic lifestyle (da Silva et al., 2017). Similarly, semi-aquatic species had relatively narrow heads, resembling their fully aquatic counterparts. Fossorial and semi-fossorial species had the shortest jaws and quadrates, likely reflecting adaptations for substrate penetration and reducing the cost of burrowing (Figure 4). Semi-fossorial species exhibited the shortest inter-ocular distances among all groups, suggesting eyes positioned on top of the head allowing to detect predators while being partially hidden in the substrate. In contrast, arboreal species had great inter-ocular and eye-nares distances, forming a more triangular head shape and reflecting their elongated and pointed head morphology. This pattern aligns with observations of arboreal snakes, which often exhibit elongated heads that facilitate depth perception and thus movement and navigation in complex three-dimensional environments (Jayne & Riley, 2007). The combined patterns of body and head morphology across habitats demonstrate generalizable evolutionary principles: environmental constraints and functional demands shape morphological diversity in predictable ways, while phylogenetic history modulates the specific solutions that arise.

Our results strengthen the idea that the physical constraints imposed by different habitats shape morphological disparity as evidenced by significant pairwise differences across all habitat use. Morphological disparity patterns reveal that semi-fossorial, semi-arboreal, and semi-aquatic species tend to resemble their terrestrial counterparts more than their fully specialized relatives. These observations support our hypothesis that highly specialized habitats exhibit more homogeneous morphological features, whereas non-specialist habitat use display significant morphological heterogeneity (Figure 4). Arboreal species exhibit an intermediate level of morphological disparity. Similarly, aquatic species tend to exhibit a broader range of morphological features compared to semi-aquatic species. Sand-dwelling and fossorial habitat use appear to be similarly disparate.

The test for morphological similarities among fossorial and aquatic species showed that species in these habitat use do not strongly resemble each other. Thus, similar functional pressures can lead to different morphological solutions, emphasizing the role of evolutionary contingency and many-to-one map-

ping (Thompson et al., 2017; Wainwright et al., 2005) alongside adaptive strictly convergent responses. Semi-aquatic species also do not show a strong morphological similarity. Similarly, semi-arboreal species show only moderate morphological similarity, and their evolutionary timing does not support a strong historical trajectory towards a shared phenotype. Semi-fossorial and sand-dwelling species do not show strong clustering in morphospace, suggesting weaker morphological association with habitat use in these groups. In contrast, terrestrial species occupy a more restricted region of morphospace, indicating that ground-dwelling species tend to share similar morphological traits. The recent study of `Tingle et al. (2024) aligns with our conclusion that functional diversity can lead to varied morphological outcomes rather than strict convergence. However, our test for convergent evolution using Stayton's distance-based metrics (C1–C4) provides a more nuanced perspective. While we found that functional constraints do not always produce identical adaptations across all groups, certain habitats—most notably the arboreal group—exhibit robust and significant convergence across all metrics. This confirms that for lineages facing the biomechanical demands of three-dimensional environments, evolution has repeatedly pulled morphology towards a highly specific adaptive optimum. Furthermore, our findings align with studies which emphasize functional constraints over strict similarity, reinforcing the idea that biomechanical pressures do not always produce identical morphological adaptations (Moon et al., 2019; Vincent et al., 2006). Nevertheless, the detection of significant convergence in terrestrial and semi-arboreal groups (C1 and C2 metrics) suggests that while evolutionary pathways may differ, there is a predictable reduction in morphological distance when lineages enter similar ecological zones. Similarly, recent studies have shown convergence in head shape and feeding systems, suggesting that specific functional traits may be more prone to convergence than an animal's overall morphology (Deepak et al., 2023; Sherratt et al., 2018). It is also important to acknowledge that current methods for detecting similarity have limitations. As highlighted by Grossnickle et al. (2024), similarity metrics can be sensitive to phylogenetic uncertainty, trait selection, and the scale of analysis, which may obscure or exaggerate true evolutionary patterns.

Our findings provide a more nuanced understanding of the constraints imposed by habitat use in species with a uniform body plan. While studies, such as those of Deepak et al. (2023) and Esquerre´ & Keogh (2016), focused on the convergence of head shape and body form in response to habitat use, our analysis extends these ideas by showing that morphological traits are not only similar among species occupying the same habitat, but also strongly influenced by ecological factors across the phylogeny. For example, in birds, macroevolutionary analyses reveal that morphological form is organized along predictable axes in relation to dietary ecology and feeding mode (Pigot et al., 2020). Similarly, in mammals, feeding ecology drives mandibular shape in carnivorans, whereas cranial morphology is strongly modulated by phylogenetic and developmental constraints (Ferreira-Cardoso et al., 2022; Law et al., 2022). This demonstrates that, across vertebrates with very different body plans, ecological pressures can channel morphological diversification along certain functional dimensions, while phylogenetic and developmental constraints modulate the exact solutions that evolve.

The comparison of raw morphometric data and size-standardized shape (LSR) provides key insights into the hierarchical nature of snake morphological evolution. In our analyses of raw measurements, a multiple-rate Brownian motion model (BMM) was favoured, indicating that evolutionary rates differ among habitats, primarily due to shifts in absolute body size. Body size is an exceptionally well-studied trait in snakes and is often considered a primary axis of diversification (Boback & Guyer, 2003; Feldman et al., 2016). Our findings align with the view that much of snake evolution is driven by selection on size itself, which in turn predictably reshapes the phenotype through allometric scaling (Pyron & Burbrink, 2009). However, after standardizing for absolute scale using LSRs, an OU model was preferred indicating that habitat use is also associated with distinct adaptive optima in allometry-retaining shape space. This suggests that while size is a dominant driver, it does not account for all morphological variation. The significant interaction between SVL and habitat use further confirms that allometric trajectories are shaped by selective pressures (Esquerré et al., 2017). As noted in other major vertebrate radiations, such as teleost fishes (Price et al., 2019), examining both size-standardized shape and allometric trajectories is essential to understanding how morphological and ecological diversity is generated. This decoupling of size and shape suggests that selection may act primarily on size in generalist lineages, but switches to target specific body proportions—such as head robustness or trunk slenderness—when species enter highly specialized niches (Sherratt et al., 2025). For example, the specialized requirements of aquatic or fossorial lifestyles appear to pull taxa away from generalized allometric trends towards isolated adaptive optima.

While our study provides insights into how habitat use is associated with repeated morphological patterns in snakes, there are limitations in the study design and data analysis. One significant limitation is the exclusion of dietary factors from our analysis. Diet plays a critical role in shaping animal morphology, particularly head size and shape (Deepak et al., 2023; Hudry & Herrel, 2025). Cranial traits are highly adapted to prey items among several species, suc as in birds or bats (Felice et al., 2019; Ramírez-Fráncel et al., 2021). By focusing primarily on habitat use, we may have overlooked how variation in diet contributes to morphological diversity. For example, skinks that specialize in herbivory developed a relatively wider heads compared to insectivorous species, whereas habitat use does not seem to be correlated with morphological features or bite force (Saulnier-Masson et al., 2023). Incorporating dietary data could provide a more comprehensive understanding of the factors driving morphological convergence. Future research should integrate dietary information to explore how diet-specific adaptations influence morphological similarity, as an understanding the relationship between habitat use, prey type, foraging mode, and head morphology is essential for revealing how ecological pressures related to feeding drive morphological evolution. Additionally, while our study provides a detailed morphometric analysis, future research could benefit from more precise descriptions using geometric morphometrics to map morphological similarity with higher precision (Melchionna et al., 2021).

Although we aimed to encompass the broad phylogenetic and ecological diversity of snakes, our sampling was ultimately constrained by the availability of specimens in museum collections. This resulted in unbalanced sample sizes across habitat use categories. Larger within-group disparity in more speciose categories (such as terrestrial species) could therefore partly reflect sampling richness rather than biological reality. Disparity metrics are known

to be sensitive to unequal sample sizes (Jones & Close, 2024), which may influence comparisons among habitat use. Future work could evaluate this effect through systematic subsampling procedures (e.g., rarefaction by randomly selecting an equal number of species per habitat use category and repeating the analysis), which would allow a more explicit assessment of sample size dependence in disparity estimates. Additionally, ontogenetic variation can influence cranial and postcranial morphology in snakes, often associated with shifts in feeding mechanics and prey type during growth (Patterson et al., 2022; Vincent et al., 2007). However, the magnitude and direction of these ontogenetic trajectories vary markedly among clades (Esquerré et al., 2017; Palci et al., 2016), suggesting that developmental effects on morphology are not uniform across lineages. Thus, while our dataset likely incorporates some degree of ontogenetic variation, these differences are unlikely to introduce a systematic bias at the macroevolutionary scale. Despite these limitations, our dataset remains representative of the major ecological strategies and phylogenetic breadth in snakes, and the observed patterns should be interpreted within this sampling context.

Finally, in this study, we defined convergence broadly as the tendency of distantly related species to exhibit similar phenotypes when occupying similar habitats, irrespective of whether these phenotypes arose from distinct ancestral morphologies. Although stricter definitions of convergence focus only on traits independently evolving from distinct ancestral states (Bolnick et al., 2018), we adopted this broader approach to test whether habitat consistently shapes morphology at macroevolutionary scales, even without explicitly reconstructing ancestral states. Our results indicate that habitat use imposes predictable selective pressures that channel morphology along similar functional axes, but we cannot confirm whether these similarities represent "true" convergence under stricter definitions. Further studies incorporating ancestral state reconstructions or phylogenetic simulations could evaluate whether the observed patterns reflect independent evolution from divergent ancestors, providing a more rigorous test of convergence across snake lineages.

Conclusion

Our study underscores the critical role of habitat use in shaping morphology in snakes, revealing how similar ecological pressures can drive the evolution of comparable traits across distinct lineages. By examining variation in absolute size, body and head shape across a diverse range of species, we provide insights into the complex interplay between morphology, ecology, and evolutionary history. While some habitat types promote morphological homogeneity, others allow for greater disparity, reflecting differing degrees of functional constraints. Importantly, our findings suggest that convergence in snake morphology is not uniform but instead results from multiple adaptive pathways rather than a single evolutionary trajectory. This nuanced perspective highlights the importance of considering both ecological constraints and functional diversity when interpreting patterns of morphological evolution. Future research integrating dietary factors, geometric morphometrics, and finer-scale ecological data will further refine our understanding of how snakes—and other taxa—navigate the balance between specialization and morphological diversity in response to their environments.

Supplementary Material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data Availability

The data that support the findings of this study are openly available on Github at https://doi.org/10.5281/zenodo.20819574. Phylogenetic tree data were reused from Title et al. (2024) and are available via Dryad at https://datadryad.org/dataset/doi:10.5061/dryad.p5hqbzkvb.

Author Contributions

David Hudry (Conceptualization [equal], Data curation [lead], Formal Analysis [supporting], Investigation [lead], Methodology [supporting], Project administration [supporting], Resources [lead], Software [lead], Visualization [lead], Writing – original draft [lead], Writing – review & editing [equal]), Anthony Herrel (Conceptualization [equal], Data curation [supporting], Formal Analysis [lead], Investigation [equal], Methodology [lead], Project administration [lead], Resources [supporting], Software [supporting], Supervision [lead], Validation [lead], Visualization [supporting], Writing – review & editing [lead])

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Conflicts of Interest

None declared.

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