



Abiotic and biotic constraints across reptile and amphibian ranges

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A long-standing macroecological hypothesis posits that species range limits are primarily determined by abiotic factors (e.g. climate) at poleward boundaries and biotic factors (e.g. competition) at equatorward boundaries. Using correlative environmental niche models we test this hypothesis for 214 amphibian and reptile species endemic to the United States (U.S.). As predicted, we find a closer association between climate and northern (poleward) range limits than at southern (equatorward) boundaries. However when we separately analyze amphibians and reptiles, only reptiles show the predicted pattern; amphibians show the opposite pattern. We also find more unoccupied, but climatically habitable, area beyond species' southern range limits for reptiles but not amphibians. This suggests that factors other than climate limit distributions at southern boundaries for reptiles and at northern boundaries for amphibians. These contrasting results suggest that even in the same biogeographic regions, this macroecological hypothesis does not hold. Further studies should investigate, preferably via experimental approaches, the proximate and ultimate mechanisms responsible for range limits.

The form, cause, and consequences of range limits have long been central themes of study in ecology, biogeography, and evolutionary biology (Kirkpatrick and Barton 1997, Gaston 2003, 2009, Holt 2003, Kubisch et al. 2014). Many ecological and evolutionary factors are known to limit species distributions (Kirkpatrick and Barton 1997, Holt 2003, Kubisch et al. 2014), including climate, dispersal barriers, species interactions, and the degree of evolutionary potential or adaptive evolution at range margins (Gaston 2003, 2009, Holt 2003, Kubisch et al. 2014, Svenning et al. 2014). Although both abiotic and biotic factors have been identified as range determinants, the relative strength of these factors across geographic space remains unclear (Parmesan et al. 2005, Gaston 2009, Sexton et al. 2009, Cahill et al. 2014). Specifically, we evaluate if the factors limiting poleward versus equatorward range boundaries differ by assaying the correspondence between predictions made with climate and actual range boundaries.

Climate is often the dominant abiotic force shaping species distributions at broad spatial scales (Hutchinson 1918, MacArthur 1972, Root 1988a, Gaston 2003, Buckley and Jetz 2007, Sexton et al. 2009). Distributions may be constrained by temperature or moisture requirements. For example, Root (1988b) found that northern range limits of 60% of wintering bird species in North America coincided with isoclines of minimum daily temperatures for January. Repasky (1991) detected an association between body size and the geographic location of northern range margins within bird species that winter in North America. Specifically, species of all body sizes occur in areas in lowest temperatures

yet few large passerines of North America have northern range limits in warm southerly areas (Repasky 1991). The close association between climate and distribution is especially apparent in ectotherms due to the tight link between environmental and body temperatures (Brattstrom 1968, Buckley and Jetz 2007, Sunday et al. 2011, 2012). Climate may also prevent successful completion of life cycles or limit reproduction (reviewed by Gaston 2003).

Species interactions also shape species distributions in a wide variety of species (Gross and Price 2000, Gaston 2003, Case et al. 2005, Holt and Barfield 2009, Price and Kirkpatrick 2009, Wiens 2011, Kubisch et al. 2014, Svenning et al. 2014). In a recent review of 111 transplant experiments, Hargreaves et al. (2013) found biotic interactions were important limiting factors at warmer, species-rich range boundaries. Biotic interactions can influence range limits in multiple ways. For example, interspecific aggression has been found to constrain the ranges of Neotropical birds (Jankowski et al. 2010). On the other hand, enemy release in plants can promote range expansion (Lakeman-Fraser and Ewers 2013). Despite few investigations into the role of biotic interactions and range limits, especially in comparison to studies on abiotic mechanisms (Cahill et al. 2014), the imprint of biotic interactions can sometimes be detected at large spatial scales (Heikkinen et al. 2007, Cunningham et al. 2009). For instance, the effects of species interactions on community assembly can be discerned at spatial scales much larger than the scale of individual territories in Danish avifauna (Gotelli et al. 2010). However, at broad geographic scales, the spatial signature of local competitive interactions

may not be detectable (Gotelli et al. 2010, Araújo and Rozenfeld 2014).

One longstanding macroecological hypothesis addressing the role of climate and species interactions in limiting range distributions was put forth by Darwin (1859) and later refined by MacArthur (1972). The hypothesis, called here the north-south hypothesis (NSH), posits that abiotic conditions (climate) determine a species' poleward range limit and biotic conditions (species interactions) determine a species' equatorward range limit (Dobzhansky 1950, MacArthur 1972, Brown et al. 1996, Gaston 2003, Parmesan et al. 2005, reviewed by Schemske et al. 2009). A large survey of the literature found that in 77% of the cases, biotic interactions were statistically stronger in the tropics, and in no case were biotic interactions more important at higher latitudes than at lower latitudes (Schemske et al. 2009). Further, a recent review of over a hundred studies supported the role of biotic interactions in limiting ranges at lower latitudes and elevations (Hargreaves et al. 2013). However controversy remains about making generalizations based on the NSH because these large reviews focused on broad comparisons across different ecosystems (e.g. temperate vs tropical systems). It is less clear whether there is a difference in the relative strength of abiotic and biotic factors across a single species' range. For example, a recent review of 105 studies that examined the cause of range limits at low elevations and latitudes of 178 plant and animal species across terrestrial and aquatic environments suggests the NSH pattern may not hold (Cahill et al. 2014). Cahill et al. (2014) found that at these warm-edge limits, most (61%) studies found evidence that temperature was at least partly responsible for the range boundary. However, few studies explicitly examined both abiotic and biotic factors and when they did biotic factors were not more important (Cahill et al. 2014).

We use correlative environmental niche models (ENM) (Maxent, Phillips and Dudik 2008) to investigate the relative role of climate in determining the northern versus southern range limits of amphibian and reptile species in the United States (U.S.). If climate primarily determines northern range limits (in the Northern Hemisphere), as predicted by the NSH, then the northern range boundary should align closely with the boundary predicted by niche models (Fig. 1). However, if species interactions constrain the southern range limit for a species, then range limits predicted solely on climate should extend beyond the currently observed southern range boundary (Fig. 1). Put another way, climate-only ENMs should perform poorly at southern range limits and better at northern range limits.

Material and methods

Focal taxa and defining actual and predicted range distributions

We used amphibian and reptile species ($n = 340$), the majority of which are endemic to the U.S., of the orders Anura, Caudata, and Squamata. However, the distribution of some species did extend across the political borders of the U.S. In those cases, the entire distribution of the species was used in the analysis. After excluding species with southern



Figure 1. Hypothetical observed range (hatched–dark gray) and predicted range (shaded–light gray). If climate drives northern range limits, then the alignment between observed and predicted ranges should be close at the northern edge. If species interactions drive southern range limits, then a predicted range, based solely on climate, should predict beyond the southern edge of the observed range limit. Offset between observed and predicted ranges will result in northern or southern misalignment of the geographic centroids of the observed (closed circle) and predicted ranges (open circle).

range limits that bordered the Gulf of Mexico a physical, hard constraint on their distribution, 214 species were used in the analysis.

We downloaded range maps for all species from NatureServe (<<http://natureserve.org>>). We predicted ranges based on climate using Maxent ver. 3.2.1 (Phillips et al. 2004). Point locality information was downloaded from HerpNet (<www.herpnet.org>) and GBIF (<www.gbif.org>) in 2008. Because taxonomy is not static, we were careful to include only points for species that reflected the most up-to-date systematic knowledge, especially in complexes under recent revision (e.g. *Plethodon glutinosus* complex). All locality information was georeferenced using GEOLocate ver. 2.0. Points defined as having low precision from GEOLocate or occurring beyond observed range limits were excluded from analysis. We used the 19 WorldClim bioclimatic layers, which are biologically relevant temperature and precipitation layers at 2.5 minute resolution for 1950–2000 to build ENMs (Hijmans et al. 2005). Twenty percent of the locality data for each species was used for training. Default values in Maxent were used for all other parameters. We used a fixed threshold value of 50% to define the range boundary (Liu et al. 2005). A fixed threshold was chosen to ensure that estimates of over- and underprediction were comparable across species. ENMs were projected using an equal area projection prior to statistical analysis.

Statistical analyses

We examined the offset of the predicted range from the actual range by calculating the length and angle of a vector extending from the observed geometric centroid of the range to that of the centroid of the predicted ENM range. We used circular statistics (R library circular) to estimate mean

bearing of the vector between the centroid of the observed and predicted ranges. We tested whether the distributions of bearings differed from null (uniform) expectations using Kuiper's and Watson's tests of uniformity (Pewsey et al. 2013). We tested for differences in bearings between subsets of species using a circular analysis of variance (ANOVA) and an Equal Kappa test for homogeneity of concentrations. We compared the ratio of predicted to actual range area (pixels) north (Pn) or south (Ps) of the observed geometric centroids. We used an Albers equal area conic projection ('aea' projection in R library sp) for both observed and predicted distributions to ensure comparability of areas. If the ratio of habitat predicted to be suitable in the south and north (Ps/Pn) is greater than one, the model overpredicts in the south more than the north as would be predicted from the NSH where species interactions eliminate otherwise climatically suitable areas from the actual species range. Analyses were conducted using R ver. 3.0.

We also examined factors that could bias our overall patterns including range size (quartiles based on range area), which roughly corresponds to environmental tolerance breadth (Slatyer et al. 2013), and biogeographic regions (i.e. eastern and western U.S.), which differ in precipitation gradients, orientation of mountain ranges, and historical biogeography. Species from formerly glaciated areas could be still expanding northward. Thus, we conducted analyses excluding species with observed range centroids north of 37°N, the southernmost extent of most past glaciers in North America. We also tested the potential for bias by excluding species with ranges abutting the Gulf of Mexico. Finally, for each species, we used the jackknife of variable importance feature in Maxent to identify the climate variable with the greatest contribution to the ENM.

Results

We predicted that northern range boundaries would be more closely aligned with predicted ENM ranges based solely on climate and that we would find more overprediction beyond the actual southern boundary. Thus, we predicted a southern shift of the predicted ENM range center compared to the center of the observed range. We found that across all 214 species, the vector extending from the centroid of the observed range to that of the predicted range pointed south with a compass bearing of 150.14° (95% bootstrapped confidence interval based on the von Mises circular normal distribution: 102.8 and 182.4°) (Fig. 2a; Supplementary material Appendix 1, Table A1, A2). The observed distribution of bearings differs significantly from a uniform distribution (Kuiper's test of uniformity: $V = 3.02$; Watson's test for circular uniformity: $U^2 = 0.65$, for von Mises Distribution: $U^2 = 0.42$).

When we analyzed amphibians and reptiles separately, we found that the bearings of the vectors differed significantly (Equal Kappa test for homogeneity of concentrations $\chi^2 = 11.3$, $DF = 3$, $p = 0.01$, Circular ANOVA $\chi^2_{(1, 214)} = 9.89$, $DF = 1$, $p = 0.001$; Table 1; Fig. 2b, c). The predicted range center was south of the actual range for reptiles (bearing = 158.5°) but north (bearing = 7.58°) for amphibians. The mean distance between observed and predicted range

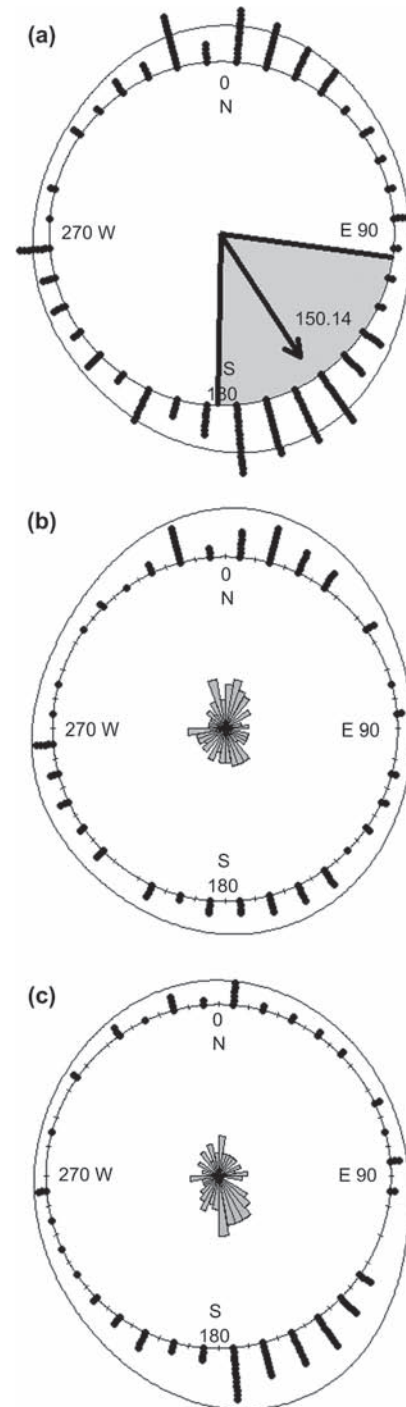


Figure 2. (a) Circular plot showing overall mean angular difference between actual and predicted centroids of ranges for all species. Individual mean angles binned in 10° intervals for all species are shown externally. The overall mean angle, 95% confidence intervals (shaded) and density line are shown. (b) Circular plot for mean angular difference between actual and predicted ranges for amphibians, overall mean 7.58°, individual mean angles externally binned in 10° intervals and density line shown. Inner rose diagram illustrating the frequency of angular offset between predicted and actual ranges, binned in 10° intervals for amphibians. (c) Circular plot for mean angular difference between actual and predicted ranges for reptiles, overall mean 158.50°, individual mean angles externally binned in 10° intervals and density line shown. Inner rose diagram illustrating the frequency of angular offset between predicted and actual ranges, binned in 10° intervals for reptiles.

Table 1. The directional offsets and linear distances between the centroid of the observed and predicted range (Offset vector) was south overall. The direction of offset was north for amphibians and south for reptiles (Circular ANOVA $\chi^2_{(1, 214)} = 9.89$, $DF = 1$, $p = 0.001$). We examined the ratio of predicted to actual range area to the south (Ps) and north (Pn) of the actual range centroid. Ps/Pn > 1 indicates greater overprediction or less underprediction in the south. Species with ranges abutting the Gulf of Mexico were excluded from the overall analysis; thus, the individual data were not included in calculation of the overall statistics shown.

Taxon (with n)	Offset vector (degrees) (95% CI)	Distance (km) mean \pm SD	Ps/Pn mean \pm SD
Overall (n = 214)	150.14 (102.83, 182.19)	214.48 \pm 246.35	1.06 \pm 0.44
Eastern species (n = 54)	214.71 (230.85, -47.33)	225.72 \pm 321.88	1.02 \pm 0.51
Western species (n = 160)	133.88 (85.65, 161.40)	210.62 \pm 216.11	1.073 \pm 0.42
Amphibians (n = 106)	7.58 (-114.25, 166.97)	232.34 \pm 303.76	1.09 \pm 0.52
Reptiles (n = 108)	158.50 (139.40, 174.92)	196.9 \pm 173.47	1.02 \pm 0.35

centroids was 232 km for amphibians and 196 km for reptiles (Table 1).

As predicted from the NSH, we found a tendency for greater overprediction of suitable habitat to the south of the observed centroid relative to that to the north, and this accounts for the offset of the centroids noted above. The ratio of the area of suitable habitat in the south and north (Ps/Pn) was close, but slightly and significantly greater than one (1.062 ± 0.060 SD; t -test $t = 2.05$, $DF = 213$, $p = 0.04$), due to a skewed distribution with a tail representing some amphibians and reptile species with more dramatic overpredictions to the south (Fig. 3). Neither group is independently driving this result.

Overall, there was no effect of range size on the bearings (Circular ANOVA $\chi^2_{(3, 214)} = 4.28$, $p = 0.233$), and excluding species in formerly glaciated regions did not alter our findings: the overall prediction was still south (162.67°). Nor did the inclusion of species with ranges abutting the Gulf of Mexico alter the overall prediction which remained

south (135.38°). Both values are within the 95% confidence interval for the prediction that included all species (Table 1). We also found no difference in bearings between biogeographic regions (Equal Kappa test for homogeneity of concentrations $\chi^2 = 0.001$, $DF = 1$, $p = 0.97$).

The climate variables of most importance in generating ENMs differed significantly between amphibians and reptiles ($\chi^2_{(1, 18)} = 92.65$, $p < 0.000$; Fig. 4). For amphibians, the climate variables of importance were mean temperature of coldest quarter, precipitation seasonality (coefficient of variation), and precipitation of driest quarter. For reptiles, the climate variables of greatest importance were precipitation of warmest quarter, mean diurnal range, and mean temperature of coldest quarter. In general, amphibian distribution models are being strongly driven by precipitation, whereas temperature is a relatively stronger driver of reptile models.

Discussion

For reptiles, our results concur with predictions based on the NSH: we detected the potential for range expansion to the south but not to the north. For amphibians, we found the opposite pattern. What might account for these results?

A comparison of thermal tolerance limits and observed distributions found that terrestrial ectotherms (reptiles, amphibians, and insects) underfill their potential range at the warm boundary but overfill their potential range at the cold boundary (Sunday et al. 2012). This finding is potentially consistent with biotic factors constraining warm range limits. We consistently predicted that reptiles should expand beyond their current southern range limits. A recent study found cold tolerance, rather than heat tolerance, shifts steadily with latitude in terrestrial ectotherms (Sunday et al. 2014) which may contribute to the strong match of predicted and observed distributions at northern range limits in reptiles. Further, the mean temperature of the coldest quarter often contributed to the predictions in reptile distribution models suggesting cold temperatures may be a strong limiting factor at northern range limits for this group. For example, the northern range limit of the painted turtle *Chrysemys picta* occurs when temperatures fall below the thermal tolerance of the species (St Clair and Gregory 1990). Our analysis exclusively considered adults. Juvenile life stages may face more severe thermal limits (Angilletta et al. 2013), which could account for predicting that species could inhabit warmer environments than they are found in.

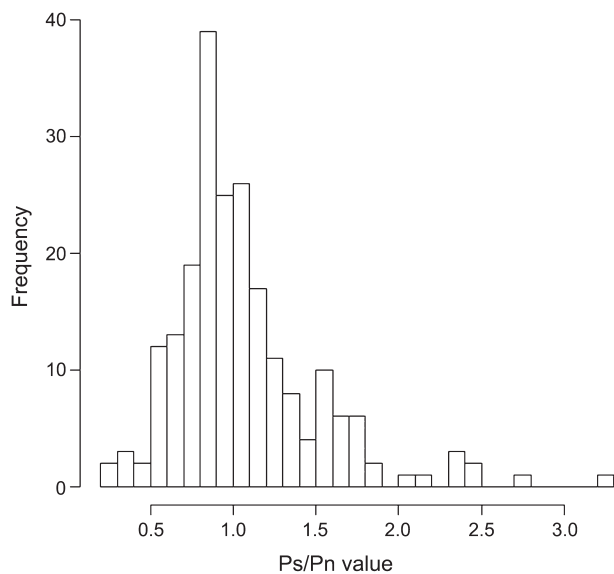


Figure 3. The ratio of predicted to actual range area north (Pn) or south (Ps) of the observed geometric centroids differed across species. If the ratio of habitat predicted to be suitable in the south and north (Ps/Pn) is greater than one, the model overpredicts in the south more than the north. Overall the long tail corresponding to Ps/Pn values greater than 1 indicates greater overprediction or less underprediction in the south, consistent with the hypothesis of more unoccupied but climatically suitable habitat in the south.

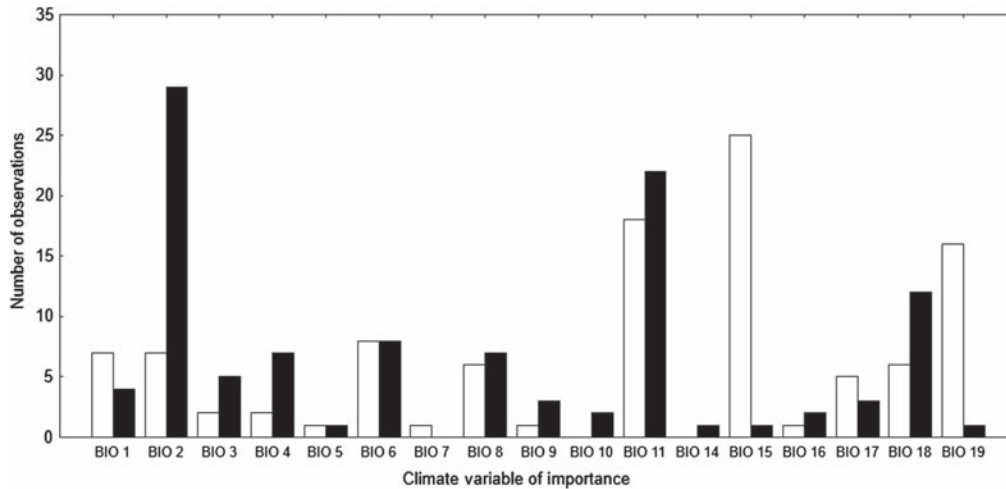


Figure 4. The climate variables of most importance in generating ecological niche models differed between amphibians (white bars) and reptiles (black bars). The variables examined are as follows: BIO 1 = annual mean temperature, BIO 2 = mean diurnal range (mean of monthly (max temp – min temp)), BIO 3 = isothermality ($\#2/\#7$) ($\times 100$), BIO 4 = temperature seasonality (standard deviation $\times 100$), BIO 5 = max temperature of warmest month, BIO 6 = min temperature of coldest month, BIO 7 = temperature annual range ($\#5-\#6$), BIO 8 = mean temperature of wettest quarter, BIO 9 = mean temperature of driest quarter, BIO 10 = mean temperature of warmest quarter, BIO 11 = mean temperature of coldest quarter, BIO 12 = annual precipitation, BIO 13 = precipitation of wettest month, BIO 14 = precipitation of driest month, BIO 15 = precipitation seasonality (coefficient of variation), BIO 16 = precipitation of wettest quarter, BIO 17 = precipitation of driest quarter, BIO 18 = precipitation of warmest quarter, BIO 19 = precipitation of coldest quarter.

One way to mitigate thermal stress in otherwise suitable habitat is via behavioral responses; thus, thermal limits on activity times and energetics, rather than acute thermal limits, may constrain range limits of ectotherms (Buckley et al. 2012). For example, at range limits where behavioral responses are required due to thermal tolerance limit, biotic interactions could potentially limit such responses. Biotic interactions such as competition for suitable basking sites, nesting areas, and refuges could impede an individual's ability to thermoregulate behaviorally. The combined effects of climatic conditions, such as temperature, and biotic interactions could result in a poor fit of reptile models at southern range margins.

Alternatively, the observed overprediction beyond southern limits of reptiles may be due to the signature of historic climate. Reptile richness in the United States peaks in the southwest. During the last glacial maximum temperatures were 5°C lower than present temperatures in the southwestern U.S. (Stute et al. 1992). Thus, distribution patterns would differ from contemporary patterns, assuming that species ranges are not at equilibrium with contemporary climates. A recent study of European herpetofauna found strong evidence that historic climate contributed to contemporary richness patterns in Europe (Araújo et al. 2008). Furthermore, evidence supports a differential impact of historic climate on species distributions. For example, narrow ranging species are not as likely as wide ranging species to be at equilibrium with current climate conditions (Webb and Gaston 2000, Araújo et al. 2008). Poor model fit at southern range limits of reptiles could be the result of nonequilibrium between all species and contemporary climate.

Amphibians showed the opposite pattern of reptiles by consistently predicting beyond northern range limits. What could account for this? In general, most aspects of amphibian physiology are temperature-dependent. For

example, Popescu and Gibbs (2009) determined that pond occupancy by mink frogs *Rana septentrionalis* at the species' southern range margin was limited by water temperature during embryo development. Additionally, a recent study investigating thermal tolerances across 697 ectotherm and 227 endotherm and 1817 plant species suggests that tolerance to heat is generally conserved across lineages while tolerances to cold varies within and between species (Araújo et al. 2013). For amphibians, variability in tolerance to cold could account for the imperfect match between observed and predicted ranges at northern limits. Mean temperature of coldest quarter was one of the three most important variables in the ENMs of amphibians. Conversely, if heat tolerances are largely conserved, as suggested by Araújo et al. (2013), this could explain the close alignment of predicted and observed ranges at southern margins.

However, unlike reptiles, amphibians are constrained in their means to thermoregulate because of the permeability of their skin (reviewed by Wells 2007). Thus, amphibians have a moisture requirement that differs from reptiles which could be driving the differing patterns of overprediction. This could account for the difference in the relative importance of various climate variables between the two groups. For example, precipitation seasonality and precipitation of driest quarter were two climate variables that contributed to amphibian ENMs but not reptile ENMs.

When sufficient moisture is available, amphibians can reduce thermal heat loads by evaporative cooling (Sunday et al. 2014). Conversely, their ability to increase body temperature through basking is severely limited because radiation increases water loss. In general, thermal-safety margins of wet-skinned amphibians increase with latitude (Sunday et al. 2014). This could result in the observed close alignment of predicted and actual southern range limits. Precipitation variables loaded strongly on amphibians ENMs

indicative of water balance contributing to the observed pattern of northern overprediction. The potential for distributions constrained by water balance to differ from expectations based on temperature is highlighted by plants tending to shift their elevational distributions downward as they track shifts in water balance through recent climate warming (Crimmins et al. 2011). Patterns of amphibian richness have also been shown to be influenced by water balance (Rodríguez et al. 2005, Aragón et al. 2010). Although we used 19 climatic variables, the complexity of water balance, temperature, and amphibian physiology may not have been captured.

Other variables, not accounted for in the ENMs, (e.g. topography, geologic features) may be contributing to the amphibian pattern of northern overprediction. For example, amphibian species that have large geographic ranges but only occupy a limited area within their range would likely show overprediction. For example, the eastern hellbender *Cryptobranchus alleganiensis*, common mudpuppy *Necturus maculosus*, and cave salamander *Eurycea lucifuga* have large geographic ranges and showed northern overprediction. Yet, these species require specific habitats, geologic features and suitable aquatic environments (reviewed by Wells 2007) that are not continuously distributed across geographic space. Considering the specific microhabitat requirements of amphibians, we might have overpredicted many amphibian species to the north based on climate (precipitation and temperature requirements) which are actually limited by the distribution of suitable microhabitats. This could especially be true of aquatic and stream dwelling amphibians. Another variable that could drive the pattern of northern overprediction is the number of consecutive days with optimal conditions for amphibian activity. For example, a lack of consecutive warm days for amphibian reproduction, feeding, and larval development beyond observed northern range limits could result in northern overprediction of ENMs based solely on climate. In fact, the number of consecutive warm days are known to limit the northern distribution of amphibian species (Wynne-Edwards 1952) and may not be captured in ENMs based solely on climate. Amphibians might be more sensitive to temperature thresholds because they rely on particular weather patterns to initiate and continue certain behaviors such as migration.

What about biotic interactions, and are there reasons to suspect that reptiles are more susceptible to biotic exclusion than amphibians? As previously mentioned, a number of studies have investigated the role of abiotic factors in setting range limits (Cahill et al. 2014), but only eight species have been tested for the relative importance of both biotic and abiotic factors. This lack of empirical, quantitative studies (but see Cunningham et al. 2009) on the relative strength of species interactions versus abiotic conditions limits our ability to understand the role of biotic interactions in determining species range distributions and shifts due to climate change (Buckley 2014). We know that both amphibians and reptiles respond to competition. Perhaps the best known case of habitat partitioning due to competitive exclusion is that of the Caribbean *Anolis* lizards (reviewed by Losos 2009). Similar patterns have been shown in the southeast Asian *Draco* lizards where interspecific competition has driven habitat and morphological change analogous to that found in *Anolis* (Ord and Klompare 2014). But amphibians also show

responses to biotic interactions. A recent study of *Plethodon* salamanders in the eastern United States, found that competitive interactions are structuring forces in these assemblages (Adams 2007). One study on salamanders used a reciprocal transplant experiment to test whether competition with a heterospecific at the southern range boundary in the slimy salamander *Plethodon glutinosus* affected body condition and survival to a greater degree than competition in the core of the species' range (Cunningham et al. 2009). Overall, the combined effects of climatic conditions at the range boundary and biotic interactions on salamanders were greater at the range boundary versus in the core of the range under more benign climatic conditions. In a separate study investigating elevational limits in montane salamanders, Gifford and Kozak (2012) found that upper elevational limits were set by biotic interactions and lower limits by physiological constraints, opposite of what is predicted by the NSH. Further, at fine spatial scales in the eastern United States, competitive interactions among streamside salamanders of the genus *Desmognathus* influence local distribution patterns; the mere presence of one key species can displace conspecifics from predominately aquatic habitats to less optimal, more terrestrial upland ones (Rissler et al. 2004, reviewed by Wells 2007). In the southern Appalachian Mountains, the geographically widespread redbacked salamander *Plethodon cinereus* prevents the geographic expansion of small, isolated populations of congeners (Highton 1971). Thus, a few studies demonstrate the importance of competition in setting range limits in both reptiles and amphibians.

It is also worth noting that some aspects of the modeling could skew the biological interpretation of our results. For example, ENMs are thought to reflect the realized rather than the fundamental niche because localities implicitly include biotic interactions (Araújo and Guisan 2006, Peterson 2006, Soberón and Nakamura 2009). How this manifests into over or under-filling particular geographic regions that are part of the fundamental niche is unclear, and further physiological and ecological experiments would need to be completed to understand the mechanisms influencing species range dynamics and range limits. Similarly, habitat specialization or adaptation to particular geographic features not included in our models (e.g. geologic substrate) may additionally constrain our estimates of environmental suitability, but we believe these are unlikely to affect the relative comparison of northern vs southern range edges because they are unlikely to occur disproportionately in one region or the other. Finally, our analysis should be robust to limited locality sampling as MAXENT has been found to perform well with sample sizes as low five (Pearson et al. 2007). The steepness of the spatial gradient in climate variables varies geographically (Burrows et al. 2011). However, differences in steepness are relatively minor at the scale of amphibians and reptile ranges and unlikely to influence our results.

Conclusions

The NSH predicts that biotic interactions determine equatorial range boundaries and abiotic factors determine poleward boundaries. Using a correlative modeling approach for reptiles and amphibians in the U.S. we find support

for this general pattern. However, when amphibians and reptiles were analyzed separately, the prediction held only for reptiles. Hence, the NSH might not generally apply even across a set of ectotherms exhibiting many ecological similarities. Understanding the proximate and ultimate mechanisms influencing macroecological patterns, like the NSH, will provide insight into the manner in which physiology, behavior, and biogeography intersect to shape species' distributions. In addition we recommend experiments that measure the relative magnitude of biotic interactions across a species range, and in temperate and tropical systems, as a way to test the NSH.

Acknowledgements – This work was conducted as part of the Species Range Dynamics Working Group supported by the National Center for Ecological Analysis and Synthesis (NCEAS), a Center funded by NSF (grant no. DEB-0553768), the Univ. of California, Santa Barbara, and the State of California, and the National Evolutionary Synthesis Center, a Center funded by the National Science Foundation (grant no. EF-0423641). Thanks to working group members for helpful comments and discussions. This work was supported in part by NSF grants EF-1065638 to LBB. HRC and LJR made equal contributions to the manuscript.

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Supplementary material (Appendix ECOG-01369 at <www.ecography.org/readers/appendix>). Appendix 1.