RESEARCH ARTICLE



Post-Pleistocene dispersal explains the Rapoport effect in North American salamanders

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Abstract

Aims: In many taxa, the latitudinal span of species' geographic ranges are positively correlated with median latitude (the Rapoport effect). This correlation is frequently explained as adaptation to contemporary climate; however, variability in post-glacial range expansion among species could also explain this observation. We analyse geographic data for North American salamanders to test the potential causes of Rapoport effects.

Location: Temperate North America.

Taxon: Salamanders (order Caudata).

Methods: We tested for a Rapoport effect by estimating correlations between the latitudinal midpoint and latitudinal range among species. Next, we manipulated species' latitudinal ranges by removing post-glacial habitat and assessing the impact of species demonstrating post-glacial range expansion in forming a Rapoport effect. We built ecological niche models for species found south of the Wisconsin Ice Sheet during the Last Glacial Maximum and transferred these models to post-glacial areas. If dispersal is important in forming a Rapoport effect, then some species may tolerate northern climates but have not expanded northward as a result of variation in geographic access to post-glacial habitats. We created binary ecological niche models by thresholding using the equal sensitivity and specificity value.

Results: We recovered a Rapoport effect that was robust to the null models we tested. Analyses that manipulated ranges and species pools supported a role for variation in post-glacial range expansion among species, especially for eastern North America. Results from transferring ecological niche models indicated that species have suitable habitat north of their range limit.

Main conclusions: Variation in post-glacial range expansion is important in shaping geographic range size clines among species in areas where climates changed rapidly, though we also found support for the climatic variability hypothesis. Post-glacial colonization and range expansion likely plays an important role in forming latitudinal biodiversity gradients in northern taxa. While ecophysiology and biotic interactions have been emphasized as important contributors to diversity gradients, our study indicates that post-glacial colonization also plays a key role in forming latitudinal gradients.

KEYWORDS

ecological niche modelling, macroecology, null models, post-glacial dispersal, Rapoport effect, salamanders

1 | INTRODUCTION

Studies of variation in species' geographic ranges are central to understanding large-scale patterns in biodiversity (Lomolino et al., 2017). In many groups of organisms, range size is positively correlated with latitude (Rapoport, 1975, 1982). This trend has been dubbed Rapoport's rule (Stevens, 1989), but following Gaston et al. (1998), we refer to it as the Rapoport effect. Stevens (1989) argued that species at extreme latitudes experience greater seasonality, which through adaptation primes them to survive in a variety of habitats (the climatic variability hypothesis), resulting in species with larger geographic ranges than species found near the equator. He further argued that the climatic variability hypothesis is causally related to the latitudinal diversity gradient in species richness because the tropics harbour more distinct habitats as a result of low seasonality, allowing many climatic specialists to exist in a small region, which in turn results in greater species richness compared to the temperate zone where species are wide-ranging climatic generalists. The climatic variability hypothesis is an extension of previous observations about seasonality and geographic distributions of tropical versus temperate taxa (Janzen, 1967).

In a meta-analysis of upper and lower thermal tolerances, Sunday et al. (2010) found that geographic patterns in ectotherm physiology support the climatic variability hypothesis, such that species at more extreme latitudes have relatively large differences between upper and lower thermal tolerances. Variation was primarily driven by changes in lower thermal tolerances, as upper thermal tolerances showed little variation among species (Addo-Bediako et al., 2000; Araújo et al., 2013; Sunday et al., 2010). Clay and Gifford (2018) found that among 12 species of woodland salamanders (genus *Plethodon*) in eastern North America, latitudinal range size was positively correlated with the breadth of physiological performance in energy assimilation, which is consistent with the predictions of the climatic variability hypothesis and its role in generating a Rapoport effect.

The Rapoport effect is a pattern with multiple potential causes beyond the climatic variability hypothesis. Selective extinction can generate a Rapoport effect if narrow-ranging species generally have more limited dispersal abilities and/or narrower climatic tolerances than species that are wide-ranging. Sandel et al. (2011) compared the speed of climatic shifts with the presence of narrowranging species and found a negative relationship between the rate of climate change and the number of narrow-ranging species present. Veter et al. (2013) examined the geography of the Cenozoic fossil record of North American mammals; a Rapoport effect was not apparent throughout most of the six most recent epochs, but was detected in the Oligocene and the Pleistocene, both times of intense cooling. They concluded that species with smaller ranges were probably eliminated during glacial events, such that species with the largest ranges survived the coldest climates. However, their conclusion was weakened when narrower time intervals were investigated (Radomski, 2021). Extinction rates have been estimated from molecular phylogenies of extant amphibians, indicating higher extinction rates in temperate areas (Pyron & Wiens, 2013; Journal of Biogeography -WILEY-

but see Rabosky, 2010 for caveats about estimating extinction rates from phylogenies of extant species). Yet, the analyses of Pyron and Wiens (2013) did not consider range size in their analyses, and thus any link to a Rapoport effect is unclear.

The niche position hypothesis predicts that variation in geographic range size is due to the amount and arrangement of different habitat types to which different species are adapted (Sheth et al., 2014). For example, a species that is well adapted to arid habitat on the African continent could have a geographic range that occupies a third of the continent due to the size of the Sahara and Namib deserts. Yet, the same species would have a much smaller geographic range in South America, as the geographic area of arid habitat is limited to the relatively small Atacama Desert. Using simulations, Saupe et al. (2019) showed that the Rapoport effect could result from different areas of habitat types: colder, poleward areas are more widespread and well connected (resulting in few, large geographic ranges), while warmer areas nearer the equator are often geographically smaller and not as well connected (resulting in many small ranges).

In addition to either climatic tolerance or extinction, geographic access to post-glacial landscapes may play an important role in generating a Rapoport effect. The leading-edge hypothesis posits that species that are closest to receding glaciers undergo exponential population growth and range expansion as they colonize recently created habitats, and that species further away from glacial boundaries form barriers to each other's expansion as a result of demographic and competitive effects (Hewitt, 1996). In support of this idea, species occurring in post-glacial landscapes often have large geographic ranges, such as warblers of Asia (Price et al., 1997). Research on European flora and fauna have suggested a strong role for post-glacial range expansion on the structure of modern-day communities and geographic ranges, with the east-west running Alps and Pyrenees mountain ranges impeding post-Pleistocene range expansion among many species (Araújo & Pearson, 2005; Normand et al., 2011; Svenning & Skov, 2004, 2007). However, research into post-glacial range expansion has rarely been framed with reference to a Rapoport effect. The hypothesis that the large geographic ranges of high-latitude species are, in part, due to postglacial dispersal is supported by many population genetic studies in which genetic diversity rapidly declines in post-glacial landscapes, a pattern that is consistent with recent colonization and range expansion (Hewitt, 1999). Pelletier and Carstens (2018) found that latitude and range size were strong predictors of genetic variation, which may intimately link a Rapoport effect and post-glacial colonization, though they did not explicitly explore such an idea. Evidence of rapid post-glacial range expansion is also well supported by the pollen record (Davis, 1983).

Temperate salamanders are species-rich in North America (over 100 species), and because they are dispersal-limited (e.g. Mathis, 1991), dispersal barriers may commonly prevent them from occupying suitable habitat. Salamanders are frequently buffered from above-ground temperatures because they can access below-ground refugia, such that critical thermal minima vary less WILEY- Journal of Biogeography

than 2.5°C when comparing microendemics to widespread generalists (Markle, 2015). The post-glacial range expansion hypothesis predicts that (i) species in post-glacial landscapes should disproportionately contribute to a Rapoport effect and (ii) many species that did not have access to post-glacial habitats could exist there given the opportunity to colonize. Several lines of evidence support our hypothesis for temperate salamanders of North America. First, many of the species crossing the glacial boundary (the southernmost extent of glaciers) during the Last Glacial Maximum (~18 kya) are habitat generalists with ecologically similar relatives south of the glacial boundary (Figure S1). Second, there is evidence that salamanders with natural distributions restricted to more southern latitudes can persist in northern areas following introduction, and thus dispersal limitation was important in forming modern-day geographic ranges. The introduction of Aneides vagrans from California to Vancouver Island (which lacks other species of Aneides) resulted in the rapid colonization of the entire island (Jackman, 1998). Third, many population genetic studies of North American salamanders have found evidence for rapid post-glacial colonization (Table 1). However, geographic dynamics differ by region; in eastern North America (ENA), glaciers advanced from north to south. In western North America (WNA), glaciers also advanced from mountain ranges, including the Olympic, Cascade, Rocky and Sierra Nevada Mountains, which would likely not contribute to latitudinal range dynamics. Geomorphological changes in WNA were probably more influential than glacial cycles in structuring salamanders' geographic ranges (Wake, 1997). Additionally, proximity of glaciers to the coast and the arid environment east of coastal mountain ranges suggest that there may have been few routes for range expansion or limited refugia (e.g. Kuchta & Tan. 2005). In this study, we investigate North American salamanders to test the hypothesis that post-glacial range

TABLE 1Phylogeographic studies that found evidence of post-
glacial range expansion among North American salamanders

Species	References
Ambystoma gracile	Titus (1990)
Ambystoma laterale	Demastes et al. (2007)
Ambystoma macrodactylum	Thompson & Russell (2005)
Ambystoma maculatum	Zamudio & Savage (2003)
Ambytoma tigrinum	Templeton et al. (1995)
Desmognathus fuscus	Markle (2006)
Dicamptodon tenebrosus	Steele & Storfer (2006)
Eurycea bislineata complex	Kozak et al. (2006)
Gyrinophilus porphyriticus	Kuchta et al. (2016)
Hemidactylium scutatum	Herman & Bouzat (<mark>2016</mark>)
Notophthalmus viridescens	Gabor & Nice (2004)
Plethodon cinereus	Radomski et al. (2020)
Plethodon idahoensis	Pelletier & Carstens (2014)
Plethodon vehiculum	Pelletier et al. (2010)
Pseudotriton ruber	Folt et al. (2016)
Taricha granulosa	Kuchta & Tan (2005)

expansion played an important role in the formation of a Rapoport effect in North America. We propose that post-glacial range expansion was, in part, a historical contingency based on access to northern landscapes, *not* that species currently occupying post-glacial habitat did so because they possessed novel exaptations (i.e. were 'pre-adapted') for these habitats.

2 | MATERIALS AND METHODS

2.1 | Geographic ranges

We downloaded range maps for temperate North American salamanders (N = 169), 25 of which cross the glacial boundary, from the International Union for the Conservation of Nature (IUCN, 2016). The latitudinal range and latitudinal midpoint of each species were calculated in ArcMap (ESRI). Latitudinal ranges varied from 0.018 to 26.167°, and latitudinal midpoints ranged from 24.267 to 48.687°.

We examined whether there was a correlation between the latitudinal midpoint of a species' range and the latitudinal span of its range. We tested the strength of this correlation by comparing it to a null model built by randomly matching mid-latitudes with latitudinal spans and calculating the correlation coefficient (r); this was repeated 1000 times to form a null distribution of r (Colwell & Hurtt, 1994; Lyons & Willig, 1997). We then tested whether the observed correlation coefficient was greater than 95% of the simulated values. Each simulated range was made by randomly drawing a latitudinal midpoint from the empirical data and matching it with a latitudinal range that was also randomly drawn from the empirical data. Because all species in our dataset are approximately between the latitudes of 25.5° and 57.5°, we treated these as boundaries for the null model; if a simulated species's geographic range crossed either of these latitudes, it was removed before estimating a null value of r, which makes the null model more difficult to reject (Colwell & Hurtt, 1994).

We manipulated latitudinal ranges of species that cross the glacial boundary during the Last Glacial Maximum (Figure 1) by removing parts of the ranges extending north of the glacial boundary. If glacial retreat is important in forming a Rapoport effect, then r should decrease. Note that most species' contemporary ranges do not cross the glacial boundary, so this is a conservative test in that a small fraction of all species' ranges are actually manipulated. Since the glacial boundary was not at a constant latitude (Figure 1), we set three latitudes whereby areas northward would be removed from the ensuing correlation. These latitudinal cut-offs were set at 48.2° in the Northwest, 40.0° south of the Great Lakes and 42.0° for the Northeast (Figure 1). Some species' ranges cross the glacial boundary in multiple places. For instance, the geographic range of Plethodon cinereus crosses the glacial boundary south of the Great Lakes and in the Northeast (Figure S1). In such cases, we removed the smaller latitudinal extent. This approach is conservative because eliminating a smaller portion of the range should be less likely to weaken a correlation that includes all areas north of the glacial boundary.



FIGURE 1 Areas in black indicate the post-glacial areas to which ENMs were transferred. The black and white line indicates the glacial boundary. Species in western North America were transferred to the area to the upper left corner of the map, while species in eastern North America were transferred to the larger area of temperate forest in eastern North America. These areas are temperate forests where at least one species of terrestrial salamander occurs. The glacial boundary was drawn following Lomolino et al. (2017). Red lines indicate the latitude above which species's ranges were reduced when adjusting ranges to remove effects of post-glacial range expansion on Rapoport effects (see Methods for explanation)

We also removed all species with ranges that cross the glacial boundary (25 species) and tested for a Rapoport effect with the hypothesis that the Rapoport effect should be eliminated if post-glacial range expansion creates the Rapoport effect. However, the removal of these species may eliminate a Rapoport effect due to including fewer species. To account for this problem, we calculated the correlation coefficient as described above and compared this to a null distribution of 1000 correlation coefficients computed by removing a random set of 25 species and inferring the relationship between the latitudinal midpoint and the latitudinal span. We conducted a twotailed randomization test to test whether removing the post-glacial colonizing species resulted in a stronger or weaker Rapoport effect.

We pruned the Lissamphibia phylogeny of Pyron (2014a, 2014b) to only include temperate North American salamanders for which there were range data available from the International Union for the Conservation of Nature (IUCN, 2016). We tested for a Rapoport effect using phylogenetic-independent contrasts (Felsenstein, 1985). Note that this dataset is necessarily smaller than the one above (N = 156) because it is limited to species included in the phylogeny. Phylogenetic-independent contrasts were calculated in the R package 'ape' (Paradis et al., 2004). We then took the original data, adjusted latitudinal spans to eliminate areas north of the glacial boundary as previously described, recalculated phylogenetic-independent contrasts and tested for a correlation again. Analyses were repeated for species in ENA and WNA.

2.2 | Ecological niche modelling

We built ecological niche models (ENMs) for 12 species whose ranges are completely south of the glacial boundary and TABLE 2 Sister species pairs based on the phylogeny of Pyron (2014a). Species in the left column have geographic ranges crossing the glacial boundary. The 'Region' column refers to the sister species in the second column. Sample sizes for building ENMs are given in the 'N' column; this number is after spatial thinning. ENMs were built for species in the second column and transferred to the area north of the glacial boundary

North of glacial boundary	Sister species	Region	N
Ambystoma macrodactylum	Ambystoma talpoideum	ENA	229
Notophthalmus viridescens	Notophthalmus perstriatus	ENA	13
Taricha granulosa	Taricha torosa	WNA	236
Plethodon idahoensis	Plethodon vandykei	WNA	14
Plethodon vehiculum	Plethdon dunni	WNA	122
Plethodon dorsalis	Plethodon ventralis	ENA	21
Plethodon cinereus	Plethodon shenandoah	ENA	10
Plethodon electromorphus	Plethodon richmondi	ENA	232
Desmognathus ochrophaeus	Desmognathus orestes	ENA	56
Aneides vagrans	Aneides ferreus	WNA	83

projected their ENMs onto areas north of the glacial boundary. We built ENMs for species whose sister species's range crosses the glacial boundary (Table 2). Using sister species pairs controls for divergence time (e.g. Kozak & Wiens, 2007; Weir & Wheatcroft, 2011), since the time since speciation may influence range size (Paul et al., 2009; Webb & Gaston, 2000). In addition WILEY Journal of Biogeography

to the sister species, we also built ENMs for two widespread species, *Batrachoseps attenuatus* (WNA) and *Plethodon serratus* (ENA). Within their respective regions, each species' contemporary range is south of the glacial boundary during the Last Glacial Maximum, yet each species has a large geographic distribution (Figure S1). In our list of species in Table 2, we included *Aneides vagrans*, though its post-glacial range is a result of recent human introduction, not 'natural' range expansion (Jackman, 1998).

The area available for projecting ENMs north of the glacial boundary was limited to temperate forest north of the glacial boundary in which at least one species of salamander is currently found (Figure 1). By limiting the total area in which we projected ENMs, we hoped to reduce inferences from spuriously over-predicting models. Two separate areas of projection were made: one for species in WNA and a second for species in ENA (Figure 1).

For occurrence data, we combined data from GBIF (GBIF.org, 2020), VertNet (vertnet.org, 2020), the Arctos Database (arctos. database.museum, 2020) and georeferenced samples from Kozak and Wiens (2010). We eliminated duplicate occurrences within raster cells and centred points within raster cells using the 'trimdupes. by.raster' function in the R package 'ENMTools' (Warren et al., 2021). We thinned occurrence records to improve ENM performance (Boria et al., 2014; Fourcade et al., 2014) by maintaining that records must be at least 2 km from each other using the R package 'spThin' (Aiello-Lammens et al., 2015). Due to few clustered occurrences in the range of *Plethodon shenandoah*, we did not spatially thin its occurrence data (N = 10 unthinned versus N = 3 thinned).

For building ENMs, we used two sets of environmental variables from Hijmans et al. (2005) at a resolution of 30 arcseconds (~1 km²). We conducted analyses using two sets of environmental variables because we did not know the exact variables that circumscribe the niche of terrestrial salamanders. Concordance of results between environmental datasets may increase confidence in inferences. First we used seven environmental variables relevant for terrestrial salamander habitat: annual mean temperature, mean diurnal range (the difference of the mean of monthly maximum temperature and monthly minimum temperature), temperature seasonality (standard deviation of temperature), temperature annual range, annual precipitation, precipitation seasonality (coefficient of variation) and precipitation of the wettest guarter. Next we used six environmental variables that are uncorrelated in North America (Kozak & Wiens, 2006): mean diurnal range, maximum temperature of the warmest quarter, minimum temperature of the coldest month, precipitation seasonality and precipitation of the driest quarter. Bioclimatic data were measured from weather stations (Hijmans et al., 2005), but as we mentioned, the salamanders considered spend most of their time below the ground. However, above-ground activity is necessary for feeding and reproduction, and the above-ground climate influences the thermal and hydric state of the soil. Thus, fossorial behaviour can buffer salamanders from major climatic variation, but they are still subject to climatic variation via surface activity, which is required to maintain positive fitness (Gifford & Kozak, 2012).

We used Maxent (Phillips et al., 2006), which performs well under a wide range of circumstances (Elith et al., 2006; Qiao et al., 2015; Valavi et al., 2021). To avoid overfitting, Maxent models were calibrated on an area including the species' IUCN range map plus a 15 km buffer area. A range of models were built by varying the regularization multiplier (a value that is inversely related to model complexity via penalizing additional parameters) from 0.5 to 2.0 in increments of 0.5 and varying the functional responses that Maxent can model using the following possible combinations: linear+quadratic, linear+quadratic+hinge, linear+quadratic+hinge+product and linear+quadratic+hinge+product+threshold. Maxent models were evaluated with the area under the curve (AUC) using the block method (Radosavljevic & Anderson, 2014) in the R package 'ENMeval' (Kass et al., 2021; Muscarella et al., 2014). ENMeval reports the average $\mathsf{AUC}_{\mathsf{TEST}}$ value from the block method. For each species and set of environmental variables, we picked one model setting that maximized AUC_{TEST} and another model setting that had the lowest AICc (Warren & Seifert, 2011). Given two environmental datasets and two criteria for choosing models, we chose four ENMs per species (Table 3).

After model settings were selected for each species, we built ENMs using all available occurrences and projected these models north of the glacial boundary. Accurately transferring ENMs is difficult under many circumstances (Elith et al., 2010; Qiao et al., 2019), so we used different methods (extrapolation, clamping, both or neither). The 'extrapolation' setting in Maxent allows an ENM's predictions to change outside the range of environmental variables on which the ENM is calibrated. The 'clamping' setting causes habitat suitability to be constant as environmental variables change outside the model calibration range. Maxent allows both features to be turned off, which means that models will have zero suitability in environments outside the calibration range. Exploring model predictions with and without clamping or extrapolation is an important way to evaluate the sensitivity of the ENM to calibration conditions. While Merow et al. (2013) noted the importance of such a sensitivity analysis, it is often ignored in studies that transfer ENMs. After transferring, we thresholded ENMs by the equal training sensitivity and specificity value to create binary maps (Liu et al., 2005, Freeman & Moisen, 2008). Among commonly used ENM thresholds, the equal sensitivity and specificity value is frequently the highest and is thus conservative for modelling potential habitat.

2.3 | Model transferability: An empirical test

In the previous section, we transferred ENMs but could not evaluate the accuracy of these projections (Bohl et al., 2019). We tested our ability to predict suitable post-glacial habitat by building ENMs for native populations of *A. vagrans* and testing the ENMs using invasive populations of *A. vagrans* north of the glacial boundary (Jackman, 1998). We built ENMs in the native range of *A. vagrans*, buffered by 15 km (N = 83), and optimal model settings were chosen using the block design and either AUC or AICc and either the

TABLE 3 Results of transferring ENMs

Variable set	Model criterion	Transfer method	Ambystoma talpoideum	Aneides ferreus	Batrachoseps attenuatus	Desmognathus orestes	Notophthalmus perstriatus	Plethodon dunni	Plethodon richmondi	Plethodon serratus	Plethodon shenandoah	Plethodon vandykei	Plethodon ventralis	Taricha torosa
Six variables	AIC	C&E	+	+	-	+	-	+	+	+	+	+	+	+
		С	-	+	-	-	-	+	+	+	-	+	-	+
		E	-	+	+	-	-	+	+	+	+	+	+	+
		NA	-	+	-	-	-	+	+	+	-	+	-	+
	AUCc	C&E	±	+	-	+	-	+	+	+	±	+	-	+
		С	-	+	-	-	-	+	+	+	-	+	-	+
		Е	±	+	-	-	+	+	+	+	-	+	-	+
		NA	-	+	-	-	-	+	+	+	-	+	-	+
Seven variables	AICc	C&E	-	-	-	+	-	+	+	+	±	+	+	+
		С	-	+	-	-	-	+	+	+	-	+	-	+
		Е	-	+	-	-	-	+	+	+	±	+	+	+
		NA	-	+	-	-	-	+	+	+	-	+	-	+
	AUC	C&E	+	-	-	+	-	+	+	+	±	-	-	+
		С	-	+	-	-	-	+	+	+	-	-	-	+
		E	+	+	-	-	-	+	+	+	±	+	-	+
		NA	-	+	-	-	-	+	+	+	-	-	-	+

Note: Minus signs (-) indicate no suitable habitat in post-glacial areas, while plus signs (+) indicate suitable habitat in post-glacial areas. In several cases, all post-glacial areas were considered suitable, which is represented as a bold, underlined plus sign (\pm). In the 'Transfer method' column, 'C' refers to clamping, 'E' refers to extrapolation, 'C&E' refers to both used simultaneously and 'NA' refers to neither extrapolation nor clamping being used.

five-variable dataset or seven-variable dataset. Under optimal model settings, we transferred ENMs to the invasive range (N = 29). To evaluate our models' abilities to predict populations in the invasive range, we thresholded ENMs using the equal training sensitivity and specificity, and we calculated the omission error (the number of false negatives relative to the total number of testing occurrences; Anderson et al., 2003). All other modelling details are identical to those described for other species in this study. We calculated omission error under each set of bioclimatic variables using different model criteria (AICc versus AUC), and transferring with or without clamping or extrapolation (resulting in 16 transferred ENMs of A. *vagrans*).

2.4 | Competing hypotheses

We tested the climatic variability hypothesis by comparing the average annual temperature range for every sister species pair listed in Table 2 using the Wilcoxon test. For species crossing the glacial boundary, we thinned occurrences to 2 km as with their sister species.

To consider the contribution of the relative area of habitat (i.e. 'niche position'), we simulated species' ranges, such that each species could tolerate mean annual temperature in intervals of 4°C, from a mean of 6–18°C; all species tolerated mean annual precipitation between 1000 and 5000 mm. We used uniform distributions to define environmental tolerances, so all simulated ENMs were binary. The temperature values represent a realistic mean and range for many salamanders of North America. From each simulated range, we eliminated slivers (polygons <10 pixels large) and separated all remaining disjunct polygons as separate species' ranges. From these

simulated ranges, we calculated a correlation between the latitudinal midpoint of suitable habitat and latitudinal extent of suitable habitat. Simulations used bioclim data at a resolution of 10 arcminutes and were implemented in the R package 'virtualspecies' (Leroy et al., 2016).

All statistical analyses, besides those using Maxent, were conducted in R (R Core Team, 2021).

3 | RESULTS

3.1 | Geographic correlations

Using the full set of range data (N = 169), the latitudinal midpoint and latitudinal range were positively correlated, consistent with a Rapoport effect (p < 0.001, r = 0.33; Figure 2). When we removed areas north of the glacial boundary, the correlation between latitudinal midpoint and latitudinal range from the full dataset remained significant but the association weakened (p < 0.001, r = 0.28). The observed correlation coefficient was greater than the simulated correlation coefficients generated by randomly matching latitudinal midpoints and latitudinal spans (p < 0.001; Figure S2), allowing us to reject the hypothesis that a Rapoport effect could be generated by chance alone. We found evidence for a Rapoport effect using the subset of data for which we calculated phylogenetic-independent contrasts on latitudinal midpoints and latitudinal range sizes (p < 0.001, r = 0.37, N = 156). When we removed areas north of the glacial boundary and recalculated phylogenetic-independent contrasts, the correlation remained significant but was weaker (p = 0.005, r = 0.23). When post-glacial colonizers were completely removed from the correlation analysis, we found no relationship

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FIGURE 2 The first column represents all species for which we had data in temperate North America, the second column contains analyses of species in WNA and the third column contains analyses of species in ENA. (First row) In all cases, there is a positive relationship between latitudinal midpoint and latitudinal span of species' ranges, indicating a Rapoport effect. (Middle row) These relationships are significant but weaker when post-glacial areas are removed from species' ranges. (Bottom row) The Rapoport effect is not found when post-glacial habitat colonist species are removed

between latitudinal span and latitudinal midpoint (p = 0.064, r = 0.15, N = 144). When we compared this correlation coefficient to our null distribution of correlation coefficients generated by randomly removing the same number of species, the Rapoport effect was significantly weaker (p = 0.014; Figure S2), supporting the role of the northernmost species in shaping a Rapoport effect.

When analysing only species in WNA (N = 49), we found evidence of a Rapoport effect using latitudinal midpoints and latitudinal ranges without phylogenetic-independent contrasts (p < 0.001, r = 0.48); this was essentially unchanged when post-glacial areas were removed (p = 0.001, r = 0.45). We rejected the null model where species' latitudinal ranges and midpoints were randomly

matched (p < 0.001). When using phylogenetic-independent contrasts on latitudinal midpoint and latitudinal range, a Rapoport effect was evident (p = 0.018, r = 0.35); this relationship was not found when post-glacial areas were removed (p = 0.078, r = 0.27). When post-glacial colonizers were removed from the correlation analysis, the relationship between latitudinal span and latitudinal midpoint was not recovered (p = 0.060, r = 0.30, N = 42). When we compared this correlation coefficient to a null distribution, the Rapoport effect was not significantly weaker than the one generated by randomly removing the same number of species (p = 0.079).

In analysing only species in ENA (N = 120), we found evidence of a Rapoport effect without phylogenetic-independent contrasts (p < 0.001, r = 0.35); this changed slightly when post-glacial areas were removed (p = 0.002, r = 0.28). We rejected the null model where species' latitudinal ranges and midpoints were randomly matched (p = 0.001). When using phylogenetic-independent contrasts, a Rapoport effect was detected (p < 0.001, r = 0.41); this relationship became weaker when post-glacial areas were removed (p = 0.016, r = 0.23). When post-glacial colonizers were completely removed from the correlation analysis, the relationship between latitudinal span and latitudinal midpoint disappeared (p = 0.146, r = 0.15, N = 102). When we compared this correlation coefficient to a null distribution of correlation coefficients generated by randomly removing the same number of species, the Rapoport effect was weaker than the one generated by randomly removing species (p = 0.024).

3.2 | Ecological niche modelling

After finding optimal Maxent settings using AICc or AUC, we projected ENMs to post-glacial areas (Table 3). Results were highly variable across model settings; all species were found to have suitable habitat under at least one model condition. In WNA, *Plethodon dunni* and *Taricha torosa* were predicted to have suitable post-glacial habitat under all model conditions. In ENA, *P. richmondi* and *P. serratus* were predicted to have suitable post-glacial habitions. Visual inspection of the multivariate environmental similarity surface (Elith et al., 2010) indicated that all ENMs were transferred to regions with non-analogue climates, though the spatial extent of non-analogue climates varied by species.

When predicting the invasive range of Aneides vagrans, omission errors were minimized when clamping and extrapolation were used together for model transfer (Table 4). ENMs built using the sevenvariable dataset transferred well when AICc was used for model selection, but when the Six-variable dataset was used, AUC was a better model criterion (Table 4). None of the ENMs of *A. vagrans* predicted suitable habitat everywhere in the invasive range (5.4–63.6% of the invasive range), indicating that the ENMs did not minimize omission errors by predicting suitable habitat everywhere.

Maxent output from all ENMs are available on DRYAD.

3.3 | Competing hypotheses

When we compared temperature seasonality among sister species, we found that eight of 10 post-glacial species inhabited environments with greater annual temperature ranges than their more southern sister species (p < 0.05). The temperature seasonality experienced by A. *vagrans* in its native range was not significantly different from that of A. *ferreus* (p = 0.36), and the difference was not significant for *P. dunni* and *P. vehiculum* (p = 0.54). All other comparisons resulted in post-glacial species inhabiting environments with greater annual temperature ranges than their more southern sister species (p < 0.05).

TABLE 4 Omission error rates from ENMs of *Aneides vagrans* built on its native range and transferred to its invasive range. Lower values indicate fewer populations incorrectly omitted from the thresholded ENMs

	Six variabl	es	Seven variables			
Transfer method	AICc	AUC	AICc	AUC		
C&E	0.28	0	0	0		
С	0.64	0.52	0.52	0.52		
E	0.28	0	0	0.4		
NA	0.64	0.52	0.52	0.52		

Note: 'Six variables' versus 'Seven variables' refers to which set of bioclimatic variables were used to build the ENM. The AICc and AUC headings indicate the model criterion for ENMs in those columns. In the 'Transfer method' column, 'C' refers to clamping, 'E' refers to extrapolation, 'C&E' refers to both used simultaneously and 'NA' refers to neither extrapolation nor clamping being used. Values in each column represent omission error rates given the transfer method, set of variables and model selection criterion.

Using virtual species, we found that the area of different thermal environments could not generate Rapoport effects in either WNA (p = 0.320, r = 0.23) or ENA (p = 0.290, r = -0.26).

4 | DISCUSSION

We found evidence of a Rapoport effect in North American salamanders and an effect of post-glacial colonization on the formation of a Rapoport effect. ENMs indicated that southern species could persist in post-glacial habitats, suggesting that their absence is caused by dispersal or biotic limitation. There was stronger evidence for the role of post-glacial range expansion in ENA, given that the correlation weakened more when removing post-glacial areas. Furthermore, removing post-glacial colonizers from WNA did not eliminate the Rapoport effect more than eliminating a random sample of species from WNA (Figure S2). Ultimately few species' ranges cross the glacial boundary (as expected because species richness declines with latitude), so removing post-glacial areas resulted in modest changes in the strength of correlation, though it always decreased. All 12 species for which we built ENMs were predicted to have suitable habitat north of the glacial boundary in at least one model setting, and four species had suitable habitat north of the glacial boundary under all settings (Table 3). We have shown that dispersal is important in the formation of the Rapoport effect in North American salamanders. However, post-glacial range expansion is not the sole cause of the Rapoport effect, as ecophysiology also contributes to range size variation (Clay & Gifford, 2018; Markle, 2015).

ENMs were extrapolated onto novel conditions, which may compromise accuracy (Qiao et al., 2019). However, analyses of *Aneides vagrans* with extrapolation lowered omission rates, indicating that extrapolation can improve model predictions. Even if one assumes that our inferences are compromised due to extrapolation, we still estimated that six species have suitable habitat north of the glacial

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boundary when no extrapolation was allowed, and four of those species had suitable habitat under all conditions investigated. We note that four species for which we built ENMs had low sample sizes (<30; Table 2). While this may decrease ENM performance, Maxent can perform well with less than 10 samples (Sheth et al., 2014). Under several model settings, *P. shenandoah* was found to have suitable habitat in post-glacial areas (Table 3), which is surprising given that its range is small and restricted to three adjacent mountaintops, suggestive of an environmental specialist (Figure S1). However, field observations and experiments have found that *P. shenandoah* is an environmental generalist that is limited to marginal, talus habitat by competition with *P. cinereus* (Jaeger, 1971a, 1971b).

When a species's distribution is shaped by dispersal limitation, ENMs tend to underestimate the range of ecological conditions that constitute suitable habitat. Yet, ENMs tend to successfully recognize poor habitat when geographic distributions are shaped by dispersal limitation (Qiao et al., 2015). Thus, ENMs should be conservative in identifying potential habitat north of the glacial boundary. Maxent relies on pseudo-absence (or background) points, meaning that models are sensitive to the calibration area over which the ENM is built, resulting in overfitted models when the calibration area is large (Barve et al., 2011), which we addressed by buffering range maps by only 15 km. In our model selection procedure, we used the block method. Traditional model testing procedures (e.g. k-folds cross-validation) do not spatially segregate training and testing data, which is problematic because spatial autocorrelation of environmental variables will inflate measures of model support (Hijmans, 2012; Radosavljevic & Anderson, 2014; Wenger & Olden, 2012). The block method encourages selection of ENMs that transfer well since the model is evaluated based on its ability to differentiate presences from pseudoabsences for spatially structured data (Radosavljevic & Anderson, 2014). Several important studies have suggested that ENMs can exhibit strong statistical support because of spatial autocorrelation while failing to capture ecological relationships between distribution and environment (Beale et al., 2008; Fourcade et al., 2018; Journé et al., 2020). Nonetheless, our analysis of A. vagrans selected models that predicted its invasive range, suggesting that predictions of post-glacial habitat using ENMs were valid for other species in this study as well.

Abiotic environments are spatially autocorrelated, so it is unsurprising that species crossing the glacial boundary (and that have large geographic ranges) experience a wider range of environments compared to their sister species that are restricted further to the south. In an analysis of salamanders of eastern North America, Markle (2015) found that critical thermal minima are positively correlated with the minimum temperature experienced, though most variance in this relationship went unexplained ($R^2 = 0.46$). Markle (2015) found that while minimum temperature experienced ranged by approximately 7°C, the critical thermal minimum varied by less than 2.5°C. The difference indicates a mismatch between the ambient temperature and that which is actually experienced by salamanders. This mismatch is likely made possible through fossoriality and the insulating effects of forests.

Our findings conflict with Whitton et al. (2012). They conducted a global analysis of amphibians and found evidence for a Rapoport effect in the northern hemisphere only. They used a data mining approach in which regression models were constructed to find a relationship between range size and a set of environmental predictors, including a binary variable of recently being glaciated (or not). However, they did not directly model range size as a response variable, but instead used the median range size for all species occurring within grid cells at a 96.5 \times 96.5 km resolution. They found little evidence for glacial retreat affecting species' present-day range sizes. We suggest that they may not have detected an effect of glaciation on present-day range size because (1) some of the variance explained by glacial history was explained by their categorical predictors of biogeographic realm and biome, (2) they did not directly model species' range sizes in their regression or (3) because they used area as opposed to latitudinal span.

We suggest that salamander dispersal should be further investigated to assess how animal movement may scale up to geographic ranges and macroecological patterns. As an example, the fully terrestrial salamander Plethodon cinereus shows limited dispersal and small home ranges of several square metres (Mathis, 1991). Yet, when Marsh et al. (2004) manipulated suitable habitat by adding cover objects (important for providing a refuge from heat and low humidity), they found that P. cinereus dispersed tens of metres. The added cover objects were quickly colonized, suggesting that P. cinereus can disperse rapidly into an altered environment, despite their usual limited dispersal. Although the experiment of Marsh et al. (2004) was conducted at a relatively small spatial extent, it helps to bridge the gap between the apparent low dispersal of P. cinereus (Mathis, 1991) and its rapid range expansion since the Last Glacial Maximum (Radomski et al., 2020). This is consistent with the observation that post-Pleistocene rates of dispersal were much greater than contemporary rates, likely facilitated by new expanses of habitat opening up and the evolution of enhanced dispersal along a shifting range edge (Clark et al., 1998). Besides 'local' dispersal experiments, macroecological tools, such as general dissimilarity modelling, can be used to indirectly infer the impact of dispersal limitation on contemporary diversity (Fitzpatrick et al., 2013).

We found positive correlations between median latitude and latitudinal span (Rapoport effects) in North American salamanders. Removing post-glacial areas weakened such correlations, consistent with a role for post-glacial range expansion in forming Rapoport effects. ENMs generally supported the hypothesis that many southern species are capable of existing in post-glacial habitat, but that dispersal limitation has prevented post-glacial range expansion. We did not find support for niche position explaining Rapoport effects, but we could not rule out the climatic variability hypothesis. In total, this supports the hypothesis that post-glacial range expansion is an important component of latitudinal variation in geographic range size in temperate species. The work presented here is correlative, based on geographic distributions and environmental data. This has the advantage of including many species over a large spatial extent. However, we suggest two additional ways of testing for the importance of post-glacial dispersal in generating a Rapoport effect. The first is to produce more biologically meaningful models of species' distributions from physiology, demography and movement (Kearney & Porter, 2009). Since such mechanistic models give an indication of energy budgets or population sizes, their interpretation is clearer than that of a correlative model, as thresholds of zero energy or abundance demarcate suitable from unsuitable habitat (e.g. Gifford & Kozak, 2012). The second way forward is from experimental manipulation of species' environments, where measures of demographic or physiological performance via transplant experiments may indicate if species can persist in habitat outside their geographic range.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Latitudinal range and latitudinal midpoint data are available in supplementary Table 1. Georeferenced data used for ecological niche modelling are available in supplementary Table 2. DOIs for GBIF are as follows: https://doi.org/10.15468/dl.wk3pio (Aneides vagrans), https://doi.org/10.15468/dl.6m4f6c (Desmognathus orestes), https://doi.org/10.15468/dl.tvdqvu (Notophthalmus perstriatus), and https://doi.org/10.15468/dl.chu4tn (Plethodon cinereus). There were no DOIs for VertNet or Arctos downloads. Range maps are available through the IUCN (https://www.iucnredlist.org/resources/spatial-data-download) Climatic data are available through the Worldclim website (https://www.worldclim.org/data/v1.4/worldclim14.html). The phylogeny (Pyron, 2014b) is available on DRYAD (https://datadryad. org/stash/dataset/doi:10.5061/dryad.jm453). Maxent model comparisons from ENMevaluate, R scripts, and Maxent output are available on Dryad (https://doi.org/10.5061/dryad.nzs7h44ss).

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SUPPORTING INFORMATION

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