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Flowing Round the World: Water Snakes (Natricidae) Show Habitat-Related Adaptive Radiation After Dispersal to the New World

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Abstract

Adaptive radiations are characterized by increases in rates of lineage and trait evolution, typically due to the opening of new ecological opportunities such as may follow from dispersal to a new region or the evolution of a trait that allows exploitation of new niches. This results in clades that have accumulated unusually high biological diversity within a relatively short evolutionary timespan and hence the phenomenon has attracted longstanding interest amongst evolutionary biologists. Natricidae is a family of snakes with a primarily Old World distribution but which have colonized the New World on a single occasion. This dispersal event coincides with an increased speciation rate that has led to a species-rich New World clade. Herein, we take a phylogenetic comparative approach to investigate a likely adaptive radiation of New World natricids. We first confirmed previously reported findings of a single origin (providing new ecological opportunity) coinciding with a burst of lineage diversification. We then estimate the rates of evolution for three ecologically important traits (body size and broad categories of diet and habitat) separately for New World and Old World natricids. Of these three traits, our results provide evidence that only transition rates between terrestrial and (semi-)aquatic habitats are higher in the New World clade. Taken together, this supports a scenario of an adaptive radiation in natricids primarily associated with differentiation by habitat as the clade spread across the New World following its arrival there. Considering other adaptive radiations alongside our evidence for Natricidae, we propose the hypothesis that there is a common distinction between spatially constrained 'island' adaptive radiations (which often diverge along trophic axes) and continental adaptive radiations, which diverge as the clade spreads across a larger spatial scale and adapts to different habitats.

Keywords: trait evolution; macroevolutionary diversification; speciation rates; historical biogeography; ecological opportunity; continental radiation

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1. Introduction

Adaptive radiations are commonly thought to be important components of biodiversity as they are typically defined as clades that have undergone high rates of both lineage and phenotypic diversification [1] (although definitions have varied amongst authors [2]). Consequently, they are expected to contribute disproportionately to the generation of biological diversity across the tree of life [3]. Hence, adaptive radiations have long been of interest amongst evolutionary biologists.

Several adaptive radiations have been well-studied and can occur in the context of different ecological niche axes. For instance, Galapagos finches, African cichlids, lemurs in Madagascar, and Canary Island *Dysdera* spiders have diverged predominantly in relation to trophic traits such as diet or foraging style [4–8]. On the other hand, a few are predominantly structured along habitat axes, for example, Caribbean *Anolis* lizards and Caribbean *Eleutherodactylus* frogs [9,10]. Although these 'island'-based examples are amongst the best known, perhaps because the spatial constraints of islands force greater competition between close relatives and hence stronger selection for adaptive differentiation [1], there are also examples of continental adaptive radiations. These tend to be structured more consistently in relation to habitat, for example in Australo-Papuan pythons, mainland *Anolis* lizards, Neotropical ovenbirds, Australian *Cryptoblepharus* skinks, and *Bradypodion* dwarf chameleons [9,11–15].

The relationship between ecological opportunity—the availability of unoccupied niches—and adaptive radiation has been discussed extensively and current understanding suggests that the former is an important component but not sufficient in itself to cause adaptive radiation [1,16–20]. Importantly, ecological opportunity can arise for many reasons. The evolution of a new phenotypic trait that makes new resources accessible, often called a key innovation, can provide access to a new niche for the species in question, even if the presence of the resource is unchanged [21,22]. Alternatively, dispersal (on a macroevolutionary scale) to new areas can provide ecological opportunity that is accessible with a species' existing traits as the resources available might be different on a newly colonized island or landmass than the area originally occupied by the species [23–25].

Not all radiations, considered as clades with higher speciation or net (lineage) diversification rates, are adaptive, yet some previous studies have treated evidence of faster diversification rates as sufficient to identify adaptive radiations [26]. The 'adaptive' component requires some understanding of the evolution of traits that are expected or (ideally) known to be linked to exploitation of ecological resources, such that adaptive radiations are driven by divergence between species along a niche axis that reflects adaptation to a diversity of resources within the clade [1,2]. In contrast, non-adaptive radiations are also known in which rapid lineage evolution has occurred but with minimal evidence of ecological diversification during the radiation [27–30]. Such non-adaptive radiations may be associated with divergence via barriers to gene flow that result in allopatric speciation under similar environmental conditions, the evolution of sexually selected characters such as ornaments, or coevolutionary processes such as host-parasite cospeciation or arms race coevolution [27,30], which provide alternative explanations for radiations with no discernable link to increased ecological diversity.

Natricidae (sometimes considered a subfamily of Colubridae but treated as a family here following [31]) are a diverse group of snakes consisting of 277 species [32] that are sometimes known as 'water snakes' due to the (semi-)aquatic habits of many, but not all, species. They include some of the most commonly encountered and familiar species in many areas, for instance the European grass snakes (*Natrix*) and the North American water and garter snakes (*Nerodia* and *Thamnophis*, respectively). Natricids are geographically widespread, occurring on all continents except South America and Antarctica, and are ecologically diverse in terms of diet and habitat [33].

Natricidae contain one subclade (New World natricids) that may represent an adaptive radiation. Previous work has reported that this clade is the result of a single macroevolutionary dispersal event, either via an early crossing of Beringia around 25 mya followed by one lineage crossing back over and dispersing to Western Eurasia (*Natrix*) and the other remaining as an exclusively New World clade, or a more recent dispersal around 14 mya by the ancestor of the New World clade [33,34]. This event likely opened up ecological opportunity as this group of snakes entered a new continent with a presumably new set of resources. The diverse ecological niches within the Natricidae [33] may also relate to an adaptability that could facilitate the exploitation of this presumed opportunity. Once entering the New World, natricids gradually dispersed southward and eastward across the North American continent [34–36], facilitating the continued encounters of new areas over time.

Analysis of diversification dynamics within Natricidae have recovered an increased speciation rate that coincides with the origin of the New World clade [33]. The origin of viviparity at the root of the New World clade was proposed as a possible key innovation that led to the burst of speciation [33], but this was not explicitly tested due to the lack of variation available (i.e., all New World natricids are viviparous and almost all Old World species are oviparous). Hence, this group of snakes appear to represent a radiation resulting from dispersal to a new continent, but there is currently less evidence available on the question of whether this is an adaptive or non-adaptive radiation. Nevertheless, an analysis of global snake diets found that the rate of diet evolution is much higher in New World natricids compared to their Old World counterparts [37], suggesting that this may be an important factor.

Herein, we investigate the evolutionary dynamics of Natricidae with the aim of evaluating the status and nature of the New World clade as an adaptive radiation. We first confirm that we can recover the single origin of New World natricids and a coincident increase in lineage diversification rates, setting the evolutionary stage for adaptive radiation with a radiation exposed to ecological opportunity. We then estimate the evolutionary rates of key ecological traits in both the New World clade and the Old World natricids to evaluate whether there is evidence of adaptive diversification in one or more niche axes.

2. Materials and Methods

2.1. Phylogenetic Tree

We obtained a phylogeny for our analyses by first extracting 100 trees from Tonini et al. [38], each containing 213 natricid species (77% of currently described species richness), using the VertLife website [39]. We then calculated the maximum clade credibility tree from this set using the phangorn 2.11.1 package [40] in R 4.0.3 [41], which was used for all subsequent analyses. Basic handling and manipulation of phylogenies was carried out with ape 5.8 [42] and windex 2.0.8 [43]. This phylogeny has better species sampling than other recent estimates of Natricidae phylogeny [33], albeit at the cost of higher levels of missing data for tips, and has been used for many recent macroevolutionary studies on snakes e.g., [37]. Nevertheless, to guard against any major influence of sampling differences on the comparability of our analyses with others, we also confirmed that we can recover the key findings of a single origin of New World natricids and a concurrent burst of lineage diversification using our dataset (Sections 2.2 and 2.3).

2.2. Historical Biogeography

We coded the geographic distribution of each species based on Holt et al.'s [44] global analysis of zoogeographic realms. This categorization covers the whole distribution of Natricidae (which are represented in all realms except Madagascar and the Neotropics) and contains a clear split between the Old World and New World, our main division of interest here. We inferred the biogeographic history of the clade using both S-DIVA [45] and DEC [46] models in RASP 4.2 [47], but although we provide full outputs of both models (see Data Availability Statement) we report only the DEC analysis because (1) both models were highly consistent across the phylogeny and especially in relation to dispersal to the New World, (2) the analytical output from the DEC analysis provides more information on inferred history, and (3) previous work comparing these two models found better performance of DEC for similar biogeographic coding to ours [33]. We did not add further constraints to the analysis as we were simply interested in making sure we could recapitulate key results from previous studies rather than obtaining the best possible estimation across the tree.

2.3. Diversification Dynamics

We estimated diversification dynamics across the phylogeny using Bayesian Analysis of Macroevolutionary Mixtures version 2.5.0 (BAMM) [48], with the R package BAMMtools 2.1.12 [49] used to analyze output. BAMM uses a Metropolis-coupled MCMC approach to estimate evolutionary rates and shifts to different macroevolutionary rate regimes (distinct diversification processes which may be time-constant or time-varying). Priors for our analysis were calculated in BAMMtools and initial values for speciation and extinction rates were estimated by fitting a simple birth-death model in phytools 2.4.4 [50]. We allowed regime shifts to occur on all branches and used an equal prior probability of time-varying vs. time-constant regimes. Four Markov chains were run for 10 million generations, sampling every 1000 generations, giving 1000 posterior samples of which the first 10% were discarded as burn-in prior to further analysis. Convergence was confirmed by examining the MCMC trace of log-likelihoods and effective sample sizes were calculated for the number of regime shifts and the log-likelihood (>200 in both cases). Because BAMM estimates rates across the phylogeny it is possible to extract a clade of interest and compare the rate dynamics over time to those from the ‘background’ rates (i.e., the rest of the tree excluding that clade). We were therefore able to directly compare the New World clade to all other natricids and use this analysis to confirm previous work that the New World clade experienced an increase in speciation rate.

2.4. Trait Evolutionary Rates

We considered three traits that were chosen to represent important ecological attributes that might be expected to respond to ecological opportunity presented during an adaptive radiation. These were body mass and broad categories of diet and habitat. Body size has widespread implications for an animal’s ecology [51,52] and can therefore be considered as a useful, if imprecise, proxy for general niche shifts, since many new ecological opportunities are likely to cause changes in optimal body size. Both diet and habitat are key ecological characteristics and are highly variable across the evolutionary history of Natricidae, such that they appear to exhibit low phylogenetic signal (though this was not quantified) and may therefore be particularly able to change in response to new opportunities and selection [33]. Moreover, diet and habitat have been shown to be involved in ecomorphological variation in this group of snakes [53], again suggesting that they are important traits in the ecology of natricids. Note that we were interested in the rates of evolution in ecologically important traits, rather than the specific changes occurring, so our interpretations of analyses are focused on this aspect and our coding strategy for categorical traits is targeted towards having good sample sizes in each category to get robust estimates of rates (while retaining the ecological meaningfulness of categories).

Body mass data were obtained from a published database of lepidosaur body sizes [54], measured in grams and log-transformed (base 10) prior to analysis. We estimated the dynamics of body size evolutionary rates using BAMM with a similar approach to the estimation of diversification rates described above, including the same MCMCMC control parameters. We used a uniform distribution bound by the minimum and maximum values in the trait data as priors on the body size states, and assigned a prior probability of 1 for time-varying regimes (as body size evolution is very likely to vary across the family due to its close ties to ecology). We set the initial value of the evolutionary process at the root of the tree to 0.5. Convergence was again confirmed by examining the MCMC trace of log-likelihoods and effective sample sizes were calculated for the number of regime shifts and the log-likelihood (>600 in both cases).

Data on diet and habitat were obtained from a prior phylogenetic comparative study on natricid ecology [33]; however, in line with our aims we recoded the categories from this dataset. We required sufficient sample sizes per category in each of the two groups we are comparing (the New World clade and the Old World grade), but some combinations contained few species, for instance only four lizard specialists in the Old World and only three mollusc specialists in the New World. Consequently, we combined categories to create larger but still ecologically meaningful designations that enabled us to estimate evolutionary rates that are comparable across Natricidae and should be responsive to adaptation resulting from new ecological opportunities (i.e., increased rates would be consistent with adaptive radiation). Specifically, we coded diet as either specialist (combining the initial categories of annelids, anurans, fish, lizards, crayfish, and molluscs) or generalist (combining the initial categories of aquatic generalist and generalist). This choice of coding is also supported by analyses of *Thamnophis* ecomorphology, which found that trophic morphology varied between generalists and specialists, suggesting that this is an important distinction in the foraging ecology of New World natricids [35]. Similarly, we coded habitat as either aquatic (combining the initial categories of semiaquatic, aquatic burrowing, and aquatic) or terrestrial (combining the initial categories of burrowing and terrestrial). Hence, we estimate transition rates between the ecologically meaningful states of dietary generalism or specialism and between (semi-)aquatic and terrestrial habitats, expecting evolutionary transition rates in both directions for a given trait to be higher in the New World if there was evolution to fill new niches as the clade spread across North America.

We analyzed our categorical traits using two approaches, both implemented in phytools. To enable these methods to address our aim of testing whether dispersal to the New World resulted in evolutionary rate increases compared to the Old World natricids, we split our phylogeny into two separate trees. Specifically, we extracted the New World clade from the total phylogeny and (conversely) pruned the New World clade out to leave the Old World grade. Note that although the Old World natricids do not represent a clade, rate estimates are related to branch length units (million years in this case) and so this approach should not bias rate estimates in the Old World grade. Because treating estimates for the Old World natricids without any influence of the New World clade is the intention, any 'biases' caused by not including this clade are nothing of the sort but rather the effect we are looking to detect with this approach.

Before fitting any models to our categorical trait data, we first assessed the suitability of these traits for modelling in a phylogenetic comparative context by calculating the phylogenetic imbalance ratio (PIR) [55] in windex. PIR values range between 0 and 1, with lower values indicating greater suitability of the data for model fitting. Although advising against strict thresholds, $PIR < 0.1$ is suggested as an indication that the traits contain sufficient information to enable reasonable parameter estimation from phylogenetic comparative models [55]. We calculated PIR for both our diet and habitat traits and separately for the New World clade and Old World lineages (to reflect our modelling approach). In all cases our data are likely to be capable of generating good parameter estimates: $PIR_{dietOW} = 0.003$, $PIR_{dietNW} = 0.037$, $PIR_{habitatOW} = 0.006$, and $PIR_{habitatNW} = 0.047$.

Our first approach was to estimate four two-state Markov models, one each for the two traits (diet and habitat) in each species group (Old World and New World), using a Bayesian MCMC approach with the mcmcMk function. We used an ARD model to allow the two transition rates within each model to differ and ran the MCMC for 100,000 generations, discarding the first 20% as burn-in. We extracted and compared the posterior distributions of both transition rates for each trait between the two species groups.

In the second approach, we conducted two likelihood ratio tests (one for each trait) to directly compare the rates of evolution between our Old World and New World phylogenies and their corresponding datasets. For this we used the ratebytree function for categorical traits, which fits two versions of an ARD Markov model simultaneously to the two trees. In the first version the transition rates on each tree are allowed to vary independently, whereas in the second version the corresponding transition rates are constrained to be the same between the two trees (i.e., assuming New World and Old World natricids have the same evolutionary dynamics for the trait in question). A likelihood ratio test is then conducted to evaluate whether the more complex model allowing different evolutionary rates between phylogenies is a significantly better fit than the simpler model constrained to have the same evolutionary rates in each tree.

3. Results

Our historical biogeographic analysis confirmed a single origin of the New World natricids, with unambiguous support for a single dispersal event to the Nearctic region (see Supplementary Materials at https://doi.org/10.6084/m9.figshare.29118986.v1 accessed on 22 June 2025 for full outputs of these analyses). There is equivocal evidence for whether this event occurred at the root of the New World clade or the immediately preceding node that represents the most recent common ancestor of the New World clade and the European grass snakes (*Natrix*). In the latter scenario, the ancestors of the genus *Natrix* must have crossed back across Beringia and spread westwards across Eurasia, but in either case the New World was colonized only once by Natricidae. Other than the possible recrossing of Beringia by the ancestor of *Natrix*, all other dispersals from the Nearctic were to the Panamanian realm (Central America), of which there were an estimated 16 events with none back to the Nearctic. This latter pattern is consistent with a continued trend of southward dispersal across the North American continent after the initial crossing of Beringia.

As similarly expected, we recovered evidence for an increase in lineage diversification rates coinciding with origin of the New World clade (Figure 1). Specifically, speciation, extinction, and net diversification rates all increased coinciding with dispersal to the New World (Figure 2). Speciation rates increased >2-fold compared to Old World lineages before slowing down slightly, consistent with the expected pattern from adaptive radiation, and net diversification rate showed the same pattern (Figure 2).

Body size evolution was highly dynamic, with a posterior mean of 14 shifts (95% HPD interval 8–22 shifts) in the rate of body size evolution (Figure 3). The location of these shifts was very unclear—there are 8226 different shift configurations in the 95% credible shift set, of which the best has only ~0.1% of the posterior probability—but they did not cluster in the New World clade and there is no clear signal of higher rates in that group (Figure 3).

Transition rates between specialist and generalist diets did not conform to the higher rates expected if diet evolution characterized the adaptive radiation in the Americas, in fact rates were likely lower in the New World clade (Figure 4). This is supported by our likelihood ratio test, which found that an independent rates model was favored in which both transition rates for diet were much lower in the New World clade compared to the Old World lineages ($\chi^2 = 9.156$, df = 2, P = 0.010). We note, however, that although unable to be analyzed due to low sample size of several categories in one or both geographic regions, the original diet categories were slightly more diverse amongst New World species than Old World species. Specifically, despite the younger age of the New World clade (14 my vs. 47 my) and the lower species richness in our dataset (58 vs. 155 species) compared to the Old World group, the former include seven diet categories in our dataset (five types of specialists plus generalists and aquatic generalists) compared to six in the Old World (four types of specialists plus the two generalist categories). Hence, it is possible that this represents relatively rapid but finer-scale differentiation in particular diet components during the adaptative radiation that was not detected in our broader scale coding. Nevertheless, with limited potential for statistical support in our study this is only a tentative indication at best.

In contrast to the limited evidence for diet, we found that transitions between terrestrial and aquatic habitats, in both directions, typically occurred at a higher rate in the New World clade (Figure 4). Although the posterior distribution of our terrestrial-to-aquatic rate estimate in the New World is slightly bimodal, and hence more difficult to interpret, the aquatic-to-terrestrial transition rate is clearly higher in the New World than in Old World lineages. Furthermore, the general pattern is also supported by our likelihood ratio test, in which a model where both transition rates for habitat were much higher in the New World clade compared to the Old World lineages was strongly favored ($\chi^2 = 22.582$, df = 2, $P = 1.2 \times 10^{-5}$). Considering the original finer-scale trait coding, as we did for diet above, offers no more insight in this case as representatives of all habitat categories are present in both New and Old World lineages.

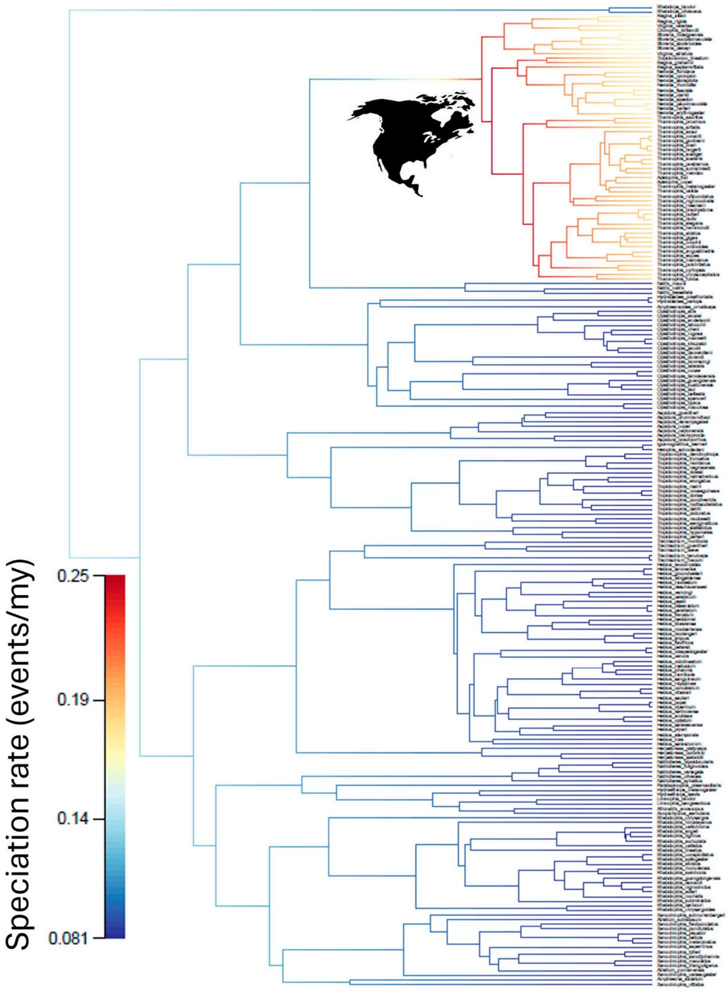

Figure 1. Most likely speciation rate dynamics for Natricidae, with a sharp increase in speciation rate at the root of the New World clade (the node with the map). This configuration had 66% of the posterior probability and another 10% recovered the same shift as shown here but one other in a different clade. Of the 95% credible shift set, all but one (holding only 8% of the posterior probability and recovering no shifts) find that an increase in speciation rate occurred either at this node at the root of the New World clade (76% of the posterior distribution) or sequentially nested nodes within this clade. Extinction and net diversification rates were estimated as having similar patterns.

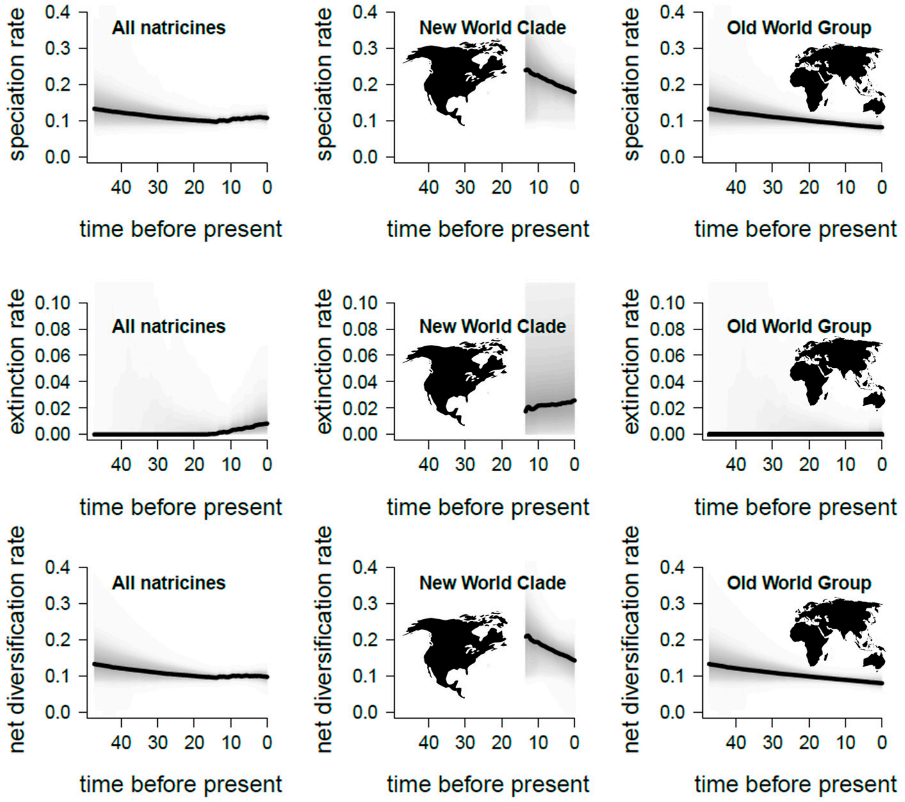

Figure 2. Diversification rate dynamics through time for all natricids combined and separately for the New World clade and the Old World grade, including speciation, extinction, and net diversification rates. A slight increase in all three rates is evident in average rates for the family in the most recent ~15 my, but this is entirely accounted for by a substantial increase at the origin of the New World clade, with the remainder of lineages showing a background pattern of a slight decrease over time.

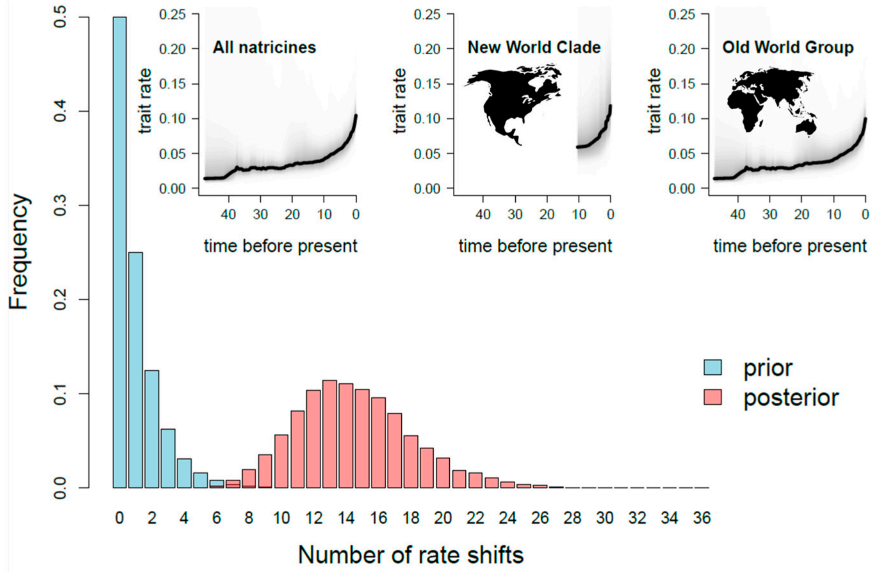

Figure 3. Prior and posterior distributions of the number of shifts in the rate of body size evolution. Although the exact number (and location) of these shifts remain unclear, the posterior estimate has diverged substantially from the prior and shows strong evidence for a large number of shifts and so a highly dynamic pattern of body size evolution in the Natricidae. Inset shows rate dynamics through time for all natricids, the New World clade, and the Old World grade, showing a general increase over time (especially the last ~5 my) but no clear pattern of higher rates in the New World.

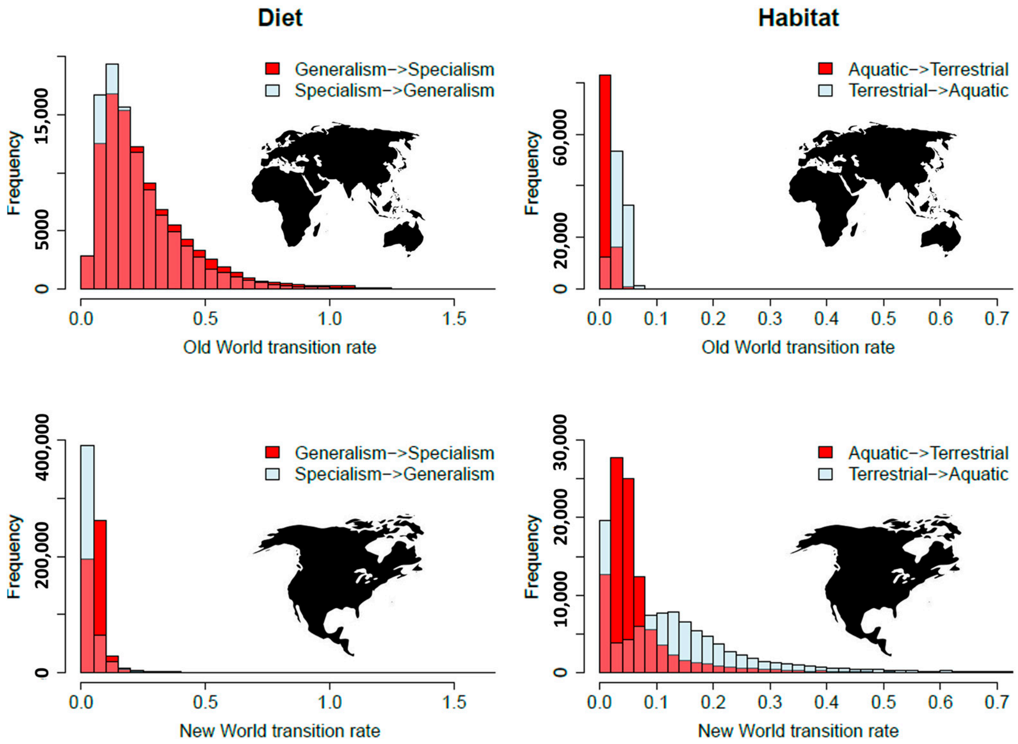

Figure 4. Posterior distributions of estimated transition rates for Markov models of diet and habitat in the Old World natricids and the New World clade. Compared to the background rates in the Old World, New World natricids switch between dietary specialists and generalists at a slower rate, whereas transition rates between aquatic and terrestrial habitats are likely higher in the New World.

4. Discussion

We took a phylogenetic comparative approach to investigate the possible adaptive radiation of the New World members of the family Natricidae. We first confirmed that our dataset recovers previously reported patterns that are key aspects of the proposed radiation: a single dispersal event across Beringia from which New World natricids arose and were exposed to the ecological opportunity of a newly encountered landmass, and that this event coincided with a burst of speciation (characterized by substantially increased diversification rates and a gradual slowing down as originally empty niches are filled throughout the new continent). Having recapitulated these results, we built on these foundations by investigating which ecologically important traits were associated with the radiation, in other words the 'adaptive' part of adaptive radiation. In doing so, we find no evidence for rapid divergence of body size and limited evidence for the involvement of diet evolution, but instead demonstrate that rates of evolutionary shifts between aquatic and terrestrial habitats increased in the New World clade. Hence, we argue that habitat was an important component of divergence as water snakes spread across the North American continent.

Our historical biogeographic analysis recovered a single dispersal event to the New World, in line with previous work [33,34], but despite higher taxon sampling we were still unable to clearly resolve whether this occurred at the origin of the New World clade or the node containing the New World clade plus *Natrix*. Single origins of New World snakes across Beringia with no dispersals back to the Old World appears to be a common pattern, including for major groups in the New World such as Dipsadidae, 'ratsnakes', pitvipers, and coral snakes [56–59]. As such, although the evidence remains equivocal we favor the dispersal event to have occurred ~15 mya at the most recent common ancestor of the New World clade. Interestingly, all but one of these groups are estimated to have arrived in North America before the natricids (the exception being pitvipers, which may have arrived at approximately the same time if the earlier dispersal of the natricids is correct), potentially reducing the availability of unoccupied niches. However, natricids are often the most common snakes in North American wetlands [60,61], suggesting that there was scope for diversifying into this habitat frequently (with terrestrial lineages perhaps better at dispersing between water bodies as the clade spread across the continent). Consistent with this tendency to specialize in aquatic habitats is that our estimated transition rates are slightly higher for terrestrial-to-aquatic shifts than vice versa.

We also found a strongly unidirectional dispersal pattern on the scale of biogeographic realms, with many independent colonizations of the Panamanian realm (Central America) from the Nearctic but none in the reverse direction. This is broadly consistent with previous studies demonstrating a typical pattern of eastward and southward spread of natricids since entering North America across Beringia [34–36]. These findings suggest a scenario of arrival and then subsequent diversification over a ‘dispersal front’, in which case lineages would have experienced new ecological opportunities on a rolling basis that would likely have generated repeated selection for niche evolution.

Although we used a different phylogeny and taxon sampling, we recovered the previously reported increase in speciation rate (a doubling in our case) at the base of the New World clade [33]. Interestingly, the latter study also found evidence of an upshift in diversification rate within a clade of Asian natricids. We did not find evidence for this additional burst of speciation, suggesting that such a result is sensitive to the phylogeny used, but importantly for our purposes the increased speciation rate of New World species held. This also translated into a marked increase in net diversification rate despite an estimated increase in extinction rate in the New World clade (but see [62] for cautions on interpreting extinction rates from extant-only phylogenies). Increases in speciation or net diversification rates of snakes are a common finding when a clade disperses to a new region, including to the New World, and likely reflects the availability of ecological opportunity in a new area [11,33,58,63].

The rate of body size evolution was highly dynamic, with frequent shifts across the phylogeny, but these were not clearly associated with the New World clade and so body size does not seem to be capturing the important ecological variation associated with an adaptive radiation. Curiously, we found that diet evolution appears to slow down in the New World, inconsistent with both diet-driven adaptive radiation and previous work showing dramatically increased rates of diet evolution in this clade [37]. However, despite a priori indications that a generalist-specialist categorization of diet is ecologically meaningful and important in these snakes [35], it seems likely that finer scale diet shifts were associated with the adaptive radiation of New World Natricidae. In line with this suggestion (and other analyses [37]), we find a slightly larger number of specialist diet categories among New Word species despite this clade having less time and fewer species to evolve specialist diets. For instance, both crayfish and mollusc specialists have evolved only in the New World clade (at least within our dataset) [33] and diet is associated with variation in head shape such as relatively wide heads and short snouts in mollusc feeders [53], albeit head shape is still more strongly associated with habitat [53]. Nevertheless, as our results show higher transition rates between terrestrial and aquatic habitats in the New World clade and that habitat shifts are likely to change the availability of particular prey categories (and hence the finer-scale diet options available), we propose that habitat was the primary axis of differentiation during the adaptive radiation of New World natricids. This is consistent with the increasing realization that adaptive radiations may take place in a hierarchical manner with multiple niche axes differentiating at different stages of the radiation [64] and that broader level traits often form the primary niche involved, with finer-scale variation evolving secondarily [65]. Intriguingly, habitat dynamics have also been recently proposed as important in the colonization and spread through the New World by pitvipers [66]—the only other snake radiation that may have dispersed to the New World at approximately the same time as natricids.

Summarizing what we now know, we consider that there is strong evidence for treating the New World clade of Natricidae as an adaptive radiation and we hypothesize the following scenario. Evolution of viviparity facilitated the dispersal across the relatively high latitude Beringia land bridge ~15 mya, as this trait is associated with lower temperature tolerance in reptiles (notwithstanding that Beringia was warmer then than it is today) [33,67]. Following their arrival in North America, natricids gradually dispersed southward and eastward away from their northwest origin point. As they did so, they encountered different habitats and, due to competition either with other natricids or other (earlier colonizing) snakes, the species' evolved to make use of primarily aquatic habitats. Repeated encounters with wetland habitats and advantages of terrestrial habits for longer distance dispersal (and hence encountering additional water bodies) generated the conditions for broad-scale ecological specialization and adaptive radiation over the continent. As an additional means of reducing competition, natricids within a given type of habitat subsequently diverged along fine-scale dietary niches. As niche space gradually filled, the rate of speciation slowed down, although still remaining high compared to Old World natricids perhaps due to continued dispersal at the southernmost edge of the range (of which there were multiple cases within the last 5 my [34,35]).

Schenk and Steppan [25] discuss in detail the implications of geographic structure and the ability of organisms to disperse across areas for adaptive radiation. Their emphasis on the combination of dispersal across an area to new regions, and adaptation to newly encountered habitats/environments as they spread, is consistent with our results. Moreover, this spatial aspect of adaptive radiation may help explain the rough division of adaptive radiations highlighted in the introduction; namely that of spatially constrained 'island' radiations differentiated primarily by trophic ecology vs. less spatially constrained 'continental' radiations primarily differentiated by habitat. Specifically, continental radiations may have sufficient space to continue dispersing and encountering new environments that will facilitate continued adaptation to these over a longer period (Figure 5). On the other hand, island radiations are less able to engage in the 'dispersal' stage as they are confined to smaller areas and hence are constrained to diversify in relation to the resources available at a given location, commonly diet (Figure 5).

This hypothesized generality of the ecological axes that are primarily exploited during adaptive radiations may not only shed light on the predictability of adaptive radiations, but also points to possible explanations for exceptions to the rule. For instance, two prominent exceptions where island adaptive radiations are likely structured primarily by habitat, *Anolis* lizards and *Eleutherodactylus* frogs [9,10], are both in the Caribbean. Since the underlying mechanism is proposed to be the more limited dispersal of island contexts, one possibility is that peculiarities of this island chain may minimize the normal constraints of island radiations. For example, if the configuration of islands in relation to ocean currents happens to facilitate dispersal between islands then a similar process may operate as in continental radiations gradually spreading across a landmass. Similarly, predictions may be made about whether exceptions to the proposed hypothesis involve organisms with especially good or poor dispersal abilities that create conditions similar to the opposing scenario. Hence, our proposed hypothesis presents opportunities to test its generality both in the form of confirmatory cases and in (specific and predictable) 'exceptions which prove the rule'. We look forward to future tests, which may include a wide range of approaches such as (1) meta-analyses of adaptive radiations, (2) further studies of particular radiations designed to distinguish the primary ecological axes, (3) investigations of ecomorphological changes in invasive species (which have, after all, 'dispersed' into a new area and so may act as experimental analogies of natural dispersal processes in evolution), (4) paleontological studies considering the expansion of habitat vs. diet niche space in fossil representatives of adaptive radiations, and (5) theoretical investigation with mathematical models.

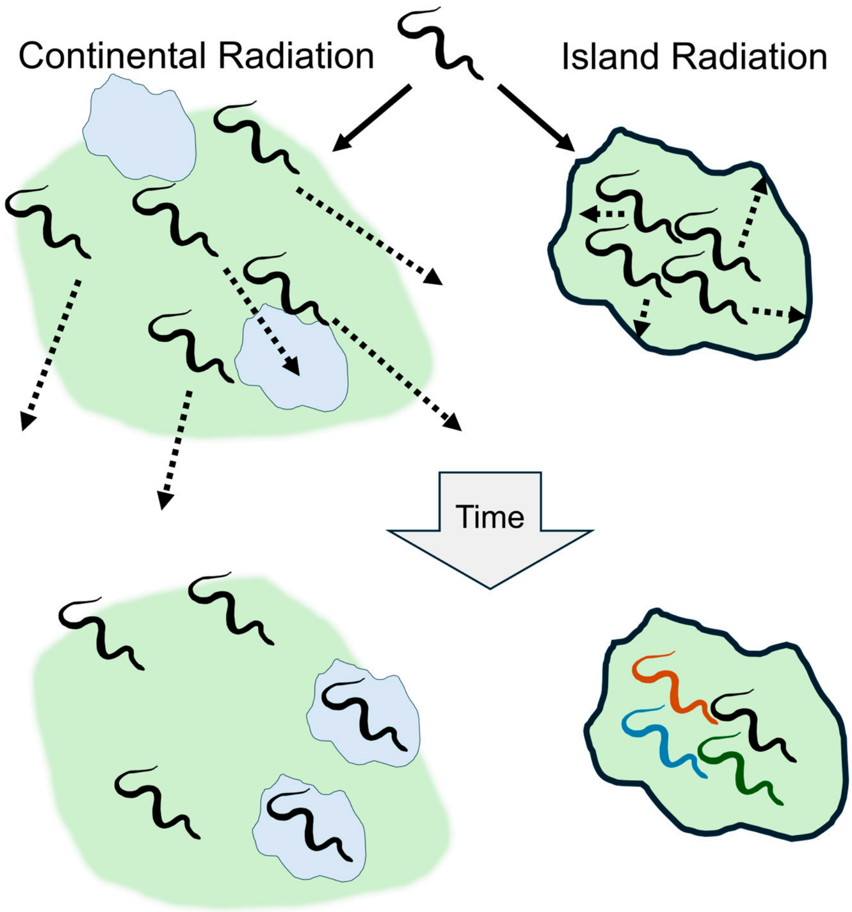

Figure 5. Diagrammatic representation of our hypothesis. When an initial lineage disperses to a new area (solid arrow), adaptive radiation may occur, facilitated by the ecological opportunity now available. If this happens on a large ('continental') landmass (left), movement (dotted arrows) is relatively unconstrained (soft boundaries) as the lineage can relatively freely spread across the landmass and encounter a range of new habitats or environments (such as water bodies) to which it can adapt on a 'rolling' basis following the dispersal front. In contrast, if the adaptive radiation is occurring under relatively tight spatial constraints (thick boundaries), such as on an island (right), further dispersal is restricted and adaptation is mainly limited to diversified use of resources in the new area such as diet specialization (colors representing different diet types).

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