

1 Title:

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

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39 Demographic processes and climate interact and vary across a species' range to determine how species'
40 distributions will respond to climate change. We predicted that populations at the extremes of a species'
41 climate envelope are most sensitive to climate shifts. We tested this using a dynamic species distribution
42 model linking demographic rates to variation in climate for wood frogs (*Lithobates sylvaticus*) in North
43 America. Sensitivity to changes in climate cannot be predicted simply by knowing locations within the
44 species' climate envelope.

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

Running head: Range position and climate sensitivity

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52 **Keywords:** bioclimatic envelope model, climate change, *Lithobates sylvaticus*, range

53 shifts, species distribution model, state space model, wood frog

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56 **Abstract**

57 Species' distributions will respond to climate change based on the relationship between

58 local demographic processes and climate and how this relationship varies based on range

59 position. A rarely tested demographic prediction is that populations at the extremes of a

60 species' climate envelope (e.g., populations in areas with the highest mean annual

61 temperature) will be most sensitive to local shifts in climate (i.e., warming). We tested

62 this prediction using a dynamic species distribution model linking demographic rates to

63 variation in temperature and precipitation for wood frogs (*Lithobates sylvaticus*) in North

64 America. Using long-term monitoring data from 746 populations in 27 study areas, we

65 determined how climatic variation affected population growth rates and how these

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

81

82 Introduction

83 A persistent theme in ecology is the need to understand the factors that shape and
84 describe species distributions (Grinnell, 1917; MacArthur, 1972; Gaston, 2009; Sexton et
85 al., 2009). These factors have been touted as a means to understand the conditions that
86 facilitate sustainable populations currently and in the future (Sexton et al., 2009). Species
87 distributions are determined by a spectrum of biotic and abiotic factors that act across
88 varying spatial and temporal scales (Anders & Post, 2006; Sexton et al., 2009). Among
89 abiotic factors, climate is thought to be one of the most important determinants of species
90 occurrence and key to the formation, maintenance and evolution of species distributions
91 (Darwin, 1859; Sexton et al., 2009; Araújo & Peterson, 2012). Climate may affect
92 species directly via constraints in physiological tolerances, indirectly via its influence on
93 community assemblages and habitats, or by complex interactions of both (Menge &
94 Olson, 1990). Understanding when and where climate constrains species' occurrence is
95 useful in predicting future responses, conserving and managing species in the face of
96 ongoing global climate change (Pearson & Dawson, 2003; Araújo & Peterson, 2012) and

97 identifying areas where other factors aside from climate are more strongly influencing
98 distributions (e.g., biotic interactions; Urban et al., 2013).

99 Attempts to quantify the role climate plays in shaping species distributions
100 frequently rely on the correlation between species occurrence and climate (i.e., a species'
101 bioclimatic envelope; Araújo & Peterson, 2012) to characterize current and to predict
102 future range dynamics. These static distribution modeling approaches are used to identify
103 broad-scale patterns contributing to range limits (Pearson & Dawson, 2003; Hijmans &
104 Graham, 2006) and to predict range-wide effects of climate change on species
105 distributions (Pearson & Dawson, 2003; Araújo et al., 2005; Thuiller et al., 2005). Under
106 bioclimatic envelope models, climatic conditions where a species is not observed are
107 assumed to prevent establishment of viable populations and thus are the environmental
108 conditions that set range limits (Araújo & Peterson, 2012). However, these
109 phenomenological models assume (1) species' ranges are in equilibrium with climate
110 conditions and (2) species responses are static across the range (Hijmans & Graham,
111 2006; Franklin, 2010). These assumptions do not realistically represent the dynamic
112 nature of the physical environment and the species themselves, especially for broadly
113 distributed species (Zurell et al., 2009). Static models of species responses to climate are
114 insufficient to understand the effect annual climate variation can have on population
115 persistence (Zurell et al., 2009; Franklin, 2010). Furthermore, the focus on species
116 occurrence data ignores the temporal variation in species responses and the demographic
117 processes that determine how a species will respond to climatic shifts (Merow et al.,
118 2014; Thuiller et al., 2014).

119 If climate shapes species distributions, changes in climate should have the greatest
120 effect on populations occurring near the climatic extremes (e.g., increased temperature
121 will have the greatest effect on populations in the warmest part of the range; MacArthur,
122 1972; Hoffman & Parsons, 1997; Parmesan et al., 2000). We test this by measuring
123 sensitivity of demographic responses to climatic variation across the range of the wood
124 frog (*Lithobates sylvaticus*). Specifically, we define sensitivity as the expected change in
125 annual population growth rate (r) with respect to change in an annual climatic measure
126 (e.g., summer extreme heat). We expect range contractions to occur when populations are
127 lost because growth rate is negative for an extended period of time. Similarly, range

128 expansions may occur when populations are gained because growth rate is positive for an
129 extended period of time. Measuring sensitivity tells us how much growth rate is expected
130 to change with a change in average annual conditions and thus how likely population
131 declines (or expansions) are to occur. We test whether sensitivity of population growth
132 rates to year-to-year variation in climate is stronger at the climatic extremes than at the
133 climatic center of a species range (i.e., the bioclimatic envelope prediction; MacArthur,
134 1972; Hoffman & Parsons, 1997; Parmesan et al., 2000). Failure to find evidence to
135 support this hypothesis could result from processes such as local adaptation, biotic
136 interactions, and other abiotic variables leading to different patterns in sensitivity to
137 change. Testing this hypothesis requires an understanding of how life history is impacted
138 and thus how demographic rates respond to climatic variation (e.g., the relationship
139 between population growth rate and temporal variation in environmental conditions;
140 Normand et al., 2014; Ross et al., 2015). This approach captures more of the process
141 underlying range shifts rather than simply the observed pattern that previous correlative
142 approaches have used to predict range shifts.

143 Amphibians make an interesting focal taxon to test the importance of population-
144 level sensitivity to climate variation in range dynamics. Amphibians are expected to be
145 particularly sensitive to the effects of climate due to their physiology and life history
146 (Hutchinson & Dupré, 1992; Duellman, 1999), generally limited dispersal abilities
147 (Beebee, 1996, but see Smith & Green, 2005), and reliance on seasonal precipitation and
148 temperature patterns to create breeding habitats and facilitate movement (Pechmann et
149 al., 1989; Rittenhouse & Semlitsch, 2007; Urban et al., 2014). Their ecological
150 importance as a link between terrestrial and aquatic systems (Ranvestel et al., 2004; Earl
151 & Semlitsch, 2012) and the decline of even common species (Stuart et al., 2004; Adams
152 et al., 2013; Grant et al., 2016) make understanding the importance of climate in
153 influencing population level dynamics important for forecasting future extinction risk.
154 Here we focus on the demographic responses to climate for a species of pond-breeding
155 frog, the wood frog, whose range extends across much of northern North America (Fig.
156 1).

157 Using a spatially and temporally rich dataset, we tested the prediction that wood
158 frog populations are most sensitive to annual climatic variation at sites near the climatic

159 extremes of their distribution (Fig. 2) and that the species distribution is shaped by the
160 interaction of long-term and annual climate conditions on population growth rates.
161 Population growth rates at sites may have three predicted responses based on their range
162 position. For example, if sensitivity of wood frog populations to variation in temperature
163 differs across the range, we predicted that 1) populations in the colder portion of the
164 range (blue; Fig. 2a) would be positively affected by warmer than average annual
165 temperatures, meaning that if warming occurred this could lead to more frequent years of
166 high population growth rates and potential range expansion; 2) populations in the warmer
167 portion of the range (red; Fig. 2a) would be negatively affected by warmer than average
168 annual temperatures, meaning that if warming occurred this would lead to more frequent
169 years of low population growth rates and potential range contraction; and 3) populations
170 in the middle of the range (black; Fig. 2a) are far from climate extremes (Fig. 2b) and
171 annual temperatures would not strongly affect population growth rates. By fitting
172 dynamic models that estimate annual changes in abundance in relation to long-term
173 climate, we can better understand which populations within a species' range are most
174 likely to respond to changing climate.

175 Study System and Methods

176 We build on previous static approaches to model bioclimatic determinants of
177 species distributions (e.g., Guisan & Zimmerman, 2000; Hijmans & Graham, 2006) by
178 measuring local demographic responses of populations using a dynamic species
179 distribution model (DSDM). The DSDM approach allowed us to test the importance of
180 range position in determining responses to climate by measuring local sensitivity of
181 population growth rate to annual variation in climate covariates. Our model takes the
182 form of a hierarchical state-space model (SSM; De Valpine & Hastings, 2002; Buckland
183 *et al.*, 2004; Kéry & Schaub, 2012; Ross *et al.* 2015), allowing us to link annual
184 population dynamics across different sites and study areas to annual variation in climatic
185 variables. The results provide a measure of climate sensitivity (i.e., the expected change
186 in mean population growth rates in response to changes in mean climate; Thuiller *et al.*,
187 2005; Thomas, 2010; Burrows *et al.*, 2014).

188 Study System and Life History

189 Wood frogs occupy an extensive range, occurring from northern Alaska to
190 Canada and south to the south central United States (USGS National Amphibian Atlas,
191 2014; Fig. 1), spanning a large gradient of climatic conditions (Fig. 1). Specific elements
192 of the wood frog life history potentially make them sensitive to changes in local climate.
193 Breeding normally occurs in early spring when rising temperatures rouse animals and
194 warm spring rains facilitate movement into breeding ponds. Adult frogs show high
195 fidelity to breeding sites (Berven & Grudzien, 1990; Green & Bailey 2015). Breeding
196 generally occurs in a short window of time, anywhere from a few consecutive evenings to
197 a few weeks in length depending on location (Authors, pers. observations; Crouch &
198 Paton, 2000). Female wood frogs become sexually mature between two and four years of
199 age and males between one and three years of age (Berven, 1982a; Berven, 2009; Green
200 & Bailey 2015), and both can live up to six years (Redmer & Trauth, 2005). Females
201 typically lay one egg mass during each breeding season, and these egg masses are
202 visually distinct and easy to locate and count (Crouch & Paton, 2000; Grant et al., 2005;
203 Green et al., 2013). Comparison of census methods show that counts of total egg masses
204 seen per season serves as a suitable proxy for total breeding females per season in a pond
205 (Crouch & Paton, 2000).

206 Field sampling

207 We used egg mass counts from 746 sites within 27 study areas across the wood
208 frog range (Fig. 1; Table S1). A site consisted of a pond or wetland (area ≤ 0.10 ha to
209 5.24 ha) that was visually sampled for wood frog egg masses during the peak of each
210 breeding season and where wood frog egg masses were observed at least once during
211 years when surveys occurred. Study areas designate geographic clusters of sites that
212 occurred within relatively close proximity (e.g., within a single national park). Sites were
213 surveyed in multiple years (range = 3-22 years, mean = 10 years; Table S1) with most,
214 but not all, sites being surveyed multiple times within each year. Surveys occurred during
215 or right after peak breeding based on the lack of calling adults and/or no additional egg
216 masses during subsequent surveys, and a maximum count at a site was recorded each
217 breeding season and used as the response variable in analyses. Wood frog egg masses are
218 conspicuous and detection probability is high ($p = 0.96 \pm 0.02$ to 0.95 ± 0.01 ; Grant et al.,
219 2005).

220 Climate covariates

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

228 We obtained global climate normal (~1960-1990, 2.5 arc-minutes resolution)
229 rasters from WorldClim (Hijmans et al., 2005) and created 30-year climate normal maps
230 of North America in program R (R Core Team, 2016). We determined 30-year mean
231 annual temperature and precipitation values across North America and within the
232 recorded range of wood frog occurrence (IUCN, 2015) to determine where the species
233 occurs within the broader North American climate space (Fig. 3). These values were used
234 to depict the climate space of wood frogs and our sampled populations in Figure 3 but
235 were not used in SSMs. Using PRISM (Daly et al., 2002) model output for the US and
236 weather station data for Canada (Environment Canada, 2015), we calculated annual
237 climate values for Precip, Hydro, Heat, and Cold at every site every year for SSMs
238 (Table 1). To model differences in long-term climate, we determined 30-year climate
239 normal (average) values (Hijmans et al., 2005) at every site over the same seasonal
240 periods as our annual climate covariates for SSMs (Table 2; nmPrecip, nmHydro,
241 nmHeat, and nmCold). For example, at northern sites we calculated total precipitation
242 values each year for February, March, and April, due to their importance in timing wood
243 frog migrations and pond filling, and averaged them for an annual spring precipitation
244 value (Precip). We then averaged total precipitation values over the same months across
245 30 years to get a long-term climate normal value (nmPrecip) that varied across but not
246 within sites. Annual climate values were standardized by 33-year (1981-2013) mean and
247 standard deviations at a site. Climate normals were standardized using the mean and
248 standard deviation from the entire extent of the wood frog range.

249 Data analysis

250 We used SSMS to estimate the effect of annual variation on population growth
251 rate (De Valpine & Hastings, 2002; Buckland et al., 2004; Kéry & Schaub, 2011; Ross et
252 al. 2015). Models were fit in JAGS (Plummer 2003) and implemented in program R via
253 the R2jags package (Su & Yajima, 2012; see Appendix S1 for JAGS code). The
254 hierarchical model allows for estimation of latent state and observation processes
255 characterizing sampled populations while simultaneously accounting for process
256 variation and observation error (Buckland et al., 2004; Kéry & Schaub, 2011). We were
257 interested in understanding how these latent processes were affected by annual climate
258 variation across the range. At the same time, the modeling framework allowed us to
259 account for observation error in counts (e.g., through variable detection, field conditions,
260 variable observer expertise) that was unrelated to the underlying population processes
261 (MacKenzie et al., 2006).

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

$$265 \quad N_{t+1} = N_t * e^r \quad (1)$$

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

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

$$275 \quad \log(N_{t+1, i}) = \log(N_{ti}) + r_{ti} \quad (2)$$

276 The now additive growth rate r_{ti} was modified to include the effects of climate
277 covariates and unexplained annual variation captured using random-error terms. Our goal
278 was to estimate the effect of annual variation in each of our four climate covariates and
279 how those effects differed across the range. We estimated these relationships using a

280 linear model that included the main effects of annual climate values and the climate
 281 normal along with the interaction of the two (Table 3). The model took the form of:

$$282 \quad r_{ti} = \beta_1 * \text{Annual Climate}_{ti} + \beta_2 * \text{Climate Normal}_i + \quad (3)$$

$$283 \quad \beta_3 * \text{Annual Climate}_{ti} * \text{Climate Normal}_i + \delta_i + \varepsilon_{ti}$$

284 The model allowed us to determine sensitivity, defined as the expected change in annual
 285 population growth rate (r) for a one standard deviation increase in annual conditions, to
 286 long-term climate normal conditions. Specifically, the interaction term allowed us to
 287 quantify the amount of change in population growth rates given an annual shift in climate
 288 in respect to the climatic range position in which a population exists. We included a
 289 random effect for site level differences, $\delta_i \sim \text{Normal}(0, \sigma^2_{\text{Site}})$. This effect served as the
 290 local site-level intercept for growth rate, which we expected to vary around a mean value
 291 of 0. We included a second random error component for additional annual variation in
 292 growth rate not explained by the climate covariates, $\varepsilon_{ti} \sim \text{Normal}(0, \sigma^2_{\text{proc}})$. To account
 293 for observation error in counts that was not explained by the population level state
 294 processes, we assumed that the log observed count of egg masses for that site and year,
 295 y_{ti} , is given by $y_{ti} \sim \text{Normal}(\log[N_{ti}], \sigma^2_{\text{obs}})$. It was also necessary to estimate a starting
 296 population size for each site. We used a prior value of $\log(N_{1i}) \sim \text{Normal}(0, 100)$.

297 We used vague priors for random effect variance components ($\sigma^2_{\text{obs}}, \sigma^2_{\text{proc}}$) with
 298 uniform distributions bounded between 0 and 5. For σ^2_{Site} we used a uniform prior
 299 bounded between 0 and 0.2 to facilitate convergence. Priors for all regression coefficients
 300 were $\beta_k \sim \text{Normal}(0, 100)$. We ran three parallel chains for 50,000 iterations each and
 301 discarded the first 1000 iterations as burn-in to allow for model convergence. Model
 302 convergence was determined visually from traceplots and Gelman Rubin statistics ($\hat{R} <$
 303 1.05; Gelman & Rubin 1992).

304 We predicted that climate covariates could have both immediate and lagged
 305 effects on annual growth rate (r_{ti} ; Fig. S1). We predicted that covariates that
 306 disproportionately impact adult survival and season-to-season variation in breeding
 307 would lead to changes in growth rate in the same year. In the case where we expected a
 308 covariate to impact the survival of eggs and tadpoles in a wetland and thus the number of
 309 potential recruits from a cohort, these were predicted to lead to changes in growth rates
 310 after a 2-year lag. Female wood frogs take approximately two years to reach sexual

311 maturity in our study sites (e.g., lowland populations; Berven, 1982a, 2009; Green &
312 Bailey 2015). Therefore the effects of reproductive failure (e.g., desiccation of tadpoles in
313 a dry year) on growth rates would not be evident in counts of egg masses in the year
314 immediately following these suboptimal conditions. We hypothesized that annual Precip
315 values affect movement of adult animals and the opportunity for successful oviposition
316 (i.e., pond filling), with low Precip values resulting in fewer egg masses laid and thus
317 reduced recruitment two years later. Hydro values reflect desiccation risk for developing
318 tadpoles (realized as altered recruitment two years later) and also drier summer
319 conditions that can decrease adult survival during foraging or return to overwintering
320 sites. Heat and Cold values reflect late summer dryness and overwintering cold stress
321 expected to impact adults. While any number of time lag combinations and effects are
322 possible, we fit the model (Eq. 3) focusing on these key periods due to their biological
323 importance and support in the literature (Table 1).

324 We were also interested in how water availability and temperature may interact to
325 explain variation in climate sensitivity. We expected that years of low precipitation
326 (Precip) would have a greater negative effect in sites with higher mean annual summer
327 temperatures (e.g., hotter areas; nmHeat) as increased water on the landscape may help
328 keep permeable amphibian skin moist and lessen desiccation risk (Rittenhouse et al.,
329 2009; Köhler et al., 2011). Similarly, we expected reduced winter severity (Cold) and its
330 indirect effect on water availability and pond filling in the spring to be greater in areas
331 that receive less spring precipitation (e.g., drier areas; nmPrecip). We tested for these
332 effects by including the interaction of different annual and long-term climate covariates
333 (e.g., Precip*nmCold, Hydro*nmHeat; Table 3). Annual covariates included the same
334 time lags as previously discussed. Models with both temperature and precipitation
335 included all annual and long-term covariates for each climate measure and an additional
336 two interaction terms allowing annual and long-term covariates to interact (Table 3). This
337 means a total of eight models testing climate hypotheses (Table 1 and 2) were run. None
338 of the selected climate covariates were strongly correlated ($|r| < 0.4$).

339 When fitting models, we tested for goodness of fit using a posterior predictive
340 check to test whether observed variability in counts was consistent with expected
341 variation. We calculated observed variance in our data for each of the sites and

342 determined if on average variance was less than or greater than the predicted variance of
343 simulated data based on our model. We report the proportion of the time that the
344 observed variance was greater than the predicted variance, with the expectation that if the
345 model fits the data well we expect this proportion to be 0.5.

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

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

351 We calculated rate of change in each of our climate variables at each of our sites
352 using linear regression where year was the predictor variable and annual values of each of
353 our climate variables over a 30-year period from 1984 to 2013 were our response
354 variables. We mapped these to geographic and climate space to highlight areas where
355 climate may currently be altering the wood frog distribution.

356 **Results**

357 Sites spanned a >23 degree range in latitude and >50 degree range in longitude from
358 North Carolina to Jasper National Park, Alberta, Canada. Study areas fell into 16
359 different states, one administrative subdivision (Washington D.C.) and one Canadian
360 province (Alberta) (Fig.1). Our data show good geographic coverage along the wood
361 frog's southern and easternmost range limit but are restricted in geographic coverage in
362 the northern and westernmost portions of the wood frog range. This was reflected in our
363 coverage in climate space (Fig. 3), with best coverage in the portion of the range with
364 warmer temperatures and higher precipitation. Therefore, we limit the presentation of
365 results and their interpretation to only the sampled portion of the wood frog range.

366 Additionally, support for models was judged by whether or not credible intervals of
367 parameter estimates overlapped zero, and we have limited our presentation of results to
368 those models with the strongest support and thus credible intervals for interaction terms
369 that did not overlap. Our posterior-predictive check values for each of our models were

370 between 0.493 and 0.541, indicating that our models did a good job of capturing actual
371 variation in growth rates.

372 Our first three models tested the effect of moisture on population growth rates,
373 with the first focused on spring precipitation and the second on late summer water
374 availability. Contrary to our predictions, we found a negative relationship between Precip
375 and wood frog population growth rates across all areas two years later (Table 4; Fig. 4a;
376 Fig. S2). The relationship of increased annual Hydro values to wood frog population
377 growth rates differed depending on if a time lag was incorporated (Table 4; Fig. 4b,c; Fig.
378 S2). The same-year effect of Hydro was dependent on long-term climate, with
379 populations in wetter areas responding most positively to wetter annual conditions as
380 compared to those in drier areas (Fig. 4b). When incorporating a two-year time lag,
381 increased values of Hydro were positively associated with growth rates only in drier areas
382 (Fig. 4c; Table 4), agreeing with our bioclimatic envelope predictions of increased
383 sensitivity to water availability in drier portions of the range.

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

395 Finally we examined how precipitation and temperature interacted to affect
396 population growth rates. We found that the two-year lag effect of annual variation in
397 spring precipitation did not depend on long-term winter climate (Precip*nmCold; Table
398 5; Fig. 5a; Fig. S2), and the effect of annual variation in winter severity did not vary
399 significantly by long-term spring precipitation (Cold*nmPrecip; Table 5; Fig. S2).

400 We found that the effect of summer water availability in the current year did not
401 differ by long-term summer heat (Hydro* Δ Heat; Table 6; Fig. 5c; Fig. S2). However,
402 the effect of warmer summers differed between drier and wetter areas. Hotter summer
403 temperatures had a positive relationship to population growth rates in wetter areas but
404 negatively impacted growth rates in drier areas (Heat* Δ Hydro; Fig. 5d; Fig. S2). We
405 found a positive relationship between increased summer water availability and wood frog
406 growth rates two years later in areas with cooler summer temperatures but a negative
407 relationship in areas with hotter summer temperatures (Table 6; Fig. 5e; Fig. S2). The
408 interaction of increased summer temperatures had a similar impact on population growth
409 rates as the summer water availability model with no time lag, with a positive effect of
410 increased summer heat in wetter versus drier areas (Table 6).

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

417 **Discussion**

418 We tested the prediction that the effect of climate on population growth rates
419 varies in a predictable pattern based on local, long-term climate (i.e., bioclimatic
420 envelope prediction; MacArthur, 1972; Hoffman & Parsons, 1997; Parmesan et al.,
421 2000). Populations near the climatic extremes of the species range were predicted to be
422 the most sensitive to annual variation in climate. Our use of hierarchical SSMs (De
423 Valpine & Hastings, 2002; Kéry & Schaub, 2012) allowed us test this broad-scale
424 prediction by simultaneously linking climate directly to demographic rates at the
425 temporal- (short-term variation in weather) and spatial- (individual populations) scales at
426 which climate acts to affect species distributions. We acknowledge that our sampled sites
427 are only a portion of the wood frog range and thus limit the interpretation of our results to
428 conditions represented in this study. Our results provided mixed evidence to support this
429 prediction, with differences in climate sensitivity often occurring in the opposite direction
430 of this prediction. For example, the effect of summer temperature was consistent with our

431 prediction – warmer summers had a more detrimental effect in the warmest part of the
432 range. The effect of summer water availability was also consistent with this prediction,
433 where increased moisture had a positive effect two years later in drier areas. On the other
434 hand, variation in spring precipitation, summer water availability in the current year, and
435 winter severity did not conform to predictions based on position within the range.

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

448 Many of the metabolic, reproductive and phenological processes in amphibians
449 are strongly linked to temperature (Berven, 1982a,b; Beebee, 1996; Gibbs & Breisch,
450 2001) and can be of key importance in structuring species distributions (Tingley et al.,
451 2009; Cahill et al., 2014). This may explain why bioclimatic envelope model predictions
452 regarding temperature, specifically heat, were better supported in our models.
453 Temperature may have a more uniform effect across the landscape and may be better
454 represented by coarse measures. Alternatively, precipitation largely acts through its effect
455 on hydrological processes during the reproductive phase and interactions between water,
456 soil, and vegetation during non-breeding periods (Drexler et al., 2004; Bauder, 2005;
457 Davis et al., in prep). Hydrologic deficits (Brooks, 2004), landscape topography (Boswell
458 & Olyphant, 2007), pond-selection by breeding animals (Pechmann et al., 1989; Skidds
459 et al., 2007; Amburgey et al., 2014), and plasticity in development (Relyea, 2002;
460 Amburgey et al., 2012) are among the many factors that may attenuate the relationships
461 between water availability and amphibian population growth rates. Our inferences are

462 also limited to the study area that we were able to sample. Limited sampling of the colder
463 and drier edge of climate space (Fig. 3) may restrict our ability to detect relationships
464 occurring at those extremes. Our study did, however, provide good coverage at the warm
465 and wet edge of the wood frog range, which is most susceptible to the effects of climate
466 change (Corn 2005; Meehl et al., 2007).

467 A multitude of other factors (e.g., local adaptation, biotic interactions, and other
468 abiotic variables) can affect populations and lead to patterns contradictory to bioclimatic
469 envelope predictions of climate sensitivity (HilleRisLambers et al., 2013; Urban et al.,
470 2013). The effect of moisture on the landscape likely depends on the form and the timing
471 of precipitation and can also impact biotic factors that likewise contribute to
472 heterogeneity in population growth rates. Increased spring precipitation may come as
473 early spring snow and ice storms that can increase adult mortality through reduced freeze
474 tolerance (Costanzo & Lee Jr., 1992) or truncate the breeding season (Berven, 1982b).
475 Increased moisture on the landscape may increase the probability of egg mass or tadpole
476 stranding in temporary flooded areas or facilitate colonization or persistence of predators
477 in ponds (Werner et al., 2009). Local adaptation to annual climate variation may alter
478 climate sensitivity, with populations nearer to climate extremes accustomed to increased
479 annual variation while populations farther away from extremes are not (e.g., Berven,
480 1982a, Laugen et al., 2003; Amburgey et al., 2012), though we cannot test this directly
481 with our approach. Local dynamics may also vary spatially, where populations near
482 climate extremes are at low enough densities that they are unable to respond to the
483 benefits of years with more suitable climate conditions.

484 Species biology may additionally structure population responses to climate and
485 result in deviations from bioclimatic envelope predictions. Wood frogs are freeze tolerant
486 (Storey & Storey, 1986; Costanzo & Lee Jr., 1992) though extended or extreme periods
487 of freezing temperatures can impact overwintering survival (Costanzo et al., 1991;
488 O'Connor & Rittenhouse, 2016). In a portion of the range that encompassed our study
489 areas, no differentiation in wood frog thermal tolerance was found (Manis & Claussen,
490 1986); however, far northern populations in Alaska have shown increased cold tolerance
491 (Larson et al., 2014). However, mild winters in colder areas may result in freeze-thaw
492 cycles that rouse animals from torpor, resulting in increased energetic demands (Storey,

493 1987), mating behavior impairment (Costanzo et al., 1997), and reduced fecundity
494 (Benard, 2015). Additionally, the life stage on which climate most strongly acts may
495 influence the population response. In amphibians, the aquatic larval stage already
496 experiences heightened mortality, and climate conditions that affects tadpole survival
497 may not lead to differential climate sensitivity at the population level as much as those
498 factors that influence terrestrial juvenile and adult survival (Biek et al., 2002; Harper et
499 al., 2008).

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

524 modeling does not include other potentially important factors (e.g., biotic interactions,
525 genetic differentiation, and geographical barriers) that may set species range limits alone
526 or in concert with climate (HilleRisLambers et al., 2013; Urban et al., 2013). However,
527 such demographic models can be modified to include such information and better inform
528 our understanding of species range dynamics.

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

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550 **References**

551 Adams MJ, Miller DAW, Muths E et al. (2013) Trends in amphibian occupancy in the
552 United States. PLoS ONE, **8**, e64347.

- 553 Amburgey S, Funk WC, Murphy M, Muths E (2012) Effects of hydroperiod duration on
554 survival, developmental rate, and size at metamorphosis in boreal chorus frog
555 tadpoles (*Pseudacris maculata*). *Herpetologica*, **68**, 456–467.
- 556 Amburgey SA, Bailey LL, Murphy M, Muths E, Funk WC (2014) The effects of
557 hydropattern and predator communities on amphibian occupancy. *Canadian*
558 *Journal of Zoology*, **92**, 927–937.
- 559 Anders AD, Post E (2006) Distribution-wide effects of climate on population densities of
560 a declining migratory landbird. *Journal of Animal Ecology*, **75**, 221–227.
- 561 Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate
562 impact models under climate change. *Global Change Biology*, **11**, 1–10.
- 563 Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling.
564 *Ecology*, **93**, 1527–1539.
- 565 Bauder ET (2005) The effects of an unpredictable precipitation regime on vernal pool
566 hydrology. *Freshwater Ecology*, **50**, 2129–2135.
- 567 Beebee TJC (1996) Ecology and conservation of amphibians. Chapman and Hall,
568 London, UK.
- 569 Beissinger SR, Westphal MI (1998) On the use of demographic models of population
570 viability in endangered species management. *The Journal of Wildlife*
571 *Management*, **62**, 821–841.
- 572 Benard MF (2015) Warmer winters reduce frog fecundity and shift breeding phenology,
573 which consequently alters larval development and metamorphic timing. *Global*
574 *Change Biology*, **21**, 1058–1065.
- 575 Berven KA (1982a) The genetic basis of altitudinal variation in the wood frog *Rana*
576 *sylvatica*. II. An experimental analysis of life history traits. *Evolution*, **36**, 962–
577 983.
- 578 Berven KA (1982b) The genetic basis of altitudinal variation in the wood frog *Rana*
579 *sylvatica*. I. An experimental analysis of life history traits. *Evolution*, **36**, 962–
580 983.
- 581 Berven KA, Grudzien TA (1990) Dispersal in the wood frog (*Rana sylvatica*):
582 implications for genetic population structure. *Evolution*, **44**, 2047–2056.

- 583 Berven KA (2009) Density dependence in the terrestrial stage of wood frogs: evidence
584 from a 21-year population study. *Copeia*, **2**, 328–338.
- 585 Biek R, Funk WC, Maxell BA, Mills LS (2002) What is missing in amphibian decline
586 research: insights from ecological sensitivity analysis. *Conservation Biology*, **16**,
587 728–734.
- 588 Boswell JS, Olyphant GA (2007) Modeling the hydrologic response of groundwater
589 dominated wetlands to transient boundary conditions: Implications for wetland
590 restoration. *Journal of Hydrology*, **332**, 467–476.
- 591 Brooks RT (2004) Weather-related effects on woodland vernal pool hydrology and
592 hydroperiod. *Wetlands*, **24**, 104–114.
- 593 Buckland ST, Newman KB, Thomas L, Koesters NB (2004) State-space models for the
594 dynamics of wild animal populations. *Ecological Modelling*, **171**, 157–175.
- 595 Burrows MT, Schoeman DS, Richardson AJ et al. (2014) Geographical limits to species-
596 range shifts are suggested by climate velocity. *Nature*, **507**, 492–507.
- 597 Cahill AE, Aiello-Lammens ME, Fisher-Reid MC et al. (2014) Causes of warm-edge
598 range limits: systematic review, proximate factors and implications for climate
599 change. *Journal of Biogeography*, **41**, 429–442.
- 600 Corn PS (2005) Climate change and amphibians. *Animal Biodiversity and Conservation*,
601 **28**, 59–67.
- 602 Costanzo JP, Lee Jr. RE, Wright MF (1991) Effect of cooling rate on the survival of
603 frozen wood frogs, *Rana sylvatica*. *Journal of Comparative Physiology*, **161**, 225–
604 229.
- 605 Costanzo JP, Lee Jr. RE (1992) Cryoprotectant production capacity of freeze-tolerant
606 wood frog, *Rana sylvatica*. *Canadian Journal of Zoology*, **71**, 71–75.
- 607 Costanzo JP, Irwin JT, Lee Jr. RE (1997) Freezing impairment of male reproductive
608 behaviors of the freeze-tolerant wood frog, *Rana sylvatica*. *Physiological*
609 *Zoology*, **70**, 158–166.
- 610 Crouch WB, Paton PWC (2000) Using egg-mass counts to monitor wood frog
611 populations. *Wildlife Society Bulletin*, **28**, 895–901.
- 612 Daly C, Gibson WP, Taylor GH, Johnson GL, Pasteris P (2002) A knowledge-based
613 approach to the statistical mapping of climate. *Climate Research*, **22**, 99–113.

- 614 Darwin CR (1859) On the Origin of Species By Means of Natural Selection, or the
615 Preservation of Favoured Races in the Struggle For Life. John Murray, London,
616 UK.
- 617 De Valpine P, Hastings A (2002) Fitting population models incorporating process noise
618 and observation error. *Ecological Monographs*, **72**, 57–76.
- 619 Dormann CF, Schymanski SJ, Cabral J et al. (2012) Correlation and process in species
620 distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–
621 2131.
- 622 Drexler JZ, Synder RL, Spano D, Paw U KT (2004) A review of models and
623 micrometeorological methods used to estimate wetland evapotranspiration.
624 *Hydrological Processes*, **18**, 2071–2101.
- 625 Duellman WE, ed (1999) Patterns of distribution of amphibians. Johns Hopkins
626 University Press, Baltimore, MD.
- 627 Earl JE, Semlitsch RD (2012) Reciprocal subsidies in ponds: does leaf input increase frog
628 biomass export? *Oecologia*, **170**, 1077–1087.
- 629 Environment Canada (2014) Canadian monthly climate data.
630 http://climate.weather.gc.ca/historical_data/search_historic_data_e.html.
631 Accessed 19 June 2015.
- 632 Franklin J (2010) Moving beyond static species distribution models in support of
633 conservation biogeography. *Diversity and Distributions*, **16**, 321–330.
- 634 Gaston KJ (2009) Geographic range limits: achieving synthesis. *Proceedings of the Royal
635 Society B: Biological Society*, **276**, 1395–1406.
- 636 Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple
637 sequences. *Statistical Science*, **7**, 457–511.
- 638 Gibbs JP, Breisch AR (2001) Climate warming and calling phenology of frogs near
639 Ithaca, New York, 1990–1999. *Conservation Biology*, **15**, 1175–1178.
- 640 Grant EHC, Miller DAW, Schmidt BR, Adams MJ, Amburgey SM, Chambert T,
641 Cruickshank SS, Fisher RN, Green DM, Hossack BR, Johnson PTJ, Joseph MB,
642 Rittenhouse TAG, Ryan ME, Waddle JH, Walls SC, Bailey LL, Fellers GM,
643 Gorman TA, Ray AM, Pilliod DS, Price SJ, Saenz D, Sadinski W, Muths E

- 644 (2016) Quantitative evidence for the effects of multiple drivers on continental-
645 scale amphibian declines. *Scientific Reports*, **6**, 25626.
- 646 Grant EHC, Jung RE, Nichols JD, Hines JE (2005) Double-observer approach to
647 estimating egg mass abundance of pool-breeding amphibians. *Wetlands Ecology*
648 *and Management*, **13**, 305–320.
- 649 Green AW, Bailey LL (2015) Reproductive strategy and carry-over effects for species
650 with complex life histories. *Population Ecology*, **57**, 175–184.
- 651 Green AW, Hooten MB, Grant EHC, Bailey LL (2013) Evaluating breeding and
652 metamorph occupancy and vernal pool management effects for wood frogs using
653 a hierarchical model. *Journal of Animal Ecology*, **50**, 1116–1123.
- 654 Grinnell J (1917) The niche-relationships of the California Thrasher. *The Auk*, **34**, 427–
655 433.
- 656 Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology.
657 *Ecological Modeling*, **135**, 147–186.
- 658 Guo Q, Taper M, Schoeneberger MM, Brandle JR (2005) Spatial-temporal population
659 dynamics across species range: from centre to margin. *Oikos*, **108**, 47–57.
- 660 Harper EB, Rittenhouse TAG, Semlitsch RD (2008) Demographic consequences of
661 terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks
662 associated with inadequate size of buffer zones. *Conservation Biology*, **22**, 1205–
663 1215.
- 664 Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the
665 effect of climate change on species distributions. *Global Change Biology*, **12**,
666 2272–2281.
- 667 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution
668 interpolated climate surfaces for global land areas. *International Journal of*
669 *Climatology*, **25**, 1965–1978.
- 670 HilleRisLambers J, Harsch MA, Ettinger AK, Ford KR, Theobald EJ (2013) How will
671 biotic interactions influence climate change-induced range shifts? *Annals of the*
672 *New York Academy of Sciences*, **1297**, 112–125.
- 673 Hoffman AA, Parsons PA (1997) *Extreme Environmental Change and Evolution*.
674 Cambridge University Press, Cambridge, UK.

- 675 Hutchinson VH, Dupré K (1992) Thermoregulation. In: Environmental Physiology of the
676 Amphibia (eds Feder ME and Burggren WW), PP. 206–249. University of
677 Chicago Press, Chicago, OH.
- 678 IUCN (International Union for Conservation of Nature) (2015) *Lithobates sylvaticus*. The
679 IUCN Red List of Threatened Species. Version 3.1. <http://www.iucnredlist.org>.
680 Downloaded on 6 October 2015.
- 681 Keith DA, Akçakaya HR, Thuiller W et al. (2008) Predicting extinction risks under
682 climate change: coupling stochastic population models with dynamic bioclimatic
683 habitat models. *Biology Letters*, **4**, 560–563.
- 684 Kéry M, Schaub M. 2012. Chapter 5 - State Space Models for Population Counts. In:
685 Bayesian Population Analysis using WinBUGS: A hierarchical perspective, PP.
686 115-132. Academic Press Waltham, MA, USA.
- 687 Köhler A, Sadowska J, Olszewska J, Trzeciak P, Berger-Tal O, Tracy CR (2011) Staying
688 warm or moist? Operative temperature and thermal preferences of common frogs
689 (*Rana temporaria*), and effects on locomotion. *Herpetological Journal*, **21**, 17–26.
- 690 Larson DJ, Middle L, Vu H, Zhang W, Serianni AS, Duman J, Barnes BM (2014) Wood
691 frog adaptations to overwintering in Alaska: new limits to freezing tolerance. The
692 *Journal of Experimental Biology*, **217**, 2193–2200.
- 693 Laugen AT, Laurila A, Räsänen K, Merilä J (2003) Latitudinal countergradient variation
694 in the common frog (*Rana temporaria*) development rate - evidence for local
695 adaptation. *Journal of Evolutionary Biology*, **16**, 996–1005.
- 696 Lawton JH (1995) Population dynamic principles. In: Extinction
697 Rates (eds Lawton JH, May RM), PP. 147–163. Oxford University
698 Press, Oxford, UK.
- 699 MacArthur RH (1972) Geographical ecology: patterns in the distribution of species.
700 Harper and Row, New York, NY.
- 701 MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006)
702 Occupancy estimation and modeling: inferring patterns and dynamics of species
703 occurrence. Academic Press, Burlington, MA, USA.
- 704 Manis ML, Claussen DL (1986) Environmental and genetic influences on the physiology
705 of *Rana sylvatica*. *Journal of Thermal Biology*, **11**, 31–36.

- 706 Meehl GA, Stocker TF, Collins WD, et al. (2007) Global Climate Projections. In:
707 Climate Change 2007: The Physical Science Basis. Contribution of Working
708 Group I to the Fourth Assessment Report of the Intergovernmental Panel on
709 Climate Change (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M,
710 Averty KB, Tignor M and Miller HL). Cambridge University Press, Cambridge,
711 UK and New York, NY, USA.
- 712 Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of
713 community structure. *Trends in Ecology and Evolution*, **5**, 52-57.
- 714 Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA (2014)
715 On using integral projection models to generate demographically driven
716 predictions of species' distributions: Development and validation using sparse
717 data. *Ecography*, **37**, 1167–1183.
- 718 Normand S, Zimmermann NE, Schurr FM, Lischke H (2014) Demography as the basis
719 for understanding and predicting range dynamics. *Ecography*, **37**, 1149–1154.
- 720 O'Connor JH, Rittenhouse TAG (2016) Snow cover and late fall movement influence
721 wood frog survival during an unusually cold winter. *Oecologia*, **181**, 635–644.
- 722 Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on
723 terrestrial biota. *Bulletin of the American Meteorological Society*, **81**, 443–450.
- 724 Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the
725 distribution of species: Are bioclimatic envelope models useful? *Global Ecology
726 and Biogeography*, **12**, 361–371.
- 727 Pechmann JHK, Scott DE, Gibbons JW, Semlitsch RD (1989) Influence of wetland
728 hydroperiod on diversity and abundance of metamorphosing juvenile amphibians.
729 *Wetlands Ecology and Management*, **1**, 3–11.
- 730 Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using
731 Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed
732 Statistical Computing (DSC 2003). Vienna, Austria.
- 733 R Core Team (2016) R: A language and environment for statistical computing. R
734 Foundation for Statistical Computing. Available at <http://www.R-project.org>.

- 735 Ranvestel AW, Lips KR, Pringle CM, Whiles MR, Bixby RJ (2004) Neotropical tadpoles
736 influence stream benthos: evidence for the ecological consequences of decline in
737 amphibian populations. *Freshwater Biology*, **49**, 274–285.
- 738 Redmer M, Trauth SE (2005) *Rana sylvatica* LeConte, 1825. Wood frog. In: *Amphibian*
739 *declines: the conservation status of United States species* (eds Lannoo M). PP.
740 590–593. University of California Press, Berkeley and Los Angeles, CA, USA.
- 741 Relyea RA (2002) Costs of phenotypic plasticity. *American Naturalist*, **159**, 272–282.
- 742 Rittenhouse TAG, Semlitsch RD (2007) Postbreeding habitat use of wood frogs in a
743 Missouri forest. *Journal of Herpetology*, **41**, 645–653.
- 744 Rittenhouse TAG, Semlitsch RD, Thompson III FR (2009) Survival costs associated with
745 wood frog breeding migrations: effects of timber harvest and drought. *Ecology*,
746 **90**, 1620–1630.
- 747 Ross BE, Hooten MB, DeVink J, Koons DN (2015) Combined effects of climate,
748 predation, and density dependence on Greater and Lesser Scaup population
749 dynamics. *Ecological Applications*, **25**, 1606–1617.
- 750 Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and Ecology of Species
751 Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–
752 436.
- 753 Skidds DE, Golet FC, Paton PWC, Mitchell JC (2007) Habitat correlates of reproductive
754 effort in wood frogs and spotted salamanders in an urbanizing watershed. *Journal*
755 *of Herpetology*, **41**, 439–450.
- 756 Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian
757 ecology and conservation: are all amphibian populations metapopulations?
758 *Ecography*, **28**, 110–128.
- 759 Storey KB (1987) Organ-specific metabolism during freezing and thawing in a freeze-
760 tolerant frog. *American Journal of Physiology- Regulatory, Integrative and*
761 *Comparative Physiology*, **253**, R292–R297.
- 762 Storey KB, Storey JM (1986) Freeze tolerance and intolerance as strategies of winter
763 survival in terrestrially-hibernating amphibians. *Comparative Biochemistry and*
764 *Physiology*, **83A**, 613–617.

- 765 Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DI, Waller RW
766 (2004) Status and trends of amphibian declines and extinctions worldwide.
767 *Science*, **306**, 1783–1786.
- 768 Su Y, Yajima M (2015) R2jags: Using R to Run 'JAGS'. R package version 0.5-7.
769 Available at <https://CRAN.R-project.org/package=R2jags>.
- 770 Thomas CD (2010) Climate, climate change and range boundaries. *Diversity and*
771 *Distributions*, **16**, 488–495.
- 772 Thuiller W, Lavorel S, Araújo MB (2005) Niche properties and geographical extent as
773 predictors of species sensitivity to climate change. *Global Ecology and*
774 *Biogeography*, **14**, 347–357.
- 775 Thuiller W, Albert C, Araújo MB et al. (2008) Predicting global change impacts on plant
776 species' distributions: Future challenges. *Perspectives in Plant Ecology,*
777 *Evolution, Systematics*, **9**, 137–152.
- 778 Thuiller W, Münkemüller T, Schiffrers KH et al. (2014) Does probability of occurrence
779 relate to population dynamics? *Ecography*, **37**, 1155–1166.
- 780 Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian
781 niche throughout a century of climate change. *Proceedings of the National*
782 *Academy of the Sciences USA*, **106**, 19637:19643.
- 783 United State Geological Survey (USGS) National Amphibian Atlas (2014) Wood frog
784 (*Lithobates sylvaticus*). Version Number 3.0 USGS Patuxent Wildlife Research
785 Center, Laurel, Maryland. Available at www.pwrc.usgs.gov/naa.
- 786 Urban MC, Zarnetske PL, Skelly DK (2013) Moving forward: dispersal and species
787 interactions determine biotic responses to climate change. *Annals of the New*
788 *York Academy of Sciences*, **1297**, 44–60.
- 789 Urban MC, Richardson JL, Freidenfelds NA (2014) Plasticity and genetic adaptation
790 mediate amphibian and reptile responses to climate change. *Evolutionary*
791 *Applications*, **7**, 88–103.
- 792 Werner EE, Relyea RA, Yurewicz KL, Skelly DK, Davis CJ (2009) Comparative
793 landscape dynamics of two anuran species: climate-driven interaction of local and
794 regional processes. *Ecological Monographs*, **79**, 503–523.

795 Williams J, Jackson ST (2007) Novel climates, no-analog communities, and ecological
796 surprises. *Frontiers in Ecology and the Environment*, **5**, 475-482.
797 Zurell D, Jeltsch F, Dormann CF, Schröder B (2009) Static species distribution models in
798 dynamically changing systems: how good can predictions really be? *Ecography*,
799 **32**, 733–744.

800

801 **Figure 1.** The wood frog is a broadly distributed species that spans most of the
802 northeastern United States into Canada and Alaska. Red dots indicate sites where egg
803 mass counts were obtained. Thirty-year annual **(a)** precipitation and **(b)** temperature
804 (Hijmans et al. 2005) maps show the broad range of climate conditions this species
805 experiences across its range (IUCN 2014).

806

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

823

824 **Figure 3.** The climate space [based on 30-year mean annual temperature ($^{\circ}\text{C} \times 10$) and
825 precipitation values (mm)] that encompasses North America (dark blue), the wood frog

826 range (light green), and our sites (red). Points on the scatterplot represent all temperature
827 by precipitation raster cell values where wood frogs occur (light green) and do not occur
828 (dark blue), with our sites in red. Precipitation values were truncated at 3500 mm for
829 visualization purposes. Histograms represent frequencies of these same 30-year annual
830 precipitation (top) and temperature (right) values in just the wood frog range. Boxplots of
831 precipitation and temperature values from our sites show the minimum, median,
832 maximum and 25th and 75th quartiles (box).

833

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

854

855 **Figure 5.** We estimated how sensitivity of wood frog population growth rates to annual
856 climate variation changed with respect to long-term climate differences (shaded regions

857 are 95% credible intervals). Sensitivity is the expected change in annual population
858 growth rate (r) for a one standard deviation increase in annual conditions (y-axis). Long-
859 term differences in mean climate are calculated using 30-year climate normals for
860 conditions during the same portion of the year that annual covariates are measured (x-
861 axis; see Tables 1 and 2) at our sampled sites. **(a)** Annual wood frog population growth
862 rate two years later did not significantly respond to spring precipitation (PRECIP lag)
863 regardless of long-term winter severity, **(b)** annual wood frog population growth rate did
864 not significantly respond to winter severity (COLD) regardless of long-term spring
865 precipitation, **(c)** annual wood frog population growth rate did not significantly respond
866 to summer water availability (HYDRO) regardless of long-term extreme summer heat,
867 **(d)** annual wood frog population growth rate responded positively to years with more
868 extreme summer temperatures (HYDRO lag) in areas where long-term average summer
869 precipitation was higher (>20 mm), **(e)** annual wood frog population growth rate two
870 years later responded negatively to increased summer water availability (HYDRO lag) in
871 areas where long-term average extreme temperature was higher ($>26.25^{\circ}\text{C}$) and
872 positively where long-term averages were lower ($<26.25^{\circ}\text{C}$).

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

Covariate	Definition	Ecological Importance
Precip = Standardized Precipitation Index 3-month (SPI3) ¹	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., Feb-Apr) 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 ^{2,3}
Hydro = Standardized Precipitation Evapotranspiration Index 3- month (SPEI3) ⁴	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 ⁵
Heat = Extreme Heat Index (EHI) ⁴	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 ^{3,5}
Cold = Air Freezing Index (AFI) ⁴	Cumulative index of freeze severity and frost depth that factors in magnitude and duration of below freezing air temperatures ⁶	Though freeze tolerance has been demonstrated in this species ⁷ , extreme cold temperatures and long durations of cold temperatures may reduce overwinter survival of juveniles and adults ⁸

¹ National Climatic Data Center, NOAA (2015)

² Rittenhouse et al. (2009)

³ Davis et al. (in prep)

⁴ Daly et al. (2002)

⁵ Brooks (2004)

⁶ Bilotta et al. (2015)

⁷ Storey and Storey (1986)

⁸ O'Connor and Rittenhouse (2016)

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1 **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.,
 2 values are constant over time). Their interaction with annual climate covariate values (Table 1) indicated if population growth rates differ
 3 in sensitivity across the range. The predicted relationship of the interaction between annual and long-term climate covariates to population
 4 growth rates across the wood frog range represent hypotheses from the bioclimatic envelope model.

Covariate	Definition	Ecological Importance	Predicted Annual and Long-term Interaction (Bioclimatic Envelope Model)
nmPrecip = Precip Normal ⁸	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	Precip * nmPrecip Negative impact of drier years in drier areas
nmHydro = Hydroperiod Normal ⁸	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	Hydro * nmHydro Negative impact of drier years in drier areas
nmHeat = Heat Normal ⁸	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	Heat * nmHeat Negative impact of hotter years in hotter areas
nmCold = Cold Normal ⁸	30-year minimum monthly temperature over similar mid-winter period as AFI	Measure of winter severity patterns, long term cold regime	Cold * nmCold Negative impact of colder years in colder areas

5 ⁸ WorldClim; Hijmans et al. (2005)

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

Model Name	Parameters
Precip (2-yr lag)	$\beta_1(\text{Precip}_{2\text{yr}}) + \beta_2(\text{nmPrecip}) + \beta_3(\text{Precip}_{2\text{yr}} * \text{nmPrecip}) + \delta_i + \varepsilon_{ti}$
Hydro	$\beta_1(\text{Hydro}) + \beta_2(\text{nmHydro}) + \beta_3(\text{Hydro} * \text{nmHydro}) + \delta_i + \varepsilon_{ti}$
Hydro (2-yr lag)	$\beta_1(\text{Hydro}_{2\text{yr}}) + \beta_2(\text{nmHydro}) + \beta_3(\text{Hydro}_{2\text{yr}} * \text{nmHydro}) + \delta_i + \varepsilon_{ti}$
Heat	$\beta_1(\text{Heat}) + \beta_2(\text{nmHeat}) + \beta_3(\text{Heat} * \text{nmHeat}) + \delta_i + \varepsilon_{ti}$
Cold	$\beta_1(\text{Cold}) + \beta_2(\text{nmCold}) + \beta_3(\text{Cold} * \text{nmCold}) + \delta_i + \varepsilon_{ti}$
Precip (2-yr lag) and Cold by long-term climate	$\beta_1(\text{Precip}_{2\text{yr}}) + \beta_2(\text{nmPrecip}) + \beta_3(\text{Precip}_{2\text{yr}} * \text{nmPrecip}) + \beta_4(\text{Cold}) + \beta_5(\text{nmCold}) + \beta_6(\text{Cold} * \text{nmCold}) + \beta_7(\text{Precip}_{2\text{yr}} * \text{nmCold}) + \beta_8(\text{Cold} * \text{nmPrecip}) + \delta_i + \varepsilon_{ti}$
Hydro and Heat by long- term climate	$\beta_1(\text{Hydro}) + \beta_2(\text{nmHydro}) + \beta_3(\text{Hydro} * \text{nmHydro}) + \beta_4(\text{Heat}) + \beta_5(\text{nmHeat}) + \beta_6(\text{Heat} * \text{nmHeat}) + \beta_7(\text{Hydro} * \text{nmHeat}) + \beta_8(\text{Heat} * \text{nmHydro}) + \delta_i + \varepsilon_{ti}$
Hydro (2-yr lag) and Heat by long-term climate	$\beta_1(\text{Hydro}_{2\text{yr}}) + \beta_2(\text{nmHydro}) + \beta_3(\text{Hydro}_{2\text{yr}} * \text{nmHydro}) + \beta_4(\text{Heat}) + \beta_5(\text{nmHeat}) + \beta_6(\text{Heat} * \text{nmHeat}) + \beta_7(\text{Hydro}_{2\text{yr}} * \text{nmHeat}) + \beta_8(\text{Heat} * \text{nmHydro}) + \delta_i + \varepsilon_{ti}$

7

1 **Table 4.** Parameter estimates from the four main climate covariate models. Precip, Hydro, Heat,
2 and Cold represent annual climate values. nmPrecip, nmHydro, nmHeat, and nmCold are the
3 long-term (~30 year) climate normal values. Interaction terms of annual and normal values (e.g.,
4 Precip*nmPrecip) represent the effect of an annual climate value by different long-term climate.
5 SD is the standard deviation of a parameter estimate, and $q_{0.025-0.975}$ represent 2.5th, 50th, and
6 97.5th quartile values.

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

7

1 **Table 5.** Parameter estimates from the interaction model of spring precipitation and winter
 2 severity. Precip and Cold represent annual climate values. nmPrecip and nmCold are the long-
 3 term (~30 year) climate normal values. Interaction terms of annual and normal values (e.g.,
 4 Precip*nmPrecip) represent the effect of an annual climate value by different long-term climate.
 5 SD is the standard deviation of a parameter estimate, and $q_{0.025-0.975}$ represent 2.5th, 50th, and
 6 97.5th quartile values.

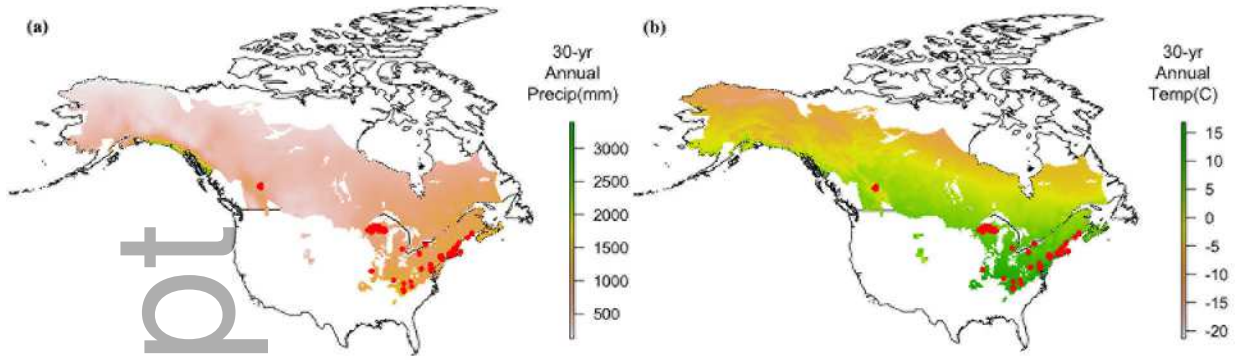
Model: Precip (2-yr lag) and Cold by long-term climate conditions					
Parameter	Mean	SD	Q_{0.025}	Q_{0.500}	Q_{0.975}
Precip (2-yr lag)	-0.192	0.126	-0.439	-0.192	0.055
nmPrecip	-8.00e-03	0.0110	-0.0300	-8.00e-03	0.0140
Precip (2-yr lag)* nmPrecip	9.00e-03	0.0170	-0.0240	9.00e-03	0.0420
Cold	-0.398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

7

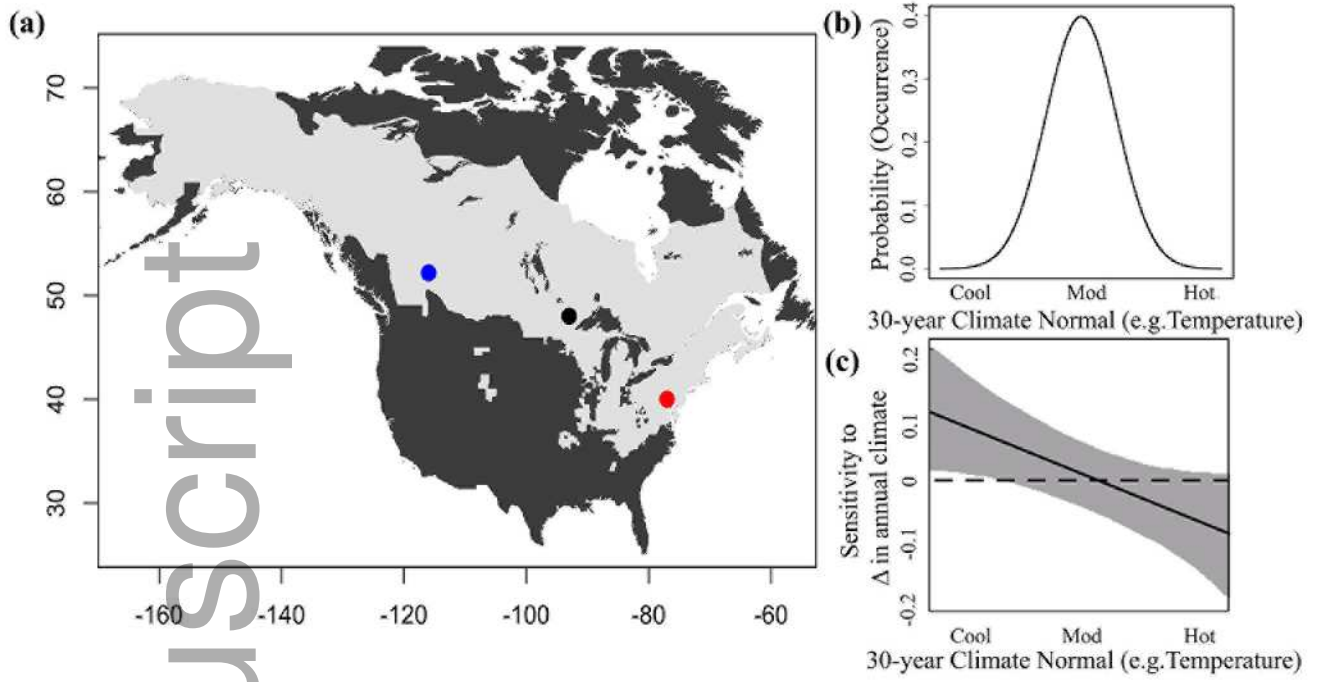
1 **Table 6.** Parameter estimates from the interaction model of summer water availability and
 2 extreme heat. Hydro and Heat represent annual climate values. nmHydro and nmHeat are the
 3 long-term (~30 year) climate normal values. Interaction terms of annual and normal values (e.g.,
 4 Hydro*nmHydro)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

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

7



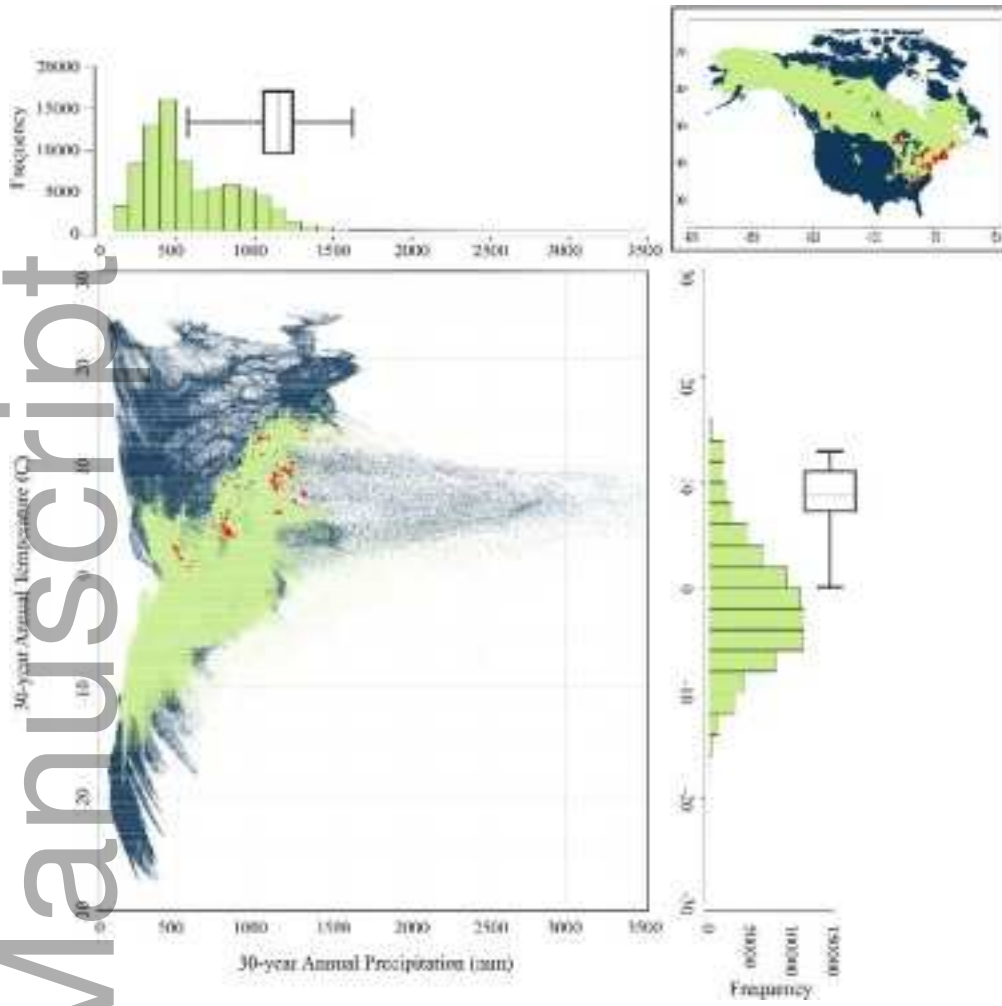
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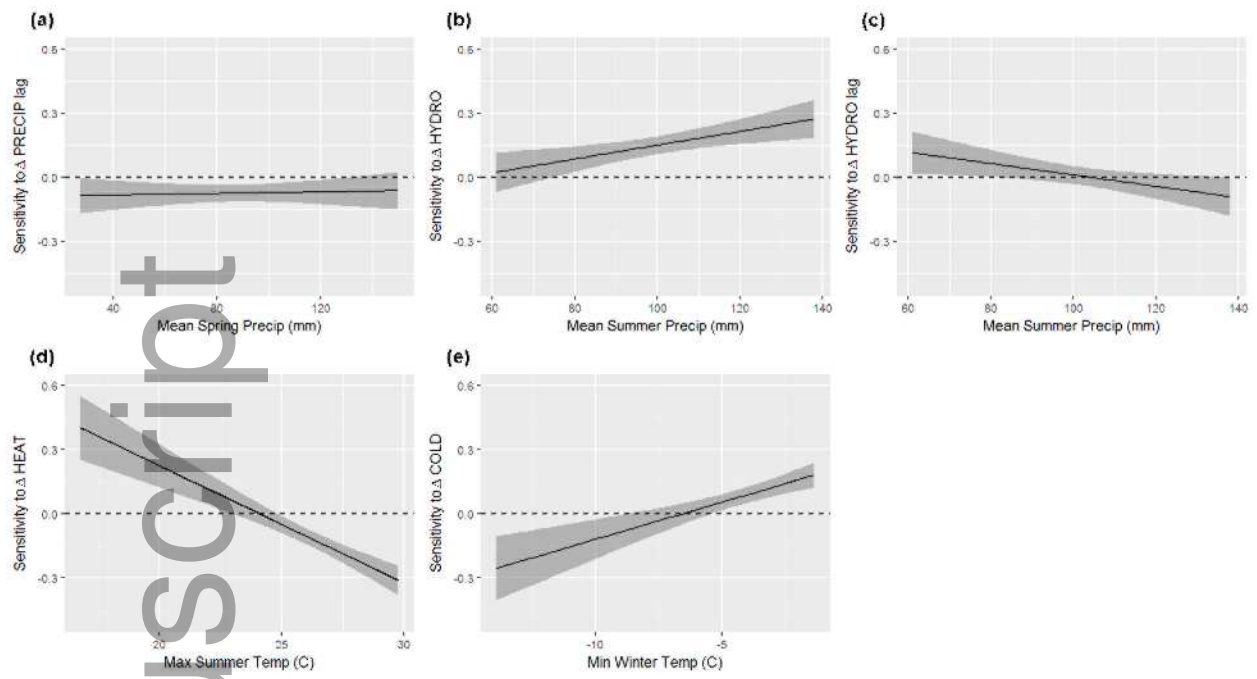
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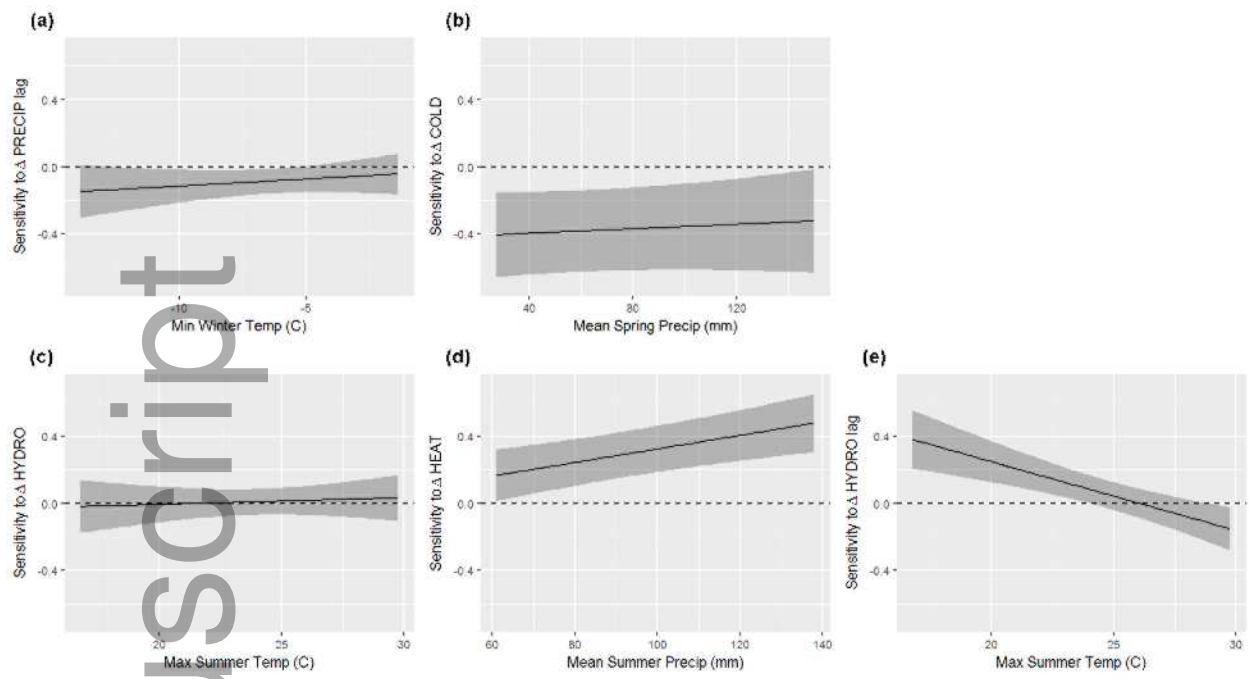
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