*Molecular Ecology*

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# Population Expansion in North American Snakes Tracks Pleistocene Climate Fluctuations and Subsequent Warming

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**Received:** 25 March 2025 | **Revised:** 17 April 2025 | **Accepted:** 25 April 2025

**Handling Editor:** Benjamin Sibbett

**Funding:** This work was supported by the National Science Foundation, IOS-2307044.

**Keywords:** population dynamics | population genetics | range expansion | snakes

How did the rapid and extensive climate oscillations of the late Pleistocene impact population expansion across ecologically distinct species? In a From the Cover article in this issue of *Molecular Ecology*, Harrington et al. (2024) reconstruct the demographic history of nine snake species or species complexes from the Eastern Nearctic to address this question. Leveraging newly generated and published genomic data, the authors test the hypothesis that these snake lineages show synchronous demographic expansion following the Last Glacial Maximum (LGM). Their findings suggest that most snake lineages tested do indeed show evidence of synchronised population expansion following the Pleistocene, though less tightly associated with post-LGM warming than expected. While some lineages exhibited exponential growth after the LGM, other lineages expanded more gradually throughout the Pleistocene. To address the broad question of what might explain variation in expansion responses across species, the authors also conduct analyses of correlations between environmental factors and genetic distances within species, and conclude that species-specific ecological traits likely explain distinct demographic patterns across species. The broad similarities in expansion timing across species provide new compelling evidence for the consistent effects of post-Pleistocene warming on ectotherm populations, such as snakes. Broadly, this study further reinforces the late Pleistocene as a valuable model for understanding species-specific responses to past climate change, and the potential of such understanding to predict how species may respond differently to future climate change.

The transitions between glacial and interglacial periods during the Pleistocene (last 2 million years), particularly the rapid warming following the Last Glacial Maximum (LGM) around 18,000 years ago, represent the most significant climatic shifts in Earth's recent history (Clark et al. 2009). As such, these climatic shifts had profound impacts on the distributions of flora and fauna, leading to corresponding shifts in the distributions and population sizes of species (Hewitt 2000), particularly those distributed in the Nearctic. These large-scale shifts were driven by multiple interconnected and non-mutually exclusive factors, including: (a) the retreat of massive ice sheets that once blanketed northern North America (Figure 1), (b) a significant temperature rise—up to 9°C in some regions (Figure 2; Annan and Hargreaves 2013)—accompanied by drier conditions, (c) the emergence of novel climate regimes absent during the glacial period, and (d) ecological reshuffling, which exposed species to new selective pressures related to food availability, predation and competition (Jackson and Overpeck 2000).

Understanding how species responded to these extreme past climate events can provide valuable insight into how distinct species may respond to future climate change. Indeed, multiple studies have examined similarities and differences in

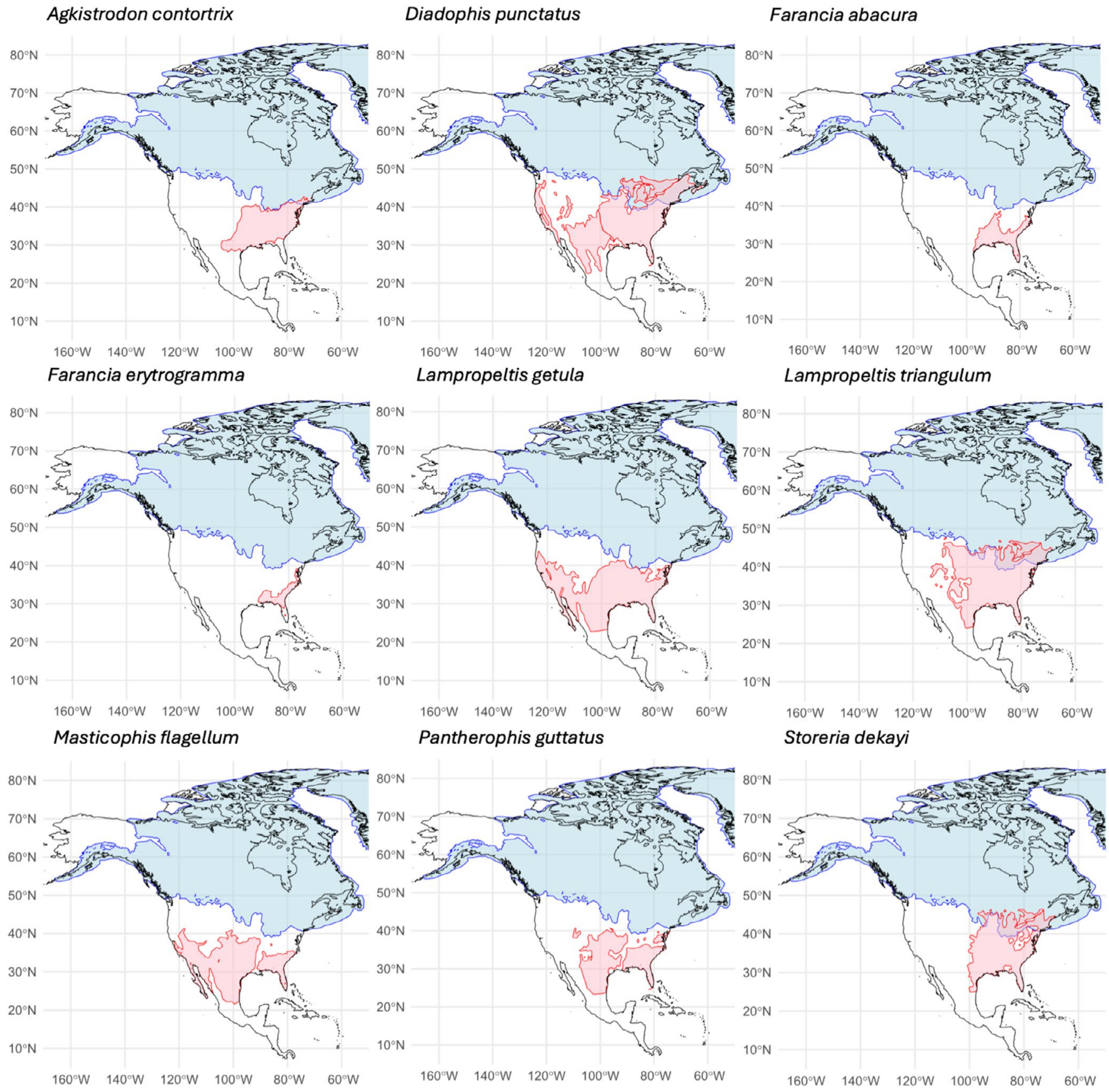

**FIGURE 1** | The current ranges (NatureServe and IUCN 2018) of snake species and species complexes studied by Harrington et al. in relation to estimates of the ice sheet extent at its maximum (i.e., 18,000 YBP; Dyke et al. 2003).

responses across species to post-LGM warming (e.g., Jackson and Overpeck 2000) and found remarkably different patterns across species in their responses. Many species adjusted to changing climates by shifting their ranges to higher latitudes or elevations to track, and thus maintain their climatic niches (Chen et al. 2011). Other species appear to have persisted within their historical ranges by expanding their niches to tolerate warmer conditions (Jezkova et al. 2011), while others colonised entirely new regions with non-analog climates, often far beyond their previous distributions (e.g., Jezkova et al. 2016; Svenning and Skov 2007).

By examining 17 distinct lineages across nine snake species or species complexes (Figure 1), Harrington et al. (2024) investigate the impact of late Pleistocene climate change on shifts in snake population sizes. Based on inferences from genomic data, they tested the broad prediction that these Nearctic snake lineages show evidence of synchronous demographic expansions that coincided with the end of the Pleistocene. The logical foundation for this expectation is based on predictions that the retreat of ice sheets and a warming climate associated with the Last Glacial Maximum (LGM) should have led to increased habitat availability for these ectothermic organisms, whose distributions are often constrained by environmental temperature. The authors find support for population expansion in all but three snake lineages. However, they also find that the extent and timing of expansion varied among the 17 lineages, and in many lineages, expansion began well before the Last Glacial Maximum (LGM),

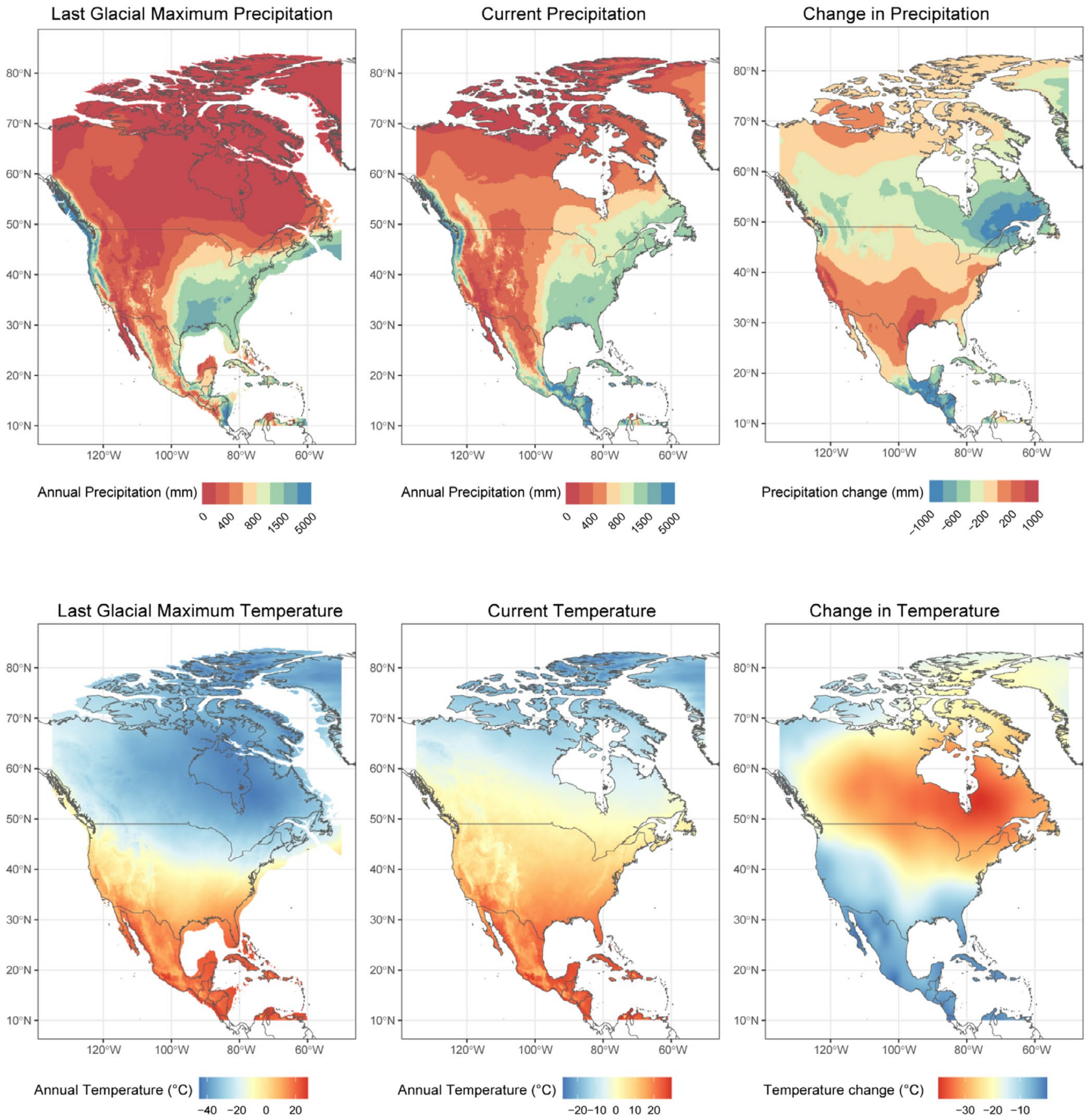

**FIGURE 2** | Annual temperature (top row) and annual precipitation (bottom row) during the Last Glacial Maximum (LGM) and Present Time. In each row, the first map represents LGM climate conditions, the second shows average values for 1970–2000, and the third displays the difference between the two. All maps are based on bioclimatic variables at a spatial resolution of 2.5 arc-minutes (~5 km) (Fick and Hijmans 2017).

in some cases as early as 2 million years before the present. The authors suggest that variation in the timing of population expansion observed across lineages is driven by species-specific responses to climatic and environmental variables. However, based on analysis of how current environmental conditions affect genetic distance across populations in the different lineages, they do not find clear trends that explain why distinct lineages show distinct expansion histories. While not directly tested in the paper, their results do seem to indicate a general trend in which northern and eastern lineages seem to show greater and more LGM-aligned expansion compared to their southern and western counterparts, likely due to the retreat of ice sheets, which opened up new competition-free habitats. Southern and western lineage expansion might have been driven by warmer temperatures overall. Additionally, larger-bodied snakes appear to exhibit expansions that are more closely tied to the timing of the LGM, possibly due to their higher dispersal capabilities and broader dietary requirements. While the authors stop short of offering specific interpretations for variation in expansion histories they observe across species, the relatively small sample size limits the potential for more extensive analyses of factors that covary with expansion patterns.

This study highlights the value of ectotherms as model systems for studying the ecological and evolutionary consequences of environmental changes, given their strong physiological dependence on environmental temperatures. Considering the ectothermic nature of snakes, it is reasonable to assume that there should be simple and consistent relationships between climate warming and population expansion. While the findings of Harrington et al. do show this trend at a coarse scale, they also provide evidence for somewhat surprisingly high variation in responsiveness to post-LGM warming across snake species. These findings raise broad questions about how different lineages of snakes may have been impacted by past climate change in fundamentally distinct ways, and how they may be differentially impacted by future climate change. The finding that many lineages appear to have undergone relatively gradual expansion throughout extended periods of the Pleistocene—prior to the Last Glacial Maximum (LGM)—is surprising and challenges the straightforward expectation that warmer temperatures directly lead to population expansion in ectotherms. Instead, it may suggest that climate shifts themselves, and perhaps habitat disturbances associated with climate change, created key opportunities that facilitated the expansion of certain lineages. Taken together, their findings highlight the complexity of variation in responses to climatic shifts across snake species, and open new questions about the complexity of climate-ecology associations that may underlie these species-specific differences.

Beyond snakes, the work of Harrington et al. provides a compelling example illustrating how studies of the responses of species to past warming events may offer key insight into how organisms may respond to future climate warming. Their findings further highlight the importance of moving beyond simplistic models that assume warming alone drives population expansion or contraction, and instead motivate consideration of the complex, multidimensional interactions among climate, landscape and species-specific biology that may more realistically portray likely responses of species to climate change. A natural next step would be to build on this and similar approaches by investigating how range expansion relates to species-specific traits, using past climate events and larger comparative sets of species as natural experiments to further test these hypotheses.

Advances in methods for inferring demographic history of lineages, along with the rapidly decreasing cost of collecting genomic data, now make it increasingly feasible to scale questions related to community-scale responses to climate change to new levels that incorporate increasingly large and diverse comparative collections of species. While the Harrington et al. study relied on using reduced-representation genome sequencing (i.e., RAD sequencing) and Site Frequency Spectra (SFS) to estimate population size through time, other more powerful approaches using whole genome resequencing data could also be leveraged to make even higher resolution demographic inferences. For example, the potential to apply Sequentially Markovian Coalescent (SMC) models to a small number of individual genomes, or even a single individual, to infer demographic history, massively increases the potential scope and scale of diversity such comparative studies could address. Going forward, there is broad and largely untapped potential to expand such comparative studies that infer historical demography of large sets of species, or even entire communities, to reconstruct past responses to climate change, and thereby estimate variation in climate responsiveness. Such approaches could provide fundamentally new insight into the potential climate change resiliency of species and help understand how variation in species-specific responses to climate change may manifest at the scales of entire ecological.

## Author Contributions

T.J. analyzed data. All authors contributed to writing the manuscript.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The authors have nothing to report.

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