


Range position and climate sensitivity: The structure of among-population demographic responses to climatic variation

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Abstract

Species' distributions will respond to climate change based on the relationship between local demographic processes and climate and how this relationship varies based on range position. A rarely tested demographic prediction is that populations at the extremes of a species' climate envelope (e.g., populations in areas with the highest mean annual temperature) will be most sensitive to local shifts in climate (i.e., warming). We tested this prediction using a dynamic species distribution model linking demographic rates to variation in temperature and precipitation for wood frogs (*Lithobates sylvaticus*) in North America. Using long-term monitoring data from 746 populations in 27 study areas, we determined how climatic variation affected population growth rates and how these

relationships varied with respect to long-term climate. Some models supported the predicted pattern, with negative effects of extreme summer temperatures in hotter areas and positive effects on recruitment for summer water availability in drier areas. We also found evidence of interacting temperature and precipitation influencing population size, such as extreme heat having less of a negative effect in wetter areas. Other results were contrary to predictions, such as positive effects of summer water availability in wetter parts of the range and positive responses to winter warming especially in milder areas. In general, we found wood frogs were more sensitive to changes in temperature or temperature interacting with precipitation than to changes in precipitation alone. Our results suggest that sensitivity to changes in climate cannot be predicted simply by knowing locations within the species' climate envelope. Many climate processes did not affect population growth rates in the predicted direction based on range position. Processes such as species-interactions, local adaptation, and interactions with the physical landscape likely affect the responses we observed. Our work highlights the need to measure demographic responses to changing climate.

KEYWORDS

bioclimatic envelope model, climate change, *Lithobates sylvaticus*, range shifts, species distribution model, state-space model, wood frog

1 | INTRODUCTION

A persistent theme in ecology is the need to understand the factors that shape and describe species distributions (Gaston, 2009; Grinnell, 1917; MacArthur, 1972; Sexton, McIntyre, Angert, & Rice, 2009). These factors have been touted as a means to understand the conditions that facilitate sustainable populations currently and in the future (Sexton et al., 2009). Species distributions are determined by a spectrum of biotic and abiotic factors that act across varying spatial and temporal scales (Anders & Post, 2006; Sexton et al., 2009). Among abiotic factors, climate is thought to be one of the most important determinants of species occurrence and key to the formation, maintenance, and evolution of species distributions (Araújo & Peterson, 2012; Darwin, 1859; Sexton et al., 2009). Climate may affect species directly via constraints in physiological tolerances, indirectly via its influence on community assemblages and habitats, or by complex interactions of both (Menge & Olson, 1990). Understanding when and where climate constrains species' occurrence is useful in predicting future responses, conserving and managing species in the face of ongoing global climate change (Araújo & Peterson, 2012; Pearson & Dawson, 2003), and identifying areas where other factors aside from climate are more strongly influencing distributions (e.g., biotic interactions; Urban, Zarnetske, & Skelly, 2013).

Attempts to quantify the role climate plays in shaping species distributions frequently rely on the correlation between species occurrence and climate (i.e., a species' bioclimatic envelope; Araújo & Peterson, 2012) to characterize current and to predict future range dynamics. These static distribution modeling approaches are

used to identify broad-scale patterns contributing to range limits (Hijmans & Graham, 2006; Pearson & Dawson, 2003) and to predict range-wide effects of climate change on species distributions (Araújo, Pearson, Thuiller, & Erhard, 2005; Pearson & Dawson, 2003; Thuiller, Lavorel, & Araújo, 2005). Under bioclimatic envelope models, climatic conditions where a species is not observed are assumed to prevent establishment of viable populations and thus are the environmental conditions that set range limits (Araújo & Peterson, 2012). However, these phenomenological models assume (1) species' ranges are in equilibrium with climate conditions and (2) species responses are static across the range (Franklin, 2010; Hijmans & Graham, 2006). These assumptions do not realistically represent the dynamic nature of the physical environment and the species themselves, especially for broadly distributed species (Zurell, Jeltsch, Dormann, & Schröder, 2009). Static models of species responses to climate are insufficient to understand the effect annual climate variation can have on population persistence (Franklin, 2010; Zurell et al., 2009; Oedekoven et al., 2017). Furthermore, the focus on species occurrence data ignores the temporal variation in species responses and the demographic processes that determine how a species will respond to climatic shifts (Merow et al., 2014; Thuiller et al., 2014).

If climate shapes species distributions, changes in climate should have the greatest effect on populations occurring near the climatic extremes (e.g., increased temperature will have the greatest effect on populations in the warmest part of the range; MacArthur, 1972; Hoffman & Parsons, 1997; Parmesan, Root, & Willig, 2000). We test this by measuring sensitivity of demographic responses to climatic variation across the range of the wood frog (*Lithobates sylvaticus*).

Specifically, we define sensitivity as the expected change in annual population growth rate (r) with respect to change in an annual climatic measure (e.g., summer extreme heat). We expect range contractions to occur when populations are lost because growth rate is negative for an extended period of time. Similarly, range expansions may occur when populations are gained because growth rate is positive for an extended period of time. Measuring sensitivity tells us how much growth rate is expected to change with a change in average annual conditions and thus how likely population declines (or expansions) are to occur. We test whether sensitivity of population growth rates to year-to-year variation in climate is stronger at the climatic extremes than at the climatic center of a species range (i.e., the bioclimatic envelope prediction; MacArthur, 1972; Hoffman & Parsons, 1997; Parmesan et al., 2000). Failure to find evidence to support this hypothesis could result from processes such as local adaptation, biotic interactions, and other abiotic variables leading to different patterns in sensitivity to change. Testing this hypothesis requires an understanding of how life history is impacted and thus how demographic rates respond to climatic variation (e.g., the relationship between population growth rate and temporal variation in environmental conditions; Normand, Zimmermann, Schurr, & Lischke, 2014; Ross, Hooten, DeVink, & Koons, 2015; Oedekoven et al., 2017). This approach captures more of the process underlying range shifts rather than simply the observed pattern that previous correlative approaches have used to predict range shifts.

Amphibians make an interesting focal taxon to test the importance of population-level sensitivity to climate variation in range dynamics. Amphibians are expected to be particularly sensitive to the effects of climate due to their physiology and life history (Duellman, 1999; Hutchinson & Dupré, 1992), generally limited dispersal abilities (Beebee, 1996; but see Smith & Green, 2005), and reliance on seasonal precipitation and temperature patterns to create breeding habitats and facilitate movement (Pechmann, Scott, Gibbons, & Semlitsch, 1989; Rittenhouse & Semlitsch, 2007; Urban, Richardson, & Freidenfelds, 2014). Their ecological importance as a link between terrestrial and aquatic systems (Earl & Semlitsch, 2012; Ranvestel, Lips, Pringle, Whiles, & Bixby, 2004) and the decline of even

common species (Adams et al., 2013; Grant et al., 2016; Stuart et al., 2004) make understanding the importance of climate in influencing population-level dynamics important for forecasting future extinction risk. Here, we focus on the demographic responses to climate for a species of pond-breeding frog, the wood frog, whose range extends across much of northern North America (Figure 1).

Using a spatially and temporally rich dataset, we tested the prediction that wood frog populations are most sensitive to annual climatic variation at sites near the climatic extremes of their distribution (Figure 2) and that the species distribution is shaped by the interaction of long-term and annual climate conditions on population growth rates. Population growth rates at sites may have three predicted responses based on their range position. For example, if sensitivity of wood frog populations to variation in temperature differs across the range, we predicted that (1) populations in the colder portion of the range (blue; Figure 2a) would be positively affected by warmer than average annual temperatures, meaning that if warming occurred this could lead to more frequent years of high population growth rates and potential range expansion, (2) populations in the warmer portion of the range (red; Figure 2a) would be negatively affected by warmer than average annual temperatures, meaning that if warming occurred this would lead to more frequent years of low population growth rates and potential range contraction, and (3) populations in the middle of the range (black; Figure 2a) are far from climate extremes (Figure 2b) and annual temperatures would not strongly affect population growth rates. By fitting dynamic models that estimate annual changes in abundance in relation to long-term climate, we can better understand which populations within a species' range are most likely to respond to changing climate.

2 | STUDY SYSTEM AND METHODS

We build on previous static approaches to model bioclimatic determinants of species distributions (e.g., Guisan & Zimmermann, 2000; Hijmans & Graham, 2006) by measuring local demographic responses of populations using a dynamic species distribution model (DSDM).

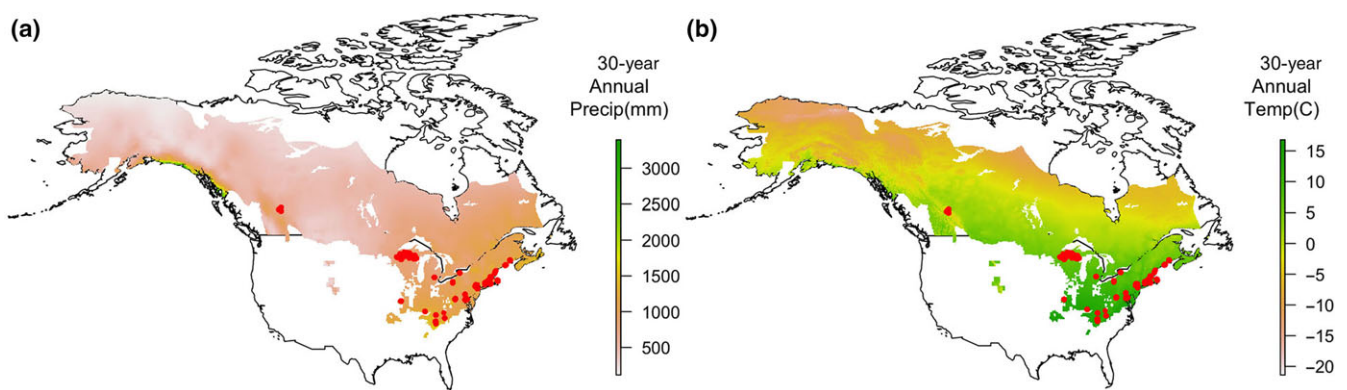


FIGURE 1 The wood frog is a broadly distributed species that spans most of the northeastern United States into Canada and Alaska. Red dots indicate sites where egg mass counts were obtained. Thirty-year annual (a) precipitation and (b) temperature (Hijmans et al., 2005) maps show the broad range of climate conditions this species experiences across its range (IUCN, Conservation International, & NatureServe 2008)

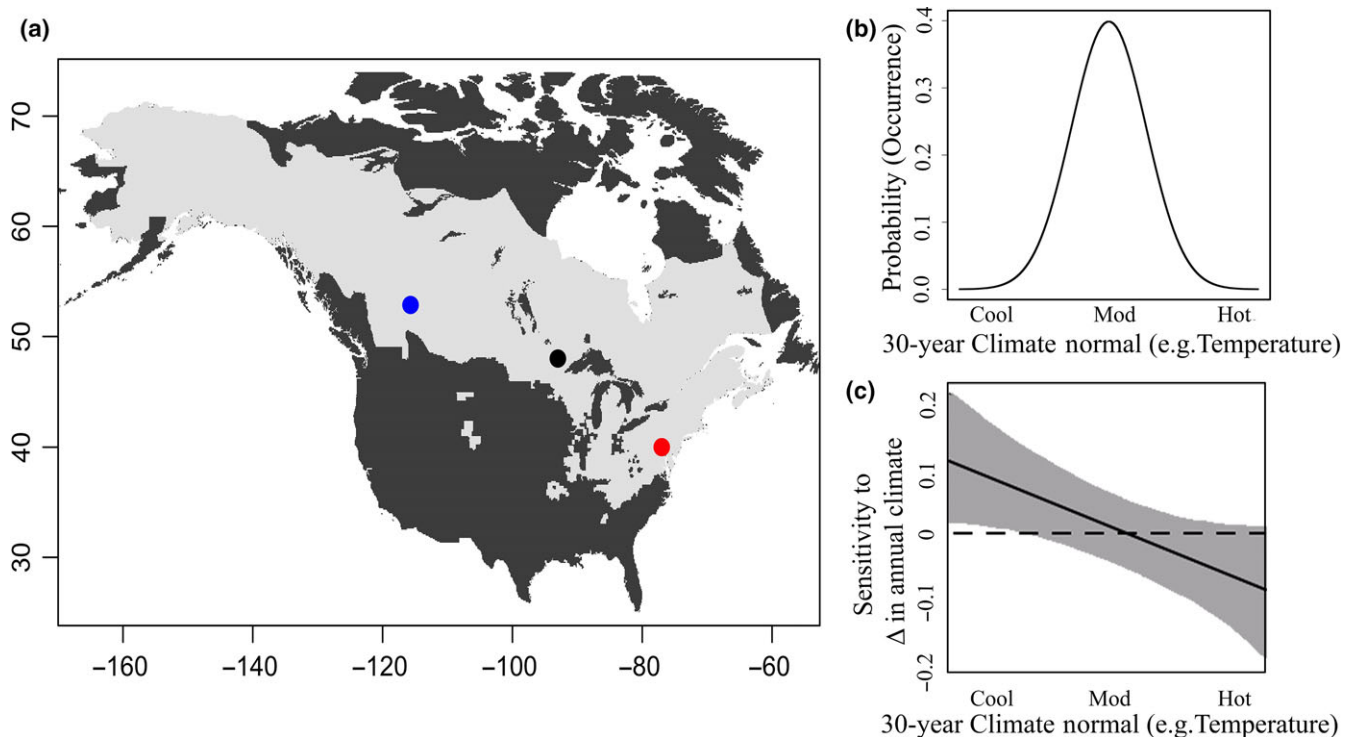


FIGURE 2 (a) The wood frog range (light gray) with an example of a northern (blue), central (black), and southern (red) population. (b) These populations come from different long-term climate normals (e.g., colder to warmer represented by mean 30 year temperature). If wood frog responses are consistent with bioclimatic envelope predictions, the probability of occurrence of wood frog peaks at some optimal temperature and declines in more extreme conditions. (c) Sensitivity of wood frog population growth rates to annual climate variation is predicted to vary by long-term climate (shaded regions are 95% credible intervals). Sensitivity is the expected change in annual population growth rate (r) for a 1 SD increase in annual conditions. We predict (1) populations in colder areas (blue) will be sensitive to warmer than average annual temperatures, leading to higher population growth rates (positive values), (2) populations in hotter areas (red) will be sensitive to warmer than average annual temperatures, leading to lower population growth rates (negative values), and (3) populations in areas far from climate extremes (black) will not be strongly affected by year-to-year deviations in temperature, leading to fairly consistent population growth rates (values around zero)

The DSDM approach allowed us to test the importance of range position in determining responses to climate by measuring local sensitivity of population growth rate to annual variation in climate covariates. Our model takes the form of a hierarchical state-space model (SSM; De Valpine & Hastings, 2002; Buckland, Newman, Thomas, & Koesters, 2004; Kéry & Schaub, 2011; Ross et al., 2015), allowing us to link annual population dynamics across different sites and study areas to annual variation in climatic variables. The results provide a measure of climate sensitivity (i.e., the expected change in mean population growth rates in response to changes in mean climate; Thuiller et al., 2005; Thomas, 2010; Burrows et al., 2014).

2.1 | Study system and life history

Wood frogs occupy an extensive range, occurring from northern Alaska to Canada and south to the south central United States (USGS National Amphibian Atlas, 2014; Figure 1), spanning a large gradient of climatic conditions (Figure 1). Specific elements of the wood frog life history potentially make them sensitive to changes in local climate. Breeding normally occurs in early spring when rising temperatures rouse animals and warm spring rains facilitate

movement into breeding ponds. Adult frogs show high fidelity to breeding sites (Berven & Grudzien, 1990; Green & Bailey, 2015). Breeding generally occurs in a short window of time, anywhere from a few consecutive evenings to a few weeks in length depending on location (E.H.C. Grant et al., personal observations; Crouch & Paton, 2000). Female wood frogs become sexually mature between 2 and 4 years of age and males between 1 and 3 years of age (Berven, 1982a, 2009; Green & Bailey, 2015), and both can live up to 6 years (Redmer & Trauth, 2005). Females typically lay one egg mass during each breeding season, and these egg masses are visually distinct and easy to locate and count (Crouch & Paton, 2000; Grant, Jung, Nichols, & Hines, 2005; Green, Hooten, Grant, & Bailey, 2013). Comparison of census methods show that counts of total egg masses seen per season serves as a suitable proxy for total breeding females per season in a pond (Crouch & Paton, 2000).

2.2 | Field sampling

We used egg mass counts from 746 sites within 27 study areas across the wood frog range (Figure 1; Table S1). A site consisted of a pond or wetland (area ≤ 0.10 –5.24 ha) that was visually sampled

for wood frog egg masses during the peak of each breeding season and where wood frog egg masses were observed at least once during years when surveys occurred. Study areas designate geographic clusters of sites that occurred within relatively close proximity (e.g., within a single national park). Sites were surveyed in multiple years (range = 3–22 years, mean = 10 years; Table S1) with most, but not all, sites being surveyed multiple times within each year. Surveys occurred during or right after peak breeding based on the lack of calling adults and/or no additional egg masses during subsequent surveys, and a maximum count at a site was recorded each breeding season and used as the response variable in analyses. Wood frog egg masses are conspicuous and detection probability is high ($p = 0.96 \pm 0.02$ to 0.95 ± 0.01 ; Grant et al., 2005).

2.3 | Climate covariates

We tested specific predictions with each model about the variation in sensitivity of population growth rates to four climate covariates (Tables 1 and 2; Fig. S1): (1) spring precipitation (*Precip*), (2) summer water availability (*Hydro*), (3) summer extreme heat (*Heat*), and (4) winter severity (*Cold*; Table 1). As our sites cover a broad geographic space, wood frog breeding was not synchronous across all study areas. Months used to calculate *Precip* and *Hydro* were benchmarked to average breeding dates in each study area, reflecting differences in seasonality across the wood frog range (Table S1).

We obtained global climate normal (~1960–1990, 2.5 arc-minutes resolution) RASTERS from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and created 30 year climate normal maps of North America in program R (R Core Team, 2016). We determined 30 year mean annual temperature and precipitation values across North America and within the recorded range of wood frog occurrence (IUCN, Conservation International, NatureServe, 2008) to determine where the species occurs within the broader North American climate space (Figure 3). These values were used to depict the climate space of wood frogs and our sampled populations in Figure 3 but were not used in SSMs. Using PRISM (Daly, Gibson, Taylor, Johnson, & Pasteris, 2002) model output for the United States and weather station data for Canada (Environment Canada, 2015), we calculated annual climate values for *Precip*, *Hydro*, *Heat*, and *Cold* at every site every year for SSMs (Table 1). To model differences in long-term climate, we determined 30 year climate normal (average) values (Hijmans et al., 2005) at every site over the same seasonal periods as our annual climate covariates for SSMs (Table 2; *nmPrecip*, *nmHydro*, *nmHeat*, and *nmCold*). For example, at northern sites we calculated total precipitation values each year for February, March, and April, due to their importance in timing wood frog migrations and pond filling, and averaged them for an annual spring precipitation value (*Precip*). We then averaged total precipitation values over the same months across 30 years to get a long-term climate normal value (*nmPrecip*) that varied across but not within sites. Annual

TABLE 1 Annual climate covariates selected for state-space models based on their potential importance in wood frog breeding and survival. Annual values at each site were used in modeling the effect of annual climate variation on wood frog population growth rates

Covariate	Definition	Ecological importance
<i>Precip</i> = Standardized Precipitation Index 3 months (SPI3) ^a	Deviation of the observed precipitation value from the estimated median for an area calculated over a 3 month period, uses only precipitation values (only inputs to the system)	Values represent the wetness of an area during the start of spring breeding (e.g., February–April) such that a more positive value indicates more precipitation than predicted. Spring precipitation is important as a cue for breeding adults to migrate to ponds and for filling ephemeral ponds ^{b,c}
<i>Hydro</i> = Standardized Precipitation Evapotranspiration Index 3 months (SPEI3) ^d	Deviation of the observed precipitation value from the estimated median for an area calculated over a 3 month period, uses precipitation and evapotranspiration values (inputs and outputs to the system)	Similar to SPI3 but includes the effect of temperature on evapotranspiration rates, considers the way these rates will influence drought severity, and can be used as a measure of water available on the landscape, calculated during summer (e.g., May–July) to get at pond drying. Hydroperiod impacts desiccation risk of tadpoles and can approximate dry summers that increase desiccation risk of adults ^e
<i>Heat</i> = Extreme Heat Index (EHI) ^d	Hottest 10 day average temperature, falls in the late summer for North America	Periods of intense heat increase the risk of heat stress and desiccation while moving between sites ^{c,e}
<i>Cold</i> = Air Freezing Index (AFI) ^d	Cumulative index of freeze severity and frost depth that factors in magnitude and duration of below freezing air temperatures ^f	Though freeze tolerance has been demonstrated in this species, ^g extreme cold temperatures and long durations of cold temperatures may reduce overwinter survival of juveniles and adults ^h

^aNational Climatic Data Center, NOAA (2015).

^bRittenhouse et al. (2009).

^cDavis et al. (in prep).

^dDaly et al. (2002).

^eBrooks (2004).

^fBilotta, Bell, Shepherd, & Arguez (2015).

^gStorey and Storey (1986).

^hO'Connor and Rittenhouse (2016).

TABLE 2 Thirty-year normal climate covariates selected for state-space models to account for long-term effects of climate at a site (i.e., values are constant over time). Their interaction with annual climate covariate values (Table 1) indicated if population growth rates differ in sensitivity across the range. The predicted relationship of the interaction between annual and long-term climate covariates to population growth rates across the wood frog range represents hypotheses from the bioclimatic envelope model

Covariate	Definition	Ecological importance	Predicted annual and long-term interaction (bioclimatic envelope model)
<i>nmPrecip</i> = Precip Normal ^a	30 year mean monthly precipitation over same 3 month period as SPI3	Measure of precipitation and water availability during spring breeding, long-term moisture dynamics of areas	<i>Precip</i> × <i>nmPrecip</i> Negative impact of drier years in drier areas
<i>nmHydro</i> = Hydroperiod Normal ^a	30 year mean monthly precipitation over same 3 month period as SPEI3	Measure of precipitation and water availability during tadpole development, long-term moisture dynamics of areas	<i>Hydro</i> × <i>nmHydro</i> Negative impact of drier years in drier areas
<i>nmHeat</i> = Heat Normal ^a	30 year maximum monthly temperature over similar late summer period as EHI	Measure of extreme heat patterns occurring during the late summer, long-term heat regime	<i>Heat</i> × <i>nmHeat</i> Negative impact of hotter years in hotter areas
<i>nmCold</i> = Cold Normal ^a	30 year minimum monthly temperature over similar mid-winter period as AFI	Measure of winter severity patterns, long-term cold regime	<i>Cold</i> × <i>nmCold</i> Negative impact of colder years in colder areas

^aWorldClim; Hijmans et al. (2005).

climate values were standardized by 33 year (1981–2013) mean and standard deviations at a site. Climate normals were standardized using the mean and standard deviation from the entire extent of the wood frog range.

2.4 | Data analysis

We used SSMs to estimate the effect of annual variation on population growth rate (De Valpine & Hastings, 2002; Buckland et al., 2004; Kéry & Schaub, 2011; Ross et al., 2015). Models were fit in JAGS (Plummer, 2003) and implemented in program R via the R2JAGS package (Su & Yajima, 2015; see Appendix S1 for JAGS code). The hierarchical model allows for estimation of latent state and observation processes characterizing sampled populations while simultaneously accounting for process variation and observation error (Buckland et al., 2004; Kéry & Schaub, 2011). We were interested in understanding how these latent processes were affected by annual climate variation across the range. At the same time, the modeling framework allowed us to account for observation error in counts (e.g., through variable detection, field conditions, variable observer expertise) that was unrelated to the underlying population processes (MacKenzie et al., 2006).

We described changes in wood frog population size (as based on egg mass counts that serve as a proxy for number of breeding females in a season) using an exponential population growth model

$$N_{t+1} = N_t \times e^{r_t}, \quad (1)$$

where population size N_{t+1} is a function of the previous population size N_t (from the previous year) and the per capita annual growth rate (r_t , the exponent of the instantaneous growth rate). Using this as a starting point, we estimated regression coefficients characterizing the relationship between annual weather and the realized growth rate (r_{ti}) for a given year (t) and a given site (i) for each climate hypothesis.

To fit the model, we reformulated Equation (1) by taking the natural logarithm of each side of the equation and indexing all parameters by year (t) and site (i) to capture annual and site-specific variation in the climate covariates and population responses. We added one to all observations to accommodate zeros in the data prior to log transformation.

$$\log(N_{t+1,i}) = \log(N_{ti}) + r_{ti}. \quad (2)$$

The now additive growth rate r_{ti} was modified to include the effects of climate covariates and unexplained annual variation captured using random-error terms. Our goal was to estimate the effect of annual variation in each of our four climate covariates and how those effects differed across the range. We estimated these relationships using a linear model that included the main effects of annual climate values and the climate normal along with the interaction of the two (Table 3). The model took the form of:

$$r_{ti} = \beta_1 \times \text{Annual Climate}_{ti} + \beta_2 \times \text{Climate Normal}_i + \beta_3 \times \text{Annual Climate}_{ti} \times \text{Climate Normal}_i + \delta_i + \varepsilon_{ti}. \quad (3)$$

The model allowed us to determine sensitivity, defined as the expected change in annual population growth rate (r) for a 1 SD increase in annual conditions, to long-term climate normal conditions. Specifically, the interaction term allowed us to quantify the amount of change in population growth rates given an annual shift in climate in respect to the climatic range position in which a population exists. We included a random effect for site-level differences, $\delta_i \sim \text{Normal}(0, \sigma_{\text{Site}}^2)$. This effect served as the local site-level intercept for growth rate, which we expected to vary around a mean value of 0. We included a second random-error component for additional annual variation in growth rate not explained by the climate covariates, $\varepsilon_{ti} \sim \text{Normal}(0, \sigma_{\text{proc}}^2)$. To account for observation error in counts that was not explained by the population-level state processes, we assumed that the log observed count of egg masses for

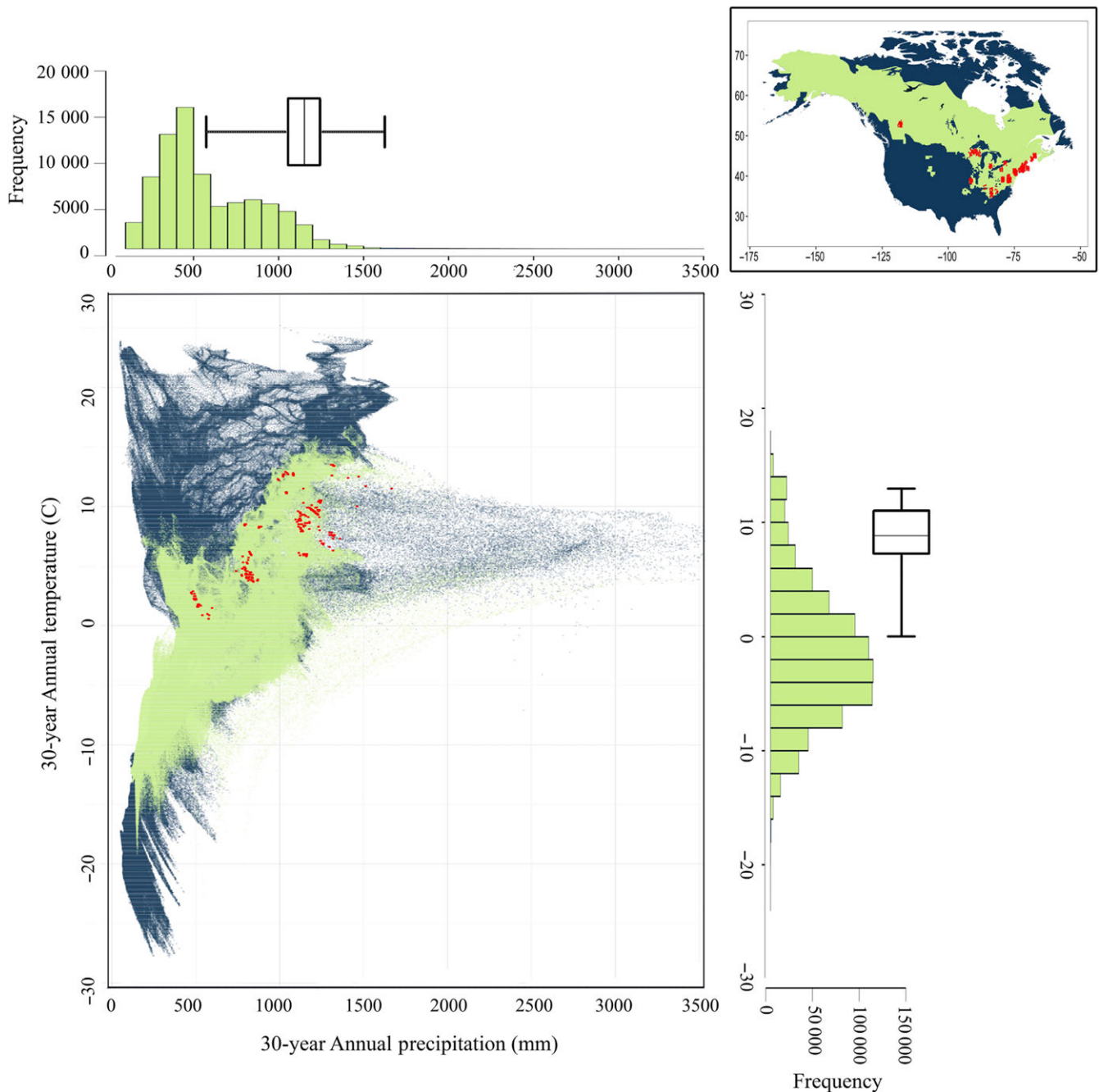


FIGURE 3 The climate space [based on 30 year mean annual temperature (°C) and precipitation values (mm)] that encompasses North America (dark blue), the wood frog range (light green), and our sites (red). Points on the scatterplot represent all temperature by precipitation raster cell values where wood frogs occur (light green) and do not occur (dark blue), with our sites in red. Precipitation values were truncated at 3,500 mm for visualization purposes. Histograms represent frequencies of these same 30 year annual precipitation (top) and temperature (right) values in just the wood frog range. Boxplots of precipitation and temperature values from our sites show the minimum, median, maximum, and 25th and 75th quartiles (box)

that site and year, y_{ti} , is given by $y_{ti} \sim \text{Normal}(\log[N_{ti}], \sigma_{\text{obs}}^2)$. It was also necessary to estimate a starting population size for each site. We used a prior value of $\log(N_{1i}) \sim \text{Normal}(0, 100)$.

We used vague priors for random effect variance components (σ_{obs}^2 , σ_{proc}^2) with uniform distributions bounded between 0 and 5. For σ_{Site}^2 , we used a uniform prior bounded between 0 and 0.2 to facilitate convergence. Priors for all regression coefficients were

$\beta_k \sim \text{Normal}(0, 100)$. We ran three parallel chains for 50,000 iterations each and discarded the first 1,000 iterations as burn-in to allow for model convergence. Model convergence was determined visually from traceplots and Gelman Rubin statistics ($\hat{R} < 1.05$; Gelman & Rubin, 1992).

We predicted that climate covariates could have both immediate and lagged effects on annual growth rate (r_{ti} ; Fig. S1). We predicted

that covariates that disproportionately impact adult survival and season-to-season variation in breeding would lead to changes in growth rate in the same year. In the case where we expected a covariate to impact the survival of eggs and tadpoles in a wetland and thus the number of potential recruits from a cohort, these were predicted to lead to changes in growth rates after a 2 year lag. Female wood frogs take approximately 2 years to reach sexual maturity in our study sites (e.g., lowland populations; Berven, 1982a, 2009; Green & Bailey, 2015). Therefore, the effects of reproductive failure (e.g., desiccation of tadpoles in a dry year) on growth rates would not be evident in counts of egg masses in the year immediately following these suboptimal conditions. We hypothesized that annual *Precip* values affect movement of adult animals and the opportunity for successful oviposition (i.e., pond filling), with low *Precip* values resulting in fewer egg masses laid and thus reduced recruitment 2 years later. *Hydro* values reflect desiccation risk for developing tadpoles (realized as altered recruitment 2 years later) and also drier summer conditions that can decrease adult survival during foraging or return to overwintering sites. *Heat* and *Cold* values reflect late summer dryness and overwintering cold stress expected to impact adults. While any number of time lag combinations and effects are possible, we fit the model (Equation 3) focusing on these key periods due to their biological importance and support in the literature (Table 1).

We were also interested in how water availability and temperature may interact to explain variation in climate sensitivity. We expected that years of low precipitation (*Precip*) would have a greater negative effect in sites with higher mean annual summer temperatures (e.g., hotter areas; *nmHeat*) as increased water on the landscape may help keep permeable amphibian skin moist and lessen desiccation risk (Köhler et al., 2011; Rittenhouse, Semlitsch, & Thompson, 2009). Similarly, we expected reduced winter severity (*Cold*) and its indirect effect on water availability and pond filling in the spring to be greater in areas that receive less spring precipitation

(e.g., drier areas; *nmPrecip*). We tested for these effects by including the interaction of different annual and long-term climate covariates (e.g., *Precip* × *nmCold*, *Hydro* × *nmHeat*; Table 3). Annual covariates included the same time lags as previously discussed. Models with both temperature and precipitation included all annual and long-term covariates for each climate measure and an additional two interaction terms allowing annual and long-term covariates to interact (Table 3). This means a total of eight models testing climate hypotheses (Tables 1 and 2) were run. None of the selected climate covariates were strongly correlated ($|r| < 0.4$).

When fitting models, we tested for goodness of fit using a posterior-predictive check to test whether observed variability in counts was consistent with expected variation. We calculated observed variance in our data for each of the sites and determined if on average variance was less than or greater than the predicted variance of simulated data based on our model. We report the proportion of the time that the observed variance was greater than the predicted variance, with the expectation that if the model fits the data well we expect this proportion to be 0.5.

In addition, we were interested in estimating the overall expected rate of change in wood frog population growth rates, dr/dt , based on our estimated climate relationships. Expected change is a function of the local sensitivity to each of our climate covariates, dr/dX , as measured in our models as well as the rate of change in mean climate over that time period, dX/dt , where:

$$\frac{dr}{dt} = \frac{dr}{dX} \frac{dX}{dt}.$$

We calculated rate of change in each of our climate variables at each of our sites using linear regression where year was the predictor variable and annual values of each of our climate variables over a 30 year period from 1984 to 2013 were our response variables. We mapped these to geographic and climate

TABLE 3 All candidate state-space models investigated for modeling wood frog egg mass counts. Each main model consists of the annual climate covariate (*Precip*, *Hydro*, *Heat*, *Cold*), the respective long-term climate normal (*nmPrecip*, *nmHydro*, *nmHeat*, *nmCold*), and the interaction between each annual and long-term covariate. Combination models are those with additional crossed interactions between annual climate covariates and long-term climate normals representing a different climate component (e.g., *Hydro* × *nmHeat* investigates the interaction between annual summer precipitation by long-term late summer maximum temperatures). The random effects of site (δ_i) and observation error (ϵ_{ti}) were included in all models

Model name	Parameters
<i>Precip</i> (2 year lag)	$\beta_1(Precip_{2\text{ year}}) + \beta_2(nmPrecip) + \beta_3(Precip_{2\text{ year}} \times nmPrecip) + \delta_i + \epsilon_{ti}$
<i>Hydro</i>	$\beta_1(Hydro) + \beta_2(nmHydro) + \beta_3(Hydro \times nmHydro) + \delta_i + \epsilon_{ti}$
<i>Hydro</i> (2 year lag)	$\beta_1(Hydro_{2\text{ year}}) + \beta_2(nmHydro) + \beta_3(Hydro_{2\text{ year}} \times nmHydro) + \delta_i + \epsilon_{ti}$
<i>Heat</i>	$\beta_1(Heat) + \beta_2(nmHeat) + \beta_3(Heat \times nmHeat) + \delta_i + \epsilon_{ti}$
<i>Cold</i>	$\beta_1(Cold) + \beta_2(nmCold) + \beta_3(Cold \times nmCold) + \delta_i + \epsilon_{ti}$
<i>Precip</i> (2 year lag) and <i>Cold</i> by long-term climate	$\beta_1(Precip_{2\text{ year}}) + \beta_2(nmPrecip) + \beta_3(Precip_{2\text{ year}} \times nmPrecip) + \beta_4(Cold) + \beta_5(nmCold) + \beta_6(Cold \times nmCold) + \beta_7(Precip_{2\text{ year}} \times nmCold) + \beta_8(Cold \times nmPrecip) + \delta_i + \epsilon_{ti}$
<i>Hydro</i> and <i>Heat</i> by long-term climate	$\beta_1(Hydro) + \beta_2(nmHydro) + \beta_3(Hydro \times nmHydro) + \beta_4(Heat) + \beta_5(nmHeat) + \beta_6(Heat \times nmHeat) + \beta_7(Hydro \times nmHeat) + \beta_8(Heat \times nmHydro) + \delta_i + \epsilon_{ti}$
<i>Hydro</i> (2 year lag) and <i>Heat</i> by long-term climate	$\beta_1(Hydro_{2\text{ year}}) + \beta_2(nmHydro) + \beta_3(Hydro_{2\text{ year}} \times nmHydro) + \beta_4(Heat) + \beta_5(nmHeat) + \beta_6(Heat \times nmHeat) + \beta_7(Hydro_{2\text{ year}} \times nmHeat) + \beta_8(Heat \times nmHydro) + \delta_i + \epsilon_{ti}$

TABLE 4 Parameter estimates from the four main climate covariate models. *Precip*, *Hydro*, *Heat*, and *Cold* represent annual climate values. *nmPrecip*, *nmHydro*, *nmHeat*, and *nmCold* are the long-term (~30 years) climate normal values. Interaction terms of annual and normal values (e.g., *Precip* × *nmPrecip*) represent the effect of an annual climate value by different long-term climate. *SD* is the standard deviation of a parameter estimate, and $q_{0.025-0.975}$ represents 2.5th, 50th, and 97.5th quartile values

Parameter	Mean	SD	$q_{0.025}$	$q_{0.500}$	$q_{0.975}$
Model: <i>Precip</i>					
<i>Precip</i> (2 year lag)	−0.0840	0.0370	−0.155	−0.0840	−0.0120
<i>nmPrecip</i>	4.00e-03	4.00e-03	−4.00e-03	4.00e-03	0.0130
<i>Precip</i> (2 year lag) × <i>nmPrecip</i>	4.00e-03	0.0140	−0.0240	4.00e-04	0.0320
Models: <i>Hydro</i>					
<i>Hydro</i>	0.0533	0.0387	−0.0229	0.0534	0.129
<i>nmHydro</i>	−0.0137	5.44e-03	−0.0243	−0.0137	−2.98e-03
<i>Hydro</i> × <i>nmHydro</i>	0.0732	0.0244	0.0255	0.0732	0.121
<i>Hydro</i> (2 year lag)	0.0925	0.0415	0.0111	0.0924	0.174
<i>nmHydro</i>	−7.21e-03	5.47e-03	−0.0179	−7.22e-03	3.57e-03
<i>Hydro</i> (2 year lag) × <i>nmHydro</i>	−0.0605	0.0253	−0.110	−0.0605	−0.0109
Model: <i>Heat</i>					
<i>Heat</i>	0.340	0.0670	0.208	0.340	0.471
<i>nmHeat</i>	7.50e-03	5.46e-03	−3.12e-03	7.51e-03	0.0183
<i>Heat</i> × <i>nmHeat</i>	−0.266	0.0383	−0.341	−0.266	−0.191
Model: <i>Cold</i>					
<i>Cold</i>	−0.438	0.117	−0.666	−0.438	−0.209
<i>nmCold</i>	0.0115	4.81e-03	2.09e-03	0.0115	0.0210
<i>Cold</i> × <i>nmCold</i>	0.258	0.0580	0.145	0.259	0.372

space to highlight areas where climate may currently be altering the wood frog distribution.

3 | RESULTS

Sites spanned a >23 degree range in latitude and >50 degree range in longitude from North Carolina to Jasper National Park, Alberta, Canada. Study areas fell into 16 different states, one administrative subdivision (Washington, DC) and one Canadian province (Alberta; Figure 1). Our data show good geographic coverage along the wood frog's southern and easternmost range limit but are restricted in geographic coverage in the northern and westernmost portions of the wood frog range. This was reflected in our coverage in climate space (Figure 3), with best coverage in the portion of the range with warmer temperatures and higher precipitation. Therefore, we limit the presentation of results and their interpretation to only the sampled portion of the wood frog range. In addition, support for models was judged by whether credible intervals of parameter estimates overlapped zero, and we have limited our presentation of results to those models with the strongest support and thus credible intervals for interaction terms that did not overlap. Our posterior-predictive check values for each of our models were between 0.493 and 0.541, indicating that our models did a good job of capturing actual variation in growth rates.

Our first three models tested the effect of moisture on population growth rates, with the first focused on spring precipitation and the second and third focused on late summer water availability. Contrary to our predictions, we found a negative relationship between

Precip and wood frog population growth rates across all areas 2 years later (Table 4; Figure 4a; Fig. S2). The relationship of increased annual *Hydro* values to wood frog population growth rates differed depending on if a time lag was incorporated (Table 4; Figure 4b,c; Fig. S2). The same-year effect of *Hydro* was dependent on long-term climate, with populations in wetter areas responding most positively to wetter annual conditions as compared to those in drier areas (Figure 4b). When incorporating a 2-year time lag, increased values of *Hydro* were positively associated with growth rates only in drier areas (Figure 4c; Table 4), agreeing with our bioclimatic envelope predictions of increased sensitivity to water availability in drier portions of the range.

Our next two models focused on the effect of extreme heat and cold severity on population growth rates. The relationship between increased values of *Heat* and wood frog population growth rates (Table 4) depended on long-term climate. Years with hotter summer temperatures had higher population growth rates in areas with cooler summer climates. However, there was a negative association between warmer summers and population growth in areas with hotter summer climates (Figure 4d; Fig. S2). This agrees with our bioclimatic envelope prediction, where we expect population growth rate to be most sensitive to warming in the warmest portion of the range. The relationship of *Cold* to population growth rates showed increased growth rates associated with milder winters across all areas (Table 4) with the most positive association in areas with milder winter climates (Figure 4e; Fig. S2).

Finally, we examined how precipitation and temperature interacted to affect population growth rates. We found that the 2-year lag effect of annual variation in spring precipitation did not depend

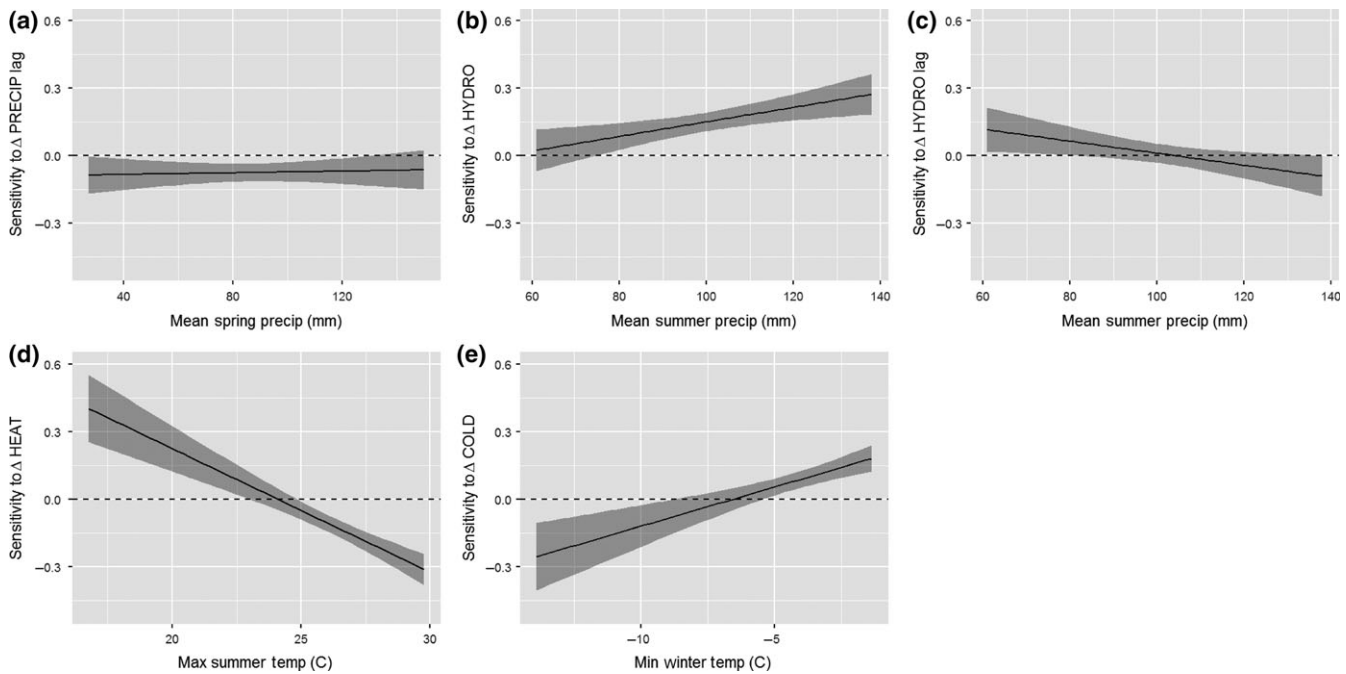


FIGURE 4 We estimated how sensitivity of wood frog population growth rates to annual climate variation changed with respect to long-term climate differences (shaded regions are 95% credible intervals). Sensitivity is the expected change in annual population growth rate (r) for a 1 SD increase in annual conditions (y-axis). Long-term differences in mean climate are calculated using 30 year climate normals for conditions during the same portion of the year that annual covariates are measured (x-axis; Tables 1 and 2) at our sampled sites. (a) Annual wood frog population growth rate 2 years later responded negatively to spring precipitation (PRECIP lag) across all areas, (b) annual wood frog population growth rate responded positively to years with more summer water availability (HYDRO) in areas where long-term average summer precipitation was higher (>50 mm), (c) annual wood frog population growth rate 2 years later responded negatively to years with more summer water availability (HYDRO lag) in areas where long-term average summer precipitation was higher (>105 mm) and positively in years where long-term averages were lower (<105 mm), (d) annual wood frog population growth rate responded negatively to extreme summer temperatures (HEAT) in areas where long-term average extreme temperature was higher ($>24^{\circ}\text{C}$) and positively where long-term averages were lower ($<24^{\circ}\text{C}$), (e) annual wood frog population growth rate responded positively to increased winter severity (COLD) in areas where long-term average minimum temperature was milder ($>-6.25^{\circ}\text{C}$) and negatively where long-term averages were colder ($<-6.25^{\circ}\text{C}$)

on long-term winter climate ($Precip \times nmCold$; Table 5; Figure 5a; Fig. S2), and the effect of annual variation in winter severity did not vary significantly by long-term spring precipitation ($Cold \times nmPrecip$; Table 5; Fig. S2).

We found that the effect of summer water availability in the current year did not differ by long-term summer heat ($Hydro \times nmHeat$; Table 6; Figure 5c; Fig. S2). However, the effect of warmer summers differed between drier and wetter areas. Hotter summer

temperatures had a positive relationship with population growth rates in wetter areas but negatively impacted growth rates in drier areas ($Heat \times nmHydro$; Figure 5d; Fig. S2). We found a positive relationship between increased summer water availability and wood frog growth rates 2 years later in areas with cooler summer temperatures but a negative relationship in areas with hotter summer temperatures (Table 6; Figure 5e; Fig. S2). The interaction of increased summer temperatures had a similar impact on population growth

Parameter	Mean	SD	$q_{0.025}$	$q_{0.500}$	$q_{0.975}$
Model: <i>Precip</i> (2 year lag) and <i>Cold</i> by long-term climate conditions					
<i>Precip</i> (2 year lag)	-0.192	0.126	-0.439	-0.192	0.055
<i>nmPrecip</i>	-8.00e-03	0.0110	-0.0300	-8.00e-03	0.0140
<i>Precip</i> (2 year lag) \times <i>nmPrecip</i>	9.00e-03	0.0170	-0.0240	9.00e-03	0.0420
<i>Cold</i>	-0.398	0.125	-0.644	-0.398	-0.152
<i>nmCold</i>	0.0210	0.0130	-4.00e-03	0.0210	0.0460
<i>Cold</i> \times <i>nmCold</i>	0.220	0.0630	0.0970	0.220	0.344
<i>Precip</i> (2 year lag) \times <i>nmCold</i>	0.0620	0.0700	-0.0760	0.0620	0.200
<i>Cold</i> \times <i>nmPrecip</i>	0.0150	0.0240	-0.0320	0.0150	0.0630

TABLE 5 Parameter estimates from the interaction model of spring precipitation and winter severity. *Precip* and *Cold* represent annual climate values. *nmPrecip* and *nmCold* are the long-term (~ 30 years) climate normal values. Interaction terms of annual and normal values (e.g., *Precip* \times *nmPrecip*) represent the effect of an annual climate value by different long-term climate. SD is the standard deviation of a parameter estimate, and $q_{0.025-0.975}$ represents 2.5th, 50th, and 97.5th quartile values

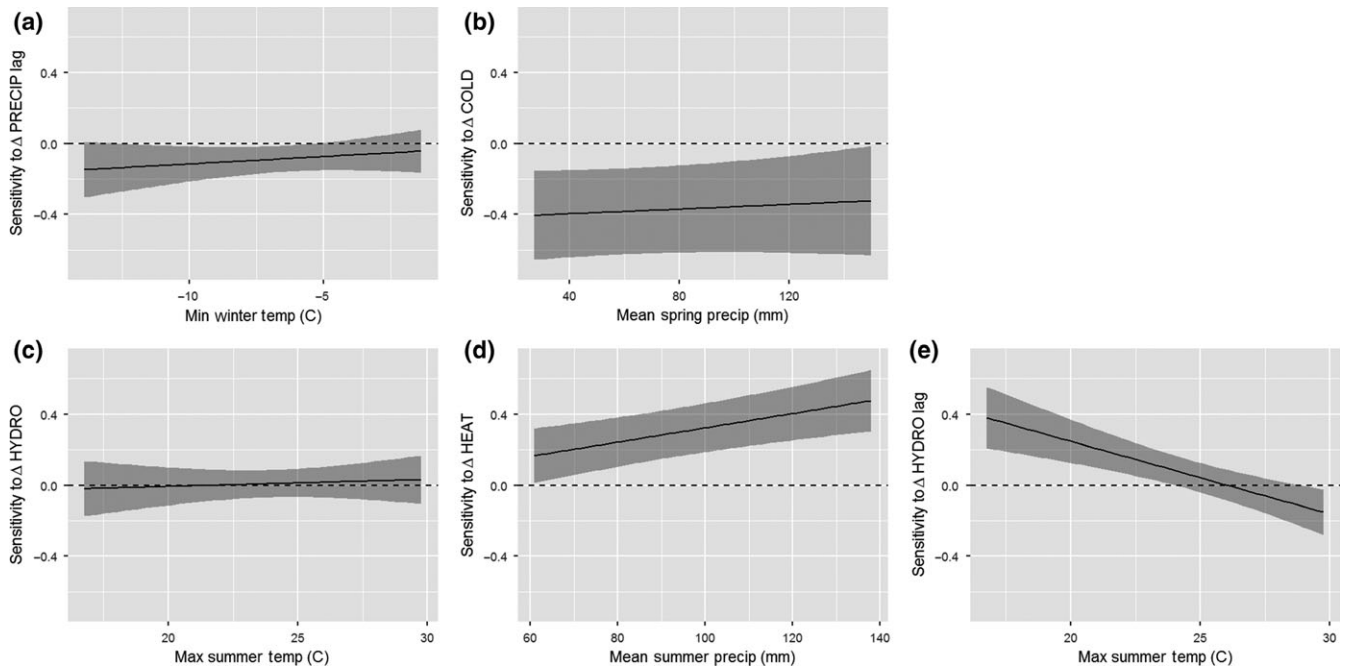


FIGURE 5 We estimated how sensitivity of wood frog population growth rates to annual climate variation changed with respect to long-term climate differences (shaded regions are 95% credible intervals). Sensitivity is the expected change in annual population growth rate (r) for a 1 SD increase in annual conditions (y-axis). Long-term differences in mean climate are calculated using 30 year climate normals for conditions during the same portion of the year that annual covariates are measured (x-axis; Tables 1 and 2) at our sampled sites. (a) Annual wood frog population growth rate 2 years later did not significantly respond to spring precipitation (PRECIP lag) regardless of long-term winter severity, (b) annual wood frog population growth rate did not significantly respond to winter severity (COLD) regardless of long-term spring precipitation, (c) annual wood frog population growth rate did not significantly respond to summer water availability (HYDRO) regardless of long-term extreme summer heat, (d) annual wood frog population growth rate responded positively to years with more extreme summer temperatures (HYDRO lag) in areas where long-term average summer precipitation was higher (>20 mm), (e) annual wood frog population growth rate 2 years later responded negatively to increased summer water availability (HYDRO lag) in areas where long-term average extreme temperature was higher ($>26.25^{\circ}\text{C}$) and positively where long-term averages were lower ($<26.25^{\circ}\text{C}$)

TABLE 6 Parameter estimates from the interaction model of summer water availability and extreme heat. *Hydro* and *Heat* represent annual climate values. *nmHydro* and *nmHeat* are the long-term (~ 30 years) climate normal values. Interaction terms of annual and normal values (e.g., *Hydro* \times *nmHydro*) represent the effect of an annual climate value by different long-term climate. SD is the standard deviation of a parameter estimate, and $q_{0.025-0.975}$ represents 2.5th, 50th, and 97.5th quartile values

Parameter	Mean	SD	$q_{0.025}$	$q_{0.500}$	$q_{0.975}$
Model: <i>Hydro</i> and <i>Heat</i> by long-term climate conditions					
<i>Hydro</i>	-0.0153	0.0701	-0.152	-0.0155	1.22e-01
<i>nmHydro</i>	-0.0404	0.0117	-0.0634	-0.0405	-1.74e-02
<i>Hydro</i> \times <i>nmHydro</i>	0.0736	0.0267	0.0210	0.0736	1.26e-01
<i>Heat</i>	0.202	0.0741	0.0562	0.202	3.47e-01
<i>nmHeat</i>	0.0383	0.0117	0.0153	0.0383	6.12e-02
<i>Heat</i> \times <i>nmHeat</i>	-0.259	0.0415	-0.340	-0.259	-1.77e-01
<i>Hydro</i> \times <i>nmHeat</i>	0.0191	0.0474	-0.0742	0.0191	1.11e-01
<i>Heat</i> \times <i>nmHydro</i>	0.0913	0.0269	0.0384	0.0914	1.44e-01
Model: <i>Hydro</i> (2 year lag) and <i>Heat</i> by long-term climate conditions					
<i>Hydro</i> (2 year lag)	0.333	0.0787	0.179	0.333	0.487
<i>nmHydro</i>	-0.0354	0.0118	-0.0585	-0.0354	-0.0122
<i>Hydro</i> (2 year lag) \times <i>nmHydro</i>	-0.0120	0.0263	-0.0635	-0.0120	0.0393
<i>Heat</i>	0.252	0.0722	0.111	0.252	0.393
<i>nmHeat</i>	0.0399	0.0117	0.0169	0.0399	0.0628
<i>Heat</i> \times <i>nmHeat</i>	-0.300	0.0390	-0.377	-0.300	-0.224
<i>Hydro</i> (2 year lag) \times <i>nmHeat</i>	-0.198	0.0475	-0.291	-0.198	-0.106
<i>Heat</i> \times <i>nmHydro</i>	0.0913	0.0267	0.0389	0.0914	0.144

rates as the summer water availability model with no time lag, with a positive effect of increased summer heat in wetter vs. drier areas (Table 6).

Expected rate of change in population growth rates over the previous 30 years that could be attributed to changes in climate showed few major increases or decreases across the wood frog range (Figs S3 and S4). The biggest changes in population growth rates were estimated to have occurred for variables related to temperature. These suggest some reductions in growth rates in the southern portion of the wood frog range due to changes in heat and cold (Figs S3d,e and S4d,e).

4 | DISCUSSION

We tested the prediction that the effect of climate on population growth rates varies in a predictable pattern based on local, long-term climate (i.e., bioclimatic envelope prediction; MacArthur, 1972; Hoffman & Parsons, 1997; Parmesan et al., 2000; Oedekoven et al., 2017). Populations near the climatic extremes of the species range were predicted to be the most sensitive to annual variation in climate. Our use of hierarchical SSMs (De Valpine & Hastings, 2002; Kéry & Schaub, 2011) allowed us test this broad-scale prediction by simultaneously linking climate directly to demographic rates at the temporal (short-term variation in weather) and spatial (individual populations) scales at which climate acts to affect species distributions. We acknowledge that our sampled sites are only a portion of the wood frog range and thus limit the interpretation of our results to conditions represented in this study. Our results provided mixed evidence to support this prediction, with differences in climate sensitivity often occurring in the opposite direction of this prediction. For example, the effect of summer temperature was consistent with our prediction—warmer summers had a more detrimental effect in the warmest part of the range. The effect of summer water availability was also consistent with this prediction, where increased moisture had a positive effect 2 years later in drier areas. However, variation in spring precipitation, summer water availability in the current year, and winter severity did not conform to predictions based on position within the range.

We also tested the climate sensitivity of populations to interactions of temperature and precipitation. We again predicted that population growth rates would be most sensitive to annual variation in one factor (e.g., increased summer heat) as they approached climate extremes of the other (e.g., drier areas). Again, we found mixed support for this prediction. Hotter summers had a positive effect on wood frog growth rates in wetter areas but a negative effect in drier areas as predicted. However, we found a contradictory positive effect of increased summer water availability 2 years later in cooler areas and no significant association of spring precipitation and winter severity to wood frog population growth rates. This suggests that expected shifts due to changing climate for wood frogs may not be strongest at the climatic extremes of the range or easily predicted solely by climate, which is surprising given the expected sensitivity of amphibians to abiotic conditions.

Many of the metabolic, reproductive, and phenological processes in amphibians are strongly linked to temperature (Beebe, 1996; Berven, 1982a, 1982b; Gibbs & Breisch, 2001) and can be of key importance in structuring species distributions (Cahill et al., 2014; Tingley, Monahan, Beissinger, & Moritz, 2009). This may explain why bioclimatic envelope model predictions regarding temperature, specifically heat, were better supported in our models. Temperature may have a more uniform effect across the landscape and may be better represented by coarse measures. Alternatively, precipitation largely acts through its effect on hydrological processes during the reproductive phase and interactions between water, soil, and vegetation during nonbreeding periods (Drexler, Synder, Spano, & Paw, 2004; Bauder, 2005; Davis et al., in preparation). Hydrologic deficits (Brooks, 2004), landscape topography (Boswell & Olyphant, 2007), pond-selection by breeding animals (Amburgey, Bailey, Murphy, Muths, & Funk, 2014; Pechmann et al., 1989; Skidds, Golet, Paton, & Mitchell, 2007), and plasticity in development (Amburgey, Funk, Murphy, & Muths, 2012; Relyea, 2002) are among the many factors that may attenuate the relationships between water availability and amphibian population growth rates. Our inferences are also limited to the study area that we were able to sample. Limited sampling of the colder and drier edge of climate space (Figure 3) may restrict our ability to detect relationships occurring at those extremes. Our study did, however, provide good coverage at the warm and wet edge of the wood frog range, which is most susceptible to the effects of climate change (Corn, 2005; Meehl et al., 2007).

A multitude of other factors (e.g., local adaptation, biotic interactions, and other abiotic variables) can affect populations and lead to patterns contradictory to bioclimatic envelope predictions of climate sensitivity (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013; Urban et al., 2013). The effect of moisture on the landscape likely depends on the form and the timing of precipitation and can also impact biotic factors that likewise contribute to heterogeneity in population growth rates. Increased spring precipitation may come as early spring snow and ice storms that can increase adult mortality through reduced freeze tolerance (Costanzo & Lee, 1992) or truncate the breeding season (Berven, 1982b). Increased moisture on the landscape may increase the probability of egg mass or tadpole stranding in temporary flooded areas or facilitate colonization or persistence of predators in ponds (Werner, Relyea, Yurewicz, Skelly, & Davis, 2009). Local adaptation to annual climate variation may alter climate sensitivity, with populations nearer to climate extremes accustomed to increased annual variation while populations farther away from extremes are not (e.g., Amburgey et al., 2012; Berven, 1982a; Laugen, Laurila, Räsänen, & Merilä, 2003), though we cannot test this directly with our approach. Local dynamics may also vary spatially, where populations near climate extremes are at low enough densities that they are unable to respond to the benefits of years with more suitable climate conditions.

Species biology may additionally structure population responses to climate and result in deviations from bioclimatic envelope predictions. Wood frogs are freeze tolerant (Costanzo & Lee, 1992; Storey & Storey, 1986) though extended or extreme periods of freezing

temperatures can impact overwintering survival (Costanzo, Lee, & Wright, 1991; O'Connor & Rittenhouse, 2016). In a portion of the range that encompassed our study areas, no differentiation in wood frog thermal tolerance was found (Manis & Claussen, 1986); however, far northern populations in Alaska have shown increased cold tolerance (Larson et al., 2014). However, mild winters in colder areas may result in freeze-thaw cycles that rouse animals from torpor, resulting in increased energetic demands (Storey, 1987), mating behavior impairment (Costanzo, Irwin, & Lee, 1997), and reduced fecundity (Benard, 2015). Additionally, the life stage on which climate most strongly acts may influence the population response. In amphibians, the aquatic larval stage already experiences heightened mortality, and climate conditions that affects tadpole survival may not lead to differential climate sensitivity at the population level as much as those factors that influence terrestrial juvenile and adult survival (Biek, Funk, Maxell, & Mills, 2002; Harper, Rittenhouse, & Semlitsch, 2008).

Currently, species distributions and range dynamics are frequently modeled using static approaches that treat climate and species responses as fixed across space and time (Franklin, 2010; Hijmans & Graham, 2006). However, species responses to climate are spatially complex, especially for those with multistage life histories. Climate shifts will likely alter species distributions by acting on demographic processes where sensitivity to change is greatest. Combining estimates of climate sensitivity with data about observed or predicted changes in climate allows for predictions about local changes in population growth rate to be made. We did this for the last 30 year period, highlighting the variability in population response across the range (Figs S3 and S4). Demographic response for some climate variables fit predictions (e.g., negative responses to warming in the warmest regions). However, estimated demographic changes related to water availability and interactions with temperature follow much less clear patterns, which would not easily be predicted using static modeling approaches. Our results demonstrate that focusing on demographic processes provides insights for understanding how species distributions may respond to change not possible with presence-absence correlative models focused on pattern (Normand et al., 2014; Ross et al., 2015). Correlative approaches based on a static snapshot of species distribution do not measure the actual mechanistic processes impacting populations (Cahill et al., 2014; Dormann et al., 2012) and do not estimate rates of change that demographic models can incorporate (Normand et al., 2014). Thus, correlations may break down with no-analog climates (Williams & Jackson, 2007) and lack the predictive power explicit estimates of climate-demography relationships can offer (Normand et al., 2014). While our model is still correlative in relating demographic rates to climatic variation, it provides a finer scale approach that provides insights to potential mechanisms while also explaining broader patterns. Bioclimatic envelope modeling does not include other potentially important factors (e.g., biotic interactions, genetic differentiation, and geographical barriers) that may set species range limits alone or in concert with climate (HilleRisLambers et al., 2013; Urban et al., 2013). However, such

demographic models can be modified to include such information and better inform our understanding of species range dynamics.

A demographic understanding of species distributions is essential to evaluating and understanding range limits, forecasting range shifts and stability, and managing species and conserving habitats. These aims will be critical in the context of changing climate. By pairing large-scale modeling studies with targeted experimental or demographic studies, we can better understand the way these broad-scale measures are realized on the landscape and influence local populations (Merow et al., 2014; Normand et al., 2014). In the future, all species are likely to experience some change to their current distributions, whether through range contractions (via altered habitat suitability through changing climate) or expansions (via altered climate facilitating colonization of new habitats; Thuiller et al., 2008). With increasingly limited conservation resources, identification and prioritization of critical areas where species are most sensitive to changing climate (Beissinger & Westphal, 1998; Keith et al., 2008) and where range shifts may occur (Thuiller et al., 2008) will allow for more efficient and effective conservation management.

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