

Local and cross-seasonal associations of climate and land use with abundance of monarch butterflies *Danaus plexippus*

Sarah P. Saunders, Leslie Ries, Karen S. Oberhauser, Wayne E. Thogmartin and Elise F. Zipkin

S. P. Saunders (<http://orcid.org/0000-0002-2688-9528>) (saund123@msu.edu) and E. F. Zipkin, Dept of Integrative Biology, Michigan State Univ., College of Natural Science, East Lansing, MI, USA. EFZ also at: Ecology, Evolutionary Biology, and Behavior Program, Michigan State Univ., East Lansing, MI, USA. – L. Ries (<http://orcid.org/0000-0002-5953-9284>), Dept of Biology, Georgetown Univ., Washington D.C., USA. – K. S. Oberhauser, Dept of Fisheries, Wildlife, and Conservation Biology, Univ. of Minnesota, St Paul, MN, USA. – W. E. Thogmartin (<http://orcid.org/0000-0002-2384-4279>), US Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI, USA.

Quantifying how climate and land use factors drive population dynamics at regional scales is complex because it depends on the extent of spatial and temporal synchrony among local populations, and the integration of population processes throughout a species' annual cycle. We modeled weekly, site-specific summer abundance (1994–2013) of monarch butterflies *Danaus plexippus* at sites across Illinois, USA to assess relative associations of monarch abundance with climate and land use variables during the winter, spring, and summer stages of their annual cycle. We developed negative binomial regression models to estimate monarch abundance during recruitment in Illinois as a function of local climate, site-specific crop cover, and county-level herbicide (glyphosate) application. We also incorporated cross-seasonal covariates, including annual abundance of wintering monarchs in Mexico and climate conditions during spring migration and breeding in Texas, USA. We provide the first empirical evidence of a negative association between county-level glyphosate application and local abundance of adult monarchs, particularly in areas of concentrated agriculture. However, this association was only evident during the initial years of the adoption of herbicide-resistant crops (1994–2003). We also found that wetter and, to a lesser degree, cooler springs in Texas were associated with higher summer abundances in Illinois, as were relatively cool local summer temperatures in Illinois. Site-specific abundance of monarchs averaged approximately one fewer per site from 2004–2013 than during the previous decade, suggesting a recent decline in local abundance of monarch butterflies on their summer breeding grounds in Illinois. Our results demonstrate that seasonal climate and land use are associated with trends in adult monarch abundance, and our approach highlights the value of considering fine-resolution temporal fluctuations in population-level responses to environmental conditions when inferring the dynamics of migratory species.

Determining the link between population processes (e.g. trends in abundance, responses to stressors) in breeding and non-breeding areas is critical for understanding the ecology of migratory species and, consequently, for conserving populations. Demographic responses to environmental conditions in a given season, density dependence, and spatially extensive environmental changes can affect population dynamics in subsequent seasons in ways that are difficult to predict (Hostetler et al. 2015). Because migratory species spend different periods of their annual cycle in geographically and ecologically distinct areas, their dynamics are a product of complex interactions occurring over large spatial and long temporal extents (Webster et al. 2002, Runge et al. 2014).

Current knowledge of how migratory species respond to climate, land cover, and land use is largely based on studies conducted at small spatial and short temporal scales (Small-Lorenz et al. 2013). These studies rarely integrate seasonal processes occurring outside the core breeding period

or range (Marra et al. 2015). Generally, it is not possible to extrapolate from local studies to range-wide population dynamics because limiting factors often vary across a species' range and through time (Sagarin et al. 2006, Rushing et al. 2016). Continuing declines in the abundances of migratory species globally (Kirby et al. 2008, Wilcove and Wikelski 2008) suggest that spatially extensive conservation action may be increasingly necessary to prevent the loss of migratory phenomena. However, because few studies have simultaneously quantified the relative contributions of breeding, non-breeding, and migratory processes to population dynamics over large areas (Wilson et al. 2011), there is little empirical information to test theoretical predictions about how seasonal interactions manifest at the population level. Therefore, understanding range-wide fluctuations in the dynamics of migratory populations and limitations on population growth require investigations of how events and conditions during different stages integrate across the annual cycle.

The annual cycle of monarch butterflies *Danaus plexippus* encompasses three stages outside of migratory periods. Unlike most migratory species, which have distinct winter non-breeding and summer breeding phases, monarchs also have a spatially distinct spring breeding phase. Consequently, the link between population dynamics from winter to spring to summer may be more complex than in other species. Data indicate that the size of the overwintering monarch population decreased from 1997 to 2015 (Fig. 1a), a trend that has steepened in the last decade (Ries et al. 2015b). Monarchs are one of the most heavily monitored species in the world, and long-term monitoring data cover a large area (Ries and Oberhauser 2015). Thus, it is possible to examine annual variation in monarch abundance, which has been linked to climate, land cover, and land use throughout their annual cycle.

Eastern North American monarchs, which comprise the largest population of the species (Brower 1986), migrate over multiple generations from wintering grounds in Mexico to breeding grounds in the United States and Canada, and their niche changes among seasons (Oberhauser and Peterson 2003, Batalden et al. 2007). In winter, they roost in oyamel fir *Abies religiosa* forests, which have a limited range in the mountains of central Mexico. Illegal logging of oyamel forests in and adjacent to overwintering sites has led to declines in the extent of winter habitat

(Vidal and Rendón-Salinas 2014, Vidal et al. 2014). In contrast, during spring and summer, monarchs are associated with open, disturbed areas where their hostplants (milkweed [Aponcynaceae, mostly *Asclepias*]) occur (Pleasants and Oberhauser 2012). Reduction in abundance of common milkweed *Asclepias syriaca*, one of their most common hostplants (Malcolm et al. 1993), is hypothesized to be a major driver of decreased monarch recruitment (Pleasants and Oberhauser 2012, Flockhart et al. 2015).

Loss of milkweed from 1999–2014 is largely attributed to the adoption of genetically modified, glyphosate-resistant (Roundup™ Ready) corn and soybean crops in the mid-western United States (Stenoien et al. 2016, Pleasants 2017). Roundup™ Ready soybean was introduced in 1996 and Roundup™ Ready corn was introduced in 1998. As of 2014, $\geq 90\%$ of both crops throughout the Midwest were herbicide resistant (USDA 2015). The resulting increase in use of glyphosate has likely contributed to the lower densities of milkweed in and adjacent to agricultural fields (Hartzler 2010, Pleasants 2015, 2017). Estimates indicate that total milkweed abundance (i.e. in both agricultural fields and non-agricultural areas) declined by approximately 58% in the Midwest from 1999 to 2010 (Pleasants and Oberhauser 2012), and by 68% in Illinois from 1997 to 2016 (Zaya et al. 2017).

The extent to which milkweed loss is contributing to population dynamics, and whether the summer population

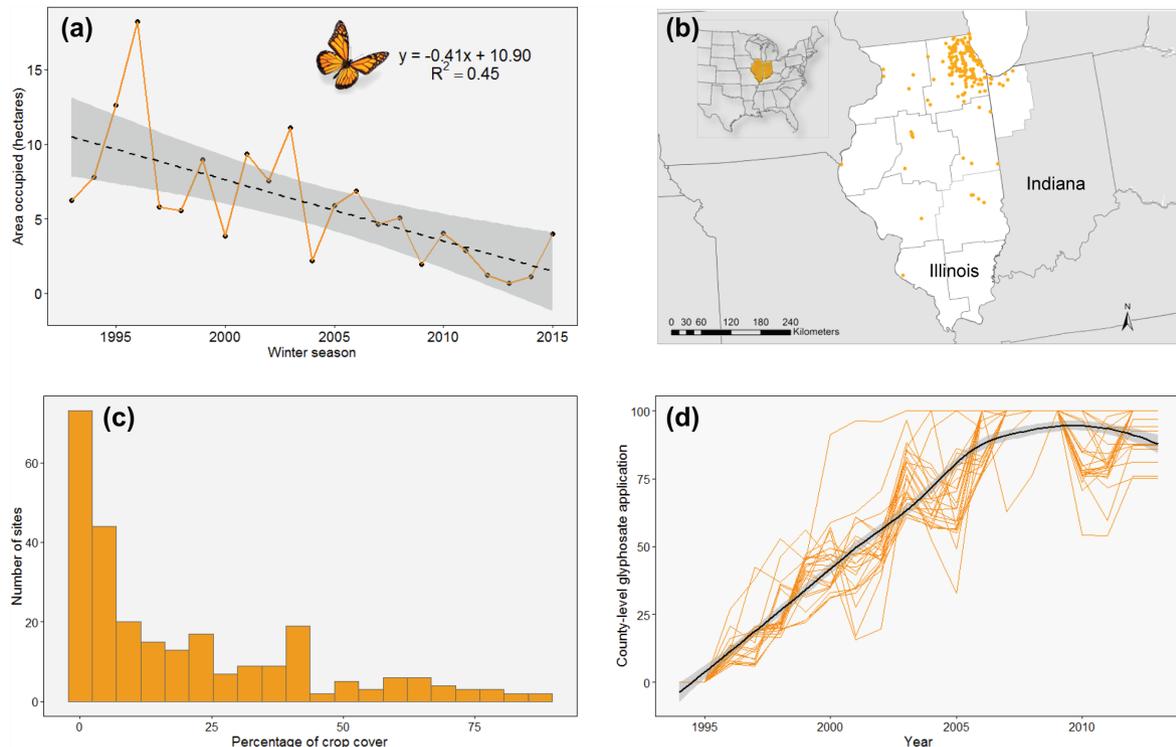


Figure 1. (a) Index of annual abundance of overwintering monarch butterflies in Mexico, measured as total area occupied by colonies in December. The dashed line is the trend and the gray shading is the 95% confidence interval. (b) Sites where monarchs were surveyed in Illinois and northwest Indiana (through the Illinois monitoring program) from 1994–2013. Delineations within the state represent US National Oceanic and Atmospheric Administration (NOAA)-defined climate divisions. (c) Percentage of crop cover within a 10 km radius of survey sites in Illinois and Indiana ($n = 262$). (d) Estimated glyphosate application (percentage of corn and soybeans sprayed) in 28 counties in Illinois and Indiana (individual orange lines) where monarch surveys occurred from 1994–2013. The black line is the smoothed trend and the gray shading is the 95% confidence interval. We assumed that the 2012 and 2013 applications were the same because data were not available for 2013.

is declining, is controversial (Brower et al. 2012a, b, Davis 2012, Ries et al. 2015a, Dyer and Forister 2016, Inamine 2016, Pleasants et al. 2016, Stenoien et al. 2016). However, summer population indices that do not indicate negative trends (Ries et al. 2015a, Inamine 2016) primarily include monarchs surveyed in non-agricultural habitats (Ries et al. 2015a, Pleasants et al. 2016). Assessments of monarch egg densities that take into account the total amount of habitat suggest a decline (Pleasants and Oberhauser 2012, Stenoien et al. 2015) and a strong correlation between egg densities and the size of the winter population (Pleasants and Oberhauser 2012). Yet no study to date has demonstrated a direct link between estimated glyphosate use and the number of adult monarchs during summer (Ries et al. 2015a), nor has any study examined the extent to which milkweed loss may be contributing to the population decline relative to other seasonal factors across the annual cycle (Dyer and Forister 2016).

Severe weather events can lead to mass mortality on the overwintering grounds (Vidal and Rendón-Salinas 2014), but a high correlation (0.74) between colony sizes at the beginning and end of winter over the last 10 yr (Ries et al. 2015a) suggests that mass mortality is infrequent and not likely the cause of recent declines. The effects of climate change on individual butterflies and the ecosystems across which they move during their annual migration also affects population dynamics (Zalucki and Rochester 2004). For example, local monarch summer abundances in the Midwest are significantly associated with temperature and precipitation during their spring migration and breeding phase in Texas (Zipkin et al. 2012, Saunders et al. 2016).

We used 20 yr of data collected in Illinois and north-west Indiana (1994–2013) to examine whether climate and land use during the winter, spring, and summer stages of the annual cycle explain annual variation in monarch abundance on their summer breeding grounds. Previous work demonstrated that spring and, to a lesser extent, local summer weather was associated with summer monarch abundances in the Midwest (Zipkin et al. 2012, Saunders et al. 2016). Here, our objective was to identify cross-seasonal and local factors associated with summer monarch abundances. We accomplished this objective by assessing whether overwintering colony size was associated with summer abundance in the subsequent year; evaluating whether spring climate (e.g. temperature and precipitation) in Texas, experienced by the year's first generation, explained fluctuations in the summer abundance of subsequent generations; and estimating the relative strengths of association of local summer climate (temperature, water availability) and land use (site-specific crop cover, county-level glyphosate application rates) with monarch abundance.

We also compared results from the 20-yr period to those from the first and second 10-yr periods (1994–2003 and 2004–2013). We chose to examine the two decades separately because several studies have demonstrated that the rate of population decline differed before and after 2004 (Crewe and McCracken 2015, Ries et al. 2015a, b, Stenoien et al. 2015), the proportion of glyphosate-tolerant corn and soybeans (and thus extent of glyphosate application) increased dramatically through 2005 (USDA 2015), and current analysis of overwintering monarch abundance suggests that

the population experienced a change in the carrying capacity and intrinsic growth rate around 2003–2004 (C. Bahlai pers. comm.). Additionally, previous analyses of the same data with similar model structure indicated that a minimum of 10 yr of data was needed for adequate model fit (Saunders et al. 2016). Population-level responses to external factors vary over time. Therefore, examining differences in these relationships at several points within a time series can reveal both differences in the strength of association between population dynamics and environmental factors, and the extent to which estimated relationships between species and aspects of their environment fluctuate over time.

Methods

Monarch population biology

The eastern migratory monarch population extends from the east coast of the United States to the Rocky Mountains during its summer breeding phase and overwinters in dense colonies in forests at the boundary of the Mexican states of Michoacán and México (Brower 1986). Each spring, individuals fly from Mexico into Texas and surrounding regions to lay eggs on milkweed. Adults that result from those eggs fly to northern breeding grounds, arriving in May and June, and produce two or three more generations throughout summer. The number of individuals in the final generation, which enters reproductive diapause by late August and flies back to the same overwintering region in Mexico, varies substantially among years (Pleasants and Oberhauser 2012). The causes of these fluctuations are not well understood, although climate is a contributing factor (Zipkin et al. 2012, Saunders et al. 2016). Reproduction in agricultural regions of the central flyway (the area between the Appalachian and Rocky Mountains) is most critical to annual population growth (Wassenaar and Hobson 1998, Oberhauser et al. 2016, Flockhart et al. 2017).

Data collection

Our analyses use statewide data collected by the Illinois Butterfly Monitoring Network (<www.bfly.org>). Because the extent of data collection grew substantially during the early 1990s and winter monitoring began in 1994, we used count data from 1994 through 2013, the last year for which data were processed and available. Monitoring sites were dispersed throughout north-central Illinois and neighboring northwest Indiana, and the majority of sites were within 160 km of Chicago (Fig. 1b); hereafter, references to Illinois also include the eight sites in Indiana. Sites were an average of 12.0 ± 26.2 km apart (\pm SD) and the centers of most sites were at least 1 km apart. Each site consisted of a single transect between 600 m and 3 km in length. The majority of transects were 1 to 1.5 km in length. Transects were not linear and spanned habitat types (e.g. old fields, gardens), but the length of each transect was consistent among years. Each transect was surveyed by a volunteer who visited their assigned site a maximum of once per week from June through mid-September, but not all sites were surveyed

every week or during every year. An observer walked along the transect and recorded all butterflies (not just monarchs) seen within approximately five meters above and ahead of the observer during each survey (Pollard 1977). The number of sites surveyed per year varied from 24 (1995) to 126 (2005), and the number of surveys conducted per site was 67 ± 35 (range 23–202). For each of the 20 yr, we included data from sites that were surveyed at least once from June through mid-September; on average, 91% of sites were surveyed ≥ 2 times. We use abundance and expected count interchangeably, but note that we are referring to apparent abundance rather than true abundance, given that we did not have data on detection probability.

Data summary

We examined the associations of climate and land use during winter, spring, and summer with monarch abundance during the ca 12-week summer recruitment phase in Illinois (28 June–20 September). Monarchs arrive in the Midwest in early May, but are relatively uncommon until mid-June through mid-July (Pryby and Oberhauser 2004), when reproduction begins in earnest; abundance continues to increase through mid-September (Brower 1986, Pryby and Oberhauser 2004).

Climate data

To assess the associations of spring and summer weather with local monarch abundances, we used temperature and water availability variables defined in two previous analyses (Zipkin et al. 2012, Saunders et al. 2016). We focused on the climate experienced by the first generation of monarchs in Texas during spring and by subsequent generations during the summer recruitment phase in Illinois. Our temperature variable was growing degree days (GDD), which measures the accumulation of the number of degrees that contribute to development (McMaster and Wilhelm 1997). GDD models assume a minimum temperature below which a species cannot develop (11.5°C for monarchs) and a maximum temperature beyond which growth no longer occurs (33°C for monarchs; Zalucki 1982). We acquired daily minimum and maximum temperatures throughout Texas (23 March through 30 April) and Illinois (3 May through 20 September) from 1994–2013 from Daymet (<http://daymet.ornl.gov>), which interpolates data from weather stations to produce spatially gridded estimates of daily weather (Thornton et al. 2014). For Texas, we used the daily minimum and maximum temperature values in a grid of points separated by 1 degree across the state (also derived from Daymet products) to calculate GDDs, and averaged the GDD values across the state to yield a single GDD spring value for each year, t ($spGDD_t$). We included a quadratic term in our model because effects of spring temperature may be nonlinear ($spGDD_t^2$; Zipkin et al. 2012, Saunders et al. 2016). We acquired Daymet temperature values at each survey site (j) in Illinois, and estimated the average cumulative GDD in the last week of the recruitment period (week of 13 September) at each site across the 20 yr ($avgGDD_j$). We used average GDD as a proxy for location

rather than latitude and longitude. Of five summer temperature covariates included in a similar analysis (Saunders et al. 2016), GDD was the only one significantly associated with summer monarch counts.

We measured local water availability with the Palmer drought index (PDI), which integrates precipitation, temperature, and soil moisture throughout the season (Stevens and Frey 2010, Zipkin et al. 2012, Saunders et al. 2016). We obtained PDI values from the Climate Data Center of the US National Oceanic and Atmospheric Administration (NOAA; <ftp://ftp.cpc.ncep.noaa.gov/htdocs/temp2>) for each of the nine NOAA-defined climate divisions in Illinois and one division in Indiana (Fig. 1b). To account for cumulative rainfall at survey locations, we used the PDI for the weeks of 28 June through 13 September within each climate division for each year ($PDI_{j,t}$; Saunders et al. 2016). Because there was a strong correlation (-0.58) between GDD and PDI in Texas, we used mean rainfall (-0.41 correlation with GDD) to account for yearly spring precipitation in Texas ($spPrec_p$, $spPrec_t^2$) instead of PDI. We calculated mean rainfall in Texas using annual state-wide summaries of cumulative rainfall for February, March, and April (from NOAA's Climate at a Glance) to align with the spring growing season of milkweed (Saunders et al. 2016).

Summer land cover and land use data

We measured the percentage of area within a 1 km radius of each site in Illinois that was unforested ($open_j$) because milkweed commonly grows in open areas. We calculated $open_j$ from the 2006 National Land Cover Database (NLCD; www.mrlc.gov/nlcd06_data.php), which has a 30 m resolution. We also calculated $open_j$ from the 2001 and 2011 NLCDs and found little variation (< 0.05 average difference) among years; thus, we treated $open_j$ as a static covariate.

As a measure of site-specific crop cover ($cropcov_j$), we quantified the proportion of land within a 10 km radius of each site that was classified as cultivated crops (-0.12 correlation with $open_j$). We also measured $cropcov_j$ within a 50 km radius of each site, but found that monarch abundance was more strongly correlated with crop cover within 10 km. Therefore, we used the 10 km covariate in all analyses. The average change in $cropcov_j$ among the 1992, 2001, 2006, and 2011 NLCDs was 0.03, so we averaged $cropcov_j$ values from the four NLCDs and treated $cropcov_j$ as static (Fig. 1c).

We estimated county-level glyphosate application (percentage of corn and soybeans sprayed; $glyApp_{j,t}$) in Illinois from 1994–2012 from data on glyphosate purchases and land cover from the U.S. Geological Survey (USGS; Stone 2013, Baker and Stone 2015). We used the 2012 values for 2013 because these data were unavailable post-2012. First, we summed area of corn and soybeans (in acres) within each county from the USDA Cropland Data Layer. Second, on the basis of expert opinion and typical protocols (C. Sprague, MSU Dept of Plant, Soil and Microbial Sciences, pers. comm.), we assumed a standard glyphosate application rate of 0.75 lbs acid equivalent (ae)/acre from 1994–2009 and 1.13 lbs ae/acre from 2010–2012. Third, we divided the total number of pounds of glyphosate purchased

per county per year by application rate to estimate the number of acres sprayed with glyphosate annually. Fourth, we divided the latter value by the area of corn and soybeans in each county to estimate the percentage of glyphosate-tolerant crops sprayed per county (0.06 correlation with $cropcov_j$; Fig. 1d). Estimated glyphosate application varied annually between 0% (all counties in 1994–1995 prior to adoption of Roundup™ Ready corn and soybeans) and 100% (several counties from 2004–2012); the mean application rate was $57.2\% \pm 31.7\%$. Our models included an interaction between $cropcov_j$ and $glyApp_{j,t}$ because we hypothesized that the effects of herbicide on local summer abundances of monarchs would depend on the area of surrounding crop cover.

Abundance of overwintering monarch butterflies

An index of the abundance of overwintering monarch butterflies ($winter_t$) is estimated annually by measuring the area occupied by all known overwintering colonies in Mexico during early winter (December). These data have been published by World Wildlife Fund since the winter of 1993–1994 (Brower et al. 2012a, b). Estimates from the winters of 1993–1994 through 2012–2013 ranged from 1.19 ha during 2012–2013 to 18.19 ha during 1996–1997 (6.58 ± 4.06 ha; Fig. 1a). We used the preceding winter's index as a covariate in models of abundance during the subsequent summer. For the analysis of 2004–2013 data, we ran models that included either the $winter_t$ covariate as defined above or the abundance of overwintering monarchs measured in late winter (February); the latter data were not available for years before 2005. The correlation between annual overwintering abundance measured in early and late winter was 0.74, but we hypothesized that because the late winter index accounts for overwintering mortality, it would explain more variation in summer abundances than the early winter index (Vidal and Rendón-Salinas 2014).

Data analysis

We developed a negative binomial regression model, fit with Bayesian inference, to estimate expected monarch counts (μ) at each survey site ($n = 262$) for each week (28 June–20 September) during each year (1994–2013). Because our count data were overdispersed (4.7 ± 12.2 individuals), the negative binomial distribution fit the data better than the Poisson distribution. We defined the count at site j in week k during year t as:

$$y_{j,k,t} \sim \text{NegBinom}(p_{j,k,t}, r) \quad (1)$$

with mean

$$\mu_{j,k,t} = \frac{p_{j,k,t} \cdot r}{1 - r} \quad (2)$$

and variance

$$\sigma_{j,k,t}^2 = \frac{p_{j,k,t} \cdot r}{(1 - r)^2}, \quad (3)$$

where r is the dispersion parameter. In addition to covariates related to climate, land cover, land use, and overwintering abundance, we included two covariates to account for the

steady increase in weekly monarch abundance ($week_k$) and the plateau in weekly abundance ($week_k^2$). We also included a random effect to control for site-specific effects (e.g. variation in effort due to transect length, observer error, and habitat quality). Random effects have been included in other analyses that were based on extensive data collected by volunteers (e.g. Breeding Bird Survey data; Sauer and Link 2011). The final global model was (see Supplementary material Appendix 1 for model code):

$$\begin{aligned} \log(\mu_{j,k,t}) = & \alpha 1 + \alpha 2 \cdot spPrec_t + \alpha 3 \cdot spPrec_t^2 \\ & + \alpha 4 \cdot spGDD_t + \alpha 5 \cdot spGDD_t^2 \\ & + \alpha 6 \cdot avgGDD_j + \alpha 7 \cdot PDI_{j,t} \\ & + \alpha 8 \cdot open_j + \alpha 9 \cdot winter_t + \alpha 10 \cdot glyApp_{j,t} \\ & + \alpha 11 \cdot cropcov_j + \alpha 12 \cdot glyApp_{j,t} \cdot cropcov_j \\ & + \alpha 13 \cdot week_k + \alpha 14 \cdot week_k^2 + \alpha 15_j \end{aligned}$$

where $\alpha 15_j$ is the random effect centered around zero with a variance (τ^2) that is estimated along with parameters $\alpha 1 - \alpha 14$. All covariates were standardized to have a mean of zero and standard deviation of one.

We estimated parameter values for all models with JAGS (Plummer 2003) called from program R (R package jagsUI; Kellner 2015). We ran three chains for 6000 iterations after a burn-in of 3000 iterations, and thinned the chains by three assuming flat normal priors for each of the covariates. Model convergence was assessed with the Rhat statistic (Gelman and Hill 2007) and visual inspection of chains. We assessed model fit by calculating a Bayesian p-value, or posterior predictive check, with a Pearson's residual discrepancy measure (Kéry 2010). A model that fits the data well has a p-value near 0.5 (Kéry 2010); p-values for global models were between 0.4 and 0.6 for each of the three time periods.

Model selection

We used a five-step forward selection approach to model fitting (Burnham and Anderson 2003). We began with a null model that included an intercept and random site effect. We then added $week_k$ and $week_k^2$ terms, and compared the fit of the two models with the deviance information criterion (DIC; Spiegelhalter et al. 2014). The model that included both week terms had the lower DIC, so we used this model as the template model. Second, we added covariates in seasonal groups: spring climate ($spGDD_j$, $spGDD_t$, $spPrec_t$ and $spPrec_t^2$), summer land use ($open_j$, $cropcov_j$, $glyApp_{j,t}$ and $cropcov_j \times glyApp_{j,t}$), summer climate ($avgGDD_j$ and $PDI_{j,t}$), and winter abundance ($winter_t$). We considered the strength of support of a given model to be high if it was within 2 DIC units of the most strongly supported model. Thus, all models within 2 DIC of the model with the lowest DIC, which contained one group of covariates, were carried forward. In the third step, we again added seasonal groups of covariates, yielding models with two groups of covariates. Again, the most strongly supported model and models within 2 DIC units were carried forward. Fourth, we repeated step three to yield models with three groups of covariates. Fifth, we added the remaining seasonal group to generate the global

model. The model with the lowest DIC after these steps was considered to be the most strongly supported.

We conducted model selection for all three time periods (1994–2013, 1994–2003, 2004–2013). For 2004–2013, we also compared the fit of early winter- and late winter-only models, and found that late winter was more strongly associated with summer abundance ($\Delta\text{DIC} = 32.7$). Therefore, we used only the late winter covariate in subsequent steps of model selection for the 2004–2013 analysis. All parameters are reported as mean and 95% credible interval (CI) unless otherwise noted; parameters with 95% credible intervals that did not overlap zero were considered significant.

Results

The most strongly supported model of summer monarch expected counts from 1994–2013 included effects of spring climate, summer climate, and summer land use (Table 1). Wetter ($\geq 5.25''$ of precipitation) and cooler (280–310 GDD) springs in Texas were associated with higher summer abundances (Fig. 2). The credible intervals of the quadratic terms for both spring GDD and precipitation overlapped zero (Table 2). The proportion of unforested area and crop cover nearby were also positively correlated with abundance (Table 2). Although county-specific glyphosate application and its interaction with crop cover were included in the summer land use group, credible intervals for both parameters overlapped zero (Table 2), indicating no significant herbicide association with summer abundance over the 20-yr period. Summer GDD and drought indices were significantly associated with abundance, although to a lesser degree than

unforested area and crop cover (Table 2); site-level abundance was greatest when accumulated GDDs were less than average (i.e. cooler) and when the PDI was slightly higher than average (i.e. sites were wetter than average). Overwintering abundance was not significantly associated with the summer abundances of monarchs from 1994–2013 (Fig. 2), and thus was not included in the most strongly supported model (but was included within the five most strongly supported models; Table 1). Site-level random effects were strongly associated with expected counts during the 20-yr period (Table 2).

The most strongly supported model of summer expected counts from 1994–2003 included spring climate as well as summer land use and summer climate, although the global model was within 0.7 DIC units (Table 1). The associations of spring climate with abundance were similar to those from 1994–2013; 5–6'' of precipitation (i.e. 10-yr average; Fig. 2a, Table 3) and 290–310 GDD (slightly above 10-yr average; Fig. 2b, Table 2, Table 3) were associated with higher expected counts. However, site-specific summer temperatures were not significantly associated with abundance, and drier than average sites were associated with greater abundances (relative to 10-yr average; Table 2). Both $open_j$ and $cropcov_j$ were positively associated with abundance (Fig. 3a). In contrast to 1994–2013, the association of abundance with county-level glyphosate application was strongly negative from 1994–2003, as was the interaction between $glyApp_{j,t}$ and $cropcov_j$ (Fig. 3a). This negative association between glyphosate and expected counts became more pronounced at sites as the percentage of crop cover surrounding the site increased (e.g. 50% decline in expected counts at sites with 50% crop cover vs 25% decline at sites with 10% crop cover; Fig. 3a). Although overwintering abundance

Table 1. The most strongly supported models of weekly summer expected counts of monarch butterflies at Illinois and northwest Indiana sites from 1994–2013, 1994–2003, and 2004–2013. Models were ranked according to differences in the deviance information criterion (ΔDIC). Spring climate refers to linear and quadratic terms for growing degree days in Texas ($spGDD_v$, $spGDD_v^2$), and linear and quadratic terms for mean rainfall during February, March, and April in Texas ($spPrec_v$ and $spPrec_v^2$). Summer (both summer land use and summer climate) refers to the percentage of unforested area within a 1 km radius of each site ($open_j$), the proportion of land within a 10 km radius of each site classified as cultivated crops ($cropcov_j$), county-level glyphosate application ($glyApp_{j,t}$), a crop cover and glyphosate interaction term ($cropcov_j \times glyApp_{j,t}$), average cumulative GDD in the week of 13 September at each site ($avgGDD_j$) and site-specific water availability from 28 June through 13 September ($PDI_{j,t}$). Summer land use refers to $open_j$, $cropcov_j$, $glyApp_{j,t}$ and $cropcov_j \times glyApp_{j,t}$. Summer climate includes $avgGDD_j$ and $PDI_{j,t}$. Winter refers to an index of overwintering monarch abundance in Mexico ($winter_t$), and global includes all 11 covariates. Models also include an intercept term, week terms ($week_{k,t}$, $week_{k,t}^2$), and survey site as a random effect.

Model	DIC	ΔDIC	Number of parameters
Abundance 1994–2013			
Spring climate + summer	29994.9	0.0	13
Spring climate + summer land use	30005.6	10.7	11
Spring climate + summer land use + winter	30007.6	12.7	12
Global (spring climate + summer + winter)	30008.3	13.4	14
Spring climate + winter	30009.4	14.5	8
Abundance 1994–2003			
Spring climate + summer	10562.5	0.00	13
Global (spring climate + summer + winter)	10563.2	0.70	14
Spring climate + summer climate + winter	10579.3	16.5	10
Spring climate + winter	10595.5	33.0	8
Spring climate + summer climate	10606.7	44.2	9
Abundance 2004–2013			
Global (spring climate + summer + winter ^a)	18612.7	0.0	14
Spring climate + summer climate + winter ^a	18694.0	81.3	10
Spring climate + summer climate	18694.8	82.1	9
Spring climate + summer	18710.9	98.2	13
Spring climate + winter ^a	18740.0	127.3	8

^aWinter refers to annual counts in February from 2004–2013.

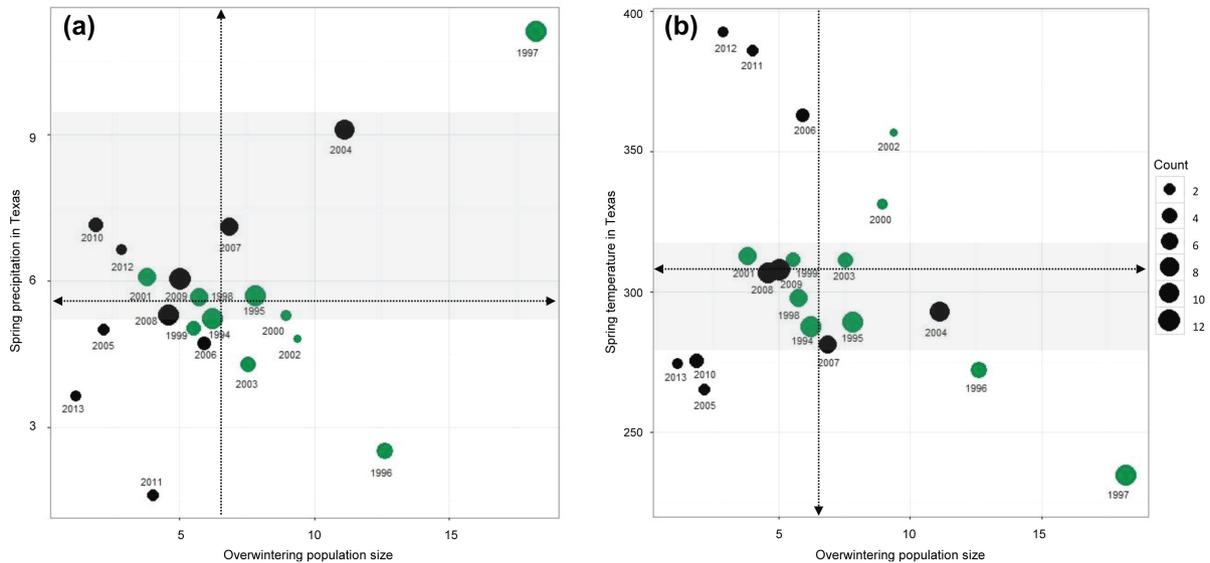


Figure 2. Average survey-specific expected counts of monarch butterflies at Illinois and northwest Indiana sites from 28 June–20 September from 1994–2003 (green points) and 2004–2013 (black points). Expected counts are plotted as a function of each year’s overwintering population size (measured as total area [ha] occupied by colonies in December) and each year’s observed (a) spring precipitation (measured as inches) or (b) spring temperature (measured as growing degree days [GDD]). Shaded rectangles indicate spring conditions associated with the highest summer abundances. The mean expected counts were derived from separate global models for each time period, and averaged across all Markov chain Monte Carlo (MCMC) iterations, surveyed sites, and weeks within each year. Dotted vertical and horizontal arrows indicate mean covariate values from 1994–2013 and the direction of the relationship with expected counts in the most strongly supported 20-yr model (Table 1).

was included in the second most strongly supported model (Table 1), the credible interval overlapped zero, indicating no strong association with summer abundance during 1994–2003 (no trend across x-axes in Fig. 2).

The global model was the most strongly supported when only data from 2004–2013 were included in model fitting; no other models were within 2 DIC units (Table 1). Again, summer expected counts were higher during springs with 5–7” of rainfall in Texas (Fig. 2a) and with 280–305 GDD (Fig. 2b, Table 3). Site-specific summer temperatures were not significantly associated with abundances, but higher PDI values (i.e. wetter sites) and abundances were positively associated (Table 2). Overwintering abundance was positively associated with summer expected counts from 2004–2013, in contrast to the lack of association during the previous decade (stronger trend across x-axes in Fig. 2). Credible intervals for both glyphosate application and the $glyApp_{j,t}$ and $cropcov_j$ interaction overlapped zero (Table 2), suggesting no significant association between herbicide application and summer abundances during 2004–2013 (Fig. 3b). Both $open_j$ and $cropcov_j$ had positive associations with abundances, as observed during the first decade (Fig. 3b). The intercept estimate for 2004–2013 ($\alpha_{1_{04-13}} = 0.85$, $CI = 0.67-1.0$) was substantially lower than that estimated for 1994–2003 ($\alpha_{1_{94-03}} = 1.19$, $CI = 0.99-1.39$), indicating that monarch expected counts were significantly lower at an average site during the second decade as compared to the first. Additionally, estimates of $week_k$ and $week_k^2$ terms differed between the two decades (Table 2), resulting in a slower rate of increase (and lower maximum) in average weekly expected counts throughout the 12-week recruitment period from 2004–2013. To compare the absolute difference in expected counts between decades given the full range of

observed data, we used the parameter estimates from the most strongly supported model for each period to calculate expected values across all MCMC iterations, surveyed sites, and weeks within each year. The expected count of monarchs averaged approximately one fewer at each site from 2004–2013 than from 1994–2003 (5.4 versus 6.3 monarchs, respectively), although the credible intervals for the two estimates partially overlapped (Fig. 4; $CI_{04-13} = 4.73-6.15$, $CI_{94-03} = 5.48-7.20$).

Discussion

This is the first study in which the weight of evidence suggests a local decline in abundance of adult monarch butterflies on their summer breeding grounds, consistent with patterns suggested less strongly by previous research (Ries et al. 2015a, Stenoien et al. 2015). By assessing indices of abundance at the site level rather than the regional level, we revealed a negative association between local abundance and county-level glyphosate application during the period when glyphosate use was increasing most quickly. The strength of this association increased as the percentage of crop cover around sites increased. Summer land use was more strongly associated with monarch abundance at sites in Illinois. Cross-seasonal associations of spring climate and overwintering abundances were also related to summer abundance in the Midwest, thus adding to the growing consensus that seasonal carry-over effects can impact long-term population dynamics (Elliott et al. 2016). Furthermore, the warmer spring temperatures in Texas from 2004–2013 (Table 3) may be contributing to the estimated decline of monarch abundance in Illinois, as cooler springs were strongly associated with

Table 2. Mean parameter estimates from the most strongly supported negative binomial regression models (top models in Table 1) estimating weekly expected counts of monarch butterflies at Illinois and northwest Indiana sites from 1994–2013, 1994–2003, and 2004–2013. The 95% credible intervals (CI) and whether intervals overlap zero are shown. See text for full covariate descriptions.

Model	Mean	95% CI	Overlap zero
1994–2013			
Intercept	1.474	1.346, 1.609	False
Open	0.318	0.202, 0.438	False
Crop cover	0.203	0.079, 0.332	False
Spring precipitation	0.161	0.114, 0.206	False
Spring precipitation ²	-0.021	-0.054, 0.011	True
Spring GDD	-0.112	-0.170, -0.055	False
Spring GDD ²	-0.002	-0.052, 0.047	True
Week	0.544	0.501, 0.586	False
Week ²	-0.119	-0.146, -0.092	False
Glyphosate application	-0.047	-0.113, 0.019	True
Glyphosate × crop cover	-0.029	-0.067, 0.008	True
Average GDD	-0.117	-0.234, -0.003	False
PDI	0.045	0.000, 0.088	False
Random site effect (τ^2)	0.722	0.575, 0.918	False
1994–2003			
Intercept	1.189	0.990, 1.391	False
Open	0.277	0.090, 0.459	False
Crop cover	0.308	0.135, 0.469	False
Spring precipitation	0.275	0.154, 0.397	False
Spring precipitation ²	1.039	0.835, 1.259	False
Spring GDD	1.115	0.806, 1.434	False
Spring GDD ²	-0.834	-1.008, -0.664	False
Week	0.941	0.866, 1.011	False
Week ²	-0.233	-0.279, -0.184	False
Glyphosate application	-0.328	-0.429, -0.229	False
Glyphosate × crop cover	-0.071	-0.135, -0.009	False
Average GDD	-0.121	-0.123, 0.044	True
PDI	-0.353	-0.424, -0.278	False
Random site effect (τ^2)	0.775	0.588, 1.066	False
2004–2013			
Intercept	0.854	0.667, 1.030	False
Open	0.248	0.110, 0.379	False
Crop cover	0.235	0.104, 0.371	False
Spring precipitation	0.282	0.199, 0.374	False
Spring precipitation ²	-0.703	-0.805, -0.703	False
Spring GDD	-0.557	-0.689, -0.429	False
Spring GDD ²	1.268	1.044, 1.509	False
Week	0.343	0.296, 0.387	False
Week ²	-0.119	-0.147, -0.092	False
Glyphosate application	-0.029	-0.097, 0.038	True
Glyphosate × crop cover	-0.030	-0.079, 0.018	True
Average GDD	-0.083	-0.216, 0.044	True
PDI	0.637	0.541, 0.736	False
Winter	0.803	0.656, 0.961	False
Random site effect (τ^2)	0.792	0.631, 1.017	False

greater summer abundances. Cumulatively, our analyses suggest that both climate and land use are associated with trends in adult monarch abundance. However, given the limited spatial extent of the survey data relative to the entire breeding range, we cannot directly assess the extent to which land use, climate, and carry-over effects are contributing to the overall decline of monarchs across eastern North America. Additional research incorporating data from a larger portion of the summer breeding range and dynamics during autumn may provide useful information on spatially extensive monarch population dynamics.

Our analysis not only highlights within- and cross-season associations of both climate and land use with abundance of a migratory species, but it also emphasizes the importance of examining associations between abundance and dynamic covariates at multiple time steps to capture fine-resolution temporal fluctuations in population-level responses to varying environmental conditions. Responses of population dynamics to climate and land use at several points in time are rarely assessed (Bertheaux et al. 2006, Kerr and Dobrowski 2013), but may be spatially and temporally complex, especially for migratory species that travel through multiple geographic regions and diverse ecosystems (Norris and Marra 2007).

The abundance index of overwintering monarchs was positively related to summer abundance from 2004–2013, indicating an association separated by, or sustained over, two stages of the annual cycle. To ensure that this result was not due to the use of the late winter rather than the early winter covariate, we replaced February counts with those from December and found a similar relationship (mean of α_9 : 0.80 and 0.78, respectively). Because the global model was within 2 DIC units of the most strongly supported model for 1994–2003, it is possible that a relationship also exists between the first decade of summer counts and late winter abundances, but data to test this hypothesis are unavailable. Overwintering abundance has decreased in recent years (Fig. 1a), which may be affecting summer abundance. Our results suggest that low winter abundance could limit the magnitude of local summer abundance in the Midwest.

We identified substantial cross-seasonal associations between spring climate and summer monarch abundance in the Midwest. Saunders et al. (2016) also found that relatively cool spring temperatures (≤ 300 GDD) and average to above-average precipitation ($\geq 6''$) in Texas were associated with greater monarch abundances in Ohio and Illinois from 1996–2011. Thus, we are reasonably confident that inference about climate drawn from this Illinois analysis can be extrapolated to a larger area of the Midwest. From 1994–2003, average to above-average spring GDD was associated with higher abundances. By contrast, from 2004–2013 and in the results of Saunders et al. (2016), below-average GDD was associated with greater abundances. However, the temperatures that were associated with greater abundances from 1994–2003 (290–310 GDD) were similar in 2004–2013; spring temperatures from 1994–2003 were merely cooler and less variable than from 2004–2013 (Fig. 2b, Table 3). This temporal variation demonstrates the difficulty in predicting population trends as climate changes, especially for migratory species.

Although data indicate that the size of the overwintering monarch population has decreased over the last 19 yr (Fig. 1a), coarse analyses of annual summer population indices (e.g. from the North American Butterfly Association's count program) do not suggest a decline (Ries et al. 2015a, Inamine 2016). To determine whether we could detect a fine-resolution decline in summer abundance in Illinois, we ran additional models (one for each decade) that included only a year effect (and the necessary week and random effect terms) and found a significant negative association between abundance and year from 2004–2013 ($\alpha_{\text{year}} = -0.09$, CI = -0.15 to -0.03), but not from 1994–2003. This result,

Table 3. Means, standard deviations (SD), and ranges of covariates included in models of weekly summer expected counts of monarch butterflies in Illinois and northwest Indiana from 1994–2003 and 2004–2013. Covariate definitions are listed in Table 1.

Covariate	1994–2003			2004–2013		
	Mean	SD	Range	Mean	SD	Range
$spPrec_t$	5.57	2.19	2.51–11.12	5.63	2.08	1.62–9.10
$spGDD_t$	295.5	33.2	234.7–356.7	314.5	48.1	265.3–392.6
$avgGDD_j$	1237.3	71.5	1121–1480	1222.3	63.4	1100–1480
$PDI_{j,t}$	-0.15	0.90	-1.65–2.12	0.76	2.53	-3.46–4.32
$Open_j$	71.5	21.6	3.1–100.0	72.7	20.0	3.1–100.0
$Winter_t$	8.59	4.17	3.83–18.19	4.58	2.93	1.19–11.12
$GlyApp_{j,t}$	41.4	24.8	0.0–62.3	80.0	18.8	52.6–100.0
$Cropcov_j$	19.5	23.3	0.0–87.5	17.4	21.6	0.0–87.4

along with the results from our main models, which indicated that mean site-level expected counts declined by nearly one individual, provides evidence of a decrease in observed monarch abundance across the study region during the two decades of data collection. Loss of milkweed in agricultural areas or phenological shifts may explain the decrease in observed abundance of monarchs in the study area, but additional research is necessary to determine the mechanisms of decline.

Our result that local summer abundance of monarchs has declined is consistent with those of other studies. Nail et al. (2015) found a decline in survival rates of immature monarchs from 1997 to 2014, Stenoien et al. (2015) detected a decline in the density of eggs per plant from 2006 to 2014, and Ries et al. (2015a) indicated a possible (but not significant) decrease from 2011–2014 in end-of-summer counts conducted by the North American Butterfly Association. Furthermore, Pleasants and Oberhauser (2012) and Pleasants (2015) showed that if milkweed loss within agriculture fields in the upper Midwest is taken into account, monarch recruitment declined from 1999–2012, consistent

with the decline observed in the overwintering population. However, because the majority of our sites were in suburban areas (10 of 262 sites were in areas with $\geq 70\%$ crop cover), we are unable to make strong inferences about monarch abundances within areas dominated by crop fields. Longer time series, additional data collection in agricultural areas, and analyses combining data collected throughout the central flyway are needed to further assess the extent to which the summer population may be declining.

The temporally consistent positive relationship between local monarch abundance and proportion of open (unforested) land suggests that this covariate may be a proxy for milkweed abundance (or a cue for monarchs to search for milkweed). Site-level abundance also increased as the proportion of cultivated crops within 10 km increased, consistent with suggestions that agricultural areas are high-quality habitat for breeding monarchs (Pleasants and Oberhauser 2012). Alternatively, because current milkweed abundance within glyphosate-resistant corn and soybean fields is nearly zero (Pleasants 2015, 2017, Stenoien et al. 2016), monarchs may be drawn to isolated, remnant habitat patches. It also

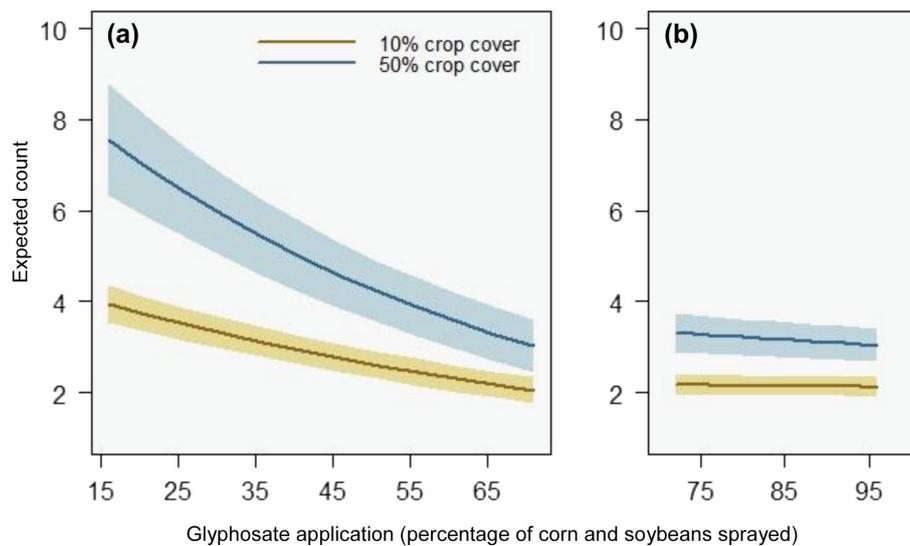


Figure 3. Expected counts of monarch butterflies at sites with 10% (yellow line) and 50% (blue line) crop cover within 10 km relative to the county-level percentage of corn and soybeans sprayed with glyphosate in Illinois and northwest Indiana from (a) 1994–2003 and (b) 2004–2013. Solid regression lines show the marginal effect of glyphosate application estimated from the most strongly supported model for each time period (i.e. two separate models; Table 1) at an average site where all other variables were held at mean values (i.e. zero). Shaded polygons represent 95% credible intervals. The x-axes in (a) and (b) represent 95% of the observed range of variation in county-level glyphosate application during 1994–2003 and 2004–2013, respectively.

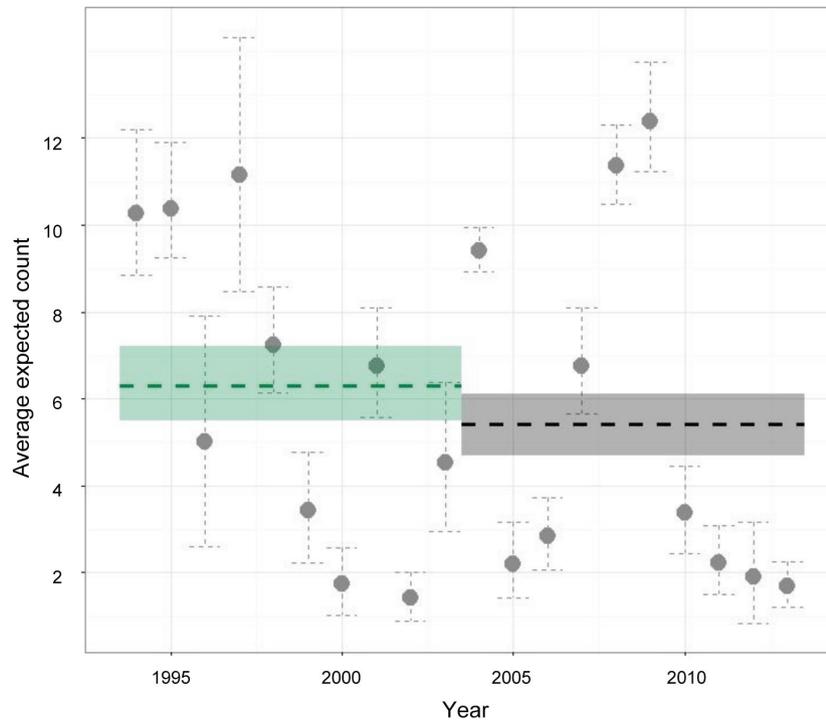


Figure 4. Average survey-specific expected counts of monarch butterflies (and 95% credible intervals) at Illinois and northwest Indiana sites from 28 June–20 September from 1994–2013. Expected counts were estimated from the most strongly supported model for each time period (i.e. two separate models; Table 1), and averaged across all MCMC iterations, surveyed sites, and weeks within each year. Dashed horizontal lines represent mean expected counts of monarchs per site during the first (green dashed line) and second (black dashed line) decades. Shaded polygons represent 95% credible intervals.

is possible that the mechanisms responsible for the relationship between abundance and land cover have changed over time. For example, we would not expect a negative correlation between local monarch abundance and crop cover after accounting for glyphosate application. The significant magnitude and variability of the site-level random effect in the models for all time periods (Table 2) also indicate unexplained spatial heterogeneity that may be contributing to observed monarch abundances.

Our results provide direct empirical evidence of a negative relationship between county-level glyphosate application rates and local monarch abundance while glyphosate-resistant crops were first being planted (1994–2003), particularly in areas of concentrated agriculture (Fig. 3a). However, our model may not be capturing the full extent of the relationship because the spatial resolution of our measure of glyphosate application is too coarse or because the locations of monarch surveys are biased (Pleasants and Oberhauser 2012). Fourteen of the 20 sites with > 60% crop cover were surveyed primarily from 1994–2003, and thus mean proportion of crop cover declined slightly in later years (Table 3). Further studies with data spanning more habitat types and agricultural intensities may help elucidate any recent trends in abundance related to glyphosate application. Additionally, future work combining several analytical approaches (e.g. mechanistic modeling, simulation models) and long-term count datasets (e.g. statewide butterfly monitoring networks, monitoring monarch larvae) should improve understanding of spatially extensive monarch dynamics and predicted changes in abundance in response to climate and land use variability.

Acknowledgements – Thank you to the many citizen science participants who helped in data collection and D. Taron of the Peggy Notebaert Nature Museum, who leads the Illinois Butterfly Monitoring Network, for access to those data. We thank R. Reeves for calculating land cover indices and E. Larsen for assembling climate variable data. We greatly appreciate the insightful comments provided by the Subject Editor E. Fleishman. Any use of trade, product, or firm names are for descriptive purposes only and do not imply endorsement by the U.S. Government.

Funding – Funding for L. Ries was provided by the National Science Foundation Award DBI-1147049.

References

- Baker, N. T. and Stone, W. W. 2015. Estimated annual agricultural pesticide use for counties of the conterminous United States, 2008–2012. – U.S. Geological Survey Data Series 907.
- Batalden, R. et al. 2007. Ecological niches in breeding generations of eastern North American monarch butterflies. – *Environ. Entomol.* 36: 1365–1373.
- Berteaux, D. et al. 2006. Constraints to projecting the effects of climate change on mammals. – *Clim. Res.* 32: 151–158.
- Brower, L. 1986. New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus* L. – In: Rankin, M. A. (ed.), *Migration: mechanisms and adaptive significance*. Marine Science Inst., pp. 748–785.
- Brower, L. P. et al. 2012a. Response to Davis: choosing relevant evidence to assess monarch population trends. – *Insect Conserv. Divers.* 5: 327–329.
- Brower, L. P. et al. 2012b. Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? – *Insect Conserv. Divers.* 5: 95–100.

- Burnham, K. P. and Anderson, D. R. 2003. Model selection and multimodel inference. – Springer.
- Crewe, T. and McCracken, J. 2015. Long-term trends in the number of monarch butterflies (Lepidoptera: Nymphalidae) counted on fall migration at Long Point, Ontario, Canada (1995–2014). – *Ann. Entomol. Soc. Am.* 108: 707–717.
- Davis, A. K. 2012. Are migratory monarchs really declining in eastern North America? Examining evidence from two fall census programs. – *Insect Conserv. Divers.* 5: 101–105.
- Dyer, L. A. and Forister, M. L. 2016. Wherefore and whither the modeler: understanding the population dynamics of monarchs will require integrative and quantitative techniques. – *Ann. Entomol. Soc. Am.* 109: 172–175.
- Elliott, K. H. et al. 2016. Experimental evidence for within- and cross-seasonal effects of fear on survival and reproduction. – *J. Anim. Ecol.* 85: 507–515.
- Flockhart, D. et al. 2015. Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. – *J. Anim. Ecol.* 84: 155–165.
- Flockhart, D. et al. 2017. Regional climate on the breeding grounds predicts variation in the natal origin of monarch butterflies overwintering in Mexico over 38 years. – *Global Change Biol.* doi: 10.1111/gcb.13589
- Gelman, A. and Hill, J. 2007. Data analysis using regression and multilevel hierarchical models. – Cambridge Univ. Press.
- Hartzler, R. G. 2010. Reduction in common milkweed (*Asclepias syriaca*) occurrence in Iowa cropland from 1999 to 2009. – *Crop Prot.* 29: 1542–1544.
- Hostetler, J. A. et al. 2015. Full-annual-cycle population models for migratory birds. – *Auk* 132: 433–449.
- Inamine, H. 2016. Linking the continental migratory cycle of the monarch butterfly to understand its population decline. – *Oikos* 125: 1081–1091.
- Kellner, k. 2015. jagsUI: a wrapper around rjags to streamline JAGS analyses. – R package ver. 1.3.5, <<https://github.com/kenkellner/jagsui>>.
- Kerr, J. T. and Dobrowski, S. Z. 2013. Predicting the impacts of global change on species, communities and ecosystems: it takes time. – *Global Ecol. Biogeogr.* 22: 261–263.
- Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. – Academic Press.
- Kirby, J. S. et al. 2008. Key conservation issues for migratory land and waterbird species on the world's major flyways. – *Bird Conserv. Int.* 18: S49–S73.
- Malcolm, S. B. et al. 1993. Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? – In: Malcolm, S. B. and Zalucki, M. P. (eds), *Biology and conservation of the monarch butterfly*. Natural History Museum of Los Angeles County, pp. 253–267.
- Marra, P. P. et al. 2015. A call for full annual cycle research in animal ecology. – *Biol. Lett.* 11: 20150552.
- McMaster, G. S. and Wilhelm, W. 1997. Growing degree-days: one equation, two interpretations. – *Agric. For. Meteorol.* 87: 291–300.
- Nail, K. R. et al. 2015. Immature monarch survival: effects of site characteristics, density, and time. – *Ann. Entomol. Soc. Am.* 108: 680–690.
- Norris, D. R. and Marra, P. P. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. – *Condor* 109: 535–547.
- Oberhauser, K. and Peterson, A. T. 2003. Modeling current and future potential wintering distributions of eastern North American monarch butterflies. – *Proc. Natl Acad. Sci. USA* 100: 14063–14068.
- Oberhauser, K. et al. 2016. A trans-national monarch butterfly population model and implications for regional conservation priorities. – *Ecol. Entomol.* doi: 10.1111/een.12351
- Pleasants, J. 2015. Monarch butterflies and agriculture. – In: Oberhauser, K. S. et al. (eds), *Monarchs in a changing world: biology and conservation of an iconic butterfly*. Cornell Univ. Press, pp. 169–178.
- Pleasants, J. 2017. Milkweed restoration in the Midwest for monarch butterfly recovery: estimates of milkweed lost, milkweed remaining and milkweeds that must be added to increase the monarch population. – *Insect Conserv. Divers.* 10: 42–53.
- Pleasants, J. M. and Oberhauser, K. S. 2012. Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. – *Insect Conserv. Divers.* 6: 135–144.
- Pleasants, J. M. et al. 2016. Conclusion of no decline in summer monarch population not supported. – *Ann. Entomol. Soc. Am.* 109: 169–171.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. – In: *Proceedings of the 3rd International workshop on Distributed Statistical Computing*. DSC, pp. 20–22.
- Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. – *Biol. Conserv.* 12: 115–134.
- Prysbly, M. D. and Oberhauser, K. S. 2004. Temporal and geographic variation in monarch densities: citizen scientists document monarch population patterns. – In: Oberhauser, K. S. and Solensky, M. J. (eds), *The monarch butterfly: biology and conservation*. Cornell Univ. Press, pp. 9–20.
- Ries, L. and Oberhauser, K. 2015. A citizen army for science: quantifying the contributions of citizen scientists to our understanding of monarch biology. – *Bioscience* 65: 419–430.
- Ries, L. et al. 2015a. The disconnect between summer and winter monarch trends for the eastern migratory population: possible links to differing drivers. – *Ann. Entomol. Soc. Am.* 108: 691–699.
- Ries, L. et al. 2015b. Connecting eastern monarch population dynamics across their migratory cycle. – In: Oberhauser, K. S. et al. (eds), *Monarchs in a changing world: biology and conservation of an iconic insect*. Cornell Univ. Press, pp. 268–281.
- Runge, C. A. et al. 2014. Conserving mobile species. – *Front Ecol. Environ.* 12: 395–402.
- Rushing, C. S. et al. 2016. Quantifying the drivers of population dynamics for a migratory bird throughout the annual cycle. – *Proc. R. Soc. B* 283: 20152846.
- Sagarin, R. D. et al. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. – *Trends Ecol. Evol.* 21: 524–530.
- Sauer, J. R. and Link, W. A. 2011. Analysis of the North American breeding bird survey using hierarchical models. – *Auk* 128: 87–98.
- Saunders, S. P. et al. 2016. Evaluating confidence in climate-based predictions of population change in a migratory species. – *Global Ecol. Biogeogr.* 25: 1000–1012.
- Small-Lorenz, S. L. et al. 2013. A blind spot in climate change vulnerability assessments. – *Nat. Clim. Change* 3: 91–93.
- Spiegelhalter, D. J. et al. 2014. The deviance information criterion: 12 years on. – *J. R. Stat. Soc.* 76: 485–493.
- Stenoien, C. et al. 2015. Habitat productivity and temporal patterns of monarch butterfly egg densities in the eastern United States. – *Ann. Entomol. Soc. Am.* 108: 670–679.
- Stenoien, C. et al. 2016. Monarchs in decline: a collateral landscape level effect of modern agriculture. – *Insect Sci.* doi: 10.1111/1744-7917.12404
- Stevens, S. R. and 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. – *J. Insect Conserv.* 14: 731–744.
- Stone, W. W. 2013. Estimated annual agricultural pesticide use for counties of the conterminous United States, 1992–2009. – U.S. Geological Survey Data Series 752.

- Thornton, P. E. et al. 2014. Daymet: daily surface weather data on a 1-km grid for North America, version 2. – Oak Ridge National Laboratory Distributed Active Archive Center, <<http://daac.ornl.gov>>.
- USDA 2011. National Agricultural Statistics Service. – United States Dept of Agriculture, <www.nass.usda.gov/Statistics_by_Subject/index.php>.
- USDA 2015. Adoption of genetically engineered crops in the U.S. – United States Dept of Agriculture, <www.ers.usda.gov/data-products/adoption-of-genetically-engineered-crops-in-the-us/recent-trends-in-ge-adoption>.
- Vidal, O. and Rendón-Salinas, E. 2014. Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico. – *Biol. Conserv.* 180: 165–175.
- Vidal, O. et al. 2014. Trends in deforestation and forest degradation after a decade of monitoring in the Monarch Butterfly Biosphere Reserve in Mexico. – *Conserv. Biol.* 28: 177–186.
- Wassenaar, L. I. and Hobson, A. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. – *Proc. Natl Acad. Sci. USA* 95: 15436–15439.
- Webster, M. S. et al. 2002. Links between worlds: unraveling migratory connectivity. – *Trends Ecol. Evol.* 17: 76–83.
- Wilcove, D. S. and Wikelski, M. 2008. Going, going, gone: is animal migration disappearing? – *PLoS Biol.* 6: e188.
- Wilson, S. et al. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. – *Ecology* 92: 1789–1798.
- Zalucki, M. P. 1982. Temperature and rate of development in *Danaus plexippus* L. and *D. chrysippus* L. (Lepidoptera: Nymphalidae). – *Aust. J. Entomol.* 21: 241–246.
- Zalucki, M. P. and Rochester, W. A. 2004. Spatial and temporal population dynamics of monarchs down-under: lessons for North America. – In: Oberhauser, K. S. et al. (eds), *The monarch butterfly: biology and conservation*. Cornell Univ. Press, pp. 219–228.
- Zaya, D. N. et al. 2017. Long-term trends in Midwestern milkweed abundances and their relevance to monarch butterfly declines. – *BioScience* doi: 10.1093/biosci/biw186
- Zipkin, E. F. et al. 2012. Tracking climate impacts on the migratory monarch butterfly. – *Global Change Biol.* 18: 3039–3049.

Supplementary material (Appendix ECOG-02719 at <www.ecography.org/appendix/ecog-02719>). Appendix 1.