Relative High Fitness and Large Genome Size May Lead to the High Diversification of Plastic Foragers

Dylan J. Padilla Perez[1,2], Martha M. Muñoz[3], David K. Skelly[2]

[1]Yale Institute for Biospheric Studies, Yale University, New Haven, CT 06511, USA.

[2]School of the Environment, Yale University, New Haven, CT 06511, USA.

[3]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA.

Corresponding author: dylan.padilla@yale.edu

Article type: Major Article

Keywords: Genetic diversity, plasticity, speciation, reproductive effort.

This manuscript includes:

Abstract: 238 words

Main Text: $\sim$ 6000 words, excluding references

Figures: 5

References: 65

Abstract

Explaining variation in diversification of species across the Tree of Life is an important challenge for evolutionary biologists. Growing evidence suggests that key innovations or historical contingency give rise to high diversification of species, but the genetic mechanisms through which this process may occur remain poorly investigated. Based on fitness landscapes, a high diversification is predicted to result from local adaptation as species navigate genotype space. To test this prediction, we conducted a comparative analysis of 997 reptile species that vary in their locomotion while foraging. The species ranged from those that travel long distances to acquire food ("active foragers") to those that barely move and acquire food in nearby sites ("sit-and-wait foragers"), or those that adopt a plastic strategy. We found that active and plastic foragers not only have higher diversification of species but also have higher fitness compared to sit-and-wait foragers. While traversing across heterogeneous environments, active and plastic foragers could accelerate the pace of evolution by exposing cryptic genetic variation to selection. This is possible in active and plastic foragers because their larger genomes and nucleotide diversity potentially facilitate variation in gene expression, allowing natural selection to operate effectively to the point where divergence by ecological speciation could occur. Restricted locomotion among sit-and-wait foragers potentially led to relatively low diversification of species via stochastic processes. We used emerging genomic data and macroevolutionary observations supported by microevolutionary processes to provide key insights into mechanisms of diversification.

Keywords: Genetic diversity, plasticity, speciation, reproductive effort.

Introduction

The process of evolution by natural selection requires differences in fitness among organisms given variation in their genomes and environments (Orr, 2009). Often, such variation in fitness arises from plastic responses pushing populations into the realm of attraction of new fitness peaks (Figure 1), which can lead to genetic differentiation over time (Price et al., 2003). Accordingly, the relationship between genes and fitness is of fundamental importance to better understand the evolutionary history of organisms. Ideally, a theory that links microevolutionary processes responsible for changes in fitness (e.g., genetic drift, mutation, selection) with macroevolutionary patterns (e.g., speciation, diversification of species) should provide the basis for describing how biodiversity arises. To develop such a theory, researchers rely on the notion of "fitness landscapes", which enables one to visualize how the process of diversification can occur (Figure 1; Wright, 1931).

Figure 1.

A prevailing prediction emerging from consideration of fitness landscapes is that many speciation events, and indeed whole adaptive radiations, result from local adaptation as species colonize new environments (Gavrilets, 1997; Wright, 1931). This prediction is based on two premises: 1) While exploring large areas of genotype space, the origin of novel allele combinations can occur as organisms with different genetic makeup reproduce. 2) The increasing likelihood of spatial sorting as organisms move

across the genotype space can cause individuals with distinct traits to accumulate at the leading edge of a population in the process of divergence (Ochocki and Miller, 2017; Shine and Baeckens, 2023). Because such premises imply the displacement of organisms across their landscapes, focusing on species that differ in their locomotion while foraging offers a good opportunity to understand how the diversification process takes place. In this regard, the foraging behaviors of organisms is highly relevant; these behaviors lie along a continuum of locomotion, ranging from species that travel long distances to acquire food ("active foragers") to species that barely move and acquire food in nearby sites ("sit-and-wait foragers"; Pianka, 1966; Reilly et al., 2007). Interestingly, the existence of species that differ in their locomotor capacity based on their foraging behavior is pervasive in nature. For instance, a meta-analysis of dispersal among marine vertebrates and invertebrates revealed that foraging behavior can influence the locomotion of organisms by affecting how far they move (Woodson and McManus, 2007). Foraging animals often seek out areas with high resource concentrations, causing them to forage in nearby sites and decreasing their overall distance traveled. Conversely, a lack of food or the presence of predators can force animals to move and disperse over long distances (Woodson and McManus, 2007). Such an ability to adjust the foraging behavior in response to environmental variations ("plastic foragers") can be especially observed in colonizing species navigating heterogeneous environments, where encountering a new environment may result in selection pressures favoring divergence from the ancestor (Price et al., 2003; Shine and Baeckens, 2023).

As plastic foragers travel across heterogeneous environments, genetic divergence is expected as gene combinations favored under the locally prevailing conditions are not

useful in distant environments (Waddington, 1961). These plastic responses might be associated with the evolution of large genomes because a substantial amount of genetic material facilitates variation in gene expression and can fuel rapid adaptation (Price et al., 2003; She et al., 2024). For instance, the expression of a novel phenotype through plasticity can reveal previously hidden genetic variation, which can be more effectively selected for (Noble et al., 2019). At the same time, however, large genomes might impose a cost of carrying around additional genetic material. Large genomes also lead to slower development, longer generation times, and potentially slower growth rates, all of which could hinder locomotion and colonization to new environments (Knight et al., 2005). By contrast, relatively small genomes may lead to smaller cell sizes and faster cell division rates, which can impact locomotor-related traits (Pyšek et al., 2018). Intriguingly, the relationship between foraging behavior and genome size has not been previously analyzed among vertebrate species, motivating us to conduct a thorough investigation that may enable us to make general conclusions about the ecology and diversification of species across the tree of life.

Here, we explored variation in net diversification of reptiles based on the foraging behavior and genomic attributes of species. Accordingly, we compared the net diversification of species resulting from a state-dependent speciation and extinction model. We also inferred the evolutionary history of foraging behaviors across the phylogeny and revealed historical patterns of radiations and mass extinctions of species within each foraging category. Our hypotheses suggested that because both plastic foragers and active foragers may more effectively explore heterogeneous environments than sit-and-wait foragers, local adaptation may have taken place if populations ex-

ploited new fitness peaks (Figure 1), leading to the relatively high diversification of species. By contrast, restricted locomotion by sit-and-wait foragers could have led to relatively low diversification of species via stochastic processes. These hypotheses are supported by the observation that local adaptation driven by natural selection to suit specific environments generally leads to faster diversification than stochastic processes (García-Pintos, 2024). Because local adaptation is directly dependent on the fitness of organisms, we predicted that the high-dispersing capacity of active and plastic foragers, compared to the low-dispersing capacity of sit-and-wait foragers (Reilly et al., 2007), may have enabled them to reach higher fitness. To test such prediction, we compared the lifetime reproductive output as a function of foraging behavior across species, which involves both their reproduction and longevity (Alif et al., 2022; Stearns, 2000). Local adaptation also relies on the presence of genetic variation, which provides the raw material for natural selection to act upon (Hoban et al., 2016). As such, we modeled the effects of genome size and foraging behavior on the species' fitnesses. In this context, we predicted that active and plastic foragers may have evolved larger genomes (or higher nucleotide diversity) and greater lifetime reproductive output than sit-and-wait foragers. However, the evolution of large genomes might have come at the cost of carrying around additional genetic material. Such a cost may be evident if active and plastic foragers have larger genomes but lower lifetime reproductive output than sit-and-wait foragers. Our study uses emerging genomic data and presents macroevolutionary observations supported by microevolutionary processes to provide key insights into the mechanisms of species' diversification.

Materials and Methods

Ecological data source

We used a comprehensive database for integrating a diverse range of physiological, behavioral, and life history data to explore patterns of diversification among reptiles (Oskyrko et al., 2024). Specifically, our analyses focused on predicting diversification rates based on the foraging behaviors of species. We classified the foraging behaviors based on whether the species have been reported as active forgers, sit-and-wait foragers, or using a plastic strategy (Meiri, 2018); a categorization that, albeit crude, remains useful to biologists for defining the extremes of a continuum. Our investigation included data of foraging behavior for 997 species of squamate reptiles distributed among 56 families. These data were mainly used for estimating net diversification of species across the reptile phylogeny.

To examine variation in fitness, we collected data of lifetime reproductive output among species. We defined lifetime reproductive output as the product between the average clutch sizes of species, their average number of clutches per year, and their longevity. We then regressed this quantity on the maximum body mass of the species (g). This way, the slope of the linear relationship can be interpreted as lifetime reproductive effort—proportion of mass allocated to reproduction—which enabled us to avoid statistical issues associated with the analysis of ratios. We also accounted for the effects of other factors such as the total area of the species' ranges and species relatedness. To estimate the area of the species' ranges, we used the species' polygonal range maps provided by Roll et al. (2017), and ran a Zonal Statistical analysis in the software QGIS (QGIS Development Team, 2025). This tool enabled us to compute the

total area across pixels of the species' range maps. To account for species relatedness, we informed our models with a time-calibrated phylogeny of squamate reptiles (Zheng and Wiens, 2016). To model the effects of these factors on diversification of species, we fitted a number of competing models and selected the most likely one based on information theory (e.g., AIC values). All models were fitted on a logarithmic scale and accounting for phylogenetic relationships using the function *gls* from the library "nlme" (Pinheiro et al., 2007) in the free software for statistical computing R (R Core Team, 2023).

Ancestral state reconstruction

Because historical factors may have played an important role in the diversification of species that we observe today (Blount et al., 2018), we inferred the evolutionary history of foraging behaviors among reptiles. To do so, we fitted a set of continuous-time, discrete-state Markov chain models to sample the character histories from their posterior probability distribution (Huelsenbeck et al., 2003), across a time-calibrated phylogeny of squamate reptiles (Zheng and Wiens, 2016). The models consisted of a an equal-rates (ER) model, in which the rate of change between the three states of the character were assumed to be equivalent. We also fitted an all-rates-different model (ARD), which enables transitions among states to occur at different rates. Lastly, we fitted a symmetrical model, which enables pairs of states to change at different rates but changes among all states are theoretically possible. To fit the models, we used the default arguments of the function *make.simmap* from the "phytools" library of R (Revell, 2012), and simulated 1×10^5 character maps. We then summarized the

number of state changes and the posterior probabilities of each internal node generated from the character map simulations. We selected the most likely model based on AIC values.

State-dependent diversification framework

To explore whether the foraging behavior of species influenced the net diversification of species, we relied on state-dependent speciation and extinction models (SSE). These models are a birth-death process in which the diversification of species are dependent on the state of an evolving character (FitzJohn et al., 2009). Because the data of foraging behavior consisted of a discrete character with 3 levels, we used the MuSSE method—a Multi-State Character extension of the Binary State Speciation and Extinction Model (BiSSE). In doing so, we first defined a likelihood function, and then optimized it as required by the library *diversitree* of R (FitzJohn, 2012). The likelihood function requires a phylogenetic tree (Zheng and Wiens, 2016), a vector of numbers ranging from 1 to 3 (where 1 = active foraging, 2 = plastic foraging, and 3 = sit-and-wait foraging), the number of states ($k = 3$), and a vector specifying the proportion of species in each character state. We computed this proportion based on the ratio of the number of species for which we had data within each foraging state to the total number of squamate species currently reported on Reptile Database (see `http://www.reptile-database.org`). Subsequently, we constrained this general likelihood function to fit different competing models. We started with a null model, in which all birth and death rates are equal between states. Next, we fitted the most complex model in which all rates of speciation and extinction depended on the char-

acter state for our multi-state character. Also, we fitted models in which only the speciation rate (λ) varied between states, only the extinction rate (μ) varied, and one in which neither λ nor μ varied, but the transition rates differed between types of transitions (e.g., ordered, unordered, etc.). As previously described, we compared the models' goodness of fit based on AIC_c and selected the most likely one for inferences. Finally, we used the most likely model to run a Bayesian Markov chain Monte Carlo simulation (MCMC) with 1×10^5 steps to take, an exponential prior distribution, and the control parameter (w) suggested by FitzJohn et al. (2009).

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.

Genomic data source

Because genetic diversity changes as organisms with distinct allele combinations reproduce, important variation in the genetic makeup among species should be observed (Waters et al., 2020). Accordingly, we examined the association between genome size and the foraging behavior of species. To do this, we obtained data of genome size from The National Center for Biotechnology Information (NCBI; `https://www.ncbi.nlm.nih.gov/`) and The Animal Genome Size Database (Gregory et al.,

2007). The genome size dataset that we compiled included 99 squamate species distributed among 29 families. Importantly, the number of species with data of genome size and genetic diversity is dramatically low compared to the availability of ecological data. Thus, our results in this context should be carefully interpreted and will require further evaluation as more data become available. To model the cost of genome size, we examined the effects of the interaction between foraging behavior and genome size on the lifetime reproductive output of species. We fitted a set of phylogenetic-corrected models and evaluated their goodness of fit based on AIC_c values. In addition to accounting for the effect of relatedness between species, we also accounted for potential confounding factors such as body mass. To do so, we used the function *gls* from the library "nlme" of R (Pinheiro et al., 2007).

Furthermore, we compared the genome-wide genetic diversity of an active forager (*Podarcis muralis*) with that of a sit-and-wait forager (*Anolis carolinensis*). To do this, we obtained whole genomes from one population of each species ($n = 5$ individuals). The genomic sequences obtained for *P. muralis* and *A. carolinenesis* are available on NCBI under the Bioproject numbers PRJNA715201 and PRJNA533001, respectively. Both populations were composed of individuals collected from distant localities across the range of the species. We performed a quality-control check of the samples (paired-end sequences) with FastQC (Andrews et al., 2012), and filtered out reads of low quality with Trimmomatic (Bolger et al., 2014). After quality control, we aligned the reads to the reference genome of *P. muralis* (PodMur_1.0) and *A. carolinensis* (rAnoCar3.1.pri) using *bwa* from samtools (Danecek et al., 2021). We then ran the *HaplotypeCaller* algorithm from the software GATK (Van der Auwera and O'Connor,

2020) to identify single nucleotide polymorphisms (SNPs) across the genomes of the study species. This pipeline generated the variant-calling format files (VCF) that we later used to compute the nucleotide diversity (π). The nucleotide diversity is a measure of genetic variation within a population, which is calculated as the average number of nucleotide differences per site in pairwise comparisons of DNA sequences. To accomplish this task, we used *vcftools* to quantify the nucleotide diversity over $10kb$ ($1\times 10^4 bp$) windows of the genome. Finally, we presented the average nucleotide diversity at the chromosome level for each species with the associated standard deviation.

Results

A state-dependent diversification framework indicated that a model in which both the rates of speciation and extinction depend on foraging behavior was strongly supported ($AIC_c = 10076.030, w = 1.000$). Overall, net diversification was indistinguishable among active and plastic foragers, but it was higher than that of sit-and-wait foragers (Figure 2C). Character state reconstruction revealed that active foraging appears to be the ancestral state of all reptiles, with a posterior probability of 0.639 at the root of the tree (Figure 2A). Although two major transitions from active foraging to sit-and-wait foraging occurred in Gekkota and Iguania, bursts of frequent transitions immediately followed within each of these clades (Figure 2B). Specifically, the highest number of transitions took place from sit-and-wait to active foraging (~ 64), followed by a similar number of transitions from sit-and-wait to plastic foraging (~ 57). The accumulation of lineages from the root of the tree to the present showed that active foragers dominated the landmasses for the first 200 million years since the origin of

reptiles in the tree of life. However, sit-and-wait foragers subsequently took over for about 100 million years (Figure 3A).

Figure 2.

A phylogenetic-informed model revealed that the evolution of lifetime reproductive output among reptiles is underlain by an interaction between body mass and foraging behavior (Figure 3B). In general, lifetime reproductive output increased strongly with body mass, but the highest rate of increase is observed in plastic foragers ($\beta = 0.241, Std.Error = 0.069, t = 3.484, p < 0.001$). The relatively high fitness of plastic foragers, however, did not seem to be influenced by their genome size (Figure 3B). Although lifetime reproductive output generally increased with genome size among species (Figure 4A), it was unlikely that such a model could explain our observations ($AIC = 79.403, AIC_c = 6.659, w = 0.014$).

Figure 3.

Interestingly, plastic foragers did not seem to incur a cost of carrying around additional genetic material (Figure 4B). Plastic foragers evolved the largest genomes on average ($\mu = 9.272\ Mb, \sigma = 0.143\ Mb, n = 10$), followed by sit-and-wait foragers ($\mu = 9.264\ Mb, \sigma = 0.089\ Mb, n = 19$). Even though active foragers have evolved the smallest genomes on average ($\mu = 9.194\ Mb, \sigma = 0.085\ Mb, n = 12, n = 28$), their genome-wide nucleotide diversity potentially exceeds that of plastic and sit-and-wait foragers (Figure 5). Yet, further studies on the association between nucleotide diversity

and genome size are needed to make robust conclusions.

Figure 4.

Figure 5.

Discussion

Based on an analysis of nearly one thousand reptile species, we found that plastic foraging and active foraging are associated with higher diversification of species (Figure 2C). 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). The observation that many sit-and-wait foragers are arboreal while most active foragers are terrestrial supports this claim (Vitt et al., 2003). Although historical contingency seems to provide good

evidence in favor of the high diversification of activate foragers, it does not necessarily explain how plastic forgers have a similar net diversification of species (Figure 2C). For example, our results not only show that active foragers and plastic forages have similar net diversification of species, but also that the number of lineages may be stabilizing in the present. By contrast, plastic-foraging lineages continue to grow almost monotonically, reflecting the diversifying effect of plasticity (Figure 3A).

Explaining variation in diversification of species across the tree of life is an important challenge for evolutionary biologists. Most of the work on this topic has focused on associations between key innovations or historical factors and species' diversification (Ricklefs, 2004). But the role of variation in fitness and its effects on diversification of species have received less attention. In this study, not only was the net diversification of plastic foragers relatively high, but they also evolved relatively high lifetime reproductive effort and large genomes. Foraging plasticity, the ability of an organism to change its foraging behavior in response to environmental variations, could then accelerate the pace of evolution, in turn accelerating species' diversification. This flexibility may be crucial for colonizing species, such as plastic and active foragers, to survive and reproduce above maintenance levels and, hence, for the persistence of species (Fusco and Minelli, 2010). Often, such plasticity is adaptive in that organisms that show a plastic response tend to have higher fitness than those that do not (Price et al., 2003). There are many examples where animals respond to heterogenous environments with immediate behavioral changes. Many bird species show a realm of exploratory foraging behaviors, occasionally resulting in quite innovative foraging techniques (Lefebvre, 2000; Lefebvre et al., 2001). These feeding innovations are correlated with species

numbers (Nicolakakis et al., 2003), reflecting the contribution of plasticity to lineage diversification. But the question of how the relatively high fitness of plastic foragers can lead to species diversification remains puzzling.

To elucidate a potential answer to this question, let us consider the ability of active and plastic foragers to colonize and survive in new environments (Sol et al., 2002). In the process of colonizing new environments, local adaptation could take place by exposing cryptic genetic variation to selection (Price et al., 2003). Perhaps, this is possible in active and plastic foragers because their large genomes potentially contain more genes, more and longer introns, and more transposable elements (Figure 4). Transposable elements often facilitate gene duplication and variation in gene expression (Krasileva, 2019; Marino et al., 2024). As variation in gene expression is expected to underlie plasticity in higher order traits, including fitness, genetic changes in sequences regulating gene expression are likely to have a key role in lineage divergence (Siddiq et al., 2024; Meyer, 1987; Kappeler and Fichtel, 2015). If selection acts on the new genetic variation supplied by gene expression, then different lineages might become adapted to and simultaneously develop genetic preferences for different ecological niches (Alatalo and Gustafsson, 1988). Eventually, species utilizing different ecological niches evolve differences in mating preferences by a process analogous to reinforcement (Gavrilets, 2010; Gavrilets and Losos, 2009). If genome size is not sufficiently large to facilitate variation in gene expression or function given a limited capacity to acquire new genes by gene duplication (Charlesworth and Barton, 2004), a high genome-wide nucleotide diversity could compensate (Figure 5A). Because nucleotide diversity (π) is directly related to the effective population size (N_e), active and plastic foragers with high nucleotide di-

versity are expected to have large effective population sizes (Charlesworth and Barton, 2004). As the efficiency of selection increases with effective population size, speciation by natural selection could occur through ecological speciation (Schluter, 2009; Nosil, 2012). Under this process, natural selection acts in contrasting directions between environments, which drives the fixation of different alleles, each advantageous in one environment but not in the other, potentially causing populations to diverge into new species (Schluter and Conte, 2009). However, if the species happen to have relatively low nucleotide diversity, as in the case of sit-and-wait foragers (Figure 5B), abundant resources and a lack of competitors might enable them to seed populations that exploit different niches at low densities, potentially leading to the diversification of species by stochastic processes like random mutation and genetic drift (Gavrilets, 2010, 2014).

Overall, we provide a set of potential scenarios by which the process of diversification could occur in reptiles. Our framework places emphasis on the ways in which variation in foraging behavior alters the locomotion of organisms, allowing them to effectively sample the genotype space and explore different fitness peaks. Although the mechanisms underlying our hypotheses sound appealing, alternative views should also be considered. For instance, some evidence suggests that a high locomotor ability is expected to favor higher rates of gene flow (Suárez et al., 2022). In contrast to the predictions of our hypotheses, over an evolutionary timescale gene flow is expected to suppress speciation events and thus clade level diversification (Claramunt et al., 2012; Weeks and Claramunt, 2014). However, recent work has shown that speciation with gene flow is also possible (Weeks and Claramunt, 2014; Feder et al., 2012). In the past decades, the emerging field of speciation genomics has enabled us to transition from

individual gene to whole genome, improving our understanding of speciation with gene flow. Our observations that plastic foragers have larger genomes and that active foragers have a relatively high genome-wide genetic diversity pave the way for others to investigate the issue of the relative importance of divergence hitchhiking and genome hitchhiking for facilitating speciation with gene flow among reptiles. Future directions should address the question of whether foraging behavior and locomotor capacity 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.

Acknowledgements

We thank David Klinges, Laura Alencar, and Raúl Araya-Donoso for their feedback on previous versions of this manuscript. The first author has been funded by the Yale Institute for Biospheric Studies (YIBS).

Data Accessibility Statement

A fully reproducible workflow of the data analyses, including R scripts and additional supporting material, is available in the following repositories: Github `https://dylan-padilla.github.io/speciation-foraging/`. A dryad link will be available upon acceptance: .

Conflict of interest

The authors have declared no competing interests.

References

Alatalo, R. V. and Gustafsson, L. (1988). Genetic component of morphological differentiation in coal tits under competitive release. *Evolution*, pages 200–203.

Alif, Ž., Dunning, J., Chik, H. Y. J., Burke, T., and Schroeder, J. (2022). What is the best fitness measure in wild populations? a case study on the power of short-term fitness proxies to predict reproductive value. *PLoS One*, 17(4):e0260905.

Andrews, S., Krueger, F., Segonds-Pichon, A., Biggins, L., Krueger, C., and Wingett, S. (2012). FastQC. Babraham Institute.

Astley, H. C. and Jayne, B. C. (2007). Effects of perch diameter and incline on the kinematics, performance and modes of arboreal locomotion of corn snakes (*Elaphe guttata*). *Journal of Experimental Biology*, 210(21):3862–3872.

Blount, Z. D., Lenski, R. E., and Losos, J. B. (2018). Contingency and determinism in evolution: Replaying life's tape. *Science*, 362(6415):eaam5979.

Bolger, A. M., Lohse, M., and Usadel, B. (2014). Trimmomatic: a flexible trimmer for illumina sequence data. *Bioinformatics*, 30(15):2114–2120.

Charlesworth, B. and Barton, N. (2004). Genome size: does bigger mean worse? *Current Biology*, 14(6):R233–R235.

Claramunt, S., Derryberry, E. P., Remsen Jr, J., and Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, 279(1733):1567–1574.

Danecek, P., Bonfield, J. K., Liddle, J., Marshall, J., Ohan, V., Pollard, M. O., Whitwham, A., Keane, T., McCarthy, S. A., Davies, R. M., and Li, H. (2021). Twelve years of SAMtools and BCFtools. *GigaScience*, 10(2).

Feder, J. L., Egan, S. P., and Nosil, P. (2012). The genomics of speciation-with-gene-flow. *Trends in genetics*, 28(7):342–350.

FitzJohn, R. G. (2012). Diversitree: comparative phylogenetic analyses of diversification in r. *Methods in Ecology and Evolution*, 3(6):1084–1092.

FitzJohn, R. G., Maddison, W. P., and Otto, S. P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic biology*, 58(6):595–611.

Fusco, G. and Minelli, A. (2010). Phenotypic plasticity in development and evolution: facts and concepts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1540):547–556.

García-Pintos, L. P. (2024). Limits on the evolutionary rates of biological traits. *Scientific Reports*, 14(1):11314.

Gavrilets, S. (1997). Evolution and speciation on holey adaptive landscapes. *Trends in ecology & evolution*, 12(8):307–312.

Gavrilets, S. (2010). High-dimensional fitness landscapes and speciation. *Evolution: the extended synthesis*, pages 45–79.

Gavrilets, S. (2014). Models of speciation: where are we now? *Journal of heredity*, 105(S1):743–755.

Gavrilets, S. and Losos, J. B. (2009). Adaptive radiation: contrasting theory with data. *Science*, 323(5915):732–737.

Gregory, T. R., Nicol, J. A., Tamm, H., Kullman, B., Kullman, K., Leitch, I. J., Murray, B. G., Kapraun, D. F., Greilhuber, J., and Bennett, M. D. (2007). Eukaryotic genome size databases. *Nucleic acids research*, 35(suppl_1):D332–D338.

Helmstetter, A. J., Glemin, S., Käfer, J., Zenil-Ferguson, R., Sauquet, H., de Boer, H., Dagallier, L.-P. M., Mazet, N., Reboud, E. L., Couvreur, T. L., et al. (2022). Pulled diversification rates, lineages-through-time plots, and modern macroevolutionary modeling. *Systematic Biology*, 71(3):758–773.

Hoban, S., Kelley, J. L., Lotterhos, K. E., Antolin, M. F., Bradburd, G., Lowry, D. B., Poss, M. L., Reed, L. K., Storfer, A., and Whitlock, M. C. (2016). Finding the genomic basis of local adaptation: pitfalls, practical solutions, and future directions. *The American Naturalist*, 188(4):379–397.

Huelsenbeck, J. P., Nielsen, R., and Bollback, J. P. (2003). Stochastic mapping of morphological characters. *Systematic biology*, 52(2):131–158.

Hyams, S. E., Jayne, B. C., and Cameron, G. N. (2012). Arboreal habitat structure affects locomotor speed and perch choice of white-footed mice (peromyscus leucopus). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 317(9):540–551.

Jud, N. A., D'Emic, M. D., Williams, S. A., Mathews, J. C., Tremaine, K. M., and Bhattacharya, J. (2018). A new fossil assemblage shows that large angiosperm trees grew in north america by the turonian (late cretaceous). *Science advances*, 4(9):eaar8568.

Kappeler, P. M. and Fichtel, C. (2015). Eco-evo-devo of the lemur syndrome: did adaptive behavioral plasticity get canalized in a large primate radiation? *Frontiers in zoology*, 12:1–16.

Knight, C. A., Molinari, N. A., and Petrov, D. A. (2005). The large genome constraint hypothesis: evolution, ecology and phenotype. *Annals of Botany*, 95(1):177–190.

Krasileva, K. V. (2019). The role of transposable elements and dna damage repair mechanisms in gene duplications and gene fusions in plant genomes. *Current Opinion in Plant Biology*, 48:18–25.

Lefebvre, L. (2000). Feeding innovations and their cultural transmission in bird populations. In *The Evolution of Cognition*. The MIT Press.

Lefebvre, L., Juretic, N., Nicolakakis, N., and Timmermans, S. (2001). Is the link between forebrain size and feeding innovations caused by confounding variables? a study of australian and north american birds. *Animal Cognition*, 4:91–97.

Marino, A., Debaecker, G., Fiston-Lavier, A.-S., Haudry, A., and Nabholz, B. (2024). Effective population size does not explain long-term variation in genome size and transposable element content in animals. *bioRxiv*, pages 2024–02.

Meiri, S. (2018). Traits of lizards of the world: Variation around a successful evolutionary design. *Global ecology and biogeography*, 27(10):1168–1172.

Meyer, A. (1987). Phenotypic plasticity and heterochrony in cichlasoma managuense (pisces, cichlidae) and their implications for speciation in cichlid fishes. *Evolution*, 41(6):1357–1369.

Nicolakakis, N., Sol, D., and Lefebvre, L. (2003). Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, 65(3):445–452.

Noble, D. W., Radersma, R., and Uller, T. (2019). Plastic responses to novel environments are biased towards phenotype dimensions with high additive genetic variation. *Proceedings of the National Academy of Sciences*, 116(27):13452–13461.

Nosil, P. (2012). *Ecological speciation*. Oxford Ecology and Evolution.

Ochocki, B. M. and Miller, T. E. (2017). Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nature communications*, 8(1):14315.

Orr, H. A. (2009). Fitness and its role in evolutionary genetics. *Nature Reviews Genetics*, 10(8):531–539.

Oskyrko, O., Mi, C., Meiri, S., and Du, W. (2024). Repttraits: a comprehensive dataset of ecological traits in reptiles. *Scientific Data*, 11(1):243.

Pianka, E. R. (1966). Convexity, desert lizards, and spatial heterogeneity. *Ecology*, 47(6):1055–1059.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R. C., et al. (2007). Linear and nonlinear mixed effects models. *R package version*, 3(57):1–89.

Price, T. D., Qvarnström, A., and Irwin, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1523):1433–1440.

Pyšek, P., Skálová, H., Čuda, J., Guo, W.-Y., Suda, J., Doležal, J., Kauzál, O., Lambertini, C., Lučanová, M., Mandáková, T., et al. (2018). Small genome separates native and invasive populations in an ecologically important cosmopolitan grass. *Ecology*, 99(1):79–90.

QGIS Development Team (2025). *QGIS Geographic Information System*. QGIS Association.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reilly, S. M., McBrayer, L. D., and Miles, D. B. (2007). *Lizard ecology*. Cambridge University Press.

Revell, L. J. (2012). phytools: an r package for phylogenetic comparative biology (and other things). *Methods in ecology and evolution*, (2):217–223.

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology letters*, 7(1):1–15.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., et al. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature ecology & evolution*, 1(11):1677–1682.

Schluter, D. (2009). Evidence for ecological speciation and its alternative. *Science*, 323(5915):737–741.

Schluter, D. and Conte, G. L. (2009). Genetics and ecological speciation. *Proceedings of the National Academy of Sciences*, 106(supplement_1):9955–9962.

She, H., Hao, Y., Song, G., Luo, X., Lei, F., Zhai, W., and Qu, Y. (2024). Gene expression plasticity followed by genetic change during colonization in a high-elevation environment. *Elife*, 12:RP86687.

Shine, R. and Baeckens, S. (2023). Rapidly evolved traits enable new conservation tools: perspectives from the cane toad invasion of australia. *Evolution*, 77(8):1744–1755.

Siddiq, M. A., Duveau, F., and Wittkopp, P. J. (2024). Plasticity and environment-specific relationships between gene expression and fitness in saccharomyces cerevisiae. *Nature Ecology & Evolution*, pages 1–11.

Sol, D., Timmermans, S., and Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal behaviour*, 63(3):495–502.

Stearns, S. C. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften*, 87:476–486.

Suárez, D., Arribas, P., Jiménez-García, E., and Emerson, B. C. (2022). Dispersal ability and its consequences for population genetic differentiation and diversification. *Proceedings of the Royal Society B*, 289(1975):20220489.

Van der Auwera, G. A. and O'Connor, B. D. (2020). *Genomics in the cloud: using Docker, GATK, and WDL in Terra*. O'Reilly Media.

van der Kooi, C. J. and Ollerton, J. (2020). The origins of flowering plants and pollinators. *Science*, 368(6497):1306–1308.

Vitt, L. J., Pianka, E. R., Cooper, Jr, W. E., and Schwenk, K. (2003). History and the global ecology of squamate reptiles. *The American Naturalist*, 162(1):44–60.

Waddington, C. H. (1961). Genetic assimilation. *Advances in genetics*, 10:257–293.

Waters, J., Emerson, B. C., Arribas, P., and McCulloch, G. (2020). Dispersal reduction: causes, genomic mechanisms, and evolutionary consequences. *Trends in Ecology & Evolution*, 35(6):512–522.

Weeks, B. C. and Claramunt, S. (2014). Dispersal has inhibited avian diversification in australasian archipelagoes. *Proceedings of the Royal Society B: Biological Sciences*, 281(1791):20141257.

Woodson, C. and McManus, M. (2007). Foraging behavior can influence dispersal of marine organisms. *Limnology and Oceanography*, 52(6):2701–2709.

Wright, S. (1931). Evolution in mendelian populations. *Genetics*, 16(2):97.

Zheng, Y. and Wiens, J. J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular phylogenetics and evolution*, 94:537–547.

Figures with captions

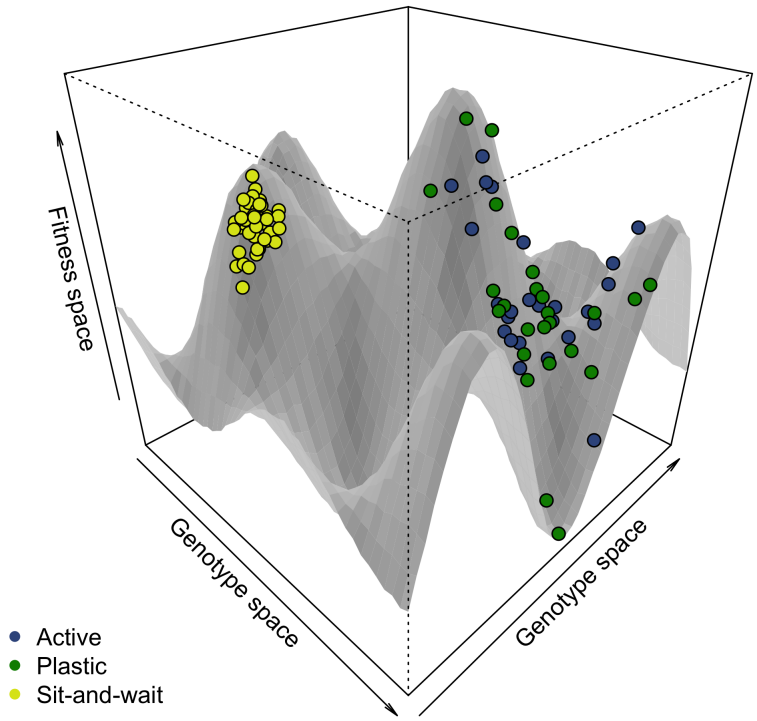

Figure 1: Populations of an active forager, a plastic forager, and a sit-and-wait forager navigating a fitness landscape. Sit-and-wait foragers occupy a single fitness peak given their restricted locomotion. By contrast, active and plastic foragers colonize new fitness peaks as a result of their high locomotor capacity. 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.

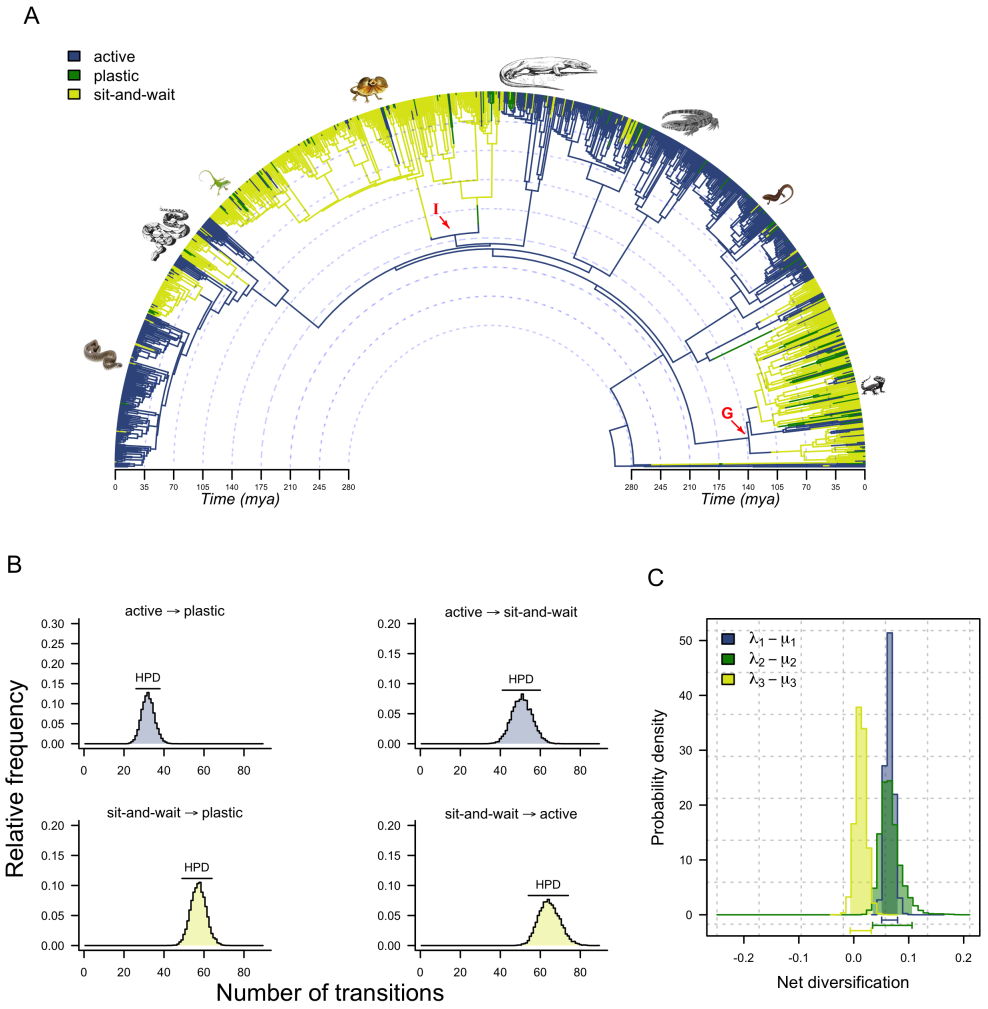

Figure 2: A) Random sample of 1×10^5 simulated character maps depicting the evolution of foraging behaviors among 997 reptile species. Clades where major transitions have occurred are indicated as follows: G = Gekkota, I = Iguania. B) Expected number of changes between the states of the character under the most likely model. The high probability density (HPD) reflects the variance of changes between states given the assumed model. C) Net diversification between clades defined by the foraging behavior of species. For each clade, the net diversification of species was computed as the difference between speciation rates (λ) and extinction rates (μ).

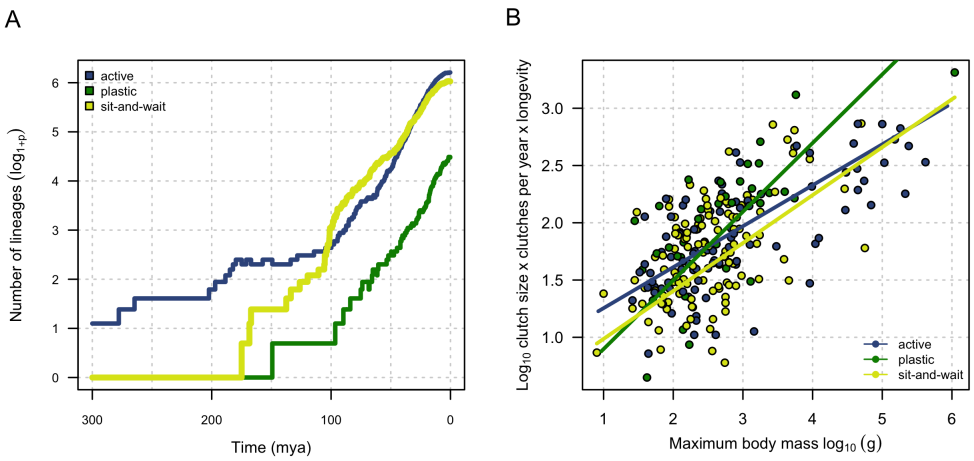

Figure 3: A) Lineage-through-time plot illustrating the accumulation of lineages within clades defined by the foraging behavior of species. B) Relationship between the lifetime reproductive output of species as a function of their body mass and foraging behavior. Dots represent species.

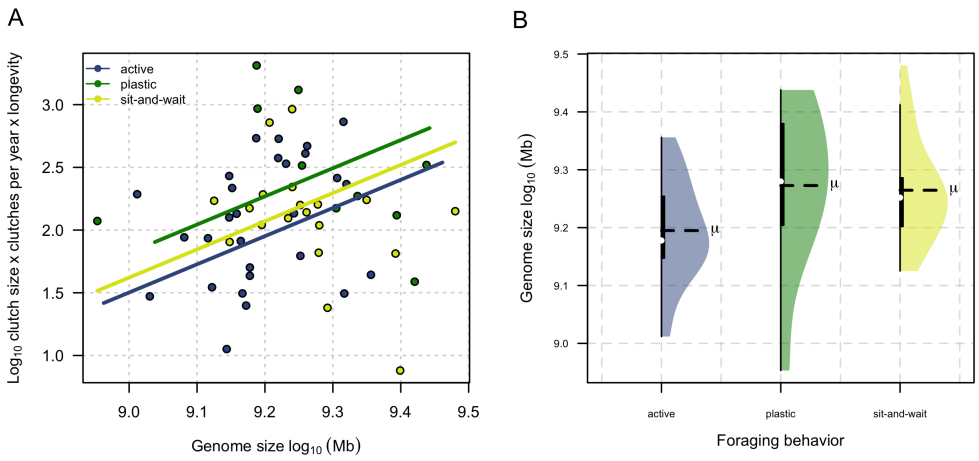

Figure 4: A) Effects of the interaction between genome size and foraging behavior on lifetime reproductive output. B) Genome size as a function of foraging behavior category. White dots represent median values and dashed lines mean values (μ)

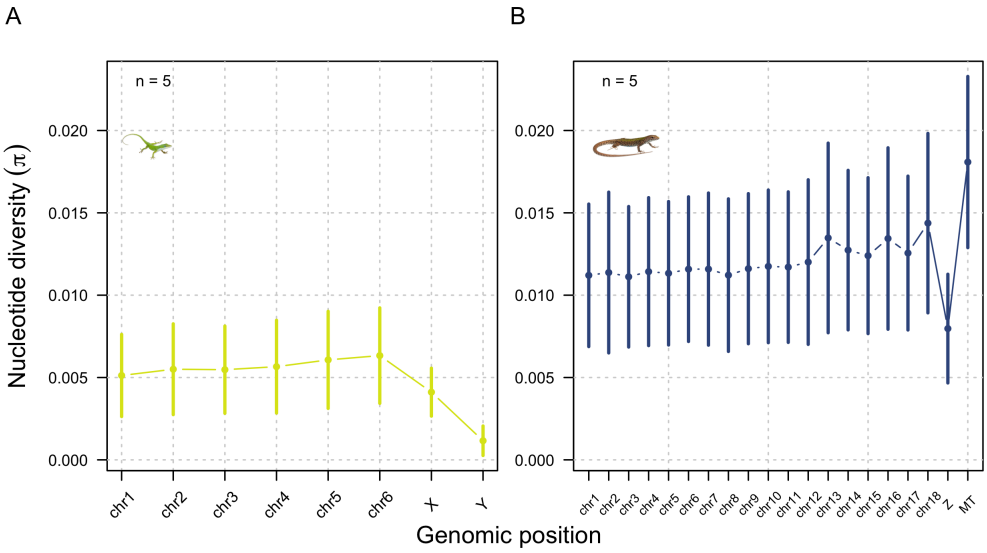

Figure 5: A) Genome-wide nucleotide diversity estimated from a population of a sit-and-wait forager (*Anolis carolinensis*). B) Genome-wide nucleotide diversity estimated from a population of an active forager (*Podarcis muralis*). Solid dots represent the average nucleotide diversity per chromosome and across the mitochondrial genome, which is abbreviated as MT. The bars associated indicate the standard deviation.