Relative High Fitness and Genome-wide Diversity May Facilitate Plastic and Active Foragers' Diversification

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Abstract

Explaining the variation in diversification rates 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 rates, 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 traverse along 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 to those that barely move and acquire food in nearby sites or those that adopt a plastic strategy. We found that plastic foragers and active foragers not only have high diversification rates but may also have higher fitness compared to sit-and-wait foragers. While traversing among heterogeneous environments, plastic foragers and active foragers could accelerate the pace of evolution by exposing cryptic genetic variation to selection. This is possible in plastic foragers because their larger genomes potentially facilitate variation in gene expression. By contrast, higher genome-wide nucleotide diversity among active foragers could make up for the small size of their genomes, allowing natural selection to operate effectively to the point where divergence by ecological speciation could occur. We used emerging genomic data and macroevolutionary observations supported by microevolutionary processes to provide key insights into mechanisms of diversification.

Keywords: Genetic diversity, genome size, foraging mode, reproductive effort.

Significance statement

The ways by which organisms seek food vary along a continuum from stationary to highly mobile foraging modes, although many species plastically switch between modes. This range of locomotion may influence the pace of evolution based on the extent to which novel genetic combinations arise as organisms encounter and colonize new environments, leading to variation in diversification rates. Our observations suggest that as plastic and active foragers colonize new environments, local adaptation could take place by exposing cryptic genetic variation to selection. As such, high diversification rates may follow through ecological speciation. By contrast, a relatively low genetic diversity and fitness among sit-and-wait foragers might lead to low diversification rates through stochastic processes like genetic drift and mutation.

Introduction

The process of evolution requires differences in fitness among individuals within species given variation in their genomes and environments (1). Often, such variation in fitness arises from plastic responses pushing populations into the realm of attraction of new fitness peaks, which can lead to genetic differentiation (2). 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) should provide the basis for describing how biodiversity evolves on Earth. To develop such a theory, researchers rely on the notion of "fitness landscapes", which enables one to analyze how the process of diversification can occur (3).

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 (4; 3). This prediction emerges from several sources, including the introduction of novel genetic combinations as organisms explore large areas of the genotype space, and the increased likelihood of spatial sorting, where organisms with distinct traits accumulate at the leading edge of a population's expansion (5; 6). To test this prediction, one could focus on species that vary in their locomotor ability while foraging. The foraging behaviors of organisms 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"; 7; 8). Importantly, the ability of organisms to change their foraging behavior in response to environmental variations ("plastic foragers") can be specially observed in colonizing species inhabiting heterogeneous environments, where encountering a new environment may result in selection pressures favoring divergence from the ancestor (2; 6).

If populations can attain high fitness in heterogeneous environments as a consequence of plastic foraging behavior, then genetic differentiation is expected as gene combinations favored under the locally prevailing conditions are not useful in distant environments (9). As populations colonize new environments, however, plasticity can be hindered by a lack of genetic variation, extensive gene flow, and genetic correlation between genes for one trait and genes for plasticity of another trait (10). Furthermore, a plastic response may come at the cost of carrying around additional genetic machinery (11). Such a cost can be assessed if one analyzes the relationship between the foraging behaviors of species and the sizes of their genomes. In this context, the cost may be evident if plastic foragers have larger genomes but lower fitness than active foragers and sit-and-wait foragers. One way to account for differences in fitness among species is to compare their annual reproductive output, which is a good predictor of lifetime fitness (12). Intriguingly, a comparison between foraging behavior, genome size, and reproductive output has not been previously evaluated 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 examined the relationship between foraging behaviors and diversification rates among 997 reptile species representing 56 families. In doing so, we considered the predictions of fitness landscapes to assess the idea that effectively traversing the genotype space might result in high diversification rate through local adaptation (13). Because both plastic foragers and active foragers may more effectively explore heterogeneous environments than sit-and-wait foragers, local adaptation may take place if populations exploit new fitness peaks, leading to a relatively high diversification rate. By contrast, restricted locomotion by sit-and-wait foragers could lead to relatively slow diversification via stochastic processes such as population bottlenecks. These expectations are supported by the idea that local adaptation driven by natural selection to suit specific environments generally leads to faster diversification than stochastic processes (14). Our study uses emerging genomic data and presents macroevolutionary observations supported by microevolutionary processes to provide key insights into the mechanisms of diversification.

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 this rate was higher than that of sit-and-wait foragers (Figure 1C). 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 1A). 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 1B). Specifically, the highest number of transitions took place from sit-and-wait to active foraging (~ 64), succeeded 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 (Figure 2A).

Figure 1.

A phylogenetic-informed model revealed that the evolution of annual reproductive output among reptiles is underlain by an interaction between body mass and foraging behavior (Figure 2B). In general, annual reproductive output increased with body mass, but the highest rate of increase is observed in plastic foragers ($\beta = 0.134, Std.Error = 0.051, t = 2.603, p = 0.009$).

Figure 2.

As with annual reproductive output, genome size also evolved in response to the interaction between body mass and foraging behavior across species (Figure 3). While genome size decreased with body mass in sit-and-wait foragers ($\beta = -0.042, Std.Error = 0.017, t = -2.363, p = 0.020$) and plastic foragers ($\beta = -0.073, Std.Error = 0.021, t = -3.403, p < 0.001$), the opposite pattern was evident in active foragers ($\beta = 9.188, Std.Error =$

$0.037, t = 246.673, p < 0.001$). However, plastic foragers had the largest genomes on average ($\mu = 9.271, \sigma = 0.133, n = 12$) followed by sit-and-wait foragers ($\mu = 9.254, \sigma = 0.089, n = 29$).

Figure 3.

Importantly, active foragers have evolved the smallest genomes on average ($\mu = 9.204, \sigma = 0.073, n = 58$), but their genome-wide nucleotide diversity potentially exceeds that of plastic and sit-and-wait foragers (Figure 4).

Figure 4.

Discussion

Based on an analysis of nearly one thousand reptile species, we found that plastic foraging and foraging actively are associated with higher diversification rates (Figure 1C). Previous hypotheses suggest that historical contingency has been a major determinant of the diversification pattern that we observe in modern-day reptiles (15). 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 2A). The subsequent rise may be linked to the emergence and spread of angiosperms (flowering plants) in the past 100 million years (16; 17). The habitat created by large sizes in 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 (18; 19). The observation that many sit-and-wait foragers are arboreal while most active foragers are terrestrial supports this claim (15). While the number of active foragers and sit-and-wait foragers may be stabilizing in the present, plastic-foraging lineages continue to grow monotonically, reflecting the diversifying effect of plasticity (Figure 2A).

Explaining variation in diversification rates 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 diversification rates (20). But the role of variation in fitness and its effects on diversification rates have received less attention. According to theoretical models, the reproductive effort of organisms should influence their lifetime fitness (21; 22; 12). Recent empirical evidence supports this idea; for example, (23) showed that the fitness of an iteroparous species was the highest at its peak annual reproductive output. In this study, not only was the net diversification of plastic foragers relatively high, but they also evolved relatively high reproductive effort (Figure 1C and Figure 2). 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 diversification rates. 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 (24). Often, such plasticity is adaptive in that organisms that show a plastic response tend to have higher fitness than those that do not (2). 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 (25; 26). These feeding innovations are correlated with species numbers (27), reflecting the contribution of plasticity to lineage diversification. But the question of how fitness variation through phenotypic plasticity can lead to species diversification remains puzzling.

To elucidate a potential answer to this question, let us consider the ability of plastic foragers to colonize and survive in new environments (e.g., 28). In the process of colonizing new environments, local adaptation could take place by exposing cryptic genetic variation to selection (2). This is possible in plastic foragers because their large genomes potentially contain more genes, more and longer introns, and more transposable elements (Figure 3). Transposable elements often facilitate gene duplication and variation in gene expression (29; 30). 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 (31; 32; 33). 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 (e.g., 34). Eventually, species utilizing different ecological niches evolve differences in mating preferences by a process analogous to reinforcement (for compelling reviews, see 35; 36). By contrast, the relatively small genomes of active foragers may limit the variation in gene expression or function given the restricted capacity to acquire new genes by gene duplication (37). Yet, a high genome-wide nucleotide diversity among active foragers could compensate for the relatively small size of their genomes (Figure 4A). Because nucleotide diversity (π) is

directly related to the effective population size (N_e), active-foraging species with high nucleotide diversity are expected to have large effective population sizes (e.g., 37). As the efficiency of selection increases with effective population size, speciation by natural selection could occur through ecological speciation (38; 39). 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 (40). However, if the species happen to have relatively low nucleotide diversity, as in the case of sit-and-wait foragers (Figure 4B), 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 (35; 41).

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 vagility of organisms, allowing them to effectively traverse along 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 dispersal ability is expected to favor higher rates of gene flow (42). 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 (43; 44). However, recent work has shown that speciation with gene flow is also possible (44; 45). 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. Although annual reproductive output can be considered a good proxy for fitness, species survival must also be examined. In essence, fitness is rather intricately associated to the reproduction and survival of organisms. Future directions should address the question of whether foraging behavior and dispersal 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 diversification rates among reptiles.

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 (e.g., 46). 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 (e.g., 47); 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.

The foraging behavior of organisms has become a paradigm in evolutionary biology because of its connection to many traits including the locomotion of species, which potentially affects their dispersal capacity (8). For example, while active foragers disperse over long distances to acquire food, sit-and-wait species barely disperse and forage in nearby sites. If these premises are met, then investigating the relationship between foraging behaviors and the fitnesses of species enables the assessment of a prevailing view of fitness landscapes. That is, effectively traversing along the genotype space might result in high diversification rates through local adaptation (13; 4; 3). To assess this prediction, we first collected data of annual reproductive output among reptile species. The annual reproductive output can be considered a good proxy for fitness because it is generally a good predictor of the long-term fitness of organisms (12; 22). We defined the annual reproductive output as the product between the average clutch sizes of species and their average number of clutches per year. We then regressed this quantity on the maximum body mass of the species (g). By regressing the product between the average clutch size and the average number of clutches per year, the slope of the linear relationship can be interpreted as reproductive effort—proportion of mass allocated to reproduction—which enabled us to avoid statistical issues associated with the analysis of ratios. To account for species relatedness, the regression was informed by a time-calibrated phylogeny of squamate reptiles (48). The regression model was fitted in the free software for statistical computing R (49), using the function *gls* from the library "nlme" (50).

Ancestral state reconstruction

Because historical contingency may have played an important role in the diversification of species that we observe today (51), 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 (52), across a time-calibrated phylogeny of squamate reptiles (48). 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 (53), 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 an information-theoretic approach such as the Akaike Information Criterion (AIC).

State-dependent diversification framework

To explore whether the foraging behavior of species influenced speciation and extinction rates, we relied on state-dependent speciation and extinction models (SSE). These models are a birth-death process where the diversification rates are dependent on the state of an evolving character (54). 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 (55). The likelihood function requires a phylogenetic tree (i.e., 48), 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 we had data for 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 character 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 (54).

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 (56). 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 impressively.

Genomic data source

Because genetic diversity changes as organisms move their alleles around the genotype space, important variation in the genetic makeup among species should be observed (57). Accordingly, we first 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 (58). The genome size dataset that we compiled included 99 squamate species distributed among 29 families. To model the association between foraging behavior and genome size among 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 (50).

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 ($n = 5$). The genomic sequences obtained for *P. muralis* and *A. carolinenesis* are available on NCBI

under the Bioproject numbers PRJNA715201 and PRJNA533001, respectively. We performed a quality-control check of the samples (paired-end sequences) with FastQC (59), and filtered out reads of low quality with Trimmomatic (60). 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 (61). We then ran the *HaplotypeCaller* algorithm from the software GATK4 (62) 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 a chromosome level for each species with the associated standard deviation.

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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 avail-

able upon acceptance: .

Conflict of interest

The authors have declared no competing interests.

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Figures with captions

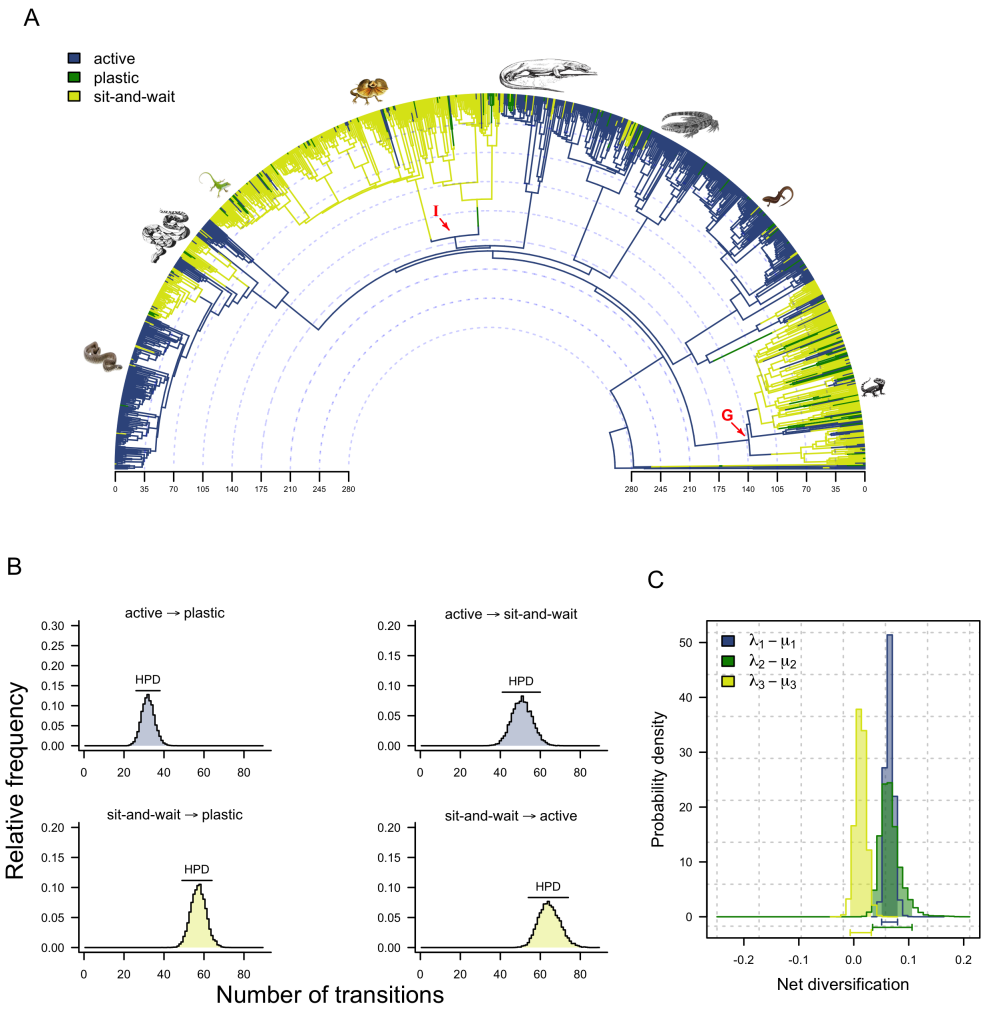

Figure 1: A) Random sample of 1×10^5 simulated character maps depicting the evolution of foraging behaviors among 997 reptile species. Clades where major transitions have occurred are indicated as follows: G = Gekkota, I = Iguania. B) Expected number of changes between the states of the character under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

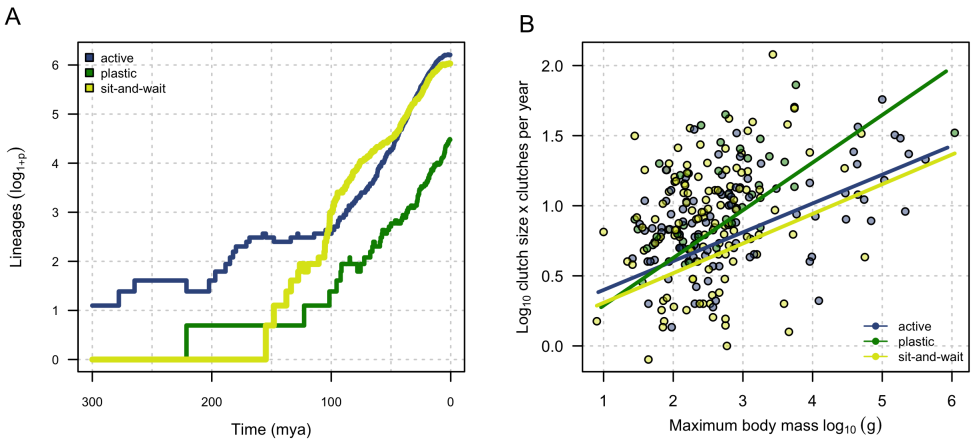

Figure 2: A) Lineage-through-time plot illustrating the accumulation of lineages within clades defined by the foraging behavior of species. B) Relationship between the annual reproductive output of species as a function of their body mass and foraging behavior.

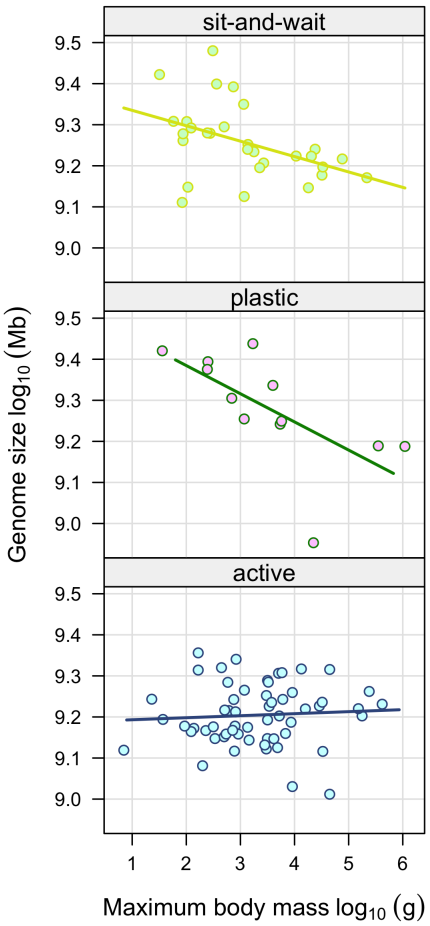

Figure 3: Evolution of genome size in response to the interaction between body mass and foraging behavior among reptile species.

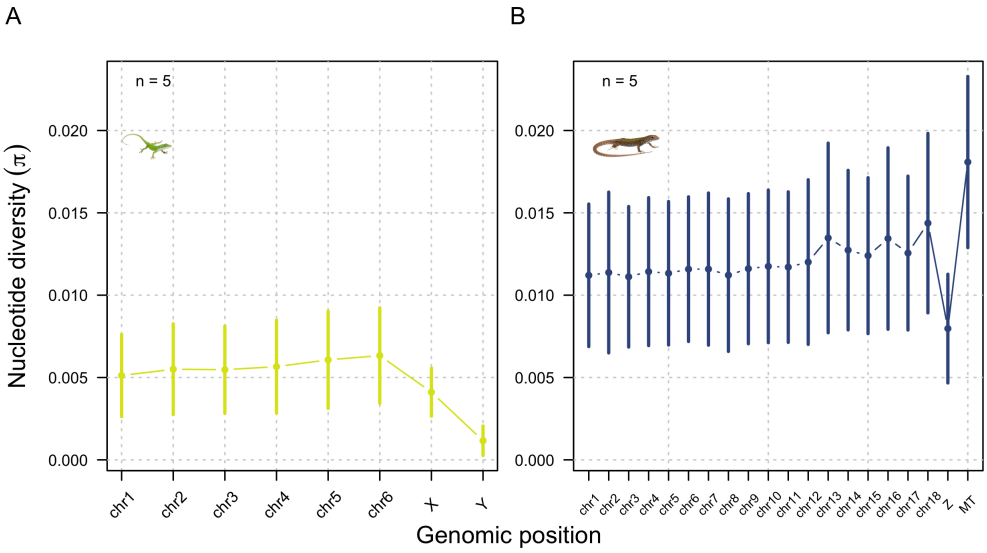

Figure 4: A) Genome-wide nucleotide diversity estimated from a population of a sit-and-wait forager (*Anolis carolinensis*). B) Genome-wide nucleotide diversity estimated from a population of an active forager (*Podarcis muralis*). Solid dots represent the average nucleotide diversity per chromosome and across the mitochondrial genome, which is abbreviated as MT. The bars associated indicate the standard deviation.