

1 RH: BIOGEOGRAPHY OF THE BLUE-SPOTTED SALAMANDER

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3 **Historical Demography and Climate Driven Range Shifts in the Blue-**  
4 **spotted Salamander Under the Climate Change Scenarios**

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16 ABSTRACT.- This study integrates phylogeography with distributional analysis  
17 to understand the demographic history and range dynamics of a limited dispersal  
18 capacity amphibian species, Blue-spotted Salamander (*Ambystoma laterale*), under  
19 several climate change scenarios. For this we used an ecological niche modeling  
20 approach, together with Bayesian based demographic analysis, to develop inferences  
21 regarding this species' demographic history and range dynamics. The current model  
22 output was mostly congruent with the present distribution of the Blue-spotted  
23 Salamander. However, under both the Last Interglacial and the Last Glacial

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24 Maximum bioclimatic conditions, the model predicted a substantially narrower  
25 distribution than the present. These predictions showed almost no suitable area in  
26 the current distribution range of the species during almost the last 22.000 y before  
27 present (ybp). The predictions indicated that the distribution of this species shifted  
28 from eastern coast of northern North America to the southern part of the current  
29 distribution range of the species. The Bayesian Skyline Plot analysis, which provided  
30 good resolution of the effective population size changes over the Blue-spotted  
31 Salamander history, was mostly congruent with ecological niche modeling  
32 predictions for this species. This study provides the first investigation of the Blue-  
33 spotted Salamander's late-Quaternary history based on ecological niche modeling  
34 and Bayesian-based demographic analysis. In terms of the main result of this study,  
35 we found that the species' present genetic structure has been substantially affected  
36 by past climate changes, and this species has reached current distribution range  
37 almost from nothing since the Last Glacial Maximum.

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## INTRODUCTION

40 The effects of late-Quaternary climate changes on North American  
41 biodiversity are considered to be dramatic (Pielou, 1991). Recent distribution  
42 patterns must have occurred from glacier-free regions during the Last Glacial  
43 Maximum (LGM). These recolonization events generally took place rapidly to  
44 preglaciated regions (G. Hewitt, 2000). It is generally accepted that these refugia  
45 were located in the south because evidence from palynological studies (Webb *et al.*,  
46 2003) shows that large changes in plant communities were also occurring rapidly.

47 Some recent studies have also shown that the distribution areas of some North  
48 American species have changed almost completely, and their distribution has shifted  
49 from south to north due to the changing climate (Perktaş and Elverici, 2020).  
50 Therefore, many northern taxa have lower genetic diversity than their southern  
51 counterparts. This is probably due to the fast post-glacial re-colonization, partial  
52 extinction, and the fast colonization events in a short time (Hewitt, 1996). Until  
53 recently, this low genetic variability has hampered our ability to detect the unique  
54 genetic structure that can be found in taxa at higher latitudes.

55 The evaluation of mitochondrial DNA (mtDNA) diversity gives an  
56 opportunity to understand species' demographic history from the recent past to the  
57 present (Freeland, 2005) Integrating mtDNA diversity with distributional analyses  
58 offers novel opportunities to understand such complex biogeographic stories (e.g.,  
59 Klicka *et al.*, 2011). The Blue-spotted Salamander (*Ambystoma laterale*) has one of the  
60 northern-most distributions in North America with very limited dispersal ability  
61 (Conant and Collins, 1991). During the Last Glacial Maximum (LGM, approx. 22,000  
62 years before present), ice coverage extended over almost the entire current  
63 distribution range of the Blue-spotted Salamander (Fig. 1). Hence, in this paper, we  
64 aim to develop an integrative biogeographic survey on the Blue-spotted Salamander  
65 to evaluate its demographic history under the climate change scenarios. This study  
66 can be considered as an integration and continuation of the work of Demastes *et*  
67 *al.* (genotype; 2007) with distributional projections derived from ecological niche  
68 models (ENMs).

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## METHODS

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### ECOLOGICAL NICHE MODELLING

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Input data – We analyzed species occurrence data from GBIF ([www.gbif.org](http://www.gbif.org)),

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ranging from 1964 to 2020 (n = 2561 after 781 duplicated occurrence records

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removed), before checking for sampling bias and spatial autocorrelation (Brown,

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2014) for occurrence records. We spatially filtered all records to eliminate multiple

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records, leaving single 20 km records across the species' distribution. For this we

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considered the low dispersal capacity of the Blue-spotted Salamander (see Ryan and

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Calhoun, 2014; Vanek *et al.*, 2019 for details). This yielded 553 unique occurrence

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records for ecological niche modelling.

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We downloaded bioclimatic data from the WorldClim database (Hijmans *et*

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*al.*, 2005, <http://www.worldclim.org>) for the Last Interglacial, three global climate

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models (CCSM4, MIROC-ESM, and MPI-ESM-P) for the Last Glacial Maximum (~22

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kybp), the mid-Holocene (~6 kybp), the present (~1960-1990), and future conditions

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based on the RCP4.5 and RCP8.5 greenhouse gas scenarios (2050 and 2070) at a

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spatial resolution of 2.5 arc-minutes. Bioclimatic data included 19 bioclimatic

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variables derived from monthly temperature and precipitation values. Previous

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studies (Campbell *et al.*, 2015; Escobar *et al.*, 2014) detected a number of apparent

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artifacts in some of the climate datasets: mean temperature of the wettest quarter,

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mean temperature of driest quarter, precipitation of the warmest quarter, and

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precipitation of the coldest quarter (BIO8–9, BIO18–19, respectively). Therefore, we

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excluded these variables from the pool of selected variables to build a model (for

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details, also see Simoes *et al.*, 2020). Since the Blue-spotted Salamander is one of the

93 rarest amphibian species in northeastern North America (Fig. 1; Ryan and Calhoun,  
94 2014), all variables were masked to include all North America (-170° to 13° W and -  
95 50° to 84° N). We then inspected correlations between these bioclimatic variables to  
96 produce three different climatic data sets based on different inter-variable  
97 correlation coefficients (0.6, 0.7, 0.8, and 0.9). These included mean diurnal range  
98 (BIO2), isothermality (BIO3), maximum temperature of warmest month (BIO5),  
99 annual temperature range (BIO7), precipitation of wettest month (BIO13) and driest  
100 month (BIO14) and precipitation seasonality (BIO15).

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#### DEMOGRAPHIC HISTORY

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We applied the Bayesian Skyline Plot (BSP) method, implemented in BEAST version 1.10.4 (Suchard *et al.*, 2018), to explore the Blue-spotted salamander demographic history. Since earlier studies have not reported any structure (Demastes *et al.*, 2007), we combined all mtDNA sequences before running the BSP analysis, and this approach made the demographic history more comparable with ecological niche modelling. Before the BSP runs, the best-fit substitution models were identified for the mtDNA control region sequences in MEGA X (Kumar *et al.*, 2018). These were the Hasegawa-Kishino-Yano (HKY, AICc = 1775.424) for the control region. Multiple independent Bayesian Skyline Plot runs were performed using the following parameters: linear models, 10 million steps, parameters sampled every 1000 steps, and a burn in of 10%. For the control region sequences, we used the strict clock model with a default mutation rate under normal prior distribution [for vertebrates, the widely-used 2%-6% substitutions/site/million years (Allio *et al.*,

116 2017; for different examples, *see also* Brito, 2005; Pereira and Baker, 2006)]. The  
117 effective sample size values of the parameters were over 200 for each run.

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## 119 RESULTS

120 We evaluated 2108 candidate models using combinations of 31 feature classes,  
121 17 regularization multipliers, and 4 climatic data sets. The best model for the Blue-  
122 spotted Salamander was provided by the third climatic data set which was had a  
123 correlation threshold of 0.8 (Set 3: BIO3, BIO5, BIO7, BIO13, BIO14 and BIO15),  
124 which was significantly different from random ( $P < 0.001$ ) and had the lowest  
125 Akeike information criteria set. The model had a regularization multiplier of 10 and  
126 included one feature class (threshold). Projections for past, present, and future  
127 performed better than a random prediction with moderate training AUC = 0.708  
128 with small standard deviation ( $sd = 0.022$ ) that indicated the robust model  
129 performance. Three bioclimatic variables contributed the most to the model  
130 (together 66.5%): BIO5 (30.5%), BIO15 (19%) and BIO7 (17%).

131 Under present bioclimatic conditions, the model's predictions were mostly  
132 congruent with the present and recent historical distribution of Blue-spotted  
133 Salamander (*see* Fig.1 for the present distribution, also *see* IUCN, 2015). The model  
134 primarily predicted areas of high suitability across habitats for the species in North  
135 America. Under the Last Glacial Maximum bioclimatic conditions, the model  
136 predicted substantially narrower distribution than the present and mid-Holocene  
137 (Fig. 2). Interestingly, predictions for the Last Glacial Maximum indicated almost no  
138 distribution in the east-coast of North America. However, predictions for the Last

139 Interglacial indicated a distribution east coast of North America. For both 2050 and  
140 2070, the model predicted that the range will most likely shift slightly northward  
141 with a wider distribution than either the past or present (Fig. 2).

142       Based on a strict molecular clock (mean 2%-4% substitutions/site/million  
143 years), the BSP result provided a good resolution of the effective population size  
144 changes over the Blue-spotted Salamander history (Fig. 3). The BSP indicated a  
145 recent demographic expansion starting after the Last Interglacial based on both  
146 mutation rates (starting approximately after 60,000 y before present).

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#### DISCUSSION

149       This study focuses on the dynamics of range shifts of the Blue-spotted  
150 Salamander from the past, the present and the near future under climate change  
151 scenarios. Accordingly, this study is therefore a continuation of the work of  
152 Demastes *et al.* (2007) with the first investigation of the late-Quaternary history of the  
153 Blue-spotted Salamander based on ecological niche modelling and Bayesian based  
154 demographic analysis.

155       The Blue-spotted Salamander showed substantially low-level genetic  
156 diversity based on 534 nucleotides of non-coding mtDNA gene region (Demastes *et*  
157 *al.*, 2007). During the Last Glacial Maximum, north-eastern North America was  
158 almost completely covered by ice (Pielou, 1991) and there is no fossil evidence to  
159 suggest that salamanders were present south of the ice sheet. Therefore, lack of  
160 mtDNA differentiation in the Blue-spotted Salamander across its distribution range  
161 suggests that populations arose recently (after the Last Glacial Maximum) from a

162 relatively homogeneous ancestral population. Phylogenetic relationships among  
163 haplotypes (*see* Fig. 2 in Demastes *et al.*, 2007) indicated most haplotypes are closely  
164 related, yet are geographically localized. The western clade separated from the east  
165 coast and central clades with high bootstrap values. All these signals suggest that  
166 populations are historically connected, but most probably due to behavioral reasons,  
167 populations are sundered by firm, and it supports recent and continuing genetic  
168 differentiation. This situation can be discussed as the absence of a long-term  
169 biogeographical barrier, but depends on the limitations in dispersal capacity of this  
170 species. The current pattern is compatible with phylogeographic category III  
171 (shallow gene tree, allopatric lineage) specified by Avise *et al.* (1987) and (Avise,  
172 2000).

173       Empirical examples that support this phylogeographic pattern from different  
174 species that spread out of the glacial line, along the southeastern coastline of North  
175 America (eg Deer Mouse, *Peromyscus polionotus*, Avise *et al.*, 1979, 1983), South  
176 America (White-Tailed Deer, *Odocoileus virginianus*, Moscarella *et al.*, 2003) has been  
177 published. However, it is well known that northeast North America has undergone  
178 remarkable topographic change because of past climatic changes, including climatic  
179 fluctuations during the last 130.000 ybp, and repeated expansion/recession of  
180 continental ice sheets during especially 22.000 ybp, and therefore habitat changes in  
181 the same time period. All these events have had dramatic effects on the genetic  
182 structuring of flora and fauna in the region (*e.g.* Pielou, 1991); and hence the genetic  
183 structure of Blue-spotted Salamander showed tight association with past climate  
184 change events.



185           The past distributional predictions of the Blue-spotted Salamander indicated  
186   substantial range-shifts from the Last Interglacial to the Present. The predicted Last  
187   Interglacial range limited to the east coast of northern North America, then the  
188   predicted Last Glacial Maximum range limited to the southern range of the  
189   distribution range of the species. Therefore, the range of Blue-spotted Salamander  
190   slided from east to south, and expanded to the north and reached the current  
191   distribution. Species looks like it experienced an almost complete extinction in its  
192   present distribution range during the Last Glacial Maximum. According to Lindsay  
193   *et al.* (2016), habitat suitability for the Blue-spotted Salamander in the Last Glacial  
194   Maximum, as ecological niche modelling approach predicts, is mostly Taiga and  
195   partly Montane Mosaic. IUCN states that there are two main suitable habitats for the  
196   species, forests and wetlands. Suitable forests are boreal (taiga) and temperate  
197   forests, so the Last Glacial Maximum vegetation model agrees with our niche  
198   modelling results. The Southern Appalachian Region was found to be a refugium for  
199   many species (Hewitt, 2004). However, this type of biogeographic pattern has not  
200   been reported for any terrestrial vertebrate species so far although some similar  
201   examples have been reported for widespread North American vertebrates (*e.g.*  
202   Klicka *et al.*, 2011; van Els *et al.*, 2012; Barrowclough *et al.*, 2018; Perktaş and Elverici,  
203   2020). The Bayesian Skyline Plot analysis showed a population increase before the  
204   Last Glacial Maximum in the ice free areas in North America, and this makes this  
205   study outputs interesting. The species, however, reached its present distribution  
206   gradually during the Holocene. Therefore, the species' demographic history  
207   supports the ecological niche modelling results. In contrast to phylogeographic

208 research on other vertebrate species (e.g. Sharp-tailed Grouse), we found no evidence  
209 of a large refugium in the ice free range of North America for this species. However,  
210 the Blue-spotted Salamander has almost completely changed its distribution since  
211 the last glacial period; that is, this species has reached current distribution range  
212 almost from nothing since the Last Glacial Maximum.

213

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217

218 *Author Contributions.*- UP conceived the study; UP developed methods and  
219 UP, CE, ÖY analyzed data; CE visualized the distributional predictions, UP wrote  
220 the paper with discussion with CE and ÖY. All authors read and approved the final  
221 manuscript.

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333 FIGURE LEGENDS:

334 Figure 1.-- Approximate distribution range of the Blue-spotted Salamander.

335 Sampling localities for ingroup taxa (1–19) are indicated based on Demastes *et al.*

336 (2007). Dashed line depicts the approximate extent of the last glacial maximum

337 Figure 2.- Ecological niche model-based distributional predictions for the Blue-

338 spotted Salamander under the different bioclimatic conditions [*i.e.* the LGM and the

339 Future (2050 and 2070)]

340 Figure 3.- The effective population size fluctuation of the Blue-spotted Salamander

341 based on the Bayesian Skyline Plot analysis







