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The Origins and Diversification of the Exceptionally Rich Gemsnakes (Colubroidea: Lamprophiidae: Pseudoxyrhophiinae) in Madagascar

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Abstract.—Processes leading to spectacular diversity of both form and species on islands have been well-documented under island biogeography theory, where distance from source and island size are key factors determining immigration and extinction resistance. But far less understood are the processes governing *in situ* diversification on the world's mega islands, where large and isolated land masses produced morphologically distinct radiations from related taxa on continental regions. Madagascar has long been recognized as a natural laboratory due to its isolation, lack of influence from adjacent continents, and diversification of spectacular vertebrate radiations. However, only a handful of studies have examined rate shifts of *in situ* diversification for this island. Here, we examine rates of diversification in the Malagasy snakes of the family Pseudoxyrhophiinae (gemsnakes) to understand if rates of speciation were initially high, enhanced by diversification into distinct biomes, and associated with key dentition traits. Using a genomic sequence-capture data set for 366 samples, we determine that all previously described and newly discovered species are delimitable and therefore useful candidates for understanding diversification trajectories through time. Our analysis detected no shifts in diversification rate between clades or changes in biome or dentition type. Remarkably, we demonstrate that rates of diversification of the gemsnake radiation, which originated in Madagascar during the early Miocene, remained steady throughout the Neogene. However, we do detect a significant slowdown in diversification during the Pleistocene. We also comment on the apparent paradox where most living species originated in the Pleistocene, despite diversification rates being substantially higher during the earlier 15 myr. [Gemsnakes; *in situ* diversification; island biogeography; Neogene; Pseudoxyrhophiinae; speciation.]

Island clades often show a pattern of rapid diversification after colonization, which is hypothesized to be a response for filling vacant niches (Schluter 2000; Losos and Ricklefs 2009; Presgraves and Glor 2010; Rabosky and Glor 2010). This standard pattern of *in situ* island diversification has provided the basic evidence for adaptive radiation (AR) via ecological opportunity and has served as the intellectual template for continental AR (Simpson 1944; Losos et al. 1998). While studies of island biogeography have firmly established that the essential properties of islands such as distance to the mainland, area, and habitat heterogeneity all influence colonization and extinction under ecological neutrality (MacArthur and Wilson 1967), less understood are the processes of *in situ* diversification as related to properties of speciation and accumulation of diverse endemic island faunas (Losos et al. 2009). Even though *in situ* island diversification is positively associated with area, and trajectories for diversification may vary among clades, most groups are expected to reveal initially high speciation rates when presented with abundant ecological opportunity upon colonization (Paulay 1994; Lomolino and Weiser 2001; Pinto et al. 2008; Losos and Ricklefs 2009; Pyron and Burbrink 2014a; Igea et al. 2015).

Several taxonomic groups across large island systems have demonstrated that speciation rates do indeed rise rapidly after colonization. For instance, the *Anolis* lizards of the West Indies (Losos et al. 2009; Rabosky and Glor 2010) and honeycreepers and silver swords in Hawaii (Carlquist et al. 2003; Lerner et al. 2011) support the classic prediction of AR as applied to island systems: rapid early speciation with associated phenotypic adaptation. This suggests that finding diversity dependence (DD), where rates of speciation are initially high but trend towards an ecologically-mediated carrying capacity, is indicative of AR over deep time scales (Losos 2010; Yoder et al. 2010). Nevertheless, there are a few examples that contradict these predictions. For instance, a diverse assemblage of snakes in the West Indies showed very little change in diversification over time (Burbrink et al. 2012b). On the other hand, typical changes in the diversification trajectory often attributed to AR may have geographic and environmental causes not linked to saturated ecological space, such as high speciation rates following rapid changes in habitat that slow as the environment stabilizes (Vrba 1985; Rosenzweig 1995; Pigot et al. 2010; Pyron and Burbrink 2012a; Quental and Marshall 2013; Moen and Morlon 2014). Moreover, AR may not be accompanied by changes in speciation rates if the adaptive traits examined do not directly affect speciation processes (Rabosky 2017).

One obstacle to understanding processes that produce diverse island communities is the difficulty obtaining reliable phylogenetic data for species-rich groups typically associated with ecologically diverse islands. For example, even if the fundamental idea of a species-diversity carrying capacity holds (and it may not, see Harmon and Harrison 2015; Rabosky and Hurlbert 2015), estimating processes and rates of diversification is often hampered by size of the phylogeny, inadequate models or disagreement among models, differing modes of speciation, insufficient taxon sampling, and undetected cryptic species (Pybus and Harvey 2000; Revell et al. 2005; Weir 2006; Rosindell et al. 2010; Pennell et al. 2012; Ruane et al. 2014). Therefore, geographically monophyletic groups are valuable for understanding diversification within large islands, where the standing diversity was generated only by intra-island speciation, and where taxon sampling is more likely to be complete.

Madagascar, at 587,041 km^2 with 3% of the worlds' biodiversity, stands out among all large islands as showing significant endemicity generated mostly by *in situ* diversification (Goodman and Benstead 2003; Vences et al. 2009). This diversity can in part be explained by its ancient isolation from Gondwanaland at 120+ millions of years ago (Ma) and India at 80 Ma (McLoughlin 2001; Collier et al. 2008) and typical island biogeographic characteristics that generate species such as area, distance from the mainland, and sharp demarcation among distinct biomes (MacArthur and Wilson 1967; Raxworthy et al. 2002, 2015; Goodman and Benstead 2003; Pearson and Raxworthy 2009; Vences et al. 2009; Samonds et al. 2013; Brown et al. 2014). For many of the diverse endemic groups on Madagascar, colonization likely happened throughout the Cenozoic, but dropped off rapidly after the mid-Miocene (von der Heydt and Dijkstra 2006; Yoder and Nowak 2006; Ali and Huber 2010; Samonds et al. 2012, 2013). Some studies have suggested that *in situ* diversification following colonization for many of these vertebrate groups remained constant through time (Crottini et al. 2012), though research on Malagasy herpetofauna (day geckos and chameleons) have shown early bursts of speciation that declined through the Quaternary (Harmon et al. 2008; Scantlebury 2013). Unfortunately, knowledge about the diversification of groups during the Cenozoic has relied on incomplete taxon sampling typically using only a handful of loci, further hindered by a wide fossil gap that excludes the critical Miocene epoch (Raxworthy Nussbaum 1997; Burney et al. 2004; Samonds et al. 2013).

We, therefore, call attention to the diverse subfamily of snakes, Pseudoxyrhophiinae (Colubroidea: Lamprophiidae), which are composed of 90 described species found in fossorial, terrestrial, aquatic, and arboreal habitats, and occur in many of the basic ecological niches snakes occupy throughout continental systems (Vitt et al. 2003; Vitt and Caldwell 2009). Because pseudoxyrhophiine snakes have no common-use name, we herein refer to them as gemsnakes, in reference to the locally well-known Malagasy legend of an endemic serpent that carries a light-emitting diamond in its stomach (Raxworthy, pers. observ.). Gemsnakes consume a wide variety of mostly prey including frogs, skinks, geckos, chameleons, other snakes, birds, mammals, and occasionally invertebrates (Nagy et al. 2003; Glaw and Vences 2007; Uetz 2009; Ruane et al. 2015). Potentially related to dietary and habitat preferences, gemsnakes can be divided into aglyphous taxa without grooved rear teeth and opisthoglyphous species, which feature enlarged, grooved rear teeth used to hold or envenomate prey (Guibé 1958; Kardong 1980; Mori and Mizuta 2006; D'Cruze 2008; Weinstein et al. 2011), though we note that aglyphous gemsnakes may also envenomate prey (Razafimahatratra et al. 2015). While dentition and diet may be correlated (Knox and Jackson 2010), for most snakes on continental systems, it is unclear if dentition type relates to general ecological or prey preferences and if this trait is phylogenetically conserved.

At least for snakes in continental communities, diversification occurs rapidly upon colonization (Burbrink et al. 2012a; Chen et al. 2017) and basic ecological niches are usually filled by the colonization and diversification of several groups across several subfamilial taxonomic ranks (Bellini et al. 2015; Burbrink and Myers 2015). In contrast, the majority of Madagascar's gemsnake diversity is suspected to have originated via *in situ* diversification from a single colonization event (Nagy et al. 2003). Importantly, Madagascar derives most of its fauna via *in situ* diversification, even when compared with other large islands such as New Guinea and Borneo (Pyron and Burbrink 2012a). It is unknown if processes of diversification leading to the large radiation of gemsnakes occurred via early bursts of speciation with downturns as niches were filled or were constant through time. Similarly, it is unclear how traits have evolved to fill niches and if primary ecology predicts key dentition types.

To address the processes of *in situ* diversification that have led to the diverse snake communities in Madagascar, we collect sequence-capture data from 366 individual gemsnakes and outgroups to first account for extant diversity among previously named taxa and phylogenetically deep cryptic lineages. Since under- or over-estimating alpha taxonomy can affect downstream estimates of diversification (Faurby et al. 2016), we confirm species delimitations of all previously and newly identified taxa using coalescent methods. We then examine the timing of colonization and processes of *in situ* species and ecological diversification, and determine if different regions of notably contrasting biomes were responsible for enhanced phylogenetic and species diversity. Our conclusions provide an alternate understanding of AR showing that constant rates (CR) of diversification throughout the Neogene can lead to spectacular diversification in species number and form.

METHODS AND MATERIALS

Data and Screening Pseudoxyrhophiine Samples for High-Throughput Sequencing

Prior to high-throughput sequencing for anchored loci used in the subsequent analyses, we Sanger-sequenced four loci for 621 individuals (583 Malagasy gemsnakes, plus outgroups, see Supplementary data available on Dryad at https://datadryad.org/resource/doi:10.5061/dryad.07h0n14): the mitochondrial locus cytochrome oxidase 1 (CO1) and the nuclear loci oocyte maturation factor mos gene (CMOS), recombination activating 2 gene (RAG2), and Nav1.4 intron 5 (NAV5) (see Supplementary data available on Dryad). Primers and sequencing conditions follow those used in Ruane et al. (2015). We inferred trees using maximum likelihood in RAxML 8.0 (Stamatakis 2014) with the GTRGAMMA model of evolution and partitioned by locus and codon position for the protein coding genes. Tree estimates used 100 independent tree searches and 5000 bootstrap replicates to retrieve support values. This procedure allowed us to confirm sample identities, determine potentially undescribed and/or cryptic taxa, and choose individuals that would encompass as much of the genetic diversity found within each species and/or genus as possible for high-throughput sequencing.

Sequence-capture data sets generating anchored hybrid enrichment loci were collected at the Center for Anchored Phylogenomics (www.anchoredphylogeny.com) following Lemmon et al. (2012) and Ruane et al. (2015; Supplementary data available on Dryad). Including new species, we sampled 109 gemsnake taxa representing 93% of extant species on Madagascar and outgroup samples from all major clades of Colubroidea, resulting in a data set comprising 366 individuals and a total 732 phased sequences (Supplementary data available on Dryad). We did not include taxa only found on Comoros *Liophidium mayottensis*, *Lycodryas cococola*, and *Lycodryas maculatus* and were unable to sample *Brygophis coulangesi*, *Ithycyphus blanci*, *Langaha pseudoalluaudi*, *Liophidium pattoni*, *Liophidium maintikibo*, *Pararhadinaea melanogaster*, *Pseudoxyrhopus ankafinaensis*, *P. kely*, and *P. sokosoko*. We note that *Pseudoxyrhopus ankafinaensis* is probably extinct (Raxworthy and Nussbaum 1994) and consider *Lycodryas carleti* (junior synonym of *L. gaimardi*), and *Phisalixella iarakaensis* (junior synonym of *P. arctifasciata*) as invalid taxa. Few genetic differences exist between these two species of *Lycodryas*; Kimura pairwise sequence differences within *L. gaimardi* (~0.043) overlap those between *L. gaimardi* and *L. carleti* (0.027–0.047). The one known *Phisalixella iarakaensis* specimen is sympatric with *P. arctifasciata*, and identical in all respects except an additional scale row on each body flank. However, as dorsal scale row variation is common in other *Phisalixella* species, we thus consider this to represent intraspecific variation.

Phylogeny

We generated three types of phylogenies based on the full (732 samples), reduced (130 samples; gemsnakes and outgroups), and core (109 samples, gemsnakes only). We used ASTRAL II (Mirarab and Warnow 2015) to infer species trees for all 732 phased terminals; this method accounts for incomplete lineage sorting. We generated support for the topology using local posterior probabilities on quadripartitions (Sayyari and Mirarab 2016). Additionally, we concatenated data and used maximum likelihood in IQ-TREE (Nguyen et al. 2015) to estimate phylogeny. Here, we partitioned each locus, assessed which among 279 models of substitution best fit each partition using Bayesian information criterion (BIC), and estimated phylogeny with support generated from 1000 bootstraps. We also estimated phylogeny using maximum likelihood on the concatenated partitioned and unpartitioned data with the GTRGAMMA model in RAxML 8.0 (Stamatakis 2014). We compared topological support between these estimators using Robinson–Foulds distances (RF; Robinson and Foulds 1981) in the R package "phangorn" (Schliep 2011) and identified nodes with distinctly different support.

Species Delimitation

It was necessary to include deeply divergent, unnamed species along with the currently recognized gemsnakes to estimate diversification and run other downstream comparative processes, and we consider 38 of these unnamed taxa as unique given that: (1) the dates of divergence were generally greater than the Calabrian; divergences for most snakes using phylogeographic species delimitations have been recorded from the mid-Pleistocene to the late Miocene (Burbrink et al. 2011; Myers et al. 2013; Ruane et al. 2014, 2016, 2018; McKelvy and Burbrink 2017), (2) the ranges of the dates of origin of these new taxa fit within the ranges of age of origin of previously named sister taxa within gemsnakes (Supplementary data available on Dryad), (3) the new taxa are geographically distinct from their sister taxa, and (4) the new taxa have morphological diagnostic characters (*in prep*).

To confirm that we can delimit all species of Malagasy gemsnakes, including previously described and new undescribed taxa, we used the program Bayesian Phylogenetics and Phylogeography (BPP v4.0; Rannala and Yang 2013). This method uses coalescent techniques to estimate the probability that species were distinct and helped confirm that they were genetically isolated on evolutionary timescales (Rannala 2015). The tree size of core gemsnakes, which includes 109 distinct species, prohibits delimitation using BPP as a whole. Therefore, using a custom script in R (*BPP_Maker*; Supplementary code available on Dryad), we broke up the phylogeny into inclusive testable groups ranging from 2 to 7 terminals and all population level-samples per taxon for a total of 32 delimitation analyses. For each analysis, we used all 370 loci, however for *Compsophis* (*Compsophis_5*) and *Madagascarophis* (*Madacascarophis_1*), we removed 244 and 232 loci, respectively, due to numerous missing individuals that would have eliminated some taxa for testing (Supplementary data available on Dryad). We used algorithm A11 to jointly delimit species and estimate a species tree (Rannala and Yang 2013), and variables were fine-tuned and updated automatically to ensure that swapping rates between Markov chain Monte Carlo (MCMC) chains were adequate. We used the new implementation of inverse gamma priors at 3, 0.004 and 3, 0.002 for ancestral population sizes (θ) and root age (τ), respectively. We ran these two times for 1×10^5 generations, following a burn in of 1×10^5generations, which were then sampled every 10 generations. We determined that all estimated sample sizes (ESS) >200 for τ only using the R package “coda” (Plummer et al. 2006). We compared the time of speciation for all new species and pairs of previously described taxa using a custom script (*BPP_Dater*) that takes all estimates of τ and converts this to time by dividing τ by substitutions/generation, obtaining substitution rate and generation time from a fitted gamma distribution for each of the 100,000 MCMC samples of τ (Angelis and Dos Reis 2015; see Supplementary code available on Dryad for details).

Reduced Phylogeny

To examine processes of species, trait, and ecological diversification in gemsnakes, we reduced the data set from 732 phased terminals down to 130 terminal taxa (including 21 outgroups) to remove population level sampling so that downstream comparative methods were calculated on trees that include only a single sample per species. The core gemsnakes were further subsampled representing 109 monophyletic pseudoxyrhophiine species that diversified within Madagascar and therefore represent *in situ* diversification; this group does not contain the African outgroup taxa *Amplorhinus*, *Duberria*, and *Ditypophis*. Phylogenies with one terminal per taxon (randomly sampled when >1 individual/species was present) were generated using (1) maximum likelihood with IQ-TREE (Nguyen et al. 2015) where each partition was tested using ModelFinder (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017) for over 279 substitutional models including up to six free rate gamma categories. Support for these trees was assessed using ultrafast nonparametric bootstrap approximation (Minh et al. 2013) over the partitioned, concatenated data sets and over the partitioned, concatenated data set where pseudoreplicates were created by resampling at the full locus level, and support using the Shimodaira–Hasegawa-like approximate likelihood ratio test (Shimodaira and Hasegawa 1999); (2) species trees generated using SVDQuartets (Chifman ane Kubatko 2014) and support from 1000 bootstraps; (3) ASTRAL II (Mirarab and Warnow 2015) with support estimated using local posterior probabilities on quadripartitions, and (4) ASTRAL II where we did not downsample the entire data set ($n=732$) but used the multiple individuals per species feature.

Divergence Dating

We dated both the full and reduced phylogeny using the penalized likelihood approach in TreePL (Smith and O′Meara 2012), MCMCTree (Yang and Rannala 2006), and BEAST2 (Bouckaert et al. 2014) and determined that all three solutions were correlated and node error was minimal. Implementing a full MCMC relaxed-clock phylogenetic method was not possible given the number of taxa and loci. Therefore, to assess error on these date estimates, we bootstrapped the concatenated and partitioned data set using IQ-TREE and estimated dated trees using TreePL with fossil constraints with hard bounds. We also used an Astral-constrained tree with concatenated data to estimate divergence dates using MCMCTree and Beast2. For MCMCTree, all calibrations were made “softer” by extending probabilities of 0.025 beyond those bounds (see Supplementary data available on Dryad for details parameterizing TreePL, MCMCTree, and BEAST2). We used the following fossil-based calibration locations and times, which according to Head (2015) and Guo et al. (2012) were reliably placed at the most recent common ancestor (mrca) with hard bounds [mean and standard deviation (SD) in parentheses for BEAST2] for the following groups: (1) Crown of Colubroidea and all trees used here (mrca of *Achalinus rufescens* and *Compsophis albiventris*) at 50.5–72.1 Ma ($\bar{X}=55.5$, SD $=9.0$), (2) stem Elapidae (mrca of *Naja melanoleuca* and *Hemerophis socotrae*), minimum 30.9 Ma ($\bar{X}=32.9$, SD $=1.0$), (3) stem Natricinae (mrca of *Thamnophis cyrtopsis* and *Helicops angulatus*) 32–36 Ma ($\bar{X}=29.5$, SD $=3.4$), and (4) crown Viperidae (mrca *Crotalus molossus* and *Bitis gabonica*) 20–23.8 Ma ($\bar{X}=22.0$, SD $=0.9$).

Ancestral Range Estimation

Previous authors have demonstrated that Madagascar was colonized twice by lamprophiid snakes from Africa, an early colonization resulting in the diversification of the core gemsnakes and a later one resulting in two species of *Mimophis* (Nagy et al. 2003; Vidal et al. 2008; Ruane et al. 2018). We tested this using our new comprehensive phylogenies that included lamprophiids from Africa and global colubroid outgroups. Using the dated 130-taxon phylogeny, we estimated ancestral areas using BioGeoBEARS (Matzke 2013, 2014). We used three base models in BioGeoBEARS (Matzke 2013): the Dispersal–Extinction–Cladogenesis (DEC) of Ree and Smith (2008); DIVALIKE, a likelihood implementation of the assumptions of the parsimony DIVA program (Ronquist 1997); and BAYAREALIKE, a likelihood implementation of the assumptions of the BayArea program (Landis et al. 2013). Models were run with and without a parameter weighting jump dispersal (+J) at cladogenesis (Matzke 2014). Terminal species were coded as occurring in one or multiple areas that included globally Asia, New World, and Europe, and regionally Africa, Socotra, and Madagascar. We estimated ancestral area and colonization times using the biogeographic model with the lowest AICc.

Diversification

We determined if diversification differs throughout the core gemsnakes, estimated with the MCMCTree using BAMM (Rabosky 2014; Rabosky et al. 2014). We estimated changes in diversification using BAMM with the initial prior estimates generated using the function *setBAMMpriors* over five Poisson rate priors of 0.1, 0.5, 1.0, 5, and 10 (Rabosky et al. 2014). We ran 10×10^6 generations for each Poisson rate prior twice to ensure consistency, thinned by every 1000, and removed 15% as burn in. Over these Poisson rate priors, we estimated the number of diversification rate shifts with the highest posterior density (HPD) in the maximum shift credibility configuration.

Because methodologies in BAMM are controversial given putative problems with the likelihood function and Poisson process prior model (Moore et al. 2016; Rabosky et al. 2017), we also used spectral densities to identify modes or clusters that may represent diversification shifts in this tree (Lewitus and Morlon 2016). Here, the phylogeny was converted into a graph Laplacian and represented as a spectral density profile of eigenvalues (λ). The primary λ and 2nd, 3rd, and 4th moments were estimated to represent shifts, asymmetry, and peakedness in the spectral profile, respectively. The number of peaks in the profile represented the number of diversification modalities across the tree. This method was implemented using the R package "RPANDA" (Morlon et al. 2016) using the *spectR* and *BICompare* functions to identify distinct patterns of diversification within the phylogeny of gemsnakes.

Diversification rates were the same over the core gemsnakes (see Results section). We determined if speciation or extinction rates have changed over time, or responded to mass extinction events. Under a typical AR model, we predicted that speciation rates should have been highest upon colonization and decrease through time. We tested this using rjMCMC CoMET (May et al. 2016) in the R package "TESS" (Höhna et al. 2015) to estimate diversification parameters over time given hyperpriors for speciation, extinction, and numbers of mass extinction generated from the empirical data using the *TESS.analysis* function with 1×10^5 iterations. We determined that convergence using rjMCMC occurred for the speciation, extinction rate, and mass extinction parameters when effective sample sizes exceeded 200. We ran CoMET on the maximum likelihood phylogeny to determine if Bayes factors support any mass extinction events. With no evidence of mass extinction, we repeated this analysis 10 times over all 1000 bootstrapped dated trees and estimated rates of speciation and extinction over time. We also determined if Bayes factors showed evidence of change in speciation and extinction over time.

To determine whether incomplete taxon sampling from undiscovered species could explain the signal for declining diversification rates in the Pleistocene, we developed code to add additional artificial taxa only in the Pleistocene without altering the height of any existing nodes (Supplementary data available on Dryad). This stress test was designed to determine how many additional undiscovered speciation events would be needed to change estimates of diversification away from declining rates during the Pleistocene. We added additional sets of ten taxa up to a total 109 cryptic species (doubling the current number of taxa) replicated 100 times per set, reran TESS, and used Bayes Factors above 5.0 to account for declining or increasing rate shifts during the Pleistocene.

To detect a signal of DD given changes in speciation and extinction rates, we used the R package "DDD" (Etienne et al. 2012) to test between CR and DD models. We estimated parameters including birth (λ), death μ, and carrying capacity (κ) for both DD and CR models. We used these estimates in the function *dd_LR* to generate a parametric bootstrapped ($n=1000$) likelihood ratio test for DD against CR given simulations generated from the estimated values of λ, μ, and κ at 0.299 (0.162), 0 (9.718×10^{-6}), and 146, respectively (CR values for λ and μ are shown in parenthesis).

In contrast, we compare results from DDD against the coalescent-derived estimators of diversification from Morlon et al. (2011) over the following models: (1 and 2) saturated diversity (most similar to DD) with either time constant or variable rates, respectively; (3) homogenous birth death; (4a–d) expanding diversity with CR; (5) expanding diversity with no extinction (Yule); and (6) expanding diversity with time-varying speciation and no extinction.

Diversity by Area

Given that Madagascar is composed of regionally distinct habitats, we tested whether habitat type was responsible for higher species richness and phylogenetic diversity by first classifying all unique lineages presented in the species tree by ecoregion. To do this, we first obtained and confirmed locality information using a combination of genetic samples, morphological samples, and previously published museum records. All genetic samples used in this study were associated with localities obtained in the field (datum: WGS84, error: Differential GPS) at 0.05 km accuracy or georeferenced using the point-radius uncertainty method (Wieczorek et al. 2004). Specimens that were not genetically sampled in this study were first assigned to a particular lineage using morphological data, then associated localities were incorporated. Additionally, previously published localities records (Glaw and Vences 2007; Brown et al. 2016) where lineage identity was certain were also included. Combined, all sources provided 864 unique locality records, ranging from 1 to 48 records per species (Supplementary data available on Dryad).

We classified distributions of all gemsnakes into six major terrestrial ecoregions of Madagascar, which include arid spiny bush, central highlands, dry deciduous forest, ericoid thicket, and evergreen rainforest (combined with the Sambirano rainforest), presented in Goodman and Benstead (2003) (as modified by Yoder and Nowak (2006); see Supplementary data available on Dryad for code and details on fitting species to region). We then estimated species richness and phylogenetic diversity in these regions. We used the richness-independent measure PSV (phylogenetic species variability) implemented in the R package "Picante" (Helmus et al. 2007; Ives and Helmus 2010; Kembel et al. 2010). To determine if phylogenetic diversity is either under or over dispersed, we compared our estimates to a random shuffling of all gemsnakes, while preserving regional species richness. We then compared areas using PSV and species richness. Similarly, we used the function *ConDivSim* in the R package "PEZ" (Pearse et al. 2015) to simulate mean pairwise distances in each community over different species richness values to determine if these communities deviated from null ($n = 100$) community estimates.

We also examined turnover between regions using the measure of phylogenetic community dissimilarity (PCD) to understand if changes between ecoregions occurred among taxa that were phylogenetically more related or less related in the R package "PEZ" (Pearse et al. 2015). We used PCD (where estimates lower than 1.0 indicate that dissimilar taxa between communities are closely related) to generate hierarchical clusters in the R package "pvclust" (Suzuki and Shimodaira 2006) over 1000 bootstraps to show which adjacent habitats have the least phylogenetic dissimilarity.

Trait Evolution

To understand the evolution of basic ecological traits in gemsnakes and examine how this group colonized and diversified across Madagascar, we scored taxa as being fossorial, terrestrial, arboreal, aquatic, or generalist. All taxa were considered as belonging to at least one of these basic ecological types taken from our knowledge of these species in the field and from Glaw and Vences (2007). Additionally, since these species show two basic dentition types: aglyphous and opisthoglyphous, where the latter is suggested to be associated with venom injection (Mori and Mizuta 2006; D'Cruze 2008), we also scored and included this dentition feature.

We estimated ancestral ecology and dentition type using the core phylogeny with the three non-Malagasy pseudoxyrhophiines (*Duberria, Amplorhnus*, and *Ditypophis*). We used the *fitdiscrete* function in the R package "geiger" (Harmon et al. 2008b) to compare the fit of models with equal rates (ER), symmetric (SYM) forwards/reverse rates, and all rates different (ARD). We used the AICc-best model to infer ancestral state probabilities. From this, we generated marginal ancestral states for the best model which was determined by lowest AICc. To compare to this maximum likelihood method, we performed stochastic character mapping over 1000 replications in the R package "phytools" (Nielsen and Huelsenbeck 2002; Huelsenbeck et al. 2003; Revell 2012) given the appropriate models determined in the *ace* function. These replicates were summed over all trees, from which we estimated the number of changes from each trait type given the proportion of time spent in each state. We then correlated the posterior probabilities from stochastic character mapping with the marginal ancestral states from the maximum likelihood method.

We also asked if dentition was correlated with primary ecology over the evolutionary history of the gemsnakes, here coded into binomial traits as arboreal (0) against all other states (1). We used this coding as we noted that aglyphous and opisthoglyphous dentition appeared to be associated with arboreal and terrestrial ecology. To assess this correlation, we used the threshold model (Felsenstein 2005, 2012) in "phytools" to examine correlated character change among dentition (aglyphous and opistoglyphous) and habitat (arboreal and non-arboreal). Tests were run for 5×10^6 generations with the first 25% of samples discarded as burn-in (ESS >200) and thinned by 1000. The mean and 95% HPD of r (correlation) were calculated from the remaining samples.

Finally, to understand if traits influence rates of diversification across the gemsnakes, we used the semiparametric correction to estimate binary, trait-driven diversification using the *traitDependentBAMM* function of Rabosky and Huang (2016) in the R package "BAMMTools". Using the function set for 1000 replicates and the Mann–Whitney U statistical test, we determined if dentition type or basic habit preference (arboreal/non-arboreal) influenced rates of diversification over the dated phylogeny of the gemsnakes. We also modeled trait influence on diversification using binary state (BiSSE) and hidden state (HiSSE) speciation and extinction methods (Maddison et al. 2007; Beaulieu and O'Meara 2016). Whereas BiSSE only examines whether a discrete character influences the rate of lineage diversification, HiSSE additionally accounts for hidden states (unsampled states) that could affect diversification rates for any of the observed states. We estimated AIC for null BiSSE and HiSSE models, alternative models where there was a binary state effect of traits on diversification, and equal and unequal hidden and observed state transitions and their effects on diversification.

RESULTS

Data and Phylogenies

We successfully sequenced 607 individuals for COI (674 bp), 571 individuals for CMOS (558 bp), 499 individuals for RAG2 (645 bp), and 436 individuals for NAV5 (599 bp). Maximum likelihood inference using RAxML with mtDNA only and with the entire concatenated data set resulted in largely congruent phylogenies with minor differences regarding some outgroup placement (Supplementary Fig. S1 available on Dryad).

We sequenced 371 anchored loci for 366 samples of gemsnakes and outgroups (359 guided from the Sanger tree; Supplementary data available on Dryad), and estimated phylogenies for 732 phased terminals. For the 732 terminals (all phased samples), our average locus length for the 371 loci was 1575 bp (SD 34, range: 532–2481) with a mean number of parsimony informative sites of 190 (SD 135.615, range: 0–534). Mean number of missing individuals per locus was 2.75% (SD = 4.1%, Range 0.13%–24.3%) when compared with the full data set of all individuals.

The ASTRAL II species tree generated high support for most nodes (Supplementary Fig. S2 available on Dryad) and the topology and support was consistent with IQ-TREE and the RAxML partitioned and unpartitioned bootstrap trees. Normalized RF distances ranged from 0.01 (RAxML vs. IQ-TREE) to 0.22 (RAxML partitioned vs. ASTRAL II; Supplementary Material available on Dryad).

All gemsnake genera were monophyletic and generic relationships among them were similar to Ruane et al. (2015) showing two major clades of generally aglyphous and opisthoglyphous snakes, see exceptions below (Fig. 1; Supplementary data available on Dryad). Outgroup colubroid relationships were typical of recent multilocus and NGS studies (Pyron et al. 2013, 2014; Streicher and Wiens 2016) showing xenodermatids as sister to the remaining colubroids, followed by pectinate relationships for pareatids, viperids, homolopsids, colubrids, elapids, and lamprophiids. Here, the Malagasy *Mimophis* was sister to the psammophiine African beaked snakes (*Rhamphiophis*). Among Pseudoxyrhophiinae, the Malagasy gemsnake radiation was sister to a clade composed of East African genera *Amplorhinus* and *Duberria*. Sister to all other pseudoxyrhophiines was the Socotran island endemic *Ditypophis* (Fig. 2). Divergence dates with the full tree generally agree with those generated with the reduced phylogeny (see below).

Species Delimitation

To examine diversification of species and traits in the gemsnakes, we reduced this phylogeny to account for only terminal species that also included undescribed candidate species. Here, using a combination of deep-time divergence between sister taxa and geographic distribution, we suggest that there are 38 unrecognized species distributed across all genera of gemsnakes (with exception to *Alluaudina*) and we included them in the reduced tree (Fig. 2, Supplementary data available on Dryad).

We confirmed these 38 species delimitations using BPP. ESS were all >300 (mean ESS across all delimitation $= 19{,}296$) for all 32 separate runs of BPP. All previously described taxa and newly identified species were delimited at a probability of 100%. In contrast to the gene/tree-based estimates of divergence times, for these coalescent estimates the average speciation time for undescribed taxa was 7.85×10^5 years (range 0.50–2.97 $\times10^6$) and for pairs of previously described taxa was 1.65 $\times10^6$ years (range 1.64–9.36 $\times10^6$). For the newly identified species, 96.1% of these speciation events (drawn from the MCMC distribution) occurred during the Pleistocene and 3.7% during the Neogene. For the previously described species, we found that 87% of speciation events occurred during the Pleistocene and 13% during the Neogene (Fig. 1). We note that for several taxa only a few individuals were sampled due to their rarity, and thus this may compromise species delimitations if greater sampling and isolation-migration models revealed high levels of migration (Zhang et al. 2011; Burbrink and Guiher 2015). However, we are confident that including these proposed taxa with such ancient divergences are useful for downstream approaches to understanding diversification.

Reduced Trees

We inferred the phylogeny for a reduced set of terminals, where each species was represented by a single individual. Over all loci, 19 different substitution models fit these data using Modelfit, with the highest number of loci ($n=82$) fit to the HKY model, whereas the most parameter-rich model, GTR, was best fit to only nine loci. All models included some form of rate heterogeneity with the FreeRate model and three categories fit to 74% of loci. Across all loci, the number of parameters to model substitution rates ranged from 3 to 10 parameters, with a median of 7 parameters.

Normalized RF distances among trees generated using partitioned bootstrapped were lowest between RAxML and IQ-TREE concatenated and locus bootstraps (0), and greatest between SVDQuartets and ASTRAL II with or without using multiple individuals per species (0.06).

All trees supported monophyly of all genera, similar species relationships, and similar relationships among genera (Figs. 1 and 2), which agree in part with Ruane et al. (2015). Nearly all nodes among methods were well supported. We found that the relationships among *Langaha*, *Micropisthodon*, and *Ithycyphus* differed among all methods, where SVDQuartets indicated a sister relationship between *Ithycyphus* and *Langaha* at 54% support, ASTRAL II showed *Micropisthodon* and *Ithycyphus* as sister taxa (98–100% support), and RAxML

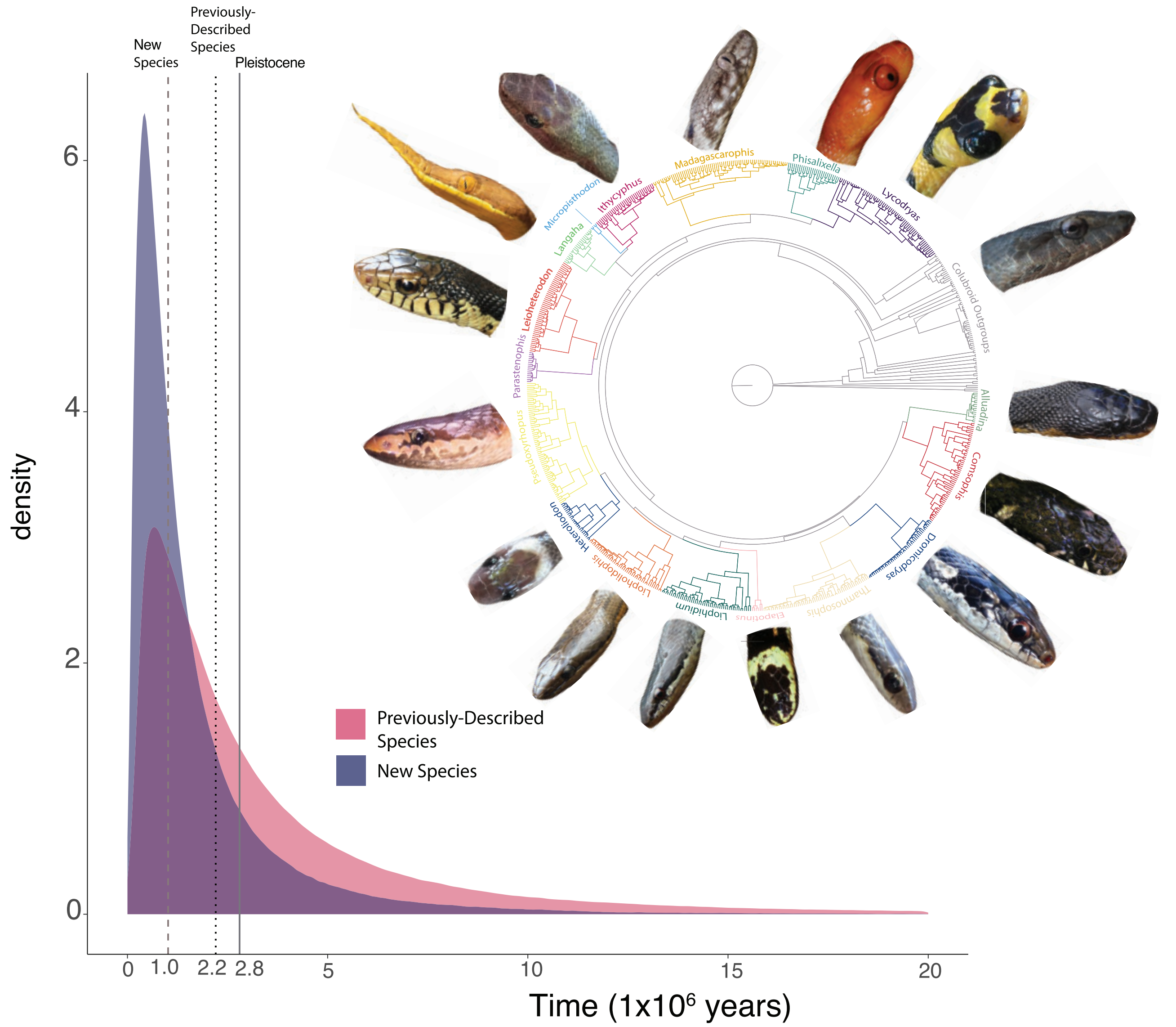

FIGURE 1. Circular phylogeny of Pseudoxyrhophiinae of all 732 phased samples from 371 loci generated in ASTRAL II (see Supplementary Fig. S2 available on Dryad for a detailed view of this phylogeny) with photographs showing representative species from all included Malagasy genera. Inset: Distribution of pairwise divergence dates for 38 newly discovered species pairs (dark blue) against previously described species pairs (light pink) using BPP.

and all IQ-TREE showed *Langaha* and *Micropisthodon* as sister taxa (93% support for RAxML, 84.7%, 82%, and 87% for SH, bootstrapped, and locus bootstrapped IQ Tree support, respectively). Among all 371 loci, 276 provided definitive sister relationships between these genera, where support was similar showing *Micropisthodon* and *Ithycyphus* at 38.7% loci, *Langaha* and *Micropisthodon* at 32.6%, and *Ithycyphus* and *Langaha* at 28.6%.

Age and Colonization

Estimating timed trees using penalized TreePL, MCMCTree, and BEAST2 produced dates that were correlated 0.96–0.99 ($P<2.2\times10^6$) with mean absolute differences between shared node dates among methods ranging from 0.33 to 0.92 my. While all dated trees were highly correlated, we note that trees and dates were not burned in after two separate long runs of BEAST2 due primarily to the size of the data set and slow parameter estimation. The BEAST2 tree was not used in any downstream calculations. The root height of this tree representing the origin of Colubroidea occurring earlier than the Cretaceous-Tertiary boundary was consistent with recent studies, though error around this estimate is high for most studies (Burbrink and Pyron 2008, 2010; Burbrink and Crother 2011; Pyron and Burbrink 2014b; Hsiang et al. 2015). Moreover, the origins of colubroid groups,

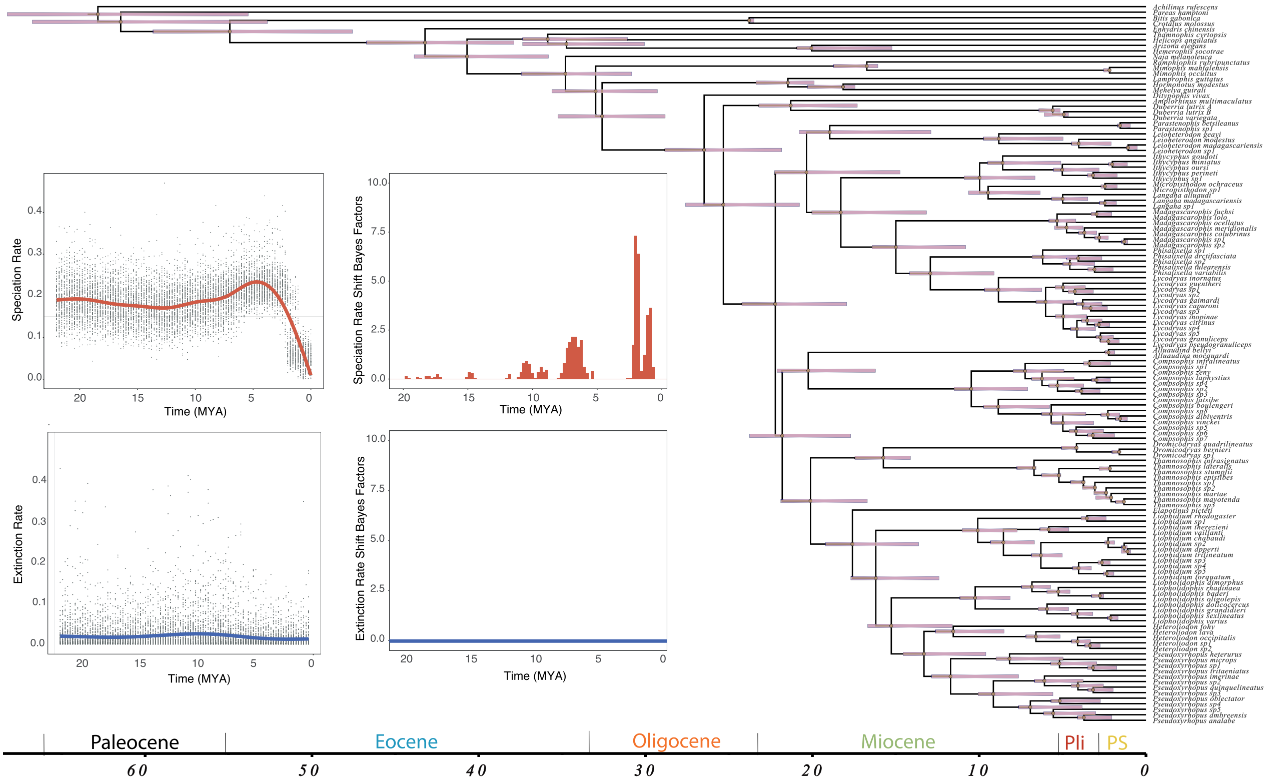

FIGURE 2. Dated phylogeny of all sampled species of Pseudoxyrhophiinae using ASTRAL II and TreePL. Estimates of speciation and extinction rates over time using CoMET with probabilities of those rates changing indicated by Bayes factors over 1000 bootstrapped phylogenies.

which included Pareidae, Viperidae, Homolopsidae, Elapidae, Lamprophiidae, and Colubridae, occurred throughout the Paleogene which was consistent with recent studies and the fossil record (Fig. 2; Burbrink and Pyron 2008; Pyron and Burbrink 2012; Head 2015; Hsiang et al. 2015).

Using the dated MCMCTree tree, we estimated the ancestral area of origin for the core gemsnakes. BioGeoBEARS shows strongest support for the DEC+J model (ΔAICc = 3.71–54.95; AICc weight = 0.86), where estimating the jump ("J" parameter) is consistent with a single over-ocean island colonization. Ancestral area estimates were the same with or without the "J" parameter. Madagascar was colonized twice by lamprophiids, first in the early-to-mid Miocene resulting in the core gemsnake radiation (Supplementary data available on Dryad) and second in the mid-to-late Miocene, resulting in the two species within the genus *Mimophis*. This agrees with previous studies attempting to date and number these colonization events, relying on mainly mtDNA data and reduced sampling of gemsnake taxa (Nagy et al. 2003; Vidal et al. 2008; Kelly et al. 2009). However, our result conflicts with other studies that found support for paraphyletic gemsnakes in Madagascar. These previous results supported more complex multiple-dispersal scenarios between Africa, Socotra, and Madagascar (Lawson et al. 2005; Pyron et al. 2011, 2013), but relied on a few independent markers with very incomplete taxon sampling.

Diversification

We tested whether diversification rates changed over the phylogeny of core gemsnakes using both BAMM and spectral distances. For all Poisson shift priors (0.1, 0.5, 1.0, 5.0), we obtained ESS >707 from BAMM and similar results for either the PLTree or MCMCTree. The posterior distribution for 0 shifts was always the highest, from 0.98 (BF>16), 0.93 (BF>7), 0.90 (BF>5), and 0.84 (BF>2.8), respectively for each Poisson shift prior. Similarly, spectral distances estimated in RPANDA only identified a single mode across the phylogeny from the eigengap metric for either tree (here asymmetry = 10.70, peakedness = 477.86, principal eigenvalue = 1.20).

Given that rates did not change within this tree, we estimated time-dependent speciation and extinction rates from the bootstrapped distribution of dated trees using CoMET producing similar results for all dated trees. There was no evidence for mass extinction in these snakes (BF <1.0). Rates of extinction, which are typically difficult to estimate using phylogeny alone (Quental and Marshall 2009; Rabosky 2010), were estimated to be low (close to 0) and constant through time (Fig. 2). Speciation rates remained constant above 0.1–0.3/myr throughout the Neogene, possibly declining by the Pliocene and certainly dropping sharply during the Pleistocene (Fig. 2, BF = 7.0–7.5). Our bootstrap likelihood ratio test for DD and CR using the program DDD for the MCMCTree showed support for rates of diversification declining

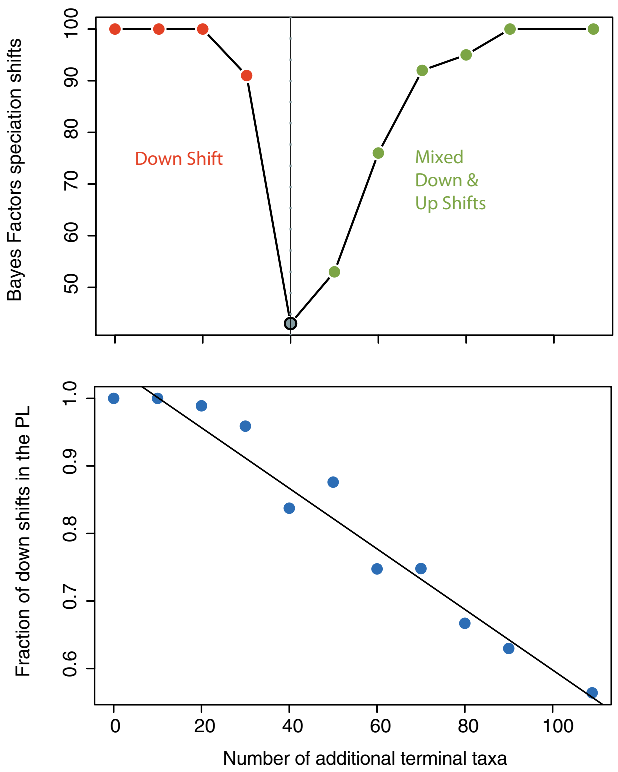

FIGURE 3. Testing the effect of unsampled taxa in the Pleistocene on predicted downshifts in diversification. The upper graph shows the percentage of Bayes factors (>5.0) from 100 simulations using the program CoMET that detect a decrease in Pleistocene speciation rates given the addition of terminal taxa imputed onto the gemsnake phylogeny occurring only in the Pleistocene. The lower graph shows the fraction of down shifts (regardless of strength of Bayes factors) in diversification during the Pleistocene detected out of 100 simulations per number of additional taxa added to the phylogeny of gemsnakes. Note that upward shifts in diversification in the Pleistocene become more common with the addition of more than 40 taxa.

against a carrying capacity [Likelihood ratio (LR) = 3.845; $P<0.0059$] with the power of this test at 0.81. This measure estimated speciation rates, extinction rates, and carrying capacities at 0.29/myr, 0.0/myr, and 146, respectively. We contrasted these results against the coalescent models from Morlon et al. (2011), which supported the saturated species diversity model with time-varying rates (Model $1=-219.110$) slightly over the declining speciation rate model (Model $6=-220.27$; Supplementary data available on Dryad).

Simulations to stress–test models of diversification where we added cryptic taxa diverging within the Pleistocene to the core gemsnakes phylogeny revealed that Bayes Factors (>5.0) using CoMET supported reduced rates of diversification in the Quaternary up to the addition of 30 species in more than 90% of simulations (Fig. 3). Above 50 imputed species, the fraction of simulations showing reduction in speciation during the Pleistocene decreased rapidly, leading to both increases and decreases in diversification during this period.

Area Diversity

Species occurred in a median of 2 ecoregions (SD $=0.98$) and 36% of all taxa were endemic to a single ecoregion. Endemicity was correlated with habitat size ($\rho=0.96$, $P=0.009$; species endemicity in parentheses): dry deciduous (13), evergreen rainforest (12), central highlands (8), arid spiny bush (3), and montane ericoid thicket (2). Species richness was lowest in the smallest ecoregion, montane ericoid thicket ($n=7$), and highest in the evergreen rainforest ($n=73$). PSV was similar among habitats and randomly dispersed across most habitats (Fig. 4). Only the dry deciduous forest showed phylogenetic underdispersion (reduced variability of phylogenetic diversity due to the absence of some humid adapted lineages; $P=0.015$; Fig. 4) yet still has an appreciably high species diversity ($n=56$). Paradoxically, habitat endemicity as a proportion of taxa was lowest in the expansive central highlands (10.6%) and largest in the region of lowest diversity, montane ericoid thicket (28.5%; see also Raxworthy and Nussbaum 1996). Both species richness and PSV increased marginally with larger biomes covering larger areas (Fig. 5). Additionally, variance in mean pairwise differences (MPD) by community increased with greater richness, which was expected when larger communities contain both a higher proportion of species and phylogenetic diversity. These communities by biome fell within the 95% confidence interval (CI) of null community MPDs given richness (Fig. 5). Finally, phylogenetic turnover as measured by PCD was lowest between communities sharing similar precipitation profiles, where PCD was lower than 1.0 between dry deciduous forests and arid spiny bush, and similarly between the central highlands/montane ericoid thickets and evergreen rainforests (Fig. 5).

Trait Origins and Diversification

Maximum likelihood and stochastic character methods of ancestral state reconstructions for all Pseudoxyrhophiinae (with non-Malagasy outgroups) were highly correlated for both habitat and dentition state reconstructions (Pearson's $r=0.999, P=2.2\times10^{-16}$). The *equal rates* character model of evolution for habitat type was always preferred (AIC weights $=0.99$). On average, 13.05 changes from arboreal to generalist ($n=3.25$) and then terrestrial to fossorial (2.88) were observed during the evolution of the gemsnakes. For dentition, the *all rates different* model of character evolution was preferred (AICweigths $=0.73$; Supplementary data available on Dryad). On average, 4.5 changes all from opisthoglyphous to aglyphous were observed with no reversals. The ancestral states for the gemsnakes upon colonization of Madagascar were opisthoglyphous and terrestrial (Fig. 6). We used the threshold model to determine if dentition type and arboreal vs. non-arboreal (generalist, aquatic, fossorial, terrestrial) ecologies were correlated. With an ESS $=437$, we found that dentition was correlated with

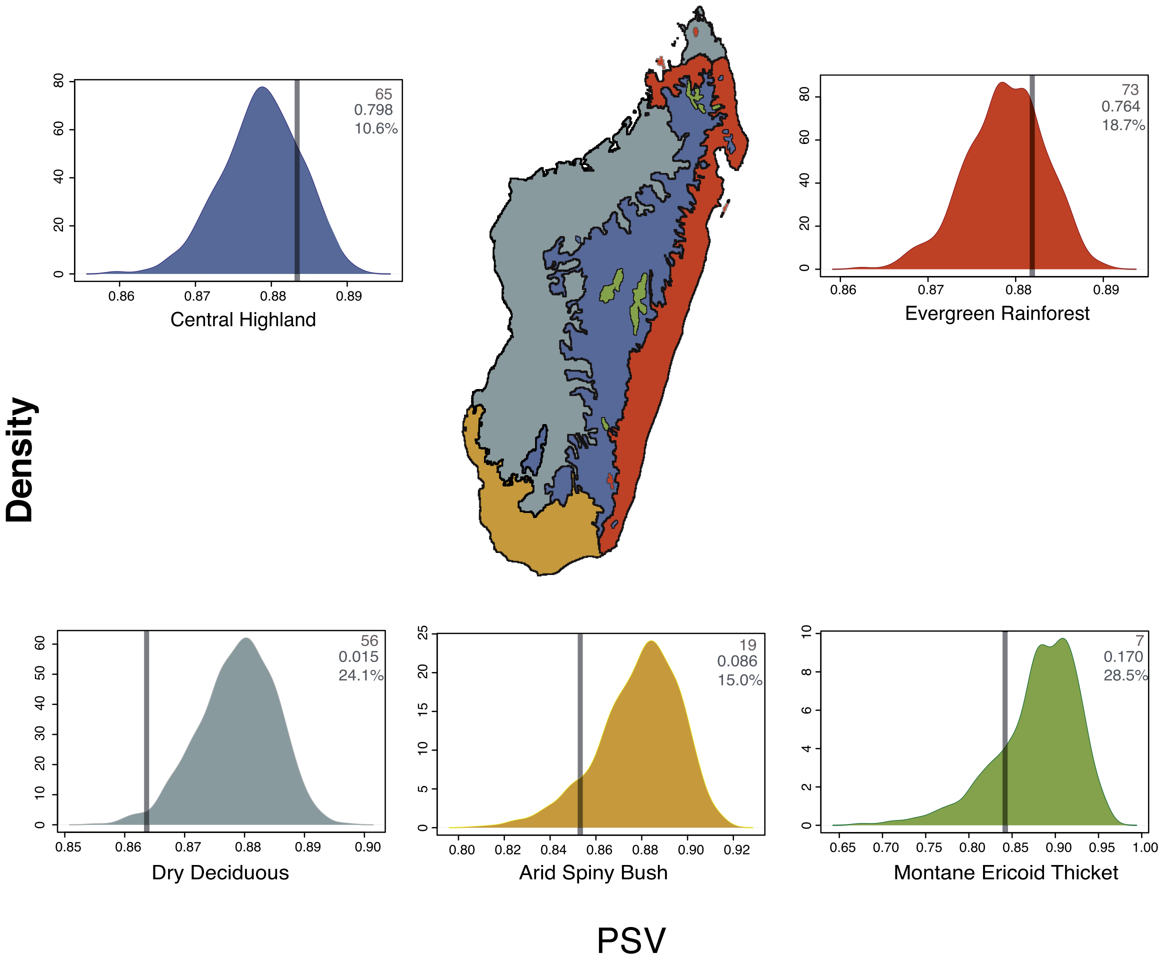

FIGURE 4. Phylogenetic species variability (PSV) for Pseudoxyrhophiinae in the five biomes of Madagascar, with null distributions showing randomly sampled taxa preserving richness relative to the actual community (vertical line). Values in the upper right-hand corner of each box are from top to bottom: species richness, P-value of observed PSV, and percentage number of ecoregion endemic species/richness.

basic ecology at a median correlation coefficient of 0.44 (Fig. 6; 95% CI 0.28–0.58).

Neither dentition or habitat type had any effect on speciation rates ($P = 0.995$ for both); species-specific rates were similar between opisthoglyphous and aglyphous taxa (0.134, 0.133) and between arboreal and terrestrial taxa (0.133, 0.134). Using HiSSE, we found greatest support for the BiSSE null model (min ΔAICc BiSSE Null and HiSSE null $= 3.56$) suggesting no connection between traits and diversification.

DISCUSSION

Diversification

The Malagasy gemsnakes show a pattern of constant diversification rates throughout the Neogene with a decline in speciation during the Plio-Pleistocene (Fig. 2). This suggests that constant speciation throughout the Neogene accounts for most of the diversification in this group. Speciation, however, declined in the last 2 myr of gemsnake history, likely due to diversity-dependence. Furthermore, there is no support for mass extinction on Madagascar in the gemsnakes. Upon colonization from Africa in the early Miocene, divergence into most of the basic ecologies occurred early, and within those groups, diversification was constant over time.

These constant rates (CR) of diversification upon colonization might seem at odds with a long-standing phylogenetic view of AR and exploration of adaptive zones (Mitter et al. 1988; Schluter 2000; Losos 2010), particularly in comparison to some other diverse reptile groups in Madagascar (Harmon et al. 2008a; Scantlebury 2013). Diversity of both species and form occurred at CR over the first 15–17 myr after colonization, though we do not know about comparative speciation rates of the related lamprophiid snakes on Africa. The process of AR can generate a diverse faunal group on Madagascar yet still be divorced from changing rates of species diversification through time (Givnish 2015; Stroud and Losos 2016; Rabosky 2017). Similar to Madagascar, evidence from both molecular and fossil studies suggest that colubroid snakes colonized North America and Europe in the late Oligocene/early

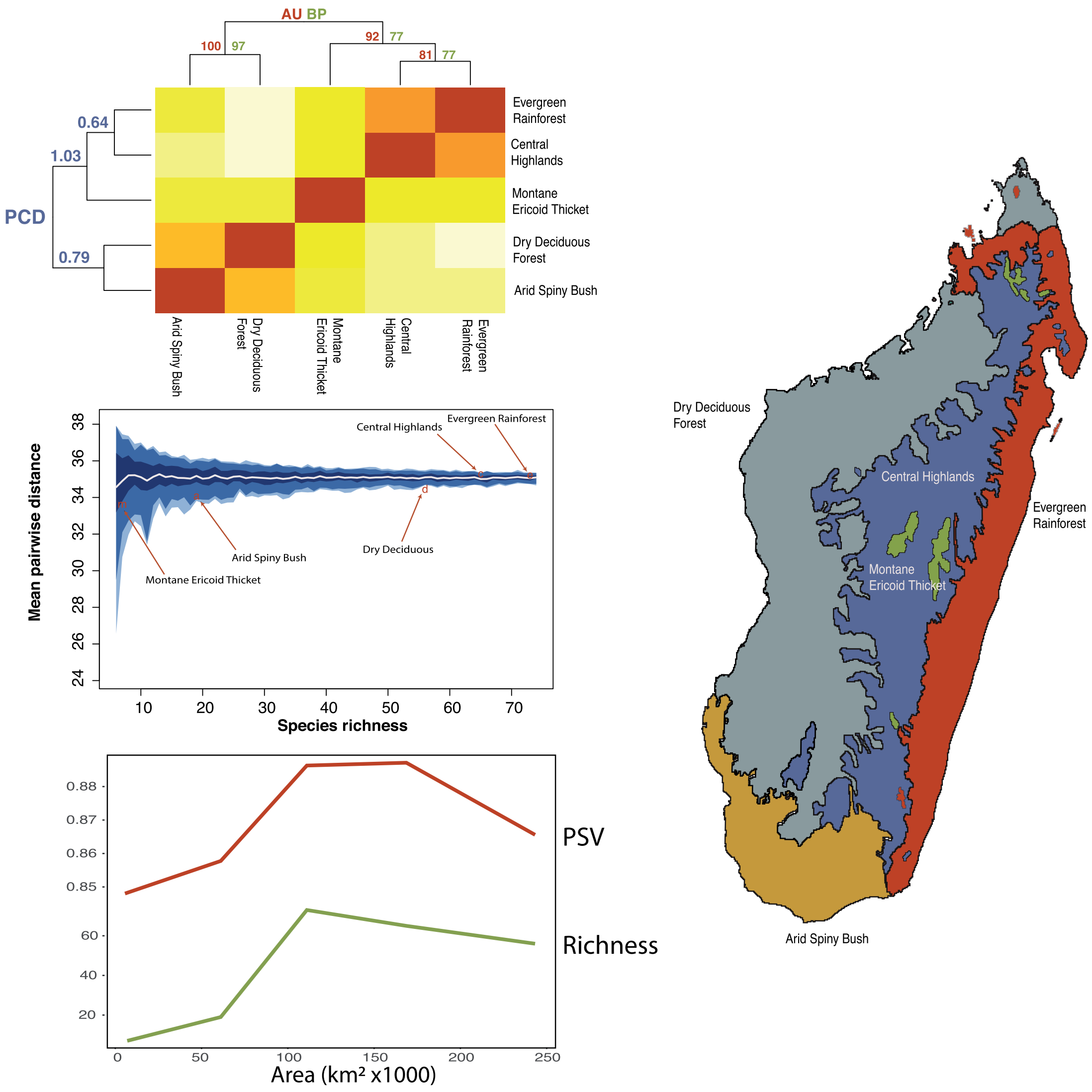

FIGURE 5. Estimating the relationships between richness, PSV, and biome. The five biomes are shown on the map to the right. Top graph shows heatmaps based on phylogenetic community differences, where values lower than one on the PCD tree (left tree) indicate turnover between biomes shows low dissimilarity (i.e., dissimilar species are closely related). The tree on the top of the heatmap shows support for these groupings based on approximate unbiased (AU) and 1000 bootstraps (BP) probabilities. The middle graph shows the relationships between richness and mean pairwise distance for each biome relative to a random sampling of individuals from the total pool relative to local species richness (dark to light representing 95% CI and white represents the median trend). Bottom graph shows the relationship between area and richness and PSV.

Miocene, and that diversification was highest in the Miocene and declined during the Pleistocene (Holman 2000; Burbrink et al. 2012a; Chen et al. 2017). While competition from other snakes could prevent an early burst of diversification, there is no evidence that other groups of colubroids ever colonized Madagascar; currently only extant blindsnakes (11 species) and boas (4 species), and extinct Late Cretaceous Madtsoiidae and Nigerophiidae snakes ever occurred in Madagascar (Glaw and Vences 2007; Laduke et al. 2010). We also did not find that Madagascar was subject to major pulses of extinction during the Neogene and speciation proceeded without major external disruption during this period. Apparently for the gemsnakes, the constant rate of speciation for 15–17 myr occurred before niches become saturated and speciation rates were reduced during the Pleistocene.

Difficulty estimating extinction rates from molecular phylogenies is well known, especially in the absence of a fossil record (Quental and Marshall 2009; Rabosky 2010). It is unclear how these estimates affect tests of diversification over time or interpretation of changing speciation rates, though we point out that these trends seen on Madagascar are similar to other large but similarly young snake groups (Burbrink et al. 2012a). Unfortunately, whereas the fossil record also supports a pattern of sustained and high diversification of snakes throughout the Miocene in Europe and North America (Holman 2000; Szyndlar 2009), a Miocene fossil record of terrestrial vertebrates is unknown for Madagascar

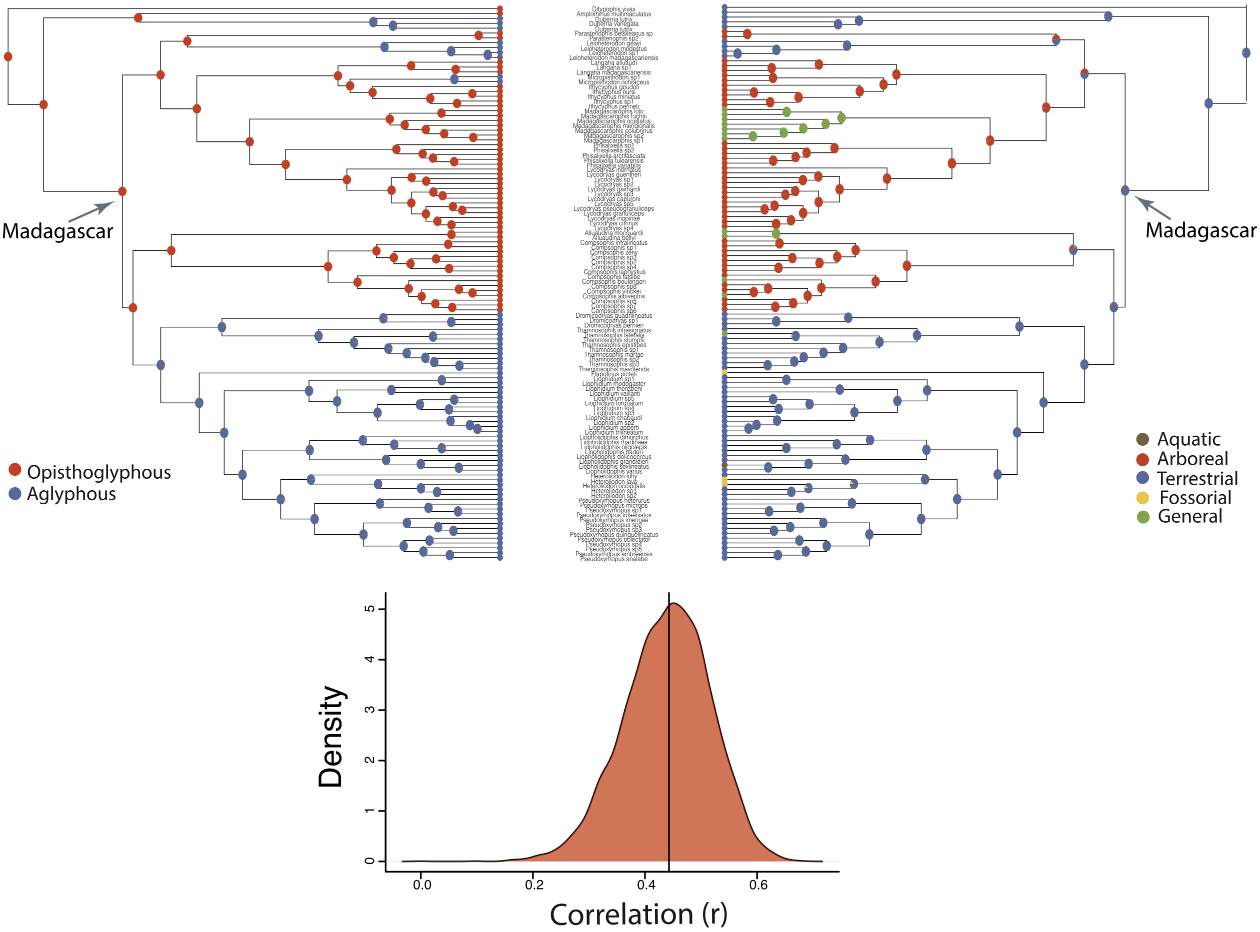

FIGURE 6. Stochastic character mapping showing ancestral dentition and ecological reconstructions for Pseudoxyrhophiinae with the distribution of correlation between dentition and habitat (arboreal v. others) over the phylogeny using the Bayesian Threshold model.

(Goodman and Benstead 2003; Samonds 2009). Marshall (2017) stressed that extinction rates may be just below speciation rates even in expanding groups, and failing to account for this may hinder reliable estimates of diversification over time using molecular phylogeny. Without credible extinction estimates, it is possible that initial diversification rates were extremely high in the gemsnakes for a short period of time upon colonization, reached saturated diversity rapidly, and then finally was reduced with enhanced extinction rates during climate change in the Pleistocene. This last phase might appear as a slowdown in speciation rates without proper estimates of extinction.

The evolution of traits allowing taxa to occupy novel niches in unique ways or, in this case, colonize empty ecological niches, may have little to do with the rate at which speciation occurs. Moreover, when considering the traits that allow taxa to colonize unique niches, it is uncertain that these same traits necessarily reduce gene flow among populations necessary for rapid speciation to occur (Servedio et al. 2011). Instead, we show that taxa evolve into distinct niches early in their history despite CR of speciation. Excluding Australia (Grundler and Rabosky 2014), this is unique among snakes, where at least in continental systems, taxa from different families assemble to fill all local niches (Burbrink and Myers 2015).

Gemsnakes occurring in the basic arboreal, terrestrial, general, fossorial, and aquatic habitats are also mostly found across the five distinct ecoregions of Madagascar, though the aquatic taxon does not occur in the montane ecoregion. Given species richness for each ecoregion, phylogenetic diversity is no different from a random draw of PSV (phylogenetic species diversity) across these regions, excluding the dry deciduous biome (Figs. 4 and 5). The largest biomes, evergreen forest, central highlands, and dry deciduous, contain the greatest diversity. However, at least within all extant biomes, no single habitat is generating most of the phylogenetic diversity. Therefore, all biomes across the island are likely responsible for gross *in situ* diversity of the gemsnakes, though realistically it is unclear if these biomes persisted continuously through the Neogene or were even responsible for the diversification of their local assemblages. Finally, among these biomes, phylogenetic dissimilarity is lowest between the two adjacent dry habitats and also among the three mesic habitats (Fig. 5), suggesting that colonization between similar biomes is related to having similar adaptive traits (e.g., as a result of having conserved ecological niches) given the reduced phylogenetic dissimilarity.

Pleistocene Divergence

While rates of speciation may have been highest throughout the Miocene, most of the standing extant diversity was likely generated during the Pleistocene (Fig. 1). Using coalescent species delimitation methods, we have shown strong support that 109 terminal species in our phylogeny are useful for understanding diversification; we assessed strong support for the existence of 38 undescribed species and date the origins of all taxa. We show for the first time a strong role for the Pleistocene generating extant diversity of a major faunal component in Madagascar. This role of Pleistocene speciation has been debated for other areas of the world (Avise et al. 1998; Klicka and Zink 1999; Knowles 2001; Weir and Schluter 2004; Carstens and Knowles 2007; Moyle et al. 2009; Ruane et al. 2014; Oliveira et al. 2015; Rull 2015), though it is likely that Pleistocene shifts in habitat due to global climate change may have generated many new species via isolation and divergence. Mirroring Last Glacial Maxima habitat changes in the Northern Hemisphere (Waltari et al. 2007; Hollingsworth and Near 2009; Burbrink et al. 2016; Gehara et al. 2017), environments throughout Madagascar were likely much cooler and drier with glacial vegetation found at lower elevations (Goodman and Benstead 2003; Burney et al. 2004; Raxworthy et al. 2008a; Goodman and Jungers 2014). Although anthropogenic effects are often highlighted as primary contributors to habitat change (e.g., Goodman and Patterson 1997; Burney et al. 2003, Salmona et al. 2017), evidence now shows forest fragmentation and modern grass communities in Madagascar predate colonization by humans (Vorontsova et al. 2016). Pleistocene fragmentation and shifting vegetation and habitats may possibly have elevated extinction risks for some species (Raxworthy et al. 2008b) and reduced rates of speciation in the gemsnakes.

It is possible that there may be many undetected Pleistocene speciation events given that young cryptic reptile species may be difficult to detect and diagnose and yet appear to be widespread in Madagascar (Raxworthy et al. 2007; Pearson and Raxworthy 2009; Florio et al. 2012; Florio and Raxworthy 2016; Ruane et al. 2018), which in turn would cast doubt that Pleistocene speciation rates declined. However, our method to stress test these conclusions show, remarkably, the results are immune even with the addition of as many as 30 unsampled taxa (Fig. 3). It is unlikely that this many new snake taxa are still remaining to be discovered given the care taken to survey across the full range of taxon distributions to identify possible cryptic species of gemsnakes, including regions predicted to have disjunct populations and unrecognized endemism (Raxworthy et al. 2003). Coalescent delimitation and dating was used to include all candidate taxa not yet described and therefore as much undetected diversity as possible was included in our estimates. Ongoing studies should help clarify population structure for poorly sampled taxa here and assess processes of speciation to provide a more granular view of diversification rates and changes in demography during the Pleistocene.

Decreases in Pleistocene diversification rates in Madagascar contradict predictions that multiple Pleistocene shifts in habitat (associated with glacial and interglacial periods) accelerate speciation as a result of enhanced isolation and divergence in allopatry. As an alternative explanation, this speciation decrease may have been due to interspecific competition as niches became saturated (Burbrink and Pyron 2010; Rabosky 2013). Our models show support for this DD relationship. In a semi-closed system over a smaller area with limited immigration like Madagascar, diversity-dependent dynamics are more likely to prevail. Harmon and Harrison (2015) suggested that there is little evidence for bounded diversity given evidence from biological invasions, the fossil record, experimental manipulation, and weak estimates from phylogenetic studies (also see Marshall and Quental 2016). Alternatively, changes in speciation rates from the Neogene to the Pleistocene may not be related to carrying capacities if: (1) rates of speciation were directly associated with environmental instability and habitats changed more rapidly in the Neogene than the Pleistocene, (2) rates were time dependent and reduced as groups failed to diversify with changing environments, or (3) extinction rates were suitably high (Vrba 1985; Rosenzweig 1995; Pigot et al. 2010; Pyron and Burbrink 2012a; Quental and Marshall 2013; Moen and Morlon 2014).

This paradox, where standing diversity was most likely generated in the Pleistocene yet may also have been a period of declining diversification rates, has been addressed in other contexts (Zink and Slowinski 1995). In summary, if we consider the life span of a species, from origin to extinction, as lasting on average 2 myr (Marshall 2017), then the probability of discovering extant species pairs originating in the Pleistocene is not remarkable given that the probability of finding divergence dates older than this declines with age as extinction probability becomes higher. This begs the question, what unique role does the Pleistocene play in speciation other than being suitably young for divergence and survival through the Holocene?

Traits History

Upon colonization of Madagascar from Africa in the Miocene via oceanic dispersal, diversification into the main ecological types were generated early with terrestrial and opisthoglyphous conditions likely being the original state at colonization (Fig. 6). Arboreal ecology and the correlated opisthoglyphous dentition originated soon after colonization. Given that rates of diversification did not change within clades of gemsnakes, it is not surprising that changes in basic ecology or dentition had no influence on speciation rates. This demonstrates that while these traits expanded ecological diversity in gemsnakes, rates of speciation and accumulation of diversity in Madagascar do not follow common patterns of trait-driven diversification seen in many other groups of taxa here and elsewhere (Agrawal et al. 2009; FitzJohn et al. 2009; FitzJohn 2010; Pyron and Burbrink 2012b).

Globally, rear-fanged snakes capable of envenomation are represented in a variety of niches, including fully terrestrial, aquatic, semi-fossorial, and arboreal habitats (Weinstein et al. 2011; Peichoto et al. 2012). However, in Madagascar, we show that opisthoglyphous dentition is correlated with arboreality, which may serve to hold or puncture prey in these habitats (Knox and Jackson 2010) where full constriction may be difficult (Harrington et al. 2018). Envenomating arboreal prey, such as lizards or frogs, may be required for successful capture, but we note that some aglyphous taxa have enlarged rear teeth, yet with no groove, but may still envenomate prey (Razafimahatratra et al. 2015). Further work on mandibular and tooth morphology here, which includes hinged teeth, gaps in tooth rows, enlarged anterior teeth, and edentulous jaws (Savitzky 1983; Cadle 1996, 1999, 2003, 2014), integrated with prey capture, envenomation, and production or constitution of venom should be examined for a more nuanced view of gemsnake trait evolution.

Taxonomy

Phylogenetic relationships among gemsnakes and the taxonomy of this group are now stable; results are similar to those in Ruane et al. (2015) showing the basic taxonomic split into opisthoglyphous and aglyphous clades (Figs. 2 and 6; Supplementary data available on Dryad). As opposed to expectation and other empirical studies (Edwards 2009; Lambert et al. 2015; Mirarab et al. 2016), our species-tree and concatenated phylogeny estimates were similar, showing the same intergeneric relationships and monophyly of all genera with high support, with the exception of the relationships among *Ithycyphus*, *Langaha*, and *Micropisthodon*. While current techniques cannot handle data sets of this size, we note that future research should consider the likelihood that the gemsnake phylogeny may not be best represented as purely bifurcating, given current research on these methods (Mallet et al. 2016; Solís-Lemus and Ané 2016) and estimates from other snakes (Burbrink and Gehara 2018). While the basic relationships are accurately captured in our phylogeny, instances of ancient reticulation may provide additional insight into diversification of endemic species on Madagascar.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.07h0n14.

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