

1 **Interaction Between Fitness and Genetic Diversity May Lead**
2 **to the Relatively High Diversification of Active Foragers**

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17 **Abstract**

18 Differences in the diversification of species across the Tree of Life may emerge from
19 the ecological and evolutionary consequences of organismal traits. Foraging behavior
20 may influence species diversification through its effects on fitness and genetic diversity.
21 Different foraging strategies can be expected to alter patterns of movement, gene flow,
22 and adaptation in different ways. Active foragers travel widely in search of food, poten-
23 tially increasing genetic divergence through local adaptation to different environments.
24 By contrast, limited movement of sit-and-wait foragers may reduce gene flow among
25 populations, prompting genetic divergence through isolation. Behavioral plasticity in
26 foraging may provide a third pathway by exposing previously hidden genetic variation
27 to selection. To test these predictions, we conducted a comparative analysis of 997
28 reptile species that vary in their locomotor behavior while foraging. We found that
29 the net diversification of reptiles depends on an interaction between foraging behavior
30 and unobserved factors. Specifically, active foragers appear to have the highest species
31 diversification. This observation may be the result of the positive association between
32 lifetime reproductive output and genetic diversity in active foragers, which may confer
33 them more potential variation for selection to act upon. By contrast, fitness of plastic
34 and sit-and-wait foragers appears to decrease with genetic diversity. In this context,
35 genetic costs associated with plastic and sit-and-wait foraging might have a constrain-
36 ing effect on species diversification. We used genomic data and macroevolutionary
37 observations supported by microevolutionary processes to provide key insights into
38 mechanisms of diversification.

39 **Keywords:** Heterozygosity, plasticity, speciation, reproductive effort.

40 Introduction

41 The process of species diversification can result from differences in fitness among organ-
42 isms given variation in their genomes and environments (Orr, 2009). Often, researchers
43 rely on the notion of “fitness landscapes” to visualize how the process of diversification
44 can occur (Wright, 1931). Variation in fitness arises through the interplay of an or-
45 ganism’s genotype, its movement across different habitats, and dynamic environmental
46 factors (Figure 1). As organisms continuously explore heterogeneous environments, ge-
47 netic and phenotypic changes may generate distinct survival and reproductive payoffs
48 (Orr, 2009; Mall et al., 2025). A prevailing prediction derived from the theory of fitness
49 landscape is that many speciation events, and indeed entire adaptive radiations, re-
50 sult from local adaptation as species explore and colonize new environments (Wright,
51 1931; Gavrillets, 2010). Because movement patterns generate consistent differences
52 in the spatial displacement of organisms across such landscapes, they offer a natural
53 comparative framework to link organismal features to macroevolutionary patterns of
54 diversification. In this context, three common types of movements could play a piv-
55 otal role in shaping species diversification: dispersal, migration, and foraging (Clobert,
56 2012; Jeltsch et al., 2013). Among reptiles, foraging movements are arguably the most
57 extensively examined (Reilly et al., 2007). Perhaps, this is because only a tiny fraction
58 (under 1%) of the roughly 12,500 known reptile species are considered true migrants
59 (Alerstam et al., 2003). While many reptiles engage in seasonal localized movements
60 to find food, overwintering dens, or nesting sites (Rutherford and Gregory, 2003), only

61 a few highly specialized groups (primarily marine turtles and some snakes) undertake
62 long-distance migrations (Southwood and Avens, 2010; Hart et al., 2021). In regard
63 to dispersal, empirical measures of dispersal are notoriously difficult to track, leaving
64 direct, high-quality data extremely rare across taxa (Driscoll et al., 2014; Rogers et al.,
65 2019; Wilkinson et al., 2025).

66 **Figure 1.**

67 Among the common types of movements described above, we focus here on for-
68 aging. While reflecting a continuum, foraging behavior tends to fall into different
69 general strategies. Active foragers can spend large fractions of each day in continual
70 movement, encountering predators, conspecifics, different habitats and associated en-
71 vironmental conditions, and a wide range of potential prey items (Pianka, 1966; Huey
72 and Pianka, 1981; Cooper, 2005; Padilla-Perez et al., 2025). Meanwhile, sit-and-wait
73 foragers can move little or not at all for days or even weeks at a time, experiencing
74 the full range of environmental variation in one spot as opposed to making frequent
75 decisions about where to be, what prey to look for, how to remain safe from predators
76 while moving (Pianka, 1966; Webb and Shine, 1997; Cooper, 2005). These foraging
77 behaviors are radically different, and yet can be found across squamate reptiles, along
78 with species exhibiting a plastic strategy that enables them to facultatively switch be-
79 tween active and sit-and-wait foraging (Greeff and Whiting, 2000). While theoretical
80 models of optimal foraging suggest that search strategies and resource tracking should
81 influence dispersal distances or probabilities (Schoener, 1971), empirical data directly
82 linking specific foraging behaviors to variation in dispersal remains scarce (Shaw, 2020).

83 However, even in the absence of direct empirical data supporting this connection, data
84 on geographic ranges can be used as proxy for dispersal, given that geographic range
85 size and dispersal capacity are positively related (Alzate and Onstein, 2022).

86 Foraging behavior may influence diversification through multiple, potentially op-
87 posing pathways. On one hand, differences in movement and dispersal may alter geo-
88 graphic range size (Castiglione et al., 2017), and therefore, opportunities for speciation
89 and buffering against extinction (Claramunt et al., 2012). On the other hand, they
90 may modify patterns of gene flow among populations, with contrasting consequences
91 for genetic differentiation and speciation (Suárez et al., 2022). Relatively long distance
92 travel by active foragers may enable species to maintain extensive geographic ranges
93 where high levels of dispersal facilitate the colonization of new habitats (see Figure 1;
94 De Fraga et al., 2017). By contrast, relatively short distance travel by sit-and-wait
95 foragers constrains the dispersal potential of species and might confine them to narrow
96 geographic ranges (see Figure 1; De Fraga et al., 2017). Plastic foragers might occupy
97 a dynamic distribution, wherein geographic range boundaries may fluctuate elastically
98 alongside the spatial predictability and seasonal availability of resources (Donihue,
99 2016). Furthermore, a high mobility in active foragers is expected to increase rates
100 of gene flow among populations, thus constraining genetic diversity (Suárez et al.,
101 2022). Over an evolutionary timescale this is expected to suppress speciation events
102 and thus clade level diversification (Claramunt et al., 2011; Weeks and Claramunt,
103 2014). By contrast, low mobility in sit-and-wait forages may favor reduced gene flow
104 among populations, which in turn results in the increased genetic variation among
105 them through random mutation and genetic drift (Gavrilets, 2014), potentially driv-

ing strong allopatric population differentiation (Burridge and Waters, 2020; Ortego et al., 2021), or parapatric speciation at the edge of the species' range (Castiglione et al., 2017). In plastic foragers, species diversification is expected because plastic responses can reveal previously hidden genetic variation that can be more effectively selected for (Noble et al., 2019). Plastic responses that result in the exposure to a novel environment may also be associated with a general increase in additive genetic variation (Gibson and Dworkin, 2004). However, plasticity may impose genetic costs that result directly from linkage between loci affecting plasticity and loci with negative fitness effects, pleiotropic effects of loci affecting plasticity and other traits, or negative epistatic interactions among loci affecting plasticity and other loci (Auld et al., 2009). The cost of plasticity can then be assessed by comparing the effects of the interaction between foraging behavior and genetic diversity on the fitness of organisms.

Together, these considerations suggest that foraging behavior could influence diversification through multiple, potentially contrasting pathways involving range dynamics, genetic diversity, and fitness. Yet, these components have largely been studied in isolation, making it difficult to assess their combined contribution to macroevolutionary patterns. This study explored variation in net diversification and speciation rates of reptiles based on the foraging behavior and genomic attributes of species. To our knowledge, foraging has been investigated in great detail over the past decades, but its implications for species diversification have been examined only in a few cases and across taxa different from reptiles (e.g., Fernández et al., 2018; López-Fernández et al., 2014). Overall, we contend that foraging is worth evaluating because it is known for most squamates and because it represents an encapsulation of important distinctions

129 in the ways that animals encounter new environments.

130 **Materials and Methods**

131 *Trait data source*

132 We used a comprehensive database of ecological, behavioral, and life-history traits to
133 investigate patterns of diversification among reptiles (Oskyrko et al., 2024). Specif-
134 ically, our analyses focused on predicting diversification rates based on the foraging
135 behaviors of species. We classified foraging behavior based on whether the species
136 have been reported as active forgers, sit-and-wait foragers, or using a combination
137 of both strategies ("plastic") contingent on the availability of resources (Meiri, 2018).
138 While relatively crude, these categorizations remain useful to biologists for defining the
139 extremes of a continuum. Our investigation included foraging behavior data for 997
140 species of squamate reptiles distributed among 56 families. These data were mainly
141 used for estimating ancestral character state and net diversification of species across
142 the reptile phylogeny. Although 997 species covers only 8% of all reptiles, our analy-
143 ses may be statistically powerful as the species examined span across lizards, snakes,
144 turtles, crocodilians, worm lizards, and the tuatara (i.e., all of the 4 existing reptile
145 orders). However, we invite future work to build upon these findings.

146 To examine variation in fitness across species, we collected data of lifetime repro-
147 ductive output corrected for the species' masses. We defined lifetime reproductive
148 output as the product between the average clutch sizes of species, their average num-
149 ber of clutches per year, and their longevity. We then regressed this quantity on the
150 maximum body mass of the species (g) and used the residuals of this regression as the

151 response variable in our models. Lifetime reproductive output is a good proxy because
 152 it integrates both major components of fitness: survival and fecundity (Van Daalen
 153 and Caswell, 2017). As ecological predictors, we included foraging behavior and area of
 154 geographic ranges of species (km^2). We also included genomic predictors in our models
 155 such as heterozygosity as describe below. To estimate the area of the species' ranges,
 156 we used the species' polygonal range maps provided by Roll et al. (2017), and ran a
 157 Zonal Statistical analysis in the software QGIS (QGIS Development Team, 2025). This
 158 tool enabled us to compute the total area across pixels of the species' range maps. To
 159 account for species relatedness, we informed our models with a time-calibrated phy-
 160 logeny of squamate reptiles (Zheng and Wiens, 2016). We fitted a number of competing
 161 models based on different interactions and main effects of our predictors, and selected
 162 the most likely one based on information theory (e.g., AIC values). All variables in
 163 the models were log-transformed, and we accounted for phylogenetic relationships in
 164 the models with the function *gls* from the library "nlme" (Pinheiro et al., 2007) in the
 165 free software for statistical computing R (R Core Team, 2023).

166 *Genomic data source*

167 Because differences in fitness could result from variation in genetic diversity as or-
 168 ganisms with distinct allele combinations interbreed (Waters et al., 2020), we ex-
 169 amined the relationship between heterozygosity and the fitness of species. To do
 170 this, we systematically obtained data of Restriction-site Associated DNA sequencing
 171 (RAD-seq) from The National Center for Biotechnology Information (NCBI; <https://www.ncbi.nlm.nih.gov/>). Subsequently, we computed estimates of heterozygosity

173 for 22 squamate species distributed among 9 families. Importantly, the number of
174 species with data of heterozygosity is dramatically low compared to the availability of
175 trait data. Thus, our results in this context should be carefully interpreted and will
176 require further evaluation as more data become available.

177 We collected RAD-seq data for species with at least 5 individuals sampled to obtain
178 a reliable estimate of heterozygosity. Also, we focused on single-end reads per species
179 to minimize potential effects of the sequencing method. We assembled and analyzed
180 the data with `ipyrad` based on its default parameter settings. To ensure high-quality
181 variant calls, we performed filtering using `bcftools v.1.21`. Genotypes with a se-
182 quencing depth (DP) of less than 10 reads were first set to missing. Subsequently,
183 we filtered the dataset to retain only biallelic single nucleotide polymorphisms (SNPs)
184 with a maximum missing data rate per site of less than 20% (`F_MISSING < 0.2`).
185 Lastly, we used `VCFtools v.0.1.17` to estimate heterozygosity (H_e). We used the
186 `--het` flag on the filtered VCF file and generated output profiles for each sample de-
187 tailing the number of homozygous sites $O(HOM)$, the total number of evaluated sites
188 (N_SITES), and the estimated inbreeding statistic (F). Heterozygosity (H_e) is the
189 proportion of total sites that are heterozygous, calculated as $H_e = \frac{N_SITES - O(HOM)}{N_SITES}$.

190 We modeled the effects of heterozygosity and its interaction with range size, body
191 mass, and foraging behavior on the lifetime reproductive output of species. To do this,
192 we fitted a set of phylogenetic-corrected models with the function `gls` from the library
193 “nlme” of R (Pinheiro et al., 2007), and evaluated their goodness of fit based on AIC_c
194 values.

195 *Ancestral state reconstruction*

196 Because historical factors may have played an important role in the diversification
197 of species that we observe today (Blount et al., 2018), we inferred the evolutionary
198 history of foraging behaviors among reptiles. Character state reconstruction accounts
199 for historical factors by capturing how early shifts in the evolution of a trait dic-
200 tates subsequent phenotypic changes. Accordingly, we fitted a set of continuous-time,
201 discrete-state Markov chain models to sample the character histories from their poste-
202 rior probability distribution (Huelsenbeck et al., 2003), across a time-calibrated phy-
203 logeny of squamate reptiles (Zheng and Wiens, 2016). The models consisted of a an
204 equal-rates (ER) model, in which the rate of change between the three states of the
205 character were assumed to be equivalent. We also fitted an all-rates-different model
206 (ARD), which enables transitions among states to occur at different rates. Lastly, we
207 fitted a symmetrical model, which enables pairs of states to change at different rates
208 but changes among all states are theoretically possible. To fit the models, we used the
209 default arguments of the function *make.simmap* from the “phytools” library of R (Rev-
210 ell, 2012), and simulated 1×10^5 character maps. We then summarized the number of
211 state changes and the posterior probabilities of each internal node generated from the
212 character map simulations. We selected the most likely model based on *AIC* values.

213 *Models of diversification*

214 To explore whether foraging behaviors influenced the speciation and net diversifica-
215 tion of species, we relied on two models of diversification: 1) a multi-state speciation
216 and extinction model (MuSSE) and 2) a multi-state speciation and extinction model

217 with hidden states (MuHISSE). These models are a birth-death process in which the
 218 diversification of species are dependent on the state of an evolving character and unob-
 219 served factors (FitzJohn et al., 2009). In the case of the MuSSE model, we first defined
 220 a likelihood function, and then optimized it as required by the library *diversitree* of
 221 R (FitzJohn, 2012). The likelihood function requires a phylogenetic tree (Zheng and
 222 Wiens, 2016), a vector of numbers ranging from 1 to 3 (where 1 = active foraging, 2 =
 223 plastic foraging, and 3 = sit-and-wait foraging), the number of states ($k = 3$), and a
 224 vector specifying the proportion of species in each character state. We computed this
 225 proportion based on the ratio of the number of species for which we had data within
 226 each foraging state to the total number of squamate species currently reported on
 227 Reptile Database (see <http://www.reptile-database.org>). Subsequently, we con-
 228 strained this general likelihood function to fit different competing models. We started
 229 with a null model, in which all birth and death rates are equal between states. Next, we
 230 fitted the most complex model in which all rates of speciation and extinction depended
 231 on the character state for our multi-state character. Also, we fitted models in which
 232 only the speciation rate (λ) varied between states, only the extinction rate (μ) varied,
 233 and one in which neither λ nor μ varied, but the transition rates differed between types
 234 of transitions (e.g., ordered, unordered, etc.). We used the most likely model to run a
 235 Bayesian Markov chain Monte Carlo simulation (MCMC) with 1×10^5 steps to take, an
 236 exponential prior distribution, and the control parameter (w) suggested by FitzJohn
 237 et al. (2009). In the case of the MuHISSE model, we treated foraging behavior as a
 238 three-state trait and recoded into binary characters to fit the multicharacter frame-
 239 work, explicitly omitting the biologically absent fourth state combination (i.e., 00 =

active, 01 = plastic, 10 = sit-and-wait). We established a model structure containing two hidden state categories (A and B) to account for unobserved heterogeneous factors influencing diversification, yielding six valid state regimes (00A = active-A, 01A = plastic-A, 10A = sit-and-wait-A, 00B = active-B, 01B = plastic-B, and 10B = sit-and-wait-B). Within this framework, we allowed net turnover rates and extinction fractions (ϵ) to vary independently across all six valid combinations of observed and hidden states. We used the MuHiSSE function in R to execute parameter optimization and maximum likelihood estimates. As previously described, we compared the models' goodness of fit based on AIC_c and selected the most likely one for inferences.

We complemented the state-dependent diversification framework with a lineage-through-time plot, which consists of a visual representation of how the number of lineages within clades changed over time, essentially tracing the diversification history of the clades (Helmstetter et al., 2022). Importantly, the interpretation of this analysis remains inconclusive because a simple comparison of the total number of species between clades of different ages does not necessarily reflect consequences of species interactions even though species numbers differed.

Results

A MuHiSSE model with two hidden states was strongly supported by our analyses ($AIC_c = 9994.115$) relative to the MuSSE model ($AIC_c = 10076.030$; see supporting code here). Based on the MuHiSSE model, the diversification of reptiles is strongly mediated through a combination of observed foraging behaviors and unobserved states. Character state reconstruction revealed that active foraging appears to be the ancestral

262 state of all reptiles, with a posterior probability of 0.639 at the root of the tree (Figure
 263 2A). Although two major transitions from active foraging to sit-and-wait foraging
 264 occurred in Gekkota and Iguania, bursts of frequent transitions immediately followed
 265 within each of these clades, with most concentrated in transitions away from sit-
 266 and-wait foraging to other strategies (Figure 2A). Specifically, the highest number
 267 of transitions took place from sit-and-wait to active foraging (≈ 64), followed by a
 268 similar number of transitions from sit-and-wait to plastic foraging (≈ 57). Speciation
 269 rates (μ) demonstrate that active foraging consistently exhibits the highest speciation
 270 rates, increasing from 0.38 lineages/mya in state A to 0.46 lineages/mya in state B
 271 (Figure 2B). Conversely, sit-and-wait foraging is characterized by negligible speciation
 272 in state A (≈ 0.00 lineages/mya) and a minor elevation to 0.16 lineages/mya in state
 273 B (Figure 2B). Notably, plastic foraging undergoes a dramatic reduction in speciation
 274 rates between regimes A and B, plunging from 0.32 lineages/mya in state A down to
 275 0.05 lineages/mya in state B (Figure 2B).

276 Additionally, active foraging consistently maintains highly positive net diversifica-
 277 tion rates regardless of the underlying evolutionary context ($r_{\text{active-A}} = 0.38$; $r_{\text{active-B}} =$
 278 0.46 ; Figure 2C). By contrast, sit-and-wait foraging remains at or near zero net diver-
 279 sification across both regimes ($r_{\text{sit-and-wait-A}} \approx 0.00$; $r_{\text{sit-and-wait-B}} = 0.01$). Interestingly,
 280 plastic foraging seems to sink in state A, in which high extinction pressures potentially
 281 drive net diversification deeply into negative values ($r_{\text{plastic-A}} = -0.63$). However, they
 282 show a marginally positive net diversification rate in state B ($r_{\text{plastic-B}} = 0.05$), suggest-
 283 ing that diversification of plastic foragers is conditional upon the unobserved regimes.

284 **Figure 2.**

285 The accumulation of lineages from the root of the phylogeny to the present shows
286 that active foragers dominated for the first 200 million years since the origin of reptiles
287 in the tree of life. However, sit-and-wait foragers subsequently exceeded the number
288 of active foragers for about 100 million years. While the number of plastic lineages
289 appears to be increasing more recently, they exhibit consistently lower rate of lineage
290 accumulation (Figure 3A). Interestingly, a phylogenetic-informed model revealed that
291 the lifetime reproductive output among reptiles generally increases with range size re-
292 gardless of foraging behavior ($\beta = 0.098$, $Std.Error = 0.023$, $t = 4.172$, $p < 0.001$). In
293 other words, an interaction between range size and foraging behavior is not supported
294 by the data (Figure 3B).

295 **Figure 3.**

296 Lastly, an interaction between heterozygosity and foraging behavior indicates that
297 plastic and sit-and-wait foragers incur genetic costs. Our results show that the lifetime
298 reproductive output of plastic and sit-and-wait foragers decrease with heterozygosity,
299 while the opposite occurs in active foragers (Figure 4). Yet, further studies on the
300 association between heterozygosity and lifetime reproductive output are needed to
301 make robust conclusions.

302 **Figure 4.**

Discussion

Based on an analysis of nearly one thousand reptile species, we found that the diversification of reptiles is contingent on an interaction between foraging behavior and unobserved factors (Figure 2C). State-dependent diversification models (e.g., MuSSE) often attribute broad patterns of diversification entirely to focal traits. However, by utilizing a hidden state framework (MuHISSE), our results reveal that foraging behavior alone does not explain patterns of diversification in reptiles. The substantial variation in net diversification between hidden states A and B for identical observed traits—particularly the drastic shift in plastic foraging—confirms that unmeasured environmental or genomic factors strongly interact with behavior to shape species diversification. This result aligns with modern phylogenetic comparative theory demonstrating that omitting hidden rate heterogeneity can create severe Type I errors or obscure localized dynamics, such as severe extinction bottlenecks within flexible or specialized lineages (Beaulieu et al., 2013; Caetano et al., 2018; Herrera-Alsina et al., 2019). Furthermore, empirical studies have shown that while foraging behaviors carry major ecological and physiological correlates (Vitt and Congdon, 1978; Baeckens et al., 2023), their net impact on diversification is non-uniform and context-dependent due to differing consequences for reproductive frequency, vulnerability to predators, and habitat variation (Boyko and Beaulieu, 2021; Baeckens et al., 2023).

Previous hypotheses suggest that historical contingency has been a major determinant of the diversification pattern that we observe in modern-day reptiles (Vitt et al., 2003). The early evolution of specialized feeding-related traits in active foragers, such as jaw prehension to capture larger prey, may have enabled them to dominate for

almost 200 million years since the origin of reptiles (Figure 3A). The subsequent rise of sit-and-wait foragers may be linked to the emergence and spread of angiosperms (flowering plants) in the past 100 million years (van der Kooi and Ollerton, 2020; Jud et al., 2018). The habitat created by large-sized angiosperms potentially conferred a competitive advantage to sit-and-wait foragers adopting arboreal lifestyles where limited movements suited the restrictions that arboreality exerts on the locomotion of organisms (Astley and Jayne, 2007; Hyams et al., 2012). We assessed this idea quantitatively by fitting a generalized hidden markov model (HMM) through the function `corHMM` in R (see supplementary material; Beaulieu et al., 2013). This model enabled us to evaluate the evolutionary association between foraging behavior and microhabitat preference (arboreal vs. terrestrial) across 430 species. Overall, sit-and-wait foraging lineages were heavily biased toward an arboreal lifestyle, accounting for 48.4% of the total tree representation compared to 28.8% for terrestrial sit-and-wait lineages (Figure 5A). Conversely, active foraging lineages exhibited the opposite pattern, predominantly occupying terrestrial environments (14.7%) rather than arboreal ones (8.1%), demonstrating that active foragers are mostly terrestrial (Figure 5A). The model placed the vast majority of these lineages within regime 1, indicating that the dominant sit-and-wait/arboreal phenotype thrives within a fast evolutionary rate category across reptiles (Figure 5B).

Figure 5.

Explaining variation in speciation and diversification of species across the tree of life is an important challenge for evolutionary biologists. Most of the work on

348 this topic has focused on associations between key innovations or historical factors
349 and species' diversification (Ricklefs, 2004). But the role of foraging behavior on
350 species diversification has received less attention. Foraging behavior becomes crucial
351 to understand patterns of species diversification because it influences the fitness of
352 an organisms by governing its energy intake, survival rate, and reproductive success
353 (Padilla-Perez et al., 2022). Natural selection strongly favors organisms that employ
354 efficient foraging strategies to maximize their net energy gain while minimizing the
355 time and energy spent searching and processing food (Schoener, 1971; Padilla-Perez
356 et al., 2025). In addition, some evidence show an association between foraging and
357 dispersal (Edelsparre et al., 2014), which ultimately determines the geographic range
358 sizes of organisms and increases opportunities for speciation in predictable ways as
359 described earlier. Interestingly, our data show that fitness generally increases with
360 range size among reptiles, but the rate of increase is not affected by the foraging
361 behavior of species (Figure 3B). Because we expected active and plastic foragers to
362 have large ranges given their high vaigility relative to sit-and-wait foragers, our results
363 do not entirely support our predictions and motivate us to further examine how active
364 and plastic foragers show higher species diversification than sit-and-wait foragers do.

365 To elucidate potential mechanisms of diversification, let us consider the variation
366 in genetic diversity among species with different foraging behaviors. Our findings in-
367 dicate that fitness of active foragers increases with heterozygosity, while the opposite
368 pattern occurs in plastic and sit-and-wait foragers (Figure 4). When fitness increases
369 with genetic diversity, there is more potential variation for selection to act upon,
370 increasing adaptive potential and population viability in the face of environmental

371 change (Reed and Frankham, 2003). By contrast, a decreased fitness with genetic
372 diversity suggests a genetic cost. In plastic species, genetic costs may generally lead
373 to constraining effects, but it could also contribute to genetic divergence (Price et al.,
374 2003). For instance, as plastic foragers travel across heterogeneous environments, ge-
375 netic divergence is expected as gene combinations favored under the locally prevailing
376 conditions are not useful in distant environments (Waddington, 1961). If selection
377 acts on the new genetic variation supplied by plasticity, then different lineages might
378 become adapted to and simultaneously develop genetic preferences for different eco-
379 logical niches (Alatalo and Gustafsson, 1988). Furthermore, if species span a large
380 or fragmented geographical range, as expected in sit-and-wait foragers, localized sub-
381 groups can accumulate distinct sets of alleles strictly by chance. In small and isolated
382 populations, random genetic drift and reduced gene flow can lead to unique genetic
383 incompatibilities, potentially driving strong allopatric speciation (Suárez et al., 2022).

384 Overall, we provide a set of potential scenarios by which the process of diversifi-
385 cation could occur in reptiles. Our framework places emphasis on the ways in which
386 variation in foraging behavior alters dispersal, allowing them to effectively explore
387 different fitness peaks. Foraging can be considered a distillation of major aspects of
388 lifestyle that can affect a wide range of physical conditions, physiological processes,
389 and ecological interactions. Selection is known to be associated with different patterns
390 of movement, different patterns of prey selection, different degrees of exposure to pre-
391 dation risk, and other factors (Padilla-Perez et al., 2022). On one level, it may not be
392 surprising that we uncovered strong patterns of association between foraging and pat-
393 terns of diversification. That relative rates have shifted across time is even stronger

evidence of the dialogue between changes in the environments of the earth and the strategies that animals use to detect and subdue prey. This positive result does not, by itself, help us to understand the cause. It is clear that additional study of associations between foraging behavior and dispersal will be well worthwhile. Whatever is found from such work, the encompassing nature of foraging mode means that evaluation of additional hypotheses will be needed as well. For instance, some evidence suggests that a high dispersal is expected to favor high rates of gene flow (Suárez et al., 2022). In contrast to our predictions, over an evolutionary timescale gene flow is expected to suppress speciation events and thus clade level diversification in active foragers (Claramunt et al., 2012; Weeks and Claramunt, 2014). Future directions should address the question of whether foraging behavior and dispersal are actually linked to each other. To our knowledge, studies comparing dispersal among reptile species varying in foraging behavior are scarce in the literature. Therefore, more compelling evidence is required to conduct meaningful comparative analyses of dispersal and its connection to the diversification of reptiles.

Data Accessibility Statement

A fully reproducible workflow of the data analyses, including R scripts and additional supporting material, is available in the following repositories: Posit connect <https://019a84d9-a4f4-2e37-1da7-b7af9aee1c62.share.connect.posit.cloud/>. A dryad link will be available upon acceptance: .

414 Conflict of interest

415 The authors have declared no competing interests.

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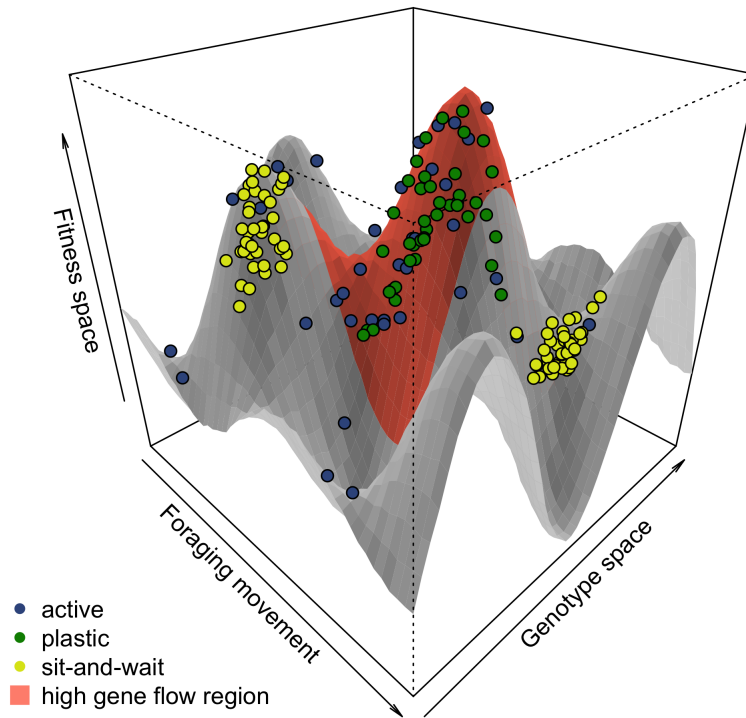


Figure 1: Hypothetical fitness landscape depicting populations of an active forager, a plastic forager, and a sit-and-wait forager navigating a fitness landscape. The “genotype space” in a fitness landscape is the multi-dimensional “ground” where every possible genotype exists as a location. The “height” at each location, or its position on the landscape, represents the fitness of that specific genotype. Therefore, the genotype space defines the relationship between all possible genetic makeups and their associated levels of fitness, which helps visualize how evolution operates. Solid dots represent individuals.

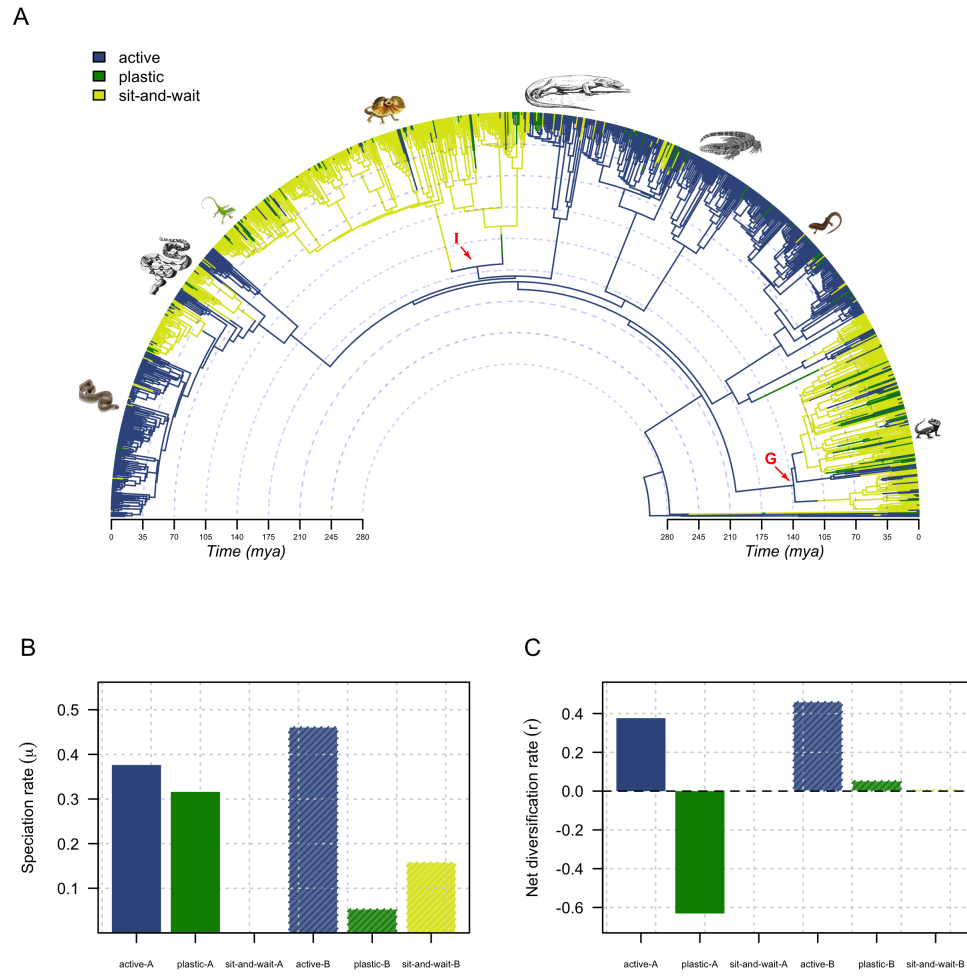


Figure 2: A) Random sample of 1×10^5 simulated character maps depicting the evolution of foraging behaviors among 997 reptile species. Clades where major transitions have occurred are indicated as follows: G = Gekkota, I = Iguania. B) Comparison of speciation rates between clades as expected by a MuHISSE model of diversification. C) Net diversification between clades as expected by a MuHISSE model of diversification.

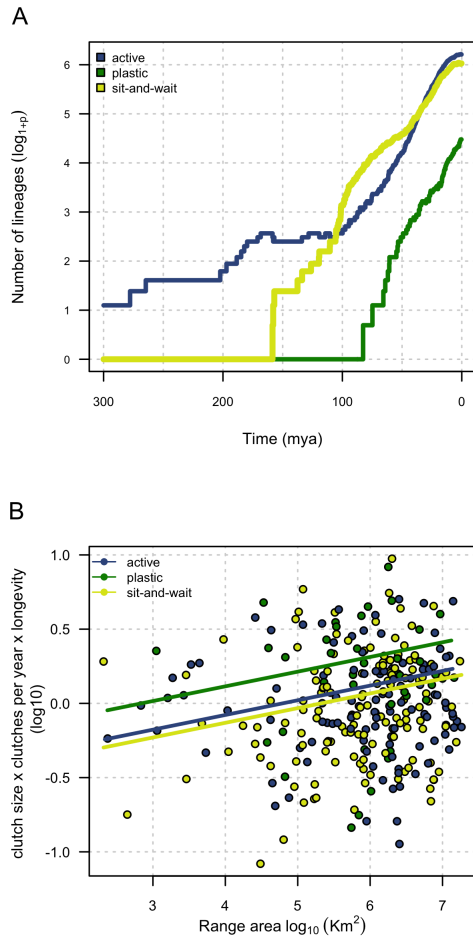


Figure 3: A) Lineage-through-time plot illustrating the accumulation of lineages within clades defined by the foraging behavior of species. B) Relationship between the lifetime reproductive output of species as a function of their geographic range sizes and foraging behaviors. Dots represent species.

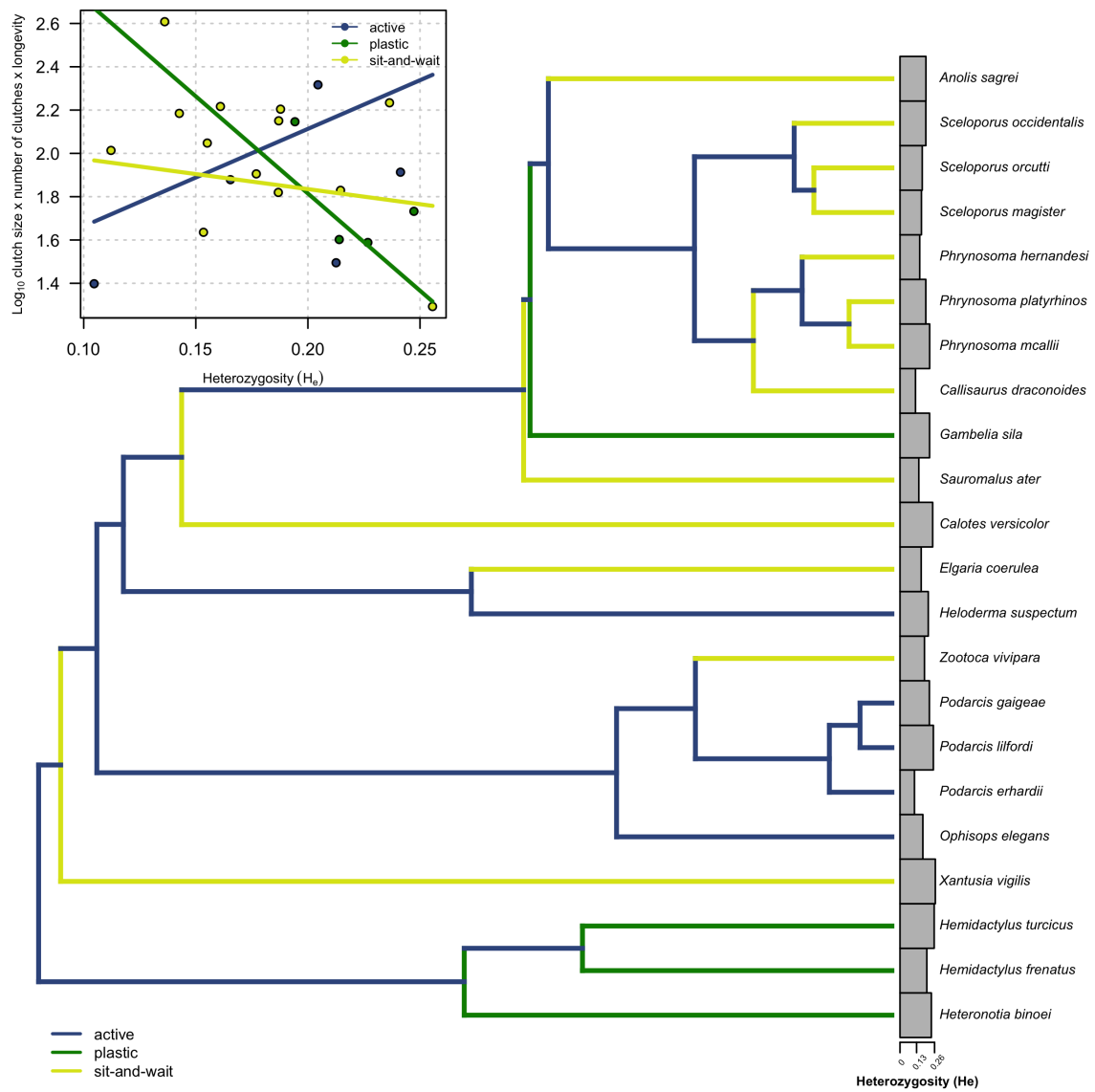


Figure 4: A) Relationship between heterozygosity, lifetime reproductive output, and foraging behavior across a squamate phylogeny. Although heterozygosity significantly affects lifetime reproductive output among species of reptiles, the scatter in the data suggests that a further evaluation of this trend is needed as more data becomes available. Dots in the scatter plot represent species.

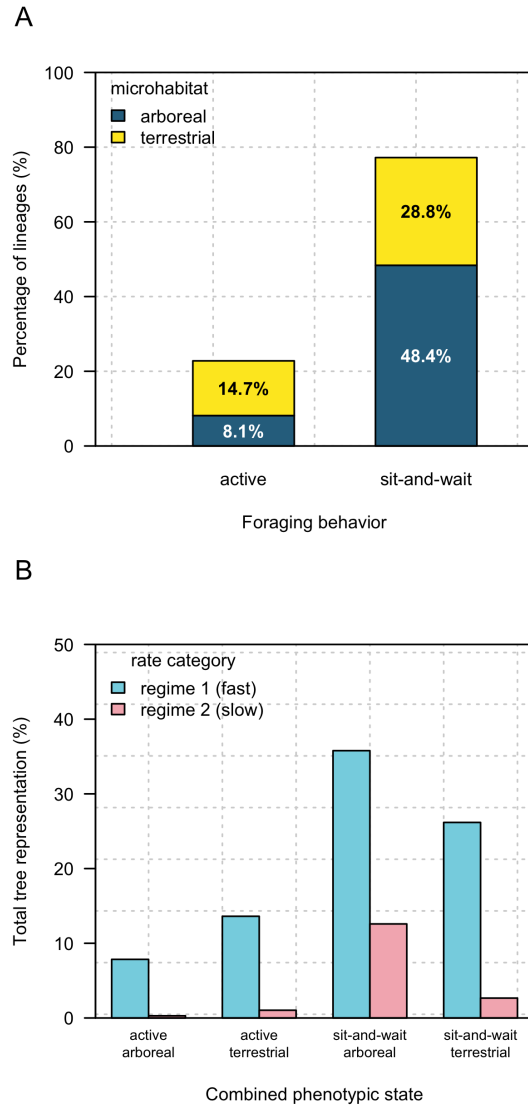


Figure 5: Marginal tip probabilities of foraging behavior and microhabitat preferences across 430 reptile species based on the best-fitting equal rates hidden markov model. A) Stacked distribution of microhabitat use (arboreal vs. terrestrial) across distinct foraging behaviors (active vs. sit-and-wait). Values inside the bars represent the total percentage of lineages reconstructed for each joint state configuration across the entire phylogeny. B) Proportional tree representation broken down by the two estimated hidden rate categories (Regime 1: fast evolutionary dynamics; Regime 2: slow evolutionary dynamics) across all four combined phenotypic states.

598 **Supplementary material**

599 *Material and Methods for corHMM analysis*

600 To evaluate the evolutionary association between foraging mode (active vs. sit-and-
601 wait) and microhabitat preference (arboreal vs. terrestrial) across 430 lizard species,
602 we implemented a Hidden Markov Model (HMM) approach using the corHMM pack-
603 age in R (Beaulieu et al., 2013). We treated both traits as binary characters and
604 constructed a four-state composite character matrix representing all joint phenotypic
605 combinations (active/arboreal, active/terrestrial, sit-and-wait/arboreal, and sit-and-
606 wait/terrestrial). To account for potential heterogeneity in evolutionary dynamics
607 across the phylogeny, we fitted models across two hidden rate categories (rate.cat =
608 2). We evaluated three alternative transition rate structures: an Equal Rates model
609 (ER), a Symmetric model (SYM), and an All Rates Different model (ARD). Model fit
610 was compared using the Akaike Information Criterion corrected for sample size (AICc),
611 which identified the ER model as the best-supported model. Marginal ancestral state
612 reconstructions at the tips revealed a pronounced evolutionary association between
613 foraging strategy and microhabitat. We filtered out plastic foragers from the analysis
614 to restrict our model to taxa with fixed, specialized foraging strategies. Microhabitats
615 were similarly reduced to binary categories (arboreal vs. terrestrial).