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## Using phylogenomics to understand the link between biogeographic origins and regional diversification in ratsnakes

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## ABSTRACT

Globally distributed groups may show regionally distinct rates of diversification, where speciation is elevated given timing and sources of ecological opportunity. However, for most organisms, nearly complete sampling at genomic-data scales to reduce topological error in all regions is unattainable, thus hampering conclusions related to biogeographic origins and rates of diversification. We explore processes leading to the diversity of global ratsnakes and test several important hypotheses related to areas of origin and enhanced diversification upon colonizing new continents. We estimate species trees inferred from phylogenomic scale data (304 loci) while exploring several strategies that consider topological error from each individual gene tree. With a dated species tree, we examine taxonomy and test previous hypotheses that suggest the ratsnakes originated in the Old World (OW) and dispersed to New World (NW). Furthermore, we determine if dispersal to the NW represented a source of ecological opportunity, which should show elevated rates of species diversification. We show that ratsnakes originated in the OW during the mid-Oligocene and subsequently dispersed to the NW by the mid-Miocene; diversification was also elevated in a subclade of NW taxa. Finally, the optimal biogeographic region-dependent speciation model shows that the uptick in ratsnake diversification was associated with colonization of the NW. We consider several alternative explanations that account for regionally distinct diversification rates.

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## 1. Introduction

Exploring the spatial and temporal modes of diversification as well as the factors influencing their patterns is critical for understanding the processes leading to biodiversity accumulation (Fritz et al., 2013). For species-rich assemblages with a global distribution, diversification is expected to be influenced by several mechanisms involving both biotic and abiotic factors (Moore and Donoghue, 2007). Adaptive radiation, defined as rapid diversification of descendants from a common ancestor into distinct environments, is considered one of the main mechanisms shaping biodiversity on earth (Simpson, 1953; Schluter, 2000). Ecological opportunity generated by the appearance of new resources, the mass extinction of competitors, or the colonization of new areas has typically been the prime motivator for adaptive radiation

(Losos, 2010; Yoder et al., 2010). Adaptive radiation via ecological opportunity predicts diversity-dependent diversification, in which speciation rates are initially rapid, filling abundant unoccupied niches and declining as available niches become saturated (Schluter, 2000; Losos, 2010). Furthermore, enhanced diversification rates should be found only in diverse taxa experiencing adaptive radiation when compared to other groups not showing heightened diversity (Glor, 2010).

Inferring diversification processes requires a comprehensive phylogeny that incorporates clade age and biogeographic information (Moore and Donoghue, 2007). Using divergence-time estimation and ancestral area reconstruction, while considering events such as dispersal, geographic isolation and mass extinction, provide a context for understanding how diversification rates change across temporal and geographic dimensions. For example, *Anolis* lizards are an important case where dispersal to new areas accelerated diversification by colonizing the abundant open niches of the West Indies, permitting a set of ecomorphs to evolve repeatedly on

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distinct islands that share similar environmental conditions (Harmon et al., 2003; Losos, 2009).

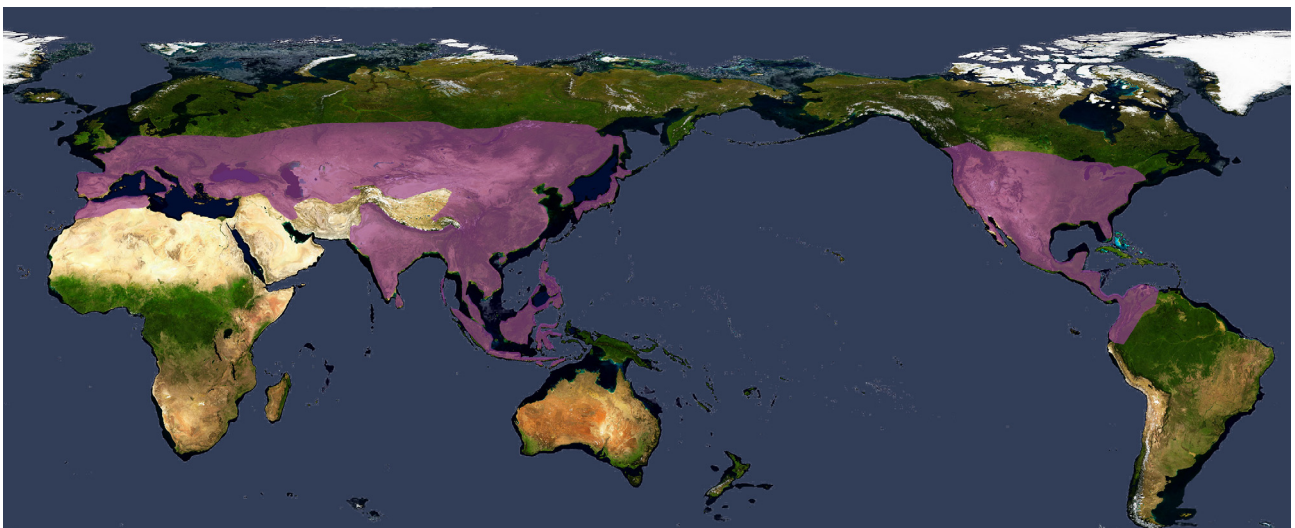
However, just because regions were free from competitors when colonized does not guarantee that rates of speciation were elevated early in the history of a particular group. For instance, a signature of rapid early radiation was not found in Caribbean alsophiine snakes despite colonizing unoccupied regions that share a similar distribution and ecological opportunity with the *Anolis* lizards (Burbrink et al., 2012). Explanations for the lack of elevated diversification in alsophiines involve the young age of this group (they may not have had sufficient time to show a reduction in speciation rates), and waiting time between island colonization (offsetting early bursts of speciation; Burbrink et al., 2012). Therefore, it is important to properly estimate divergence time, ancestral area, and species diversification so that a comprehensive view of biodiversity accumulation is properly assessed.

While many examples of diversification and adaptive radiation have occurred in geographically more controlled areas such as islands, several continentally distributed examples are relevant as well. The ratsnakes (Coronellini), which historically have been used for systematics, ecological, behavioral, and physiological research (Boulenger, 1894; Underwood, 1967; Lawson and Dessauer, 1981; Schulz, 1996; Schulz and Gumprecht, 2013), are important examples of continental-level adaptive radiation, given their rapid diversification into unique ecological niches in biogeographically distinct regions. The ratsnakes, composed of 88 species (Table S1; Uetz, 2014), are widely distributed throughout the Palearctic, northern part of the Oriental, the Nearctic and portions of the Neotropical Zoogeographic regions (Fig. 1). Given their global distribution, ratsnakes occupy very heterogeneous habitats, including mountain forests, grassland, deserts, and tropical rain and dry forests (Schulz, 1996), which likely provided ecological opportunity for rapid divergence within this group. Unlike many other ectothermic animals, ratsnakes have attained their highest diversity in both the Old World (OW) and the New World (NW) temperate regions.

Previous biogeographic studies supported a tropical Asian origin of ratsnakes with dispersal to OW temperate regions and subsequent Beringian dispersal to the NW (Burbrink and Lawson, 2007; Burbrink and Pyron, 2010; Chen et al., 2013). This Cenozoic Beringian Dispersal Hypothesis (CBDH; Guo et al., 2012) is supported in several squamate groups as well as various plant and other animal

groups. This unidirectional dispersal was likely important in shaping temperate Eurasian and North American faunas and floras (Enghoff, 1995; Wen, 1999; Smith et al., 2005; Burbrink and Lawson, 2007; Brandley et al., 2011). Importantly, diversification of the NW clade of ratsnakes, Lampropeltini, occurred rapidly upon arrival in the Americas (Burbrink and Lawson, 2007; Burbrink and Pyron, 2010). However, under similar environmental conditions, it is possible that the rapid bursts of diversification in the NW lineages were an extension of broadly rapid Holarctic diversification and not a phenomenon isolated to the Americas. Alternatively, after divergence between OW and NW clades, these lineages may have diversified uniquely in terms of tempo and trajectory of species accumulation in their respective regions. Nevertheless, neither of these hypotheses was tested in a biogeographical context where rates of diversification were examined across the phylogeny of ratsnakes while at the same time considering region of origin.

We use the Anchored phylogenomics platform to sample and sequence hundreds of loci across the entire ratsnake genome (Lemmon et al., 2012) to infer a dated species tree using coalescent-model based methods to overcome potential gene-tree/species-tree conflicts from incomplete-lineage sorting (Pamilo and Nei, 1988; Maddison, 1997; Page and Charleston, 1997; Slowinski et al., 1997; Slowinski and Page, 1999; Edwards, 2009). This represents the first attempt to infer phylogeny using genomic data across most species and all 20 genera of ratsnakes (Utiger et al., 2002, 2005; Burbrink and Lawson, 2007). Specifically, with this dated tree we examine monophyly of all genera and tribes (Coronellini and Lampropeltini) and estimate ancestral area and dispersal probabilities to test the CBDH, previously examined only using 2 loci (Burbrink and Lawson, 2007). With phylogenomic estimates, we examine species diversification as the interaction between speciation and extinction for understanding the buildup of biodiversity (Ricklefs, 2007; Morlon et al., 2010; Pyron and Burbrink, 2013). With clade age, diversity, branch length, and topology available, we use time- and taxon-dependent models to examine speciation and extinction rate changes to understand the potential factors influencing diversification patterns (Rabosky and Lovette, 2008a, 2008b; Morlon et al., 2010, 2011; Etienne et al., 2011; Stadler, 2011). Finally, linking diversification back to biogeography, we determine if diversification processes are heterogeneous across different lineages (Alfaro et al., 2009; Rabosky, 2014) and test correlation between diversification



**Fig. 1.** The global distribution of ratsnakes (colored in purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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