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RESEARCH PAPER

Evaluating confidence in climate-based predictions of population change in a migratory species

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ABSTRACT

Aim Forecasting ecological responses to climate change is a common objective, but there are few methods for evaluating confidence in such predictions. For migratory species, in particular, it is also essential to consider the extent of spatial synchrony among separate breeding populations in range-wide predictions. We develop a quantitative method to evaluate the accuracy of climate-based ecological predictions and use this approach to assess the extent of spatio-temporal synchrony among distinct regions within the breeding range of a single migratory population.

Location We model weekly site-specific summer abundances (1996–2011) of monarch butterflies (*Danaus plexippus*) in the Midwestern USA as a function of climate conditions experienced during a shared spring migration/breeding phase in Texas and separate summer recruitment periods in Ohio and Illinois.

Methods Using negative binomial regression models, we evaluate spatio-temporal synchrony between monarchs in the two states and develop a novel quantitative assessment approach to determine the temporal predictive strength of our model with Bayesian *P*-values.

Results Monarchs breeding in the Midwest exhibit spatio-temporal synchrony in Ohio and Illinois; cooler spring temperatures, average to above average precipitation in Texas and cooler than average summer temperatures are associated with higher population abundances in both states. At least 10 years of data are needed for adequate model predictability of average future counts. Because annual spring weather conditions in Texas primarily drive yearly abundances, as opposed to localized summer effects, year-specific counts are often difficult to predict reliably, specifically when predictive spring conditions are outside the range of typical regional conditions.

Main conclusions Our assessment method can be used in similar analyses to more confidently interpret ecological responses to climate change. Our results demonstrate the relative importance of climatic drivers in predicting abundances of a migratory species and the difficulties in producing reliable predictions of animal populations in the face of climate change.

Keywords

Climate change, *Danaus plexippus*, forecasting, migratory, monarch butterflies, negative binomial model, prediction, spatial synchrony.

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INTRODUCTION

As environmental and climate conditions change, forecasting future distributions of species (Brooker *et al.*, 2007; Mustin *et al.*, 2009; Kubisch *et al.*, 2013), population sizes (Roy *et al.*, 2001; Huntley *et al.*, 2010) and changes in range-wide habitat suitability (Brotons *et al.*, 2004) are vitally important for the development of effective conservation strategies via proactive preservation and restoration measures. One common approach to predicting the potential effects of climate change employs statistical models, which use empirical data to define relationships between current species distributions/ abundances and environmental drivers (Iverson & Prasad, 2001). The environment (e.g. covariate values) is then 'changed' according to expert opinion and/or model-based projections of land use or climate change (i.e. forecasting models; Berteaux *et al.*, 2006), and the statistical relationships are extrapolated forward to define new possible species distributions and abundances (e.g. Roy *et al.*, 2001; Acevedo *et al.*, 2010; Stewart *et al.*, 2015). Commonly employed statistical models for this purpose include general linear models, general additive models, regression tree models and multivariate adaptive regression splines (Iverson & Prasad, 2001).

This method of prediction from observational studies assumes that the climatic relationships demonstrated during a given study period will hold true under future conditions. Yet this assumption is rarely tested (Berteaux *et al.*, 2006; Raffa *et al.*, 2008; Jamieson *et al.*, 2012; Kerr & Dobrowski, 2013). Model validation for such analyses frequently involves omitting a random subset of data and assessing the accuracy of predicted omitted values. Typically, these predictions occur over the same time period and spatial extent as the data that are included in the model (i.e. semi-independent model validation; Lawler *et al.*, 2009), leading to problems of temporal and spatial autocorrelation in the calibration and validation sets (Araújo *et al.*, 2005). Population-level predictions under future climate scenarios commonly occur outside the observed parameter space from which measurements are available. Little guidance exists on how to evaluate confidence in these predictions from statistical models (Berteaux *et al.*, 2006; Kerr & Dobrowski, 2013), even as models to evaluate the impacts of climate change predictions become ever more sophisticated (Lawler *et al.*, 2009). Thus, predictions from such studies are prone to over-interpretation (Ehrlén & Morris, 2015), given that ecological processes may be responding to climate at finer temporal scales than that of the study period or altogether dissimilarly in ecologically and geographically distinct areas. Finally, future climate conditions may be outside the range for which data are available and thus parameter estimates on climate covariates may not characterize future conditions well. Establishing a level of confidence for these types of predictions is an essential next step in understanding the climatic drivers of population dynamics and distributions.

Predicting the impacts of climate change on migratory species is especially complicated, given that they travel through several climates that change differentially throughout their migratory range. Understanding how seasonal interactions (e.g. carry-over effects, environmental changes) affect distinct populations of a migratory species can reveal the extent of migratory connectivity across a region (Norris & Marra, 2007; Pasinelli *et al.*, 2011), and consequently help predict the impacts of climate change. Migratory insects in particular are expected to be substantially affected by climate change because they are responsive to temperature and have relatively short life cycles and high reproductive capacity (Stange & Ayres, 2010). Yet few long-term studies have investigated the effects of present and future climate on migratory insects, typically due to difficulties in defining appropriate fine-scale spatio-temporal climate metrics (but see Olfert et al., 2011; Zipkin *et al.*, 2012). Furthermore, many migratory insect species have a wide geographical extent, but investigations of spatial synchrony among populations in response to climate conditions are rare. This is most likely due to sparse spatial data collected concurrently over a multi-year period (with the exception of insect outbreak studies; e.g. Williams & Liebhold, 2000). Thus, it is difficult to establish whether responses measured in a particular study area are applicable throughout a species' range.

The monarch butterfly (*Danaus plexippus*) is an ideal focal species for analyzing current and predicting future climate responses; it has a broad migratory range and the available monitoring data encompass a wide spatial and temporal extent (Ries *et al.*, 2015). Climate (e.g. temperature, precipitation) directly affects monarch juvenile development (Zalucki, 1982; York & Oberhauser, 2002; Couture *et al.*, 2015; Nail *et al.*, 2015), adult survival (Alonso-Mejia & Arellano-Guillermo, 1992) and reproduction (Barker & Herman, 1976). Monarchs are also affected indirectly by climatic impacts on the growth and vitality of their host plants (Zalucki *et al.*, 2004). Couture *et al.* (2015) demonstrated that elevated temperatures and periodic water stress affected the growth of common milkweed (*Asclepias syriaca*) and performance of monarch larvae, and York & Oberhauser (2002) and Nail *et al.* (2015) documented both lethal and sublethal effects of extreme temperatures on larvae. Additionally, an increase in extreme weather events (with lethal conditions for monarch survival) due to climate change has been suggested as a significant factor affecting the future viability of present-day overwintering sites in central Mexico (Barve *et al.*, 2012). Therefore, climate is an important driver of annual fluctuations in monarch population dynamics, albeit a complex factor, given the geographical extent of their migratory range.

This study uses long-term (1996–2011) monarch data from two independent state-wide monitoring programs in Ohio and Illinois to examine how climate conditions experienced during a shared spring migration/breeding phase in Texas, as well as during subsequent arrival and summer breeding in separate recruitment areas, explain variation in year-to-year fluctuations in abundance on monarch summer breeding grounds. We outline a novel quantitative assessment method, employing Bayesian *P*-values (a goodness of fit metric), to evaluate confidence in population-level predictions of expected counts, using a subset of the survey data to generate predictions and then testing those predictions using actual observed weather conditions in other years. Our method considers both data availability and model structure, allowing for a more rigorous evaluation of predictive ability, both spatially and temporally. More specifically, by comparing climate impacts on breeding monarch butterflies in different portions of their breeding range over a 16-year period, we determine: (1) how confidently we can extrapolate results from one study region to another by examining spatial synchrony in results from two independent datasets, and (2) how confidently we can extrapolate predictions to future climate conditions, especially if climate projections are outside the parameter region for which data are available. Our assessment method can be used in similar analyses to: (1) understand the predictive limitations of a given dataset and regression model, and (2) determine a level of confidence when interpreting the ecological responses of a population to a changing climate.

METHODS

Focal species

We focus on the eastern migratory monarch population, the larger of two nearly separate populations in North America (Brower, 1986; Pyle, 2015). The eastern migratory population extends from the east coast to the Rocky Mountains during its summer breeding phase and overwinters in dense forest colonies at the boundary of the Mexican states of Michoacán and México (Brower, 1986). Spring migrants move into Texas and surrounding areas by mid March (Cockrell *et al.*, 1993; Malcolm & Zalucki, 1993) and lay eggs on host plants in the subfamily Asclepiadoidae (milkweeds), which are found throughout much of North America. The eggs laid by the spring migrants are that year's first generation, which subsequently colonizes more northerly areas of eastern North America beginning in early May. Throughout the remainder of the summer, the population grows by an additional two or three generations, with the bulk of recruitment occurring in the Midwestern United States (Wassenaar & Hobson, 1998). The final generation, which migrates to Mexico, varies substantially in size each year (Pleasants & Oberhauser, 2013); the causes of such fluctuations are not well understood, although climate (Zalucki *et al.*, 2004; Zipkin *et al.*, 2012) and habitat availability (Pleasants & Oberhauser, 2013) are contributing factors. Beginning in mid August, monarchs enter reproductive diapause and start to move southward, with most flying to the Mexican overwintering sites (Brower, 1986).

Monarch data collection

Our analysis used state-wide butterfly monitoring data collected in Ohio and Illinois. Both states have a well-established network of volunteers who surveyed consistently during the study period and are within the main area of monarch recruitment. The Ohio program was initiated in 1995 by the Ohio Lepidopterist Society, and we included data collected at 116 locations from 1996 to 2011 ($n = 13{,}038$ surveys). The annual number of survey locations varied between 13 (1996) and 60 (2003), and the mean number of surveys conducted per site was 129 ± 89 (SD; range 6–369). Locations were dispersed throughout the state (Fig. 1), and several kilometers usually separated the closest sites (with none closer than 1 km). Although the Illinois monitoring program began collecting data in 1987, our analysis used data from 1996–2011 to allow direct comparison with Ohio. The Illinois program also manages sites in Indiana (close to the Illinois border; Fig. 1), which we included in our analyses. The annual number of survey locations in Illinois varied annually between 29 (1996) and 94 (2005), and the mean number of surveys conducted per site was 53 ± 28 (range 20–129). We excluded under-surveyed locations (i.e. surveyed on fewer than 20 occasions between 1996 and 2011; 12% of survey data), yielding a total of 133 locations for analysis (Fig. 1; $n = 6{,}506$ surveys). Locations were dispersed throughout northern and central Illinois, with the majority of sites occurring within 160 km of Chicago; all sites were at least 1 km apart. In both states, each location was surveyed by a volunteer who visited his or her assigned location up to once weekly during the peak study period (June through August), but not all locations were surveyed every week or during every year. At each survey point, the observer walked a fixed transect of variable length and recorded all butterflies (not just monarchs) seen within approximately 5 m (Pollard, 1977). Transect lengths varied between sites, but remained fixed at sites from year to year. Observers recorded the time spent on each survey to account for variable transect lengths and monitoring effort.

Data summary and analyses

Our analysis examined the impacts of climate experienced by the first generation of monarchs in Texas and during summer recruitment phases in Ohio and Illinois (subsequent generations). We sequentially numbered each week in the season, beginning with the migration from Mexico that occurs in the beginning of March; thus, week 1 begins on 1 March. Spring breeding in Texas occurs between the last week in March up to the end of April (weeks 4–9; Prysby & Oberhauser, 2004). Emerging adults in the spring then arrive in the Midwest (e.g. Ohio and Illinois) by the first week in May (week 10; Howard & Davis, 2004), and increase in abundance during mid June to mid July (weeks 15–20; Prysby & Oberhauser, 2004). Population growth continues through to the beginning of September (week 28; Brower, 1986; Prysby & Oberhauser, 2004).

Climate data

The influence of temperature on monarch abundances was quantified via growing degree days (GDD), which measure

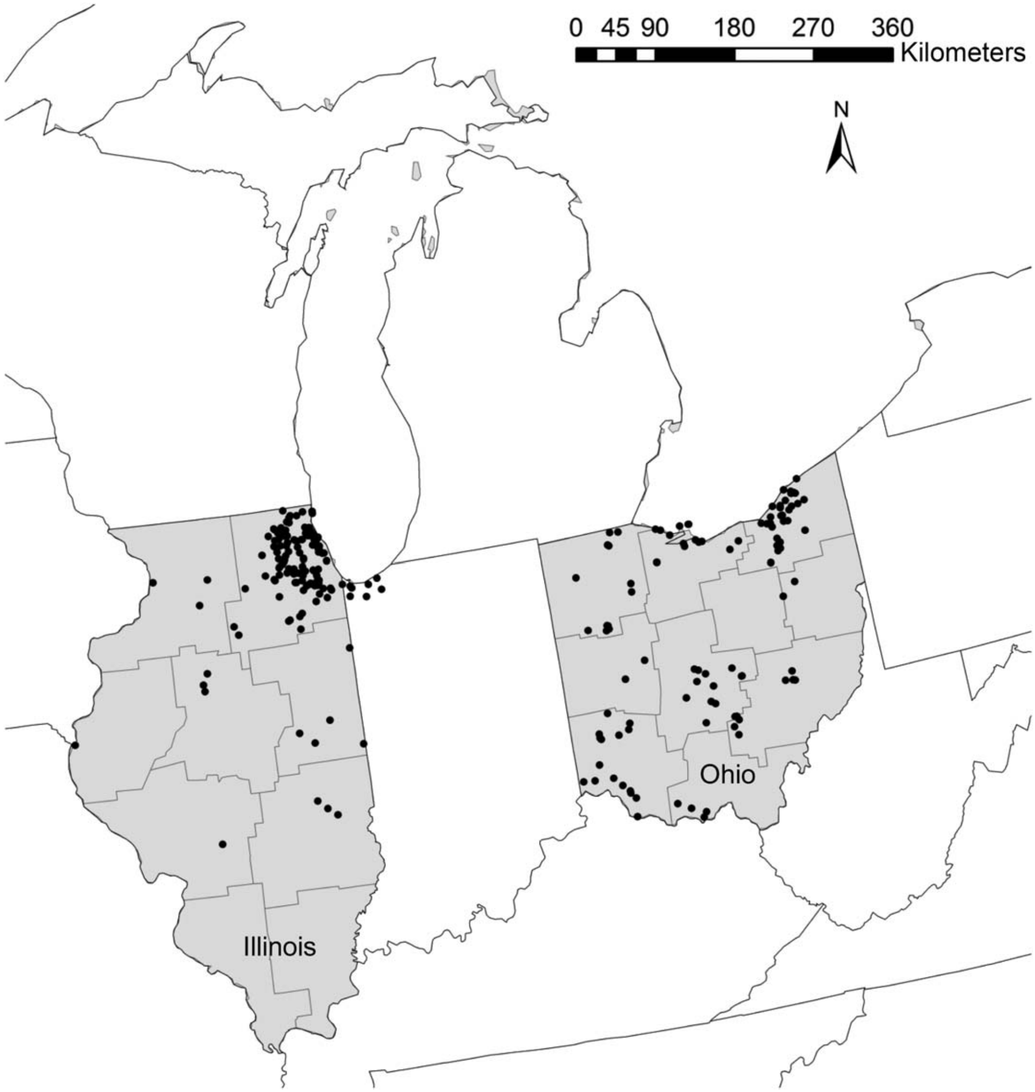

Figure 1 Monarch survey locations in Illinois (left; $n = 133$) and Ohio (right; $n = 116$) for 1996–2011. Delineations shown within each state represent the nine NOAA-defined climate divisions in Illinois and ten divisions in Ohio. Locations shown in Indiana (center) are part of the Illinois monitoring program.

the accumulation of the number of degrees that contribute to development (McMaster & Wilhelm, 1997). GDD models assume a minimum temperature (11.5 °C for monarchs) below which a species cannot develop and a maximum temperature (33 °C) beyond which growth no longer occurs (Zalucki, 1982). For monarchs, a total of 352 GDDs are, on average, required for an egg to develop into an adult (Zalucki, 1982). GDDs are calculated by summing the total GDD accumulated each day using the mean of that day's high (up to a maximum of 33 °C) and low temperatures (Baskerville & Emin, 1969). We acquired daily minimum and maximum temperatures throughout Texas (weeks 4–9), Ohio (weeks 10–28) and Illinois (weeks 10–28) from 1996 to 2011 from Daymet, a collection of algorithms designed to interpolate values from daily meteorological observations to produce spatially gridded estimates of daily weather patterns (Thornton *et al.*, 2014). For Texas, we used the values of daily minimum and maximum temperature during weeks 4–9 in a grid of 1° points spread evenly throughout the state (also derived from Daymet products), and averaged values across the entire state to yield a single GDD spring value for each year. In Ohio and Illinois, we acquired Daymet site-specific temperature values at each survey location (at a 1-km resolution) and accumulated daily GDDs from week 10 up to the week in which each survey was conducted.

To assess the influence of drought on monarch population dynamics, we used the Palmer drought index (PDI), which integrates precipitation, temperature and soil moisture throughout the season. Although this metric can be confounded with temperature (Hu & Wilson, 2000), it is a more biologically meaningful measure than rainfall alone (Heim, 2002), and has been used in previous studies of monarchs (Stevens & Frey, 2010; Zipkin *et al.*, 2012). We obtained values from the National Oceanic and Atmospheric

Administration (NOAA) Climate Data Center (ftp://ftp.cpc.ncep.noaa.gov/htdocs/temp2) for each of the 10 NOAA-defined climate divisions in Ohio and 10 divisions in Illinois (including one division in Indiana; Fig. 1). To account for accumulated rainfall at each survey location in Ohio and Illinois, we used the PDI calculated for weeks 10 to 28 within each climate division (Zipkin *et al.*, 2012). However, because there was a strong correlation between GDD and PDI in Texas, we opted to use mean rainfall (which was only weakly correlated with GDD) to account for yearly precipitation patterns in Texas only. We used annual state-wide summaries of total monthly rainfall for February, March and April from NOAA's Climate at a Glance (http://www.ncdc.noaa.gov/cag) to correlate with the growing season of milkweed.

Habitat suitability data

As a measure of site-specific habitat availability at Ohio and Illinois locations, we included a variable ($open_j$) to account for the proportion of area along the given transect j that was unforested. Because milkweed commonly grows in open areas, the inclusion of this covariate controls for variation in abundance that is due to habitat suitability (milkweed availability) at a given survey site. We calculated $open_j$ using national land-cover data for 2006 (http://www.mrlc.gov/nlcd06_data.php) at a 30-m resolution. We classified habitat categories as open or closed, and then calculated the percentage of pixels representing open habitat within a 1-km radius of each site.

Data analysis

To evaluate spatial synchrony among monarch populations, we used a negative binomial regression model to estimate expected monarch counts ($\lambda_{j,k,t}$) at each survey site (j) within Ohio and Illinois during the summer breeding season by week (denoted as k) in each year (t), according to spring and summer climate metrics. Poisson generalized linear models are typically used in analyses of count data, but the assumption of equal mean and variance is quite restrictive, as there can be large variation in numbers of observed individuals. For the monarch surveys used in this analysis, a high variance to mean ratio is likely due to differences in habitat suitability across locations [2.1 ± 6.6 (SD) monarchs at Ohio sites; 5.0 ± 11.7 monarchs at Illinois sites]. Because of this overdispersion, the negative binomial distribution produced a better fit to the data than the Poisson distribution. Thus, the count at site j in week k during year t was defined as:

$$y_{j,k,t} \sim \text{neg binom}\left(p_{j,k,t}, r\right) \tag{1}$$

with mean

$$\lambda_{j,k,t} = \frac{p_{j.k.t}\, r}{1-r} \tag{2}$$

and variance

$$\sigma^2_{j.k.t} = \frac{p_{j.k.t}\, r}{(1-r)^2} \tag{3}$$

Our model estimated the expected counts during weeks 10–28 (the first week of May to the first week of September) of the summer breeding season using climate variables from both spring (weeks 4–9) in Texas and summer in Ohio and Illinois. We conducted separate analyses for Ohio and Illinois to compare the similarity of results at the regional scale. Summer populations in Ohio and Illinois experience the same spring conditions in Texas and summer breeding occurs within similar ecoregions, each experiencing a similar range of land-use practices. Thus, we hypothesized that climate variables would be likely to influence monarchs similarly across the two states, and expected strong synchrony and agreement in model parameters. We modelled expected monarch counts, $\lambda_{j,k,t}$, at each survey location j ($n = 116$ in Ohio, $n = 133$ in Illinois) in week k (10–28) within year t (1996–2011) on the log scale using an intercept term (α_1) and 16 parameters (α_2–α_{17}) that we hypothesized could affect counts by site (j), week (k) and year (t) (Table 1; Zipkin *et al.*, 2012). All covariates were standardized such that each had a mean of zero and standard deviation of one (note that standardization was done separately for the Ohio and Illinois datasets).

As in Zipkin *et al.* (2012), we included a week covariate (α_2, linear term) because local monarch abundances increase over the course of the summer. Parameters α_3–α_8 (Table 1) relate to spring conditions in Texas, including linear and quadratic terms (α_3 and α_4) for spring precipitation ($spPREC_t$), and linear and quadratic terms (α_5 and α_6) for spring GDD ($spGDD_t$). We included interaction terms of spring precipitation/GDD and week (α_7 and α_8) because we hypothesized that spring conditions in Texas may affect monarch abundances in Ohio and Illinois differently throughout the summer.

Parameters α_9–α_{13} (Table 1) relate to the accumulating GDDs at each survey site j. Since GDD increases throughout the spring and summer, we used the difference from the mean GDD ($GDDdiff_{j,k,t}$) at a given site j across all 16 years to capture whether the GDDs accumulated by the end of each week of the survey were above or below average for that site during the time period of data collection (α_9). Average GDD ($avgGDD_j$) is the average accumulated GDD in week 28 (end of the summer) at site j across all 16 years. Average GDD serves as a proxy for location (rather than latitude and longitude) because it captures a biologically relevant relationship: the influence of relatively warmer or cooler sites on monarch abundances at the end of the season. The covariate also allows for the direct comparison between Ohio and Illinois because site-specific latitudes and longitudes are not used to explain any of the variation in expected counts. We included linear and quadratic terms for $avgGDD_j$ (α_{10} and α_{11}). We included an interaction term (α_{12}) between $GDDdiff_{j,k,t}$ and week, as well as a three-way interaction between $avgGDD_j$, $GDDdiff_{j,k,t}$ and week (α_{13}). The $PDI_{j,t}$ covariate is the annual value of the drought index at each survey location averaged for weeks 10–28; we included linear

Table 1 Descriptions of parameters used in negative binomial regression models to estimate weekly expected monarch abundances at Ohio and Illinois survey locations from 1996 to 2011.

Parameter	Covariate	Description
α_1	NA	Intercept
α_2	$week_k$	Week in breeding season
α_3	$spPREC_t$	Spring precipitation in Texas (linear)
α_4	$spPREC_t^2$	Spring precipitation in Texas (squared)
α_5	$spGDD_t$	Spring GDD in Texas (linear)
α_6	$spGDD_t^2$	Spring GDD in Texas (squared)
α_7	$spPREC_t \times week_k$	Spring precipitation and week interaction
α_8	$spGDD_t \times week_k$	Spring GDD and week interaction
α_9	$GDDdiff_{j,k,t}$	Weekly GDD differential at transects in Ohio and Illinois
α_{10}	$avgGDD_j$	Average cumulative GDD at transects in Ohio and Illinois (linear)
α_{11}	$avgGDD_j^2$	Average cumulative GDD at transects in Ohio and Illinois (squared)
α_{12}	$GDDdiff_{j,k,t} \times week_k$	GDD differential and week interaction
α_{13}	$GDDdiff_{j,k,t} \times avgGDD_j \times week_k$	GDD differential, average GDD, and week interaction
α_{14}	$PDI_{j,t}$	Annual PDI (weeks 10–28) at sites in Ohio and Illinois (linear)
α_{15}	$PDI_{j,t}^2$	Annual PDI (weeks 10–28) at sites in Ohio and Illinois (squared)
α_{16}	$PDI_{j,t} \times week_k$	Annual PDI and week interaction
α_{17}	$open_j$	Proportion of unforested habitat at transects in Ohio and Illinois

The subscripts represent transect location (j), week within season (k), and survey year (t).
GDD, growing degree days; PDI, Palmer drought index.

(α_{14}) and quadratic (α_{15}) terms, and an interaction with week (α_{16}; Table 1). Parameter α_{17} ($open_j$; Table 1) is location-specific habitat availability (i.e. milkweed grows in open areas). We controlled for variable survey durations and transect lengths using a log($effort_{j,k,t}$) covariate, where effort was standardized by survey hours.

We build on a previous analysis (Zipkin *et al.*, 2012) that assessed the impacts of climate on monarchs breeding in Ohio during 1996 to 2008. In that model, Zipkin *et al.* (2012) estimated monarch abundances using site-specific summer temperature data and drought indices, as well as spring weather conditions (temperature, precipitation) experienced by monarchs during their stopover in Texas. We defined climate variables similarly, but our implementation differed in four main ways. First, we used a negative binomial distribution, rather than a Poisson distribution, which allowed us to model overdispersion in the counts. Second, we used daily mean minimum and maximum temperatures obtained via the recently developed Daymet algorithms, a dataset of daily surface weather and climatological summaries at a 1 km × 1 km spatial resolution (Thornton *et al.*, 2014). Given the fine-scale resolution of these data, the temperatures we used are a more accurate representation of the accumulated number of degrees that can contribute to monarch development. Third, we incorporated three additional years of Ohio monarch surveys, as well as data from Illinois during the same time period, thus capturing more variation in end-of-summer abundances. Fourth, our spring precipitation values were updated by NOAA.

We analysed models for Ohio and Illinois separately and estimated parameter values using a Bayesian framework with programs R and JAGS (using the R package jagsUI; Kellner, 2015). We ran three chains for 4000 iterations after a burn-in of 1000 iterations and thinned the chains by three assuming flat normal priors on each of the 17 covariates. Model convergence was assessed using the Rhat statistic (Gelman & Hill, 2006) and visual inspection of chains.

Assessment of model fit and predictive ability

We assessed model fit by calculating a Bayesian *P*-value, or posterior predictive check, using a discrepancy measure (Kéry, 2010). A posterior predictive check compares the fit of the model for the actual dataset with the fit to replicated ‘ideal’ datasets as generated for each Markov chain Monte Carlo (MCMC) iteration using the parameter estimates. The ‘ideal’ datasets conform perfectly to model assumptions (Kéry, 2010). Thus, if the model fits the data well, then replicated data generated under the model should look similar to observed data. A discrepancy measure is computed for both the actual and ideal datasets at every iteration of the MCMC run. A Bayesian *P*-value quantifies the proportion of MCMC iterations when the discrepancy measure for the ideal dataset is greater than the discrepancy measure computed for the actual dataset. A model that fits the data well has a *P*-value near 0.5, indicating that the model is not consistently under-predicting (*P*-value near 0) or over-predicting (*P*-value near 1) counts at sites. We consider *P*-values in the range 0.3 to 0.7 to be adequate for model fit (Kéry, 2010). As is typical for negative binomial models, we

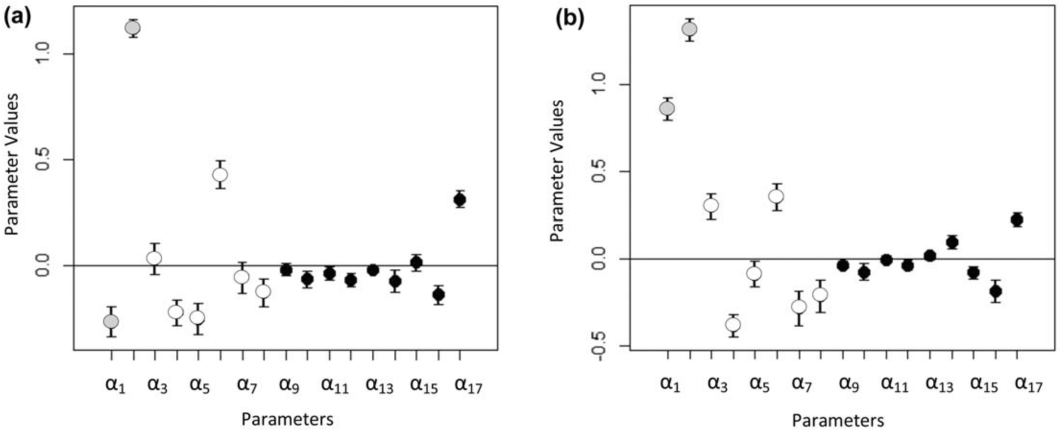

Figure 2 Parameter estimates from negative binomial regression models for (a) Ohio and (b) Illinois estimating weekly expected monarch abundances at survey locations for 1996 to 2011. Error bars represent 95% credible intervals. White circles represent spring effects, black circles represent summer effects and grey circles represent the intercept and week effect. α1, intercept; α2, $week_k$; α3, $spPREC_t$; α4, spPREC_t^2; α5, $spGDD_t$; α6, $spGDD_t^2$; α7, $spPREC_t \times week_k$; α8, $spGDD_t \times week_k$; α9, $GDDdiff_{j,k,t}$; α10, $avgGDD_j$; α11, avgGDD_j^2; α12, $GDDdiff_{j,k,t} \times week_k$; α13, $GDDdiff_{j,k,t} \times avgGDD_j \times week_k$; α14, $PDI_{j,t}$; α15, $PDI_{j,t}^2$; α16, $PDI_{j,t} \times week_k$; α17, $open_j$.

defined the discrepancy measure as the sum of squared Pearson's residuals:

$$\sum \left(\frac{n_{j,k,t} - E[n_{j,k,t}]}{\sigma^2_{j,k,t}} \right)^2 \tag{4}$$

where $n_{j,k,t}$ is the observed count by site (j), week (k) and year (t), $E[n_{j,k,t}]$ is the expected count per site, week and year, and $\sigma^2_{j,k,t}$ is the variance of the expected count.

To explore the predictive abilities of our model, we modified the Bayesian posterior predictive check to quantitatively assess the temporal predictive strength of our model. First, we partitioned the Ohio and Illinois data into subsets based on 8 (1996–2003), 10 (1996–2005), 12 (1996–2007) and 14 (1996–2009) years of data. Next, we used the parameter estimates from each of those four runs to predict expected end-of-summer counts (week 28) based on the subsequent year's spring and summer conditions (i.e. covariate values not used during parameter estimation). For example, we used parameter estimates from the 1996–2003 model run to predict the mean monarch abundance per site expected during week 28 in Ohio and Illinois under actual spring and summer conditions (temperature and precipitation) experienced during each year from 2004 to 2011. We then compared each year's expected count per site during week 28, from all 3000 iterations, with observed counts (i.e. the 'ideal' dataset) using the posterior predictive check method to assess whether the model was overestimating or underestimating counts on average and in each year.

Lastly, to more thoroughly assess year-specific predictive ability, we separately divided the Ohio and Illinois datasets into 16 different 15-year subsets (i.e. each dataset excluded exactly 1 year of data from 1996 to 2011). We then used the parameter estimates from each of the 16 model runs to predict the omitted year's expected end-of-summer count based on that year's spring and summer conditions (e.g. we used parameter estimates from the 1997–2011 model run to predict expected end-of-summer count during 1996 with covariate values observed in 1996). This procedure allowed us to utilize all available data to determine how confidently we could predict annual peak monarch counts under the best circumstances when climate conditions are known. The BUGS code for the negative binomial regression model and the discrepancy assessment procedure (for an example 8-year subset) are provided in Appendix S1 in Supporting Information.

RESULTS

Adult monarch counts in Ohio and Illinois exhibited strong spatial synchrony. Spring weather conditions (parameters α_3–α_8) in Texas had a greater influence on summer abundances in both Ohio and Illinois than local summer conditions (parameters α_9–α_{16}; Fig. 2a, b). Specifically, cooler, wetter springs led to higher end-of-summer abundances in both locations (Fig. 2a, b, parameters α_3 $spPREC_t$ and α_5 $spGDD_t$; Fig. 3a, b). In Illinois, warmer springs also tended to yield slightly higher average abundances (Fig. 3b); this trend was not apparent in Ohio. The magnitude of the effect of spring temperature on summer abundances was greater than that of spring precipitation in both locations.

Monarchs in Ohio and Illinois also responded similarly to site-specific summer temperatures. Abundances were greatest in both Ohio and Illinois when accumulated GDDs were less than average (i.e. cooler; Fig. 2a, b, parameter α_{10} $avgGDD_j$). This effect was strongest at the warmest sites in Ohio and at the coolest sites in Illinois, but the effect was weaker in Illinois. Precipitation had a minimal and inconsistent impact on abundances in both states (Fig. 2a, b, parameters α_{14} $PDI_{j,t}$ and α_{15} $PDI^2_{j,t}$). When all other covariates were held constant,

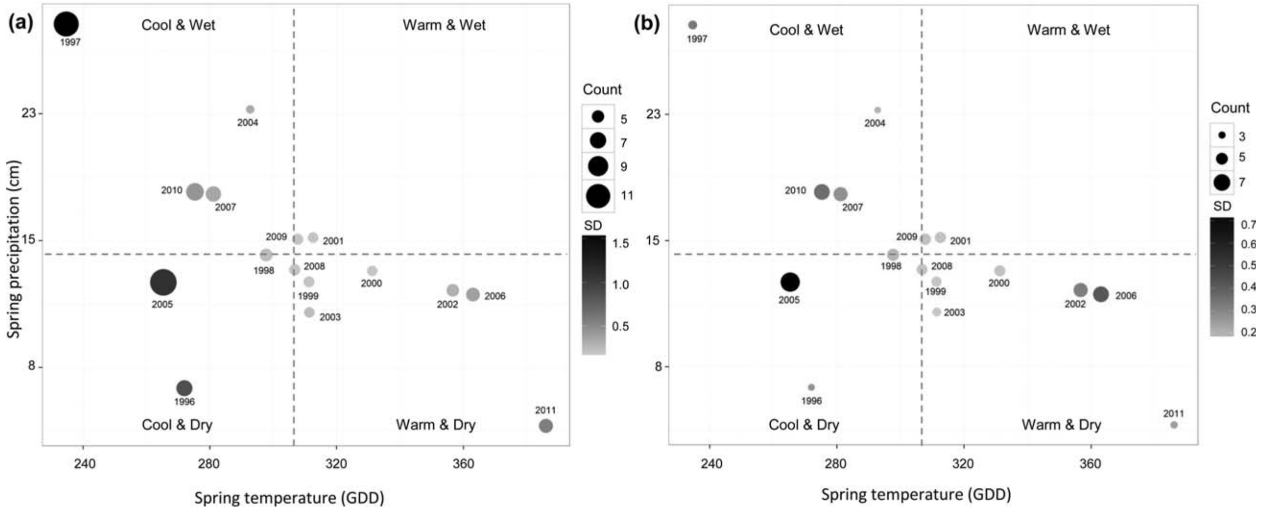

Figure 3 Expected monarch abundances per site at the end of the summer (week 28) for each year's observed spring weather conditions (temperature and precipitation) in (a) Ohio and (b) Illinois. Larger point size indicates higher counts. Shading of points indicates standard deviation (SD) of a given year's abundance estimate. Dotted vertical and horizontal lines indicate mean values of spring temperature and precipitation, respectively, for 1996 to 2011. Relative conditions (e.g. 'warm', 'wet') of each quadrant are shown.

higher abundances were expected at drier Ohio sites, whereas higher abundances were expected at wetter Illinois locations. (See Appendix S2 for more details on specific model results.)

Ohio and Illinois models yielded Bayesian *P*-values of 0.42 and 0.50, respectively, indicating an adequate model fit. We assessed the predictive strength of our model by partitioning Ohio and Illinois data into year subsets and comparing expected counts with those that were observed. We found that our model fitted poorly (Bayesian *P*-value = 0.1) with only 8 years of survey data (1996–2003) in Ohio, and was unable to accurately predict annual counts for 2004–2011 (Table 2, top row). Model fit was somewhat adequate with 8 years of Illinois survey data (Bayesian *P*-value = 0.3), but most year-specific *P*-values were not between 0.3 and 0.7 (Table 2). We ran two additional 8-year random subsets to confirm that Ohio and Illinois models consistently gave poor fits with only 8 years of survey data; *P*-values indicated that this was the case for years even with survey data included ('year subset'; Ohio *P*-values 0.20, 0.09; Illinois *P*-values 0.23,

Table 2 Model predictive strength for subsets of Ohio and Illinois data.

Year subset	Bayesian *P*-value (year subset)	Bayesian *P*-value (subsequent years combined)	Bayesian *P*-values (subsequent years)							
			2004	2005	2006	2007	2008	2009	2010	2011
Ohio										
1996–2003	0.10	0.95	1.00	0.90	0.88	0.93	1.00	1.00	0.88	0.10
1996–2005	0.40	0.44	-	-	0.74	0.93	0.90	0.84	0.80	0.10
1996–2007	0.50	0.49	-	-	-	-	0.80	0.76	0.70	0.06
1996–2009	0.54	0.42	-	-	-	-	-	-	0.62	0.03
Illinois										
1996–2003	0.32	0.77	1.00	0.93	0.15	0.03	0.88	0.30	0.13	0.14
1996–2005	0.42	0.40	-	-	0.15	0.11	0.88	0.30	0.16	0.14
1996–2007	0.56	0.52	-	-	-	-	0.72	0.51	0.22	0.10
1996–2009	0.60	0.30	-	-	-	-	-	-	0.27	0.10

Data from each state were divided into 8-, 10-, 12- and 14-year subsets and Bayesian *P*-values were used to evaluate whether predictions were consistently underestimated (closer to 0), overestimated (closer to 1), or neither (closer to 0.5) compared with observed values. Bayesian *P*-values are shown for years for which survey data were included ('year subset' column) and for years for which survey data were omitted ('subsequent years combined' and individual year columns). 'Year subset' *P*-values indicate how well the model fits the observed data for the specified years. *P*-values in the third column ('subsequent years combined') indicate how well the model predicts counts, on average, for the subsequent years (e.g. the first row is for 2004–2011, the second row for 2006–2011, etc.) under observed climate conditions during those years. Remaining columns indicate how well the model predicts counts year-by-year (individual year columns) under climate conditions for subsequent years, as compared with observed counts.

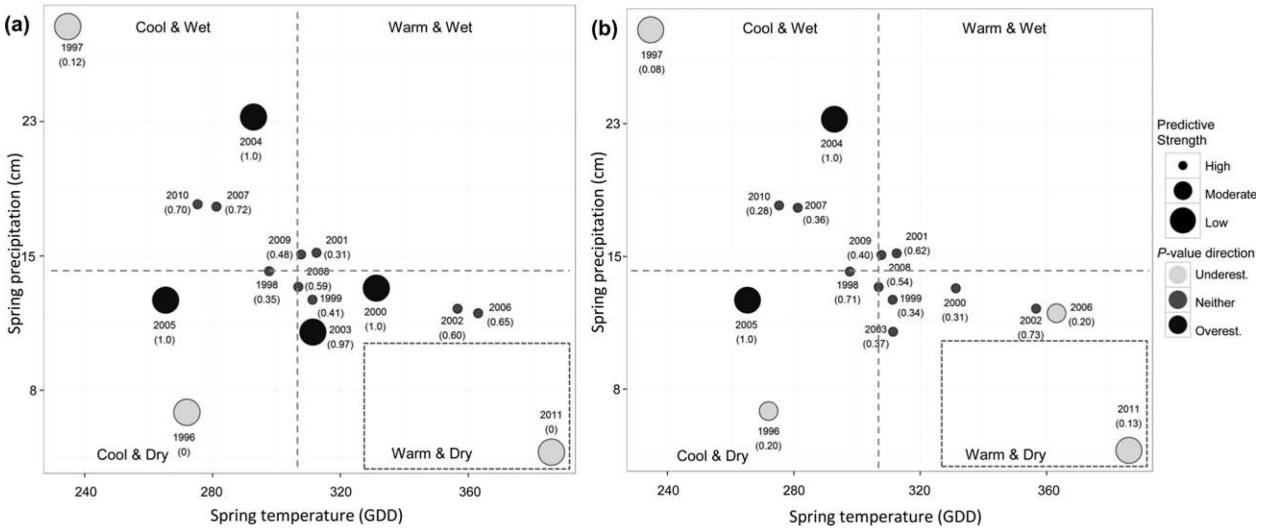

Figure 4 Year-specific predictive accuracy for average monarch abundance across all sites during week 28 in (a) Ohio and (b) Illinois. Annual Bayesian *P*-values shown in parentheses represent the ability of our model to accurately predict expected counts for that year, compared with observed counts, given the parameter estimates from a model fit using the remaining 15 years of data. Predictive strength was categorized as high (small point size; *P*-values 0.25–0.74), moderate (medium point size; *P*-values 0.15–0.24 and 0.75–0.84) and low (large point size; *P*-values 0–0.14 and 0.85–1.0). Years where counts were underestimated on average are shaded light grey (*P*-values < 0.3), overestimated counts are shaded in black (*P*-values > 0.7) and those not strongly under- or overestimated in either direction are shaded in medium grey (*P*-values 0.3–0.7). The dotted box outlines indicate the warmer and drier spring conditions expected in Texas by 2100 under climate models (CMIP5 multi-model mean projections; IPCC, 2014) where no data are currently available on which to base predictions.

0.18), and when predicting subsequent years combined ('subsequent years combined'; Ohio *P*-values 0.90, 0.84; Illinois *P*-values 0.80, 0.82).

The addition of 2 years of Ohio data substantially improved model fit and also improved predictions for subsequent years combined, although *P*-values for any given year were not consistently in the acceptable range of 0.3–0.7 (Table 2, second row). Model fit and overall prediction accuracy generally improved for 12- and 14-year Ohio and Illinois subsets, as well as for some individual years (e.g. 2009 in Illinois and 2010 in Ohio), although there was some degree of over- and underestimation of counts (Table 2). Interestingly, years with consistently under-predicted counts in Ohio were not necessarily under-predicted in Illinois (e.g. 2006 counts were overestimated in Ohio and underestimated in Illinois).

To further explore the year-specific predictive ability of our model, we used parameter estimates from 16 different model runs where we systematically removed 1 year from the dataset and then used model results and true covariate values for the missing year to predict monarch abundances during week 28, separately in both Ohio and Illinois. We found that predictive strength was high for most years that had average spring precipitation and temperature values for the 16-year period (e.g. 1998, 1999, 2001, 2008, 2009, Bayesian *P*-values between 0.31 and 0.71 for both states; Fig. 4a, b). Additionally, Bayesian *P*-values were closer to 0.5 when predicting a given year's count if another year with similar spring conditions was already present in the data (e.g. 2002 and 2006; 2007 and 2010; Fig. 4a, b). Years with atypical spring temperature and precipitation values (e.g. 1996, 1997, 2004, 2005, 2011) were consistently either under- or over-predicted, with *P*-values close to 0 and 1, suggesting little predictive ability in extreme covariate space.

DISCUSSION

Monarchs of a single population breeding in two distinct regions responded similarly, and with varying degrees of sensitivity, to climate conditions experienced during a shared breeding phase in Texas and during separate recruitment phases in Ohio and Illinois. Despite differences in collection methods (i.e. the number of surveys per site, number and geographical distribution of sites) between the two datasets, the impacts of climate on monarch abundances were remarkably similar in the two regions. Likewise, a previous study examining spatial synchrony among UK butterfly populations as part of the Butterfly Monitoring Scheme found partial synchrony at the regional scale (i.e. sample sites up to 200 km apart) due to regionally correlated weather patterns (Sutcliffe *et al.*, 1996). At such a large scale, local environmental heterogeneity averaged out so that spatial correlation in weather became the dominant factor influencing the population dynamics of several butterfly species (Sutcliffe *et al.*, 1996). From our results, we can be reasonably confident that conclusions drawn from analyses using data from either monitoring network can be extrapolated to a regional scale. However, it is important to continue collecting data in both states and to continually reassess spatial synchrony to evaluate any potential divergence due to ongoing climate change.

Quantitative assessment of the temporal predictive ability of our model revealed substantial uncertainty in year-specific predictions of abundances, specifically when spring climate conditions were at the margins of covariate space. When spring temperature and precipitation values were close to the 16-year averages, or when values were similar to those already included in the data (even if far from average), predictive ability was generally good (*P*-value range 0.3–0.7). However, for years when spring climate was atypical for the period, predictive strength was poor (*P*-values close to 0 and 1). This low predictive ability is a result of attempting to predict outside observed parameter space as well as simply a lack of year-specific model fit for years with 'extreme' spring conditions (e.g. 1996, 1997, 2004, 2005, 2011; results not shown). By 2100, springs in Texas are predicted to be approximately 1.7 °C warmer (i.e. GDD ranges of 330–390) and precipitation is expected to decrease by approximately 10% (i.e. precipitation ranges of 3.5–12.0 cm) relative to 1986–2005 means (CMIP5 multi-model; IPCC, 2014), conditions that are outside the observed range of our study period (Fig. 4, dashed boxes; except 2011). If this is the case, our ability to predict future summer population abundances of monarchs in both Ohio and Illinois is tenuous.

Both spring and summer climate conditions affect abundances of breeding monarchs in Ohio and Illinois. However, like Zipkin *et al.* (2012), we found that spring conditions in Texas had a greater influence on abundances than summer conditions (but there were some minor differences in the patterns of the relationship; see Appendix S2 for details). Because annual spring climate variables were most important for determining monarch abundance, it is necessary to have a long time series with sufficient annual variation to accurately estimate the effects of spring precipitation and temperature on monarch abundance. Thus, we found poor model fit and predictability when using only 8 years of data to estimate parameters. The addition of only 2 years (2004 and 2005) of data dramatically improved model fit for the Ohio and Illinois datasets. Our model was consistently accurate in predicting counts for subsequent years combined, on average, once 10 years of data were included in both datasets. This suggests that predicting average annual counts over a number of years (and climate conditions) may be more accurate than predicting monarch counts under a specific temperature–precipitation scenario (e.g. spring conditions in a a given year). For example, our Ohio model substantially overestimated counts (*P*-values close to 1) in 2000 and 2003, years that had springs which were only moderately warmer and drier than average, suggesting a given year's additional unexplained variation is affecting predictive power. We found that weekly mean monarch counts (averaged across all sites) peaked after week 28 in 2000 (peak week 29) and 2003 (week 31). This difference, along with very low observed counts in both years in Ohio (Fig. S1) and a wide longitudinal and environmental gradient (compared with Illinois), makes year-specific predictions quite difficult, even in the case of fairly average spring conditions.

Understanding the impacts of climate on migratory species is challenging because such species travel through several climates that may be differentially changing. Our study demonstrates how analyzing distinct areas of a species' migratory range, and assessing the temporal predictive power of a given model, can enhance our understanding of the nuances of spatial synchrony among populations and our ability to make accurate predictions about future abundances. Because breeding monarch populations in Ohio and Illinois closely mirrored one another in their responses to climate, future changes in the Texan climate can have a geographically widespread impact on subsequent stages in the annual cycle. Our results also demonstrate how difficult it can be to accurately predict future annual monarch abundances. Counts during several years (2006, 2007 and 2010) were not consistently over- or underestimated in both Ohio and Illinois, which suggests there is unaccounted variation in monarch abundances that cannot be explained by climate factors. For instance, the size of the population in Mexico at the end of winter has been shown to influence summer abundance (Ries *et al.*, 2015), but these data have only been collected since 2005, so were not included in this study. To fully understand all the factors affecting monarch populations, future analyses should include data on wintering populations as well as other habitat and environmental covariates, including annual milkweed availability (Pleasants & Oberhauser, 2013) and disease and parasitism rates (Oberhauser, 2012).

Multiple climate factors will continue to change in their means, variabilities, extremes and in the correlations between them (Ehrlén & Morris, 2015). Forecasting future ecological conditions based on long-term observational studies is a useful practice, but it has limitations (Kerr & Dobrowski, 2013) that are not typically acknowledged (e.g. Acevedo *et al.*, 2010; Stewart *et al.*, 2015). This is especially true when attempting to anticipate events occurring across large spatial scales or at extreme covariate values (Berteaux *et al.*, 2006). Predictions of how the geographical ranges or abundances of individual species may change as climates alter have the potential to be accurate, but there are too many uncertainties to accept those predictions without rigorous, temporal validation (Kerr & Dobrowski, 2013). Our assessment approach can lend credibility to such analyses by quantifying the reliability of model predictions. This is particularly important for threatened and/or declining species like the iconic monarch butterfly.

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REFERENCES

Acevedo, P., Ruiz-Fons, F., Estrada, R., Marquez, A.L., Miranda, M.A., Gortázar, C. & Lucientes, J. (2010) A broad assessment of factors determining *Culicoides imicola* abundance: modelling the present and forecasting its future in climate change scenarios. *PLoS One*, **5**, e14236.

Alonso-Mejia, A. & Arellano-Guillermo, A. (1992) Influence of temperature, surface body moisture and height aboveground on survival of monarch butterflies overwintering in Mexico. *Biotropica*, **24**, 415–419.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.

Barker, J.F. & Herman, W.S. (1976) Effect of photoperiod and temperature on reproduction of the monarch butterfly, *Danaus plexippus*. *Journal of Insect Physiology*, **22**, 1565–1568.

Barve, N., Bonilla, A.J., Brandes, J. *et al.* (2012) Climate-change and mass mortality events in overwintering monarch butterflies. *Revista Mexicana de Biodiversidad*, **83**, 817–824.

Baskerville, G. & Emin, P. (1969) Rapid estimation of heat accumulation for maximum and minimum temperatures. *Ecology*, **50**, 514–517.

Berteaux, D., Humphries, M., Krebs, C. *et al.* (2006) Constraints to projecting the effects of climate change on mammals. *Climate Research*, **32**, 151–158.

Brooker, R.W., Travis, J.M., Clark, E.J. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245**, 59–65.

Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence–absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.

Brower, L.P. (1986) New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus L. Migration: mechanisms and adaptive significance* (ed. by M.A. Rankin), pp. 748–785. Marine Science Institute, University of Texas at Austin, Port Aransas, TX.

Cockrell, B.J., Malcolm, S.B. & Brower, L.P. (1993) Time, temperature, and latitudinal constraints on the annual recolonization of eastern North America by the monarch butterfly. *Biology and conservation of the monarch butterfly* (ed. by S.B. Malcolm and M.P. Zalucki), pp. 233–251. Natural History Museum of Los Angeles County, Los Angeles, CA.

Couture, J.J., Serbin, S.P. & Townsend, P.A. (2015) Elevated temperature and periodic water stress alter growth and quality of common milkweed (*Asclepias syriaca*) and monarch (*Danaus plexippus*) larval performance. *Arthropod–Plant Interactions*, **9**, 149–161.

Ehrlén, J. & Morris, W.F. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, **18**, 303–314.

Gelman, A. & Hill, J. (2006) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge.

Heim, R.R., Jr (2002) A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society*, **83**, 1149–1165.

Howard, E. & Davis, A.K. (2004) Documenting the spring movements of monarch butterflies with Journey North, a citizen science program. *The monarch butterfly: biology and conservation* (ed. by K.S. Oberhauser and M.J. Solensky), pp. 105–114. Cornell University Press, Ithaca, NY.

Hu, Q. & Wilson, G.D. (2000) Effects of temperature anomalies on the Palmer drought severity index in the central United States. *International Journal of Climatology*, **20**, 1899–1911.

Huntley, B., Barnard, P., Altwegg, R. *et al.* (2010) Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography*, **33**, 621–626.

IPCC (2014) *Climate change 2014: impacts, adaptations, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (ed. by V.R. Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCraken, P.R. Mastrandrea and L.L. White), Chapter 26: North America. Cambridge University Press, Cambridge.

Iverson, L.R. & Prasad, A.M. (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems*, **4**, 186–199.

Jamieson, M.A., Trowbridge, A.M., Raffa, K.F. & Lindroth, R.L. (2012) Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, **160**, 1719–1727.

Kellner, K. (2015) *jagsUI: a wrapper around rjags to streamline JAGS analyses*. R package version 1.3.5. Available at: https://github.com/kenkellner/jagsUI.

Kerr, J.T. & Dobrowski, S.Z. (2013) Predicting the impacts of global change on species, communities, and ecosystems: it takes time. *Global Ecology and Biogeography*, **22**, 261–263.

Kéry, M. (2010) *Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses*. Academic Press, Burlington, MA.

Kubisch, A., Degen, T., Hovestadt, T. & Poethke, H.J. (2013) Predicting range shifts under global change: the balance between local adaptation and dispersal. *Ecography*, **36**, 873–882.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90**, 588–597.

McMaster, G.S. & Wilhelm, W. (1997) Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology*, **87**, 291–300.

Malcolm, S.B. & Zalucki, M.P. (1993) *Biology and conservation of the monarch butterfly*. Natural History Museum of Los Angeles County, Los Angeles, CA.

Mustin, K., Benton, T.G., Dytham, C. & Travis, J.M. (2009) The dynamics of climate-induced range shifting; perspectives from simulation modelling. *Oikos*, **118**, 131–137.

Nail, K.R., Batalden, R.V. & Oberhauser, K.S. (2015) What's too hot and what's too cold? Lethal and sublethal effects of extreme temperatures on developing monarchs. *Monarchs in a changing world: biology and conservation of an iconic butterfly* (ed. by K.S. Oberhauser, K.R. Nail and S. Altizer), pp. 99–108. Cornell University Press, Ithaca, NY.

Norris, D.R. & Marra, P.P. (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor*, **109**, 535–547.

Oberhauser, K. (2012) Tachinid flies and monarch butterflies: citizen scientists document parasitism patterns over broad spatial and temporal scales. *American Entomologist*, **58**, 19–22.

Olfert, O., Weiss, R. & Kriticos, D. (2011) Application of general circulation models to assess the potential impact of climate change on potential distribution and relative abundance of *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae) in North America. *Psyche: a Journal of Entomology*, **2011**, 9. doi:10.1155/2011/80372.

Pasinelli, G., Schaub, M., Häfliger, G., Frey, M., Jakober, H., Müller, M., Stauber, W., Tryjanowski, P., Zollinger, J.L. & Jenni, L. (2011) Impacts of density and environmental factors on population fluctuations in a migratory passerine. *Journal of Animal Ecology*, **80**, 225–234.

Pleasants, J.M. & Oberhauser, K.S. (2013) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conservation and Diversity*, **6**, 135–144.

Pollard, E. (1977) A method for assessing changes in the abundance of butterflies. *Biological Conservation*, **12**, 115–134.

Prysby, M.D. & Oberhauser, K.S. (2004) Temporal and geographic variation in monarch densities: citizen scientists document monarch population patterns. *The monarch butterfly: biology and conservation* (ed. by K.S. Oberhauser and M.J. Solensky), pp. 9–20. Cornell University Press, Ithaca, NY.

Pyle, R.M. (2015) Monarchs in the mist: new perspectives on monarch distribution in the Pacific Northwest. *Monarchs in a changing world: biology and conservation of an iconic butterfly* (ed. by K.S. Oberhauser, K.R. Nail and S. Altizer), pp. 236–246. Cornell University Press, Ithaca, NY.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G. & Romme, W.H. (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience*, **58**, 501–517.

Ries, L., Taron, D.J., Rendón-Salinas, E. & Oberhauser, K.S. (2015) Connecting eastern monarch population dynamics across their migratory cycle. *Monarchs in a changing world: biology and conservation of an iconic butterfly* (ed. by K.S. Oberhauser, K.R. Nail and S. Altizer), pp. 268–281. Cornell University Press, Ithaca, NY.

Roy, D.B., Rothery, P., Moss, D., Pollard, E. & Thomas, J. (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201–217.

Stange, E.E. & Ayres, M.P. (2010) Climate change impacts: insects. *Encyclopedia of life sciences (ELS)* (ed. by J.K. Govindjee, J. Messinger, and J. Whitmarsh). John Wiley & Sons, Chichester.

Stevens, S.R. & Frey, D.F. (2010) Host plant pattern and variation in climate predict the location of natal grounds for migratory monarch butterflies in western North America. *Journal of Insect Conservation*, **14**, 731–744.

Stewart, J.A., Perrine, J.D., Nichols, L.B., Thorne, J.H., Millar, C.I., Goehring, K.E., Massing, C.P. & Wright, D.H. (2015) Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*, **42**, 880–890.

Sutcliffe, O.L., Thomas, C.D. & Moss, D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, **65**, 85–95.

Thornton, P.E., Thornton, M.M., Mayer, B.W., Wilhelmi, N., Wei, Y., Devarakonda, R. & Cook, R.B. (2014) *Daymet: daily surface weather data on a 1-km grid for North America, Version 2. Data set.* Available online from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. http://daac.ornl.gov.

Wassenaar, L.I. & Hobson, A. (1998) Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences USA*, **95**, 15436–15439.

Williams, D.W. & Liebhold, A.M. (2000) Spatial synchrony of spruce budworm outbreaks in eastern North America. *Ecology*, **81**, 2753–2766.

York, H.A. & Oberhauser, K.S. (2002) Effects of duration and timing of heat stress on monarch butterfly (*Danaus plexippus*) (Lepidoptera: Nymphalidae) development. *Journal of the Kansas Entomological Society*, **75**, 290–298.

Zalucki, M.P. (1982) Temperature and rate of development in *Danaus plexippus* L. and *D. chrysippus* L. (Lepidoptera:

Nymphalidae). *Australian Journal of Entomology*, **21**, 241–246.

Zalucki, M.P., Rochester, W.A., Oberhauser, K. & Solensky, M. (2004) Spatial and temporal population dynamics of monarchs down-under: lessons for North America. *The monarch butterfly: biology and conservation* (ed. by K.S. Oberhauser and M.J. Solensky), pp. 78–83, Cornell University Press, Ithaca, NY.

Zipkin, E.F., Ries, L., Reeves, R., Regetz, J. & Oberhauser, K.S. (2012) Tracking climate impacts on the migratory monarch butterfly. *Global Change Biology*, **18**, 3039–3049.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Observed and expected monarch end-of-summer abundances in Ohio and Illinois shown on comparable scales.

Appendix S1 BUGS code for the negative binomial model and assessment procedure example.

Appendix S2 Detailed comparison of this study's results with those of Zipkin *et al.* (2012).

BIOSKETCH

The authors aim to understand the impacts of climate change on future distributions and abundances of species, especially those in decline. Specifically, they seek to develop advanced statistical models using long-term datasets to investigate broad-scale patterns and processes. Their research encompass a wide variety of taxa, including birds, amphibians and insects.

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