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HISTORICAL DEMOGRAPHY AND CLIMATE DRIVEN RANGE SHIFTS IN THE BLUE-SPOTTED SALAMANDER UNDER THE CLIMATE CHANGE SCENARIOS

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Abstract.

*This study integrates phylogeography with distributional analysis to understand the demographic history and range dynamics of a limited dispersal capacity amphibian species, Blue-spotted Salamander (*Ambystoma laterale*), under several climate change scenarios. For this we used an ecological niche modeling approach, together with Bayesian based demographic analysis, to develop inferences regarding this species' demographic history and range dynamics. The current model output was mostly congruent with the present distribution of the Blue-spotted Salamander. However, under both the Last Interglacial and the Last Glacial Maximum bioclimatic conditions, the model predicted a substantially narrower distribution than the present. These predictions showed almost no suitable area in the current distribution range of the species during almost the last 22.000 y before present (ybp). The predictions indicated that the distribution of this species shifted from eastern coast of northern North America to the southern part of the current distribution range of the species. The Bayesian Skyline Plot analysis, which provided good resolution of the effective population size changes over the Blue-spotted Salamander history, was mostly congruent with ecological niche modeling predictions for this species. This study provides the first investigation of the Blue-spotted Salamander's late-Quaternary history based on ecological niche modeling and Bayesian-based demographic analysis. In terms of the main result of this study, we found that the species' present genetic structure has been substantially affected by past climate changes. It is worth noting that the species faced near-extinction within its present distribution range during the Last Glacial Maximum.*

Introduction

The impact of climate changes during the late-Quaternary period on North American biodiversity cannot be underestimated. It is widely acknowledged that the Last Glacial Maximum (LGM) led to significant shifts in distribution patterns, as species had to rapidly recolonize glacier-free regions (Pielou, 1991; G. Hewitt, 2000). These refugia, predominantly located in the southern regions, played a crucial role in facilitating the migration of plant communities, as evidenced by palynological studies (Webb et al., 2003). Furthermore, recent research has highlighted the profound effects of changing climate on the distribution areas of various North American species, resulting in a complete shift from south to north (Perktas and Elverici, 2020). Consequently, it is not surprising that many northern taxa exhibit lower genetic diversity compared to their southern counterparts, owing to the rapid post-glacial re-colonization, partial extinction, and accelerated colonization events (Hewitt, 1996). However, until recently, this reduced genetic variability has hindered our ability to detect the unique genetic structure found in taxa inhabiting higher latitudes.

The evaluation of mitochondrial DNA (mtDNA) diversity provides a valuable opportunity to unravel a species' demographic history, shedding light on its past and present (Freeland, 2005). By integrating mtDNA diversity with distributional analyses, we can gain novel insights into the complex biogeographic narratives that unfold (e.g., Klicka et al., 2011). One such species with a particularly limited dispersal ability is the Blue-spotted Salamander (Ambystoma laterale), which boasts one of the northernmost distributions in North America (Conant and Collins, 1991). During the Last Glacial Maximum, the ice coverage extended across almost the entirety of the Blue-spotted Salamander's current range (Fig. 1).

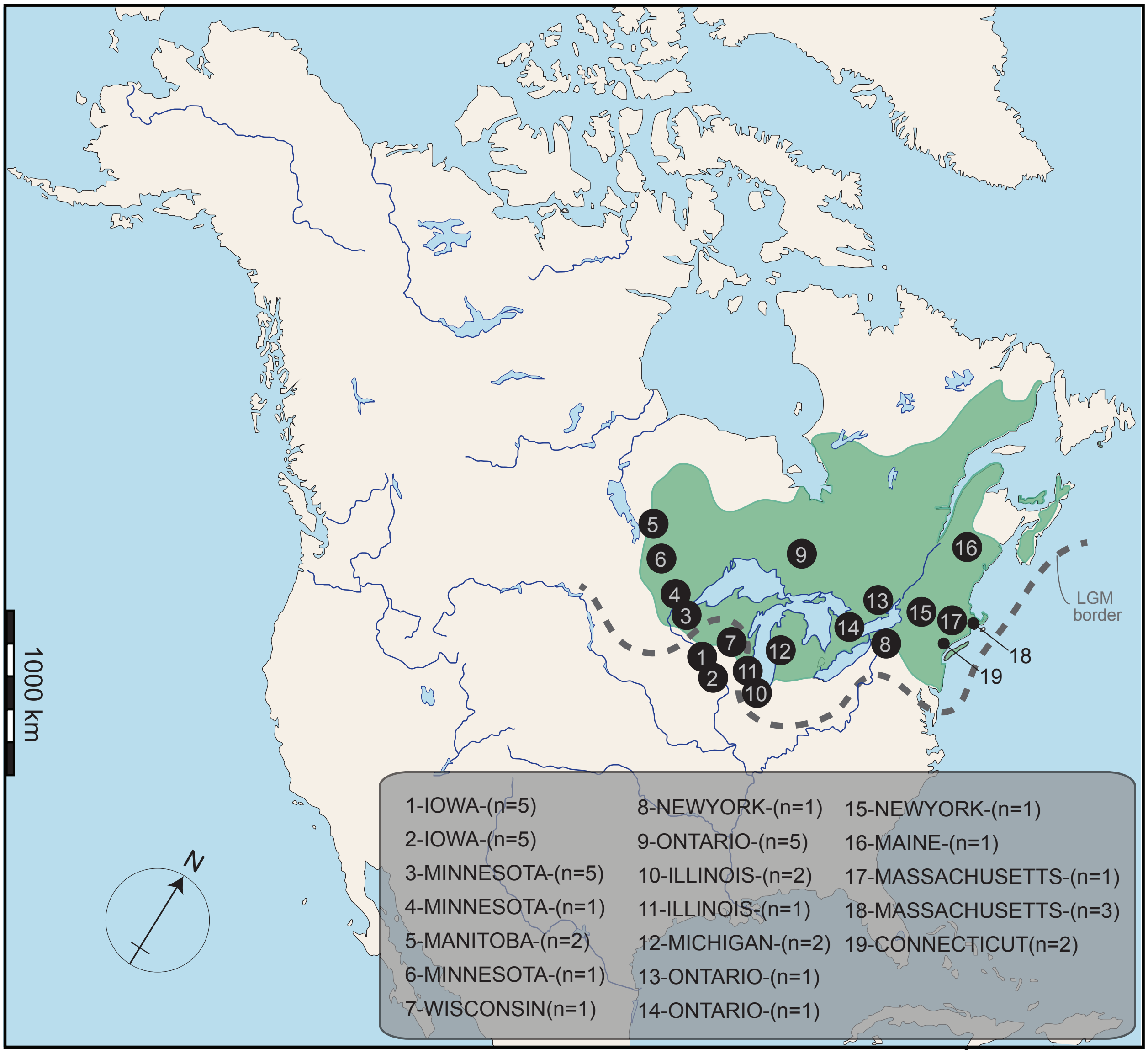

Figure 1. Approximate distribution range of the Blue-spotted Salamander. Sampling localities for ingroup taxa are indicated based on Demastes et al. (2007). Dashed line depicts the approximate extent of the last glacial maximum.

Therefore, the objective of this study is to conduct an integrative biogeographic survey on the Blue-spotted Salamander, aiming to evaluate its demographic history under different climate change scenarios. This research builds upon and expands the work of Demastes et al. (genotype; 2007), incorporating distributional projections derived from ecological niche models.

Methods

Ecological Niche Modelling

To conduct our analysis, we utilized species occurrence data obtained from GBIF (www.gbif.org) spanning from 1964 to 2020 (n = 2561 after removing 781 duplicated occurrence records). Before proceeding, we carefully examined the data for any sampling bias and spatial autocorrelation, following the methodology outlined by Brown (2014). To ensure accuracy, we spatially filtered the records, retaining only single occurrences within a 20 km radius across the species' distribution. This approach was particularly important considering the Blue-spotted Salamander's limited dispersal capacity, as documented by Ryan and Calhoun (2014) and Vanek et al. (2019). Consequently, we obtained a total of 553 unique occurrence records suitable for ecological niche modeling.

To complement our species occurrence data, we obtained bioclimatic data from the WorldClim database (Hijmans et al., 2005, http://www.worldclim.org). This included data for the Last Interglacial, as well as three global climate models (CCSM4, MIROC-ESM, and MPI-ESM-P) representing the Last Glacial Maximum (~22 kybp), the mid-Holocene (~6 kybp), the present (~1960-1990), and future conditions based on the RCP4.5 and RCP8.5 greenhouse gas scenarios (2050 and 2070). All data were acquired at a spatial resolution of 2.5 arc-minutes and encompassed 19 bioclimatic variables derived from monthly temperature and precipitation values.

To ensure the reliability of our analysis, we took into account previous studies (Campbell et al., 2015; Escobar et al., 2014) that identified potential artifacts in certain climate datasets. Specifically, we excluded variables such as mean temperature of the wettest quarter, mean temperature of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter (BIO8–9, BIO18–19, respectively) from our selection of variables used to build our model. For further details on this process, please refer to Simoes et al. (2020).

Given the rarity of the Blue-spotted Salamander in northeastern North America (Fig. 1; Ryan and Calhoun, 2014), we ensured that all variables were masked to encompass the entire North American region (-170° to 13° W and - 50° to 84° N). Additionally, we examined the correlations between the selected bioclimatic variables and generated three distinct climatic datasets based on different inter-variable correlation coefficients (0.6, 0.7, 0.8, and 0.9). These datasets included variables such as mean diurnal range (BIO2), isothermality (BIO3), maximum temperature of the warmest month (BIO5), annual temperature range (BIO7), precipitation of the wettest month (BIO13) and driest month (BIO14), as well as precipitation seasonality (BIO15).

Demographic History

To gain insights into the demographic history of the Blue-spotted salamander, we employed the Bayesian Skyline Plot (BSP) method using BEAST version 1.10.4 (Suchard et al., 2018). Previous studies (Demastes et al., 2007) did not report any population structure, so we combined all mtDNA sequences for the BSP analysis. This approach allowed for better comparability with our ecological niche modeling efforts.

Additionally, we employed a network approach to analyze the mtDNA dataset. This choice stems from the recognition that several fundamental assumptions underpinning traditional tree-building methods can be compromised in intraspecific studies, as indicated by Posada and Crandall (2001). We conducted this analysis using PopART (Population Analysis with Reticulate Trees) v.1.7.2, and for more details, please refer to Figure 3.

Before running the BSP analysis, we determined the best-fit substitution models for the mtDNA control region sequences using MEGA X (Kumar et al., 2018). The Hasegawa-Kishino-Yano (HKY) model was identified as the most suitable (AICc = 1775.424) for the control region. Subsequently, we performed multiple independent Bayesian Skyline Plot runs with the following parameters: linear models, 10 million steps, sampling of parameters every 1000 steps, and a burn-in period of 10%.

For the control region sequences, we employed the strict clock model with a default mutation rate under a normal prior distribution. In the case of vertebrates, the widely-used mutation rate ranges from 2% to 6% substitutions per site per million years (Allio et al., 2017). Additional examples can be found in studies by Brito (2005) and Pereira and Baker (2006). The effective sample size values for each run exceeded 200, ensuring reliable parameter estimation.

Results

Our analysis involved evaluating a staggering 2108 candidate models, considering various combinations of 31 feature classes, 17 regularization multipliers, and 4 climatic data sets. The most optimal model for the Blue-spotted Salamander emerged from the third climatic data set, which exhibited a correlation threshold of 0.8 (Set 3: BIO3, BIO5, BIO7, BIO13, BIO14, and BIO15). This model not only stood significantly apart from random ($P < 0.001$) but also boasted the lowest Akaike information criteria set, indicating its performance. With a regularization multiplier of 10 and the inclusion of a single feature class (threshold), the model demonstrated remarkable accuracy in projecting past, present, and future scenarios. Its training AUC of 0.708, accompanied by a small standard deviation (sd = 0.022), underscored its robustness. Among the bioclimatic variables, three stood out as major contributors, collectively accounting for 66.5% of the model's significance: BIO5 (30.5%), BIO15 (19%), and BIO7 (17%).

When applied to present bioclimatic conditions, the model's predictions aligned closely with the current and recent historical distribution of the Blue-spotted Salamander (refer to Fig. 1, also see IUCN, 2015). Notably, the model predominantly identified areas of high suitability across various habitats in North America. However, when projected onto the Last Glacial Maximum bioclimatic conditions, the model indicated a considerably narrower distribution compared to the present and mid-Holocene (Fig. 2). Intriguingly, predictions for the Last Glacial Maximum suggested an almost complete absence of distribution along the east coast of North America. Conversely, predictions for the Last Interglacial pointed to a distribution encompassing the east coast of North America. Looking ahead to 2050 and 2070, the model anticipated a slight northward shift in the range, accompanied by a broader distribution than both the past and present (Fig. 2).

Incorporating a strict molecular clock (mean 2%-4% substitutions/site/million years), our BSP analysis provided valuable insights into the changes in effective population size throughout the history of the Blue-spotted Salamander (Fig. 3). The BSP revealed a recent demographic expansion that began after the Last Interglacial, aligning with mutation rates (approximately 60,000 years before the present). This expansion is also evident in the haplotype network within this timeframe (Fig. 3).

Discussion

In this study, we delve into the captivating dynamics of range shifts exhibited by the Blue-spotted Salamander, spanning the past, present, and near future under the looming threat of climate change. Building upon the pioneering work of Demastes et al. (2007), we embark on an unprecedented exploration of the late-Quaternary history of this remarkable creature, employing cutting-edge ecological niche modelling and Bayesian-based demographic analysis.

Previous research has revealed the Blue-spotted Salamander to possess remarkably low-level genetic diversity, as evidenced by the analysis of 534 nucleotides of non-coding mtDNA gene region (Demastes et al., 2007). Intriguingly, during the Last Glacial Maximum, the vast expanse of northeastern North America lay ensnared beneath a thick blanket of ice, with no fossil evidence to suggest the presence of salamanders south of this icy barrier (Pielou, 1991). Consequently, the lack of mtDNA differentiation across the distribution range of the Blue-spotted Salamander implies that populations emerged relatively

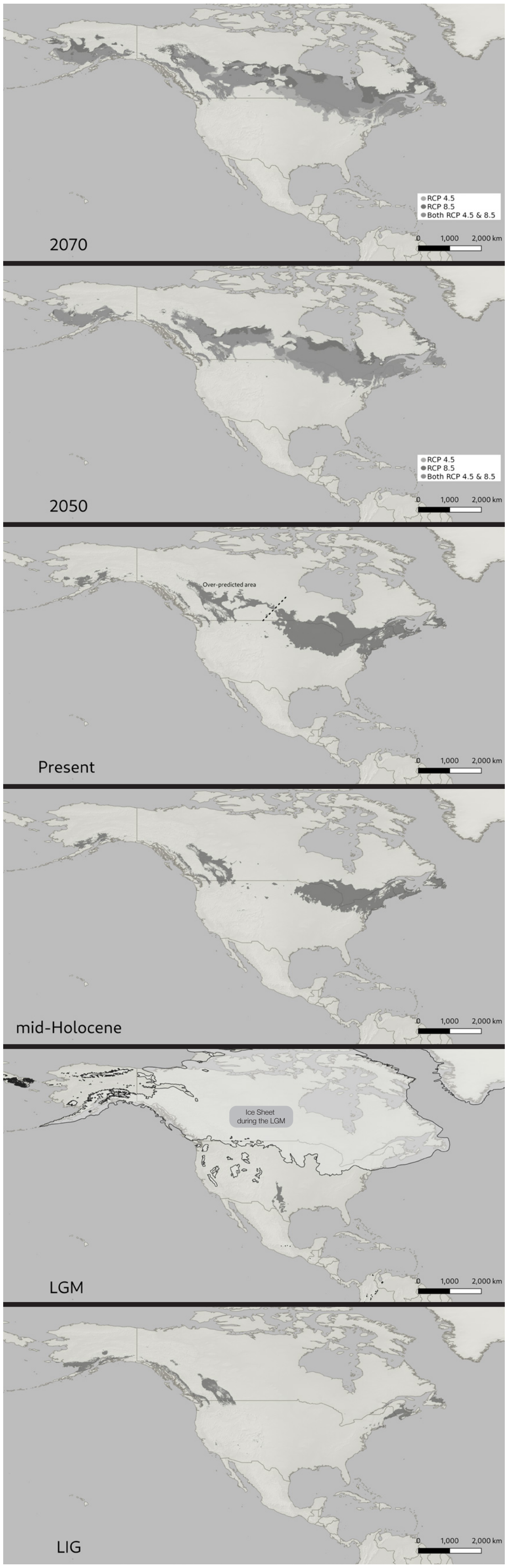

Figure 2. Ecological niche model-based distributional predictions for the Blue-spotted Salamander under the different bioclimatic conditions [i.e. the LGM and the Future (2050 and 2070)].

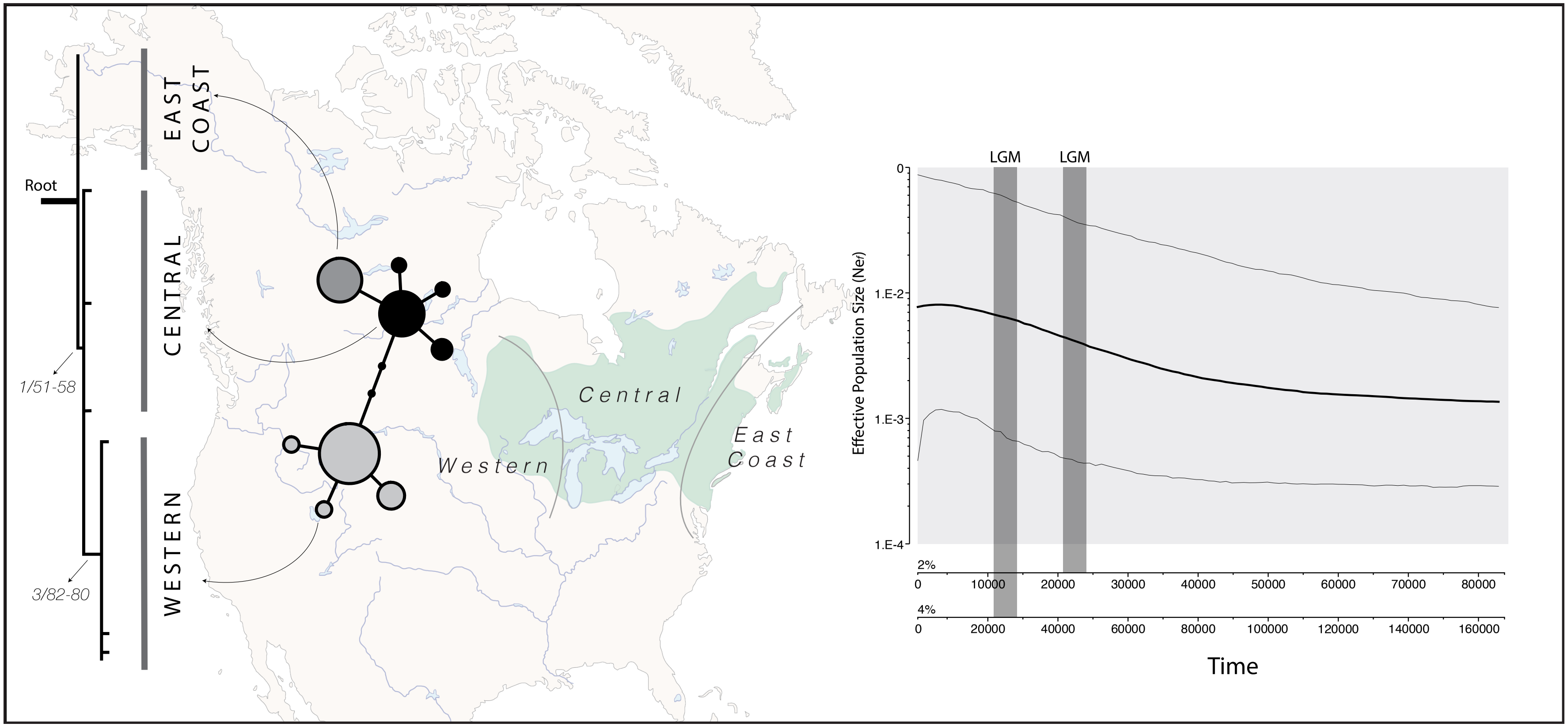

Figure 3. Maximum likelihood tree for Ambystoma laterale, derived from 534 base pairs of mtDNA, encompassing 19 sampled populations and the outgroup *A. jeffersonianum*. The numbers above branches indicate absolute branch lengths, and those below denote bootstrap values (ML/parsimony), for details, see Demastes et al., 2007. The haplotype network was constructed using PopART (Population Analysis with Reticulate Trees) v.1.7.2, incorporating the median joining network criteria from NETWORK (Bandelt et al., 1999), with circle sizes representing sample sizes. The background map illustrates the species' distribution range and the approximate positioning of haplogroups. The Bayesian Skyline Plot analysis revealed temporal fluctuations in the effective population size of the Blue-spotted Salamander, and the x-axis has been adjusted according to varying mutation rates.

recently, following the retreat of the ice sheet, from a relatively homogeneous ancestral population.

Phylogenetic analysis of haplotypes (refer to Fig. 2 in Demastes et al., 2007) has unveiled close relationships among most haplotypes, albeit with distinct geographical localization. Notably, the western clade has diverged significantly from the east coast and central clades, as indicated by robust bootstrap values. These findings suggest historical connectivity among populations, yet the presence of firm barriers, likely driven by behavioral factors, has fostered recent and ongoing genetic differentiation. While this situation may be interpreted as the absence of a long-term biogeographical barrier, it ultimately hinges upon the limitations in the dispersal capacity of this species.

The current pattern aligns with the phylogeographic category III, characterized by a shallow gene tree and allopatric lineage, as defined by Avise et al. (1987) and (Avise, 2000). Empirical evidence supporting this phylogeographic pattern has been documented in various species that migrated beyond the glacial line, along the southeastern coastline of North America (e.g., Deer Mouse, *Peromyscus polionotus*, Avise et al., 1979, 1983), as well as in South America (White-Tailed Deer, *Odocoileus virginianus*, Moscarella et al., 2003). However, it is crucial to acknowledge that northeastern North America has undergone profound topographic transformations due to past climatic fluctuations, including those occurring over the last 130,000 years, along with the repeated expansion and recession of continental ice sheets, particularly around 22,000 years ago. These events have exerted a profound influence on the genetic structuring of flora and fauna in the region (e.g., Pielou, 1991), thereby establishing a tight association between the genetic structure of the Blue-spotted Salamander and past climate change events.

Predictions regarding the past distribution of the Blue-spotted Salamander have unveiled substantial range shifts from the Last Interglacial period to the present day. During the Last Interglacial, the species was confined to the east coast of northern North America, only to witness its range shrink to the southern regions during the Last Glacial Maximum. Consequently, the Blue-spotted Salamander underwent a remarkable journey, sliding from east to south, expanding northward, and ultimately reaching its current distribution. It is worth noting that the species faced near-extinction within its present distribution range during the Last Glacial Maximum.

According to Lindsay et al. (2016), the habitat suitability for the Blue-spotted Salamander during the Last Glacial Maximum, as predicted by ecological niche modelling, predominantly comprised Taiga and partially Montane Mosaic. The International Union for Conservation of Nature (IUCN) identifies forests and wetlands as the two primary suitable habitats for this species. Specifically, suitable forests encompass boreal (taiga) and temperate forests, aligning with the vegetation model derived from the Last Glacial Maximum, thus corroborating our niche modelling results. The Southern Appalachian Region emerges as a refuge for numerous species (Hewitt, 2004). However, it is noteworthy that this particular biogeographic pattern has not been reported for any terrestrial vertebrate species thus far, although similar examples have been documented for widespread North American vertebrates (e.g., Klicka et al., 2011; van Els et al., 2012; Barrowclough et al., 2018; Perktas and Elverici, 2020).

The Bayesian Skyline Plot analysis has shed light on a population increase preceding the Last Glacial Maximum within the ice-free areas of North America, adding an intriguing dimension to our study. Remarkably, the Blue-spotted Salamander gradually expanded its range during the Holocene, ultimately culminating in its present distribution. Thus, the species' demographic history aligns harmoniously with the outcomes derived from ecological niche modelling. In contrast to phylogeographic research conducted on other vertebrate species (e.g., Sharp-tailed Grouse), we have found no evidence of a large refugium within the ice-free regions of North America for the Blue-spotted Salamander. Nevertheless, it is awe-inspiring to witness how this species has undergone a complete transformation in its distribution since the last glacial period, effectively establishing its current range from virtually nothing since the Last Glacial Maximum.

Acknowledgment

This study was initially submitted to the American Midland Naturalist. However, following the closure of the journal (their last publication being the October 2022 issue) after the evaluation, we chose to resubmit the study to the European Journal of Ecology. In doing so, we took into consideration the assessments provided by reviewers from the original journal. Editors, Piotr Tryjanowski and Jakub Kosicki, meticulously reviewed this resubmission, considering the feedback from the previous referees.

We express our sincere gratitude to everyone involved in the process. Additionally, we extend our thanks to the remaining members of the Biogeography Research Laboratory for their continuous support and assistance across various phases of this project.

Author Contributions

UP conceived the study; UP developed methods and UP, CE, ÖY analyzed data; CE visualized the distributional predictions, UP wrote the paper with discussion with CE and ÖY. All authors read and approved the final manuscript.

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