UC Davis
UC Davis Previously Published Works

Title

Understanding a migratory species in a changing world: climatic effects and demographic declines in the western monarch revealed by four decades of intensive monitoring

Permalink

https://escholarship.org/uc/item/0900q49t

Journal

Oecologia, 181(3)

ISSN

0029-8549

Authors

Espeset, Anne E
Harrison, Joshua G
Shapiro, Arthur M
et al.

Publication Date

2016-07-01

DOI

10.1007/s00442-016-3600-y

Peer reviewed

Metadata of the article that will be visualized in OnlineFirst

---

Please note: Images will appear in color online but will be printed in black and white.

ArticleTitle	Understanding a migratory species in a changing world: climatic effects and demographic declines in the western monarch revealed by four decades of intensive monitoring
Article Sub-Title	
Article CopyRight	Springer-Verlag Berlin Heidelberg (This will be the copyright line in the final PDF)
Journal Name	Oecologia

Corresponding Author	Family Name	**Espeset**
	Particle	
	Given Name	**Anne E.**
	Suffix	
	Division	Program in Ecology, Evolution, and Conservation Biology, Department of Biology
	Organization	University of Nevada
	Address	Reno, NV, USA
	Division	
	Organization	
	Address	1664 North Virginia Street, 89509, Reno, NV, USA
	Email	aespeset@nevada.unr.edu

Author	Family Name	**Harrison**
	Particle	
	Given Name	**Joshua G.**
	Suffix	
	Division	Program in Ecology, Evolution, and Conservation Biology, Department of Biology
	Organization	University of Nevada
	Address	Reno, NV, USA
	Email	

Author	Family Name	**Shapiro**
	Particle	
	Given Name	**Arthur M.**
	Suffix	
	Division	Center for Population Biology
	Organization	University of California
	Address	Davis, CA, USA
	Email	

Author	Family Name	**Nice**
	Particle	
	Given Name	**Chris C.**
	Suffix	
	Division	Department of Biology

	Organization	Texas State University
	Address	San Marcos, TX, USA
	Email	
Author	Family Name	**Thorne**
	Particle	
	Given Name	**James H.**
	Suffix	
	Division	Department of Environmental Science and Policy
	Organization	University of California
	Address	Davis, CA, USA
	Email	
Author	Family Name	**Waetjen**
	Particle	
	Given Name	**David P.**
	Suffix	
	Division	Department of Environmental Science and Policy
	Organization	University of California
	Address	Davis, CA, USA
	Email	
Author	Family Name	**Fordyce**
	Particle	
	Given Name	**James A.**
	Suffix	
	Division	Ecology and Evolutionary Biology
	Organization	University of Tennessee
	Address	37996, Knoxville, TN, USA
	Email	
Author	Family Name	**Forister**
	Particle	
	Given Name	**Matthew L.**
	Suffix	
	Division	Program in Ecology, Evolution, and Conservation Biology, Department of Biology
	Organization	University of Nevada
	Address	Reno, NV, USA
	Email	

Abstract	Migratory animals pose unique challenges for conservation biologists, and we have much to learn about how migratory species respond to drivers of global change. Research has cast doubt on the stability of the eastern monarch butterfly (*Danaus plexippus*) population in North America, but the western monarchs have not been as intensively examined. Using a Bayesian hierarchical model, sightings of western monarchs over approximately 40 years were investigated using summer flight records from ten sites along an elevational transect in Northern California. Multiple weather variables were examined, including local and regional temperature and precipitation. Population trends from the ten focal sites and a subset of western overwintering sites were compared to summer and overwintering data from the eastern migration.

Records showed western overwintering grounds and western breeding grounds had negative trends over time, with declines concentrated early in the breeding season, which were potentially more severe than in the eastern population. Temporal variation in the western monarch also appears to be largely independent of (uncorrelated with) the dynamics in the east. For our focal sites, warmer temperatures had positive effects during winter and spring, and precipitation had a positive effect during spring. These climatic associations add to our understanding of biotic-abiotic interactions in a migratory butterfly, but shifting climatic conditions do not explain the overall, long-term, negative population trajectory observed in our data.

Keywords (separated by '-')	Climate change - *Danaus plexippus* - Hierarchical model - Monarch butterfly - Western population
Footnote Information	Communicated by Klaus Fischer. **Electronic supplementary material** The online version of this article (doi:10.1007/s00442-016-3600-y) contains supplementary material, which is available to authorized users.

CrossMark

POPULATION ECOLOGY – ORIGINAL RESEARCH

Understanding a migratory species in a changing world: climatic effects and demographic declines in the western monarch revealed by four decades of intensive monitoring

Anne E. Espeset[1,6] · Joshua G. Harrison[1] · Arthur M. Shapiro[2] · Chris C. Nice[3] ·
James H. Thorne[4] · David P. Waetjen[4] · James A. Fordyce[5] · Matthew L. Forister[1]

Abstract Migratory animals pose unique challenges for conservation biologists, and we have much to learn about how migratory species respond to drivers of global change. Research has cast doubt on the stability of the eastern monarch butterfly (*Danaus plexippus*) population in North America, but the western monarchs have not been as intensively examined. Using a Bayesian hierarchical model, sightings of western monarchs over approximately 40 years were investigated using summer flight records from ten sites along an elevational transect in Northern California. Multiple weather variables were examined, including local and regional temperature and precipitation. Population trends from the ten focal sites and a subset of western overwintering sites were compared to summer and overwintering data from the eastern migration. Records showed western overwintering grounds and western breeding grounds had negative trends over time, with declines concentrated early in the breeding season, which were potentially more severe than in the eastern population. Temporal variation in the western monarch also appears to be largely independent of (uncorrelated with) the dynamics in the east. For our focal sites, warmer temperatures had positive effects during winter and spring, and precipitation had a positive effect during spring. These climatic associations add to our understanding of biotic-abiotic interactions in a migratory butterfly, but shifting climatic conditions do not explain the overall, long-term, negative population trajectory observed in our data.

Communicated by Klaus Fischer.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3600-y) contains supplementary material, which is available to authorized users.

✉ Anne E. Espeset
aespeset@nevada.unr.edu

1 Program in Ecology, Evolution, and Conservation Biology, Department of Biology, University of Nevada, Reno, NV, USA

2 Center for Population Biology, University of California, Davis, CA, USA

3 Department of Biology, Texas State University, San Marcos, TX, USA

4 Department of Environmental Science and Policy, University of California, Davis, CA, USA

5 Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

6 1664 North Virginia Street, Reno, NV 89509, USA

Introduction

Issues of spatial and temporal scale have always been among the greatest challenges that face ecologists wishing to extrapolate beyond single species and local conditions (McGill 2010; Chave 2013). These concerns have been brought to the fore by recent decades of anthropogenic influence on the environment, as the public looks to ecologists for predictions regarding changes in regional or continental floras and faunas (Morisette et al. 2008; Tylianakis et al. 2008). An important advance in the process has involved meta-analyses that allow global phenomena to be perceived through the accumulation of smaller-scale case studies (Parmesan 2006; Wu et al. 2011; Mantyka-Pringle et al. 2012). A further key contribution has come from the

Springer

development of hierarchical models that can effectively estimate parameters (such as the influence of weather) across large numbers of species and locations (Royle and Dorazio 2008; Ponciano et al. 2009; Congdon 2014; Nice et al. 2014). A logical implementation of such models involves species that utilize large regions, and migratory species are of particular interest because of complex life cycles that integrate climatic variation across heterogeneous local climates (Zipkin et al. 2012).

A prominent migratory animal in North America is the monarch butterfly (*Danaus plexippus*). This species has two independent migratory populations or subpopulations that together traverse much of the continent (Brower 1995; Brower and Malcolm 1991). In general, monarchs east of the Rocky Mountains migrate to Mexico while monarchs west of the Rocky Mountains migrate to locations along the Pacific coast of California (Urquhart and Urquhart 1977), aggregating in groves of Monterey pine (*Pinus radiata*), Monterey cypress (*Cupressus macrocarpa*), and blue gum (*Eucalyptus globulus*) (Weiss et al. 1991). Genetic studies have suggested that these populations are not distinct (Brower and Malcolm 1991; Lyons et al. 2012; Zhan et al. 2014), and some western monarchs potentially overwinter in Mexico (Dingle et al. 2005; Morris et al. 2015). Both populations depend on host plants in the genus *Asclepias*, the milkweeds. These plants are ruderal in nature, and have experienced declines in recent years in some areas, potentially in association with increased herbicide use on agricultural lands (Hartzler 2010; Pleasants and Oberhauser 2012; Zalucki and Lammers 2010). For the overwintering monarchs in Mexico, severe weather and forest degradation are further stressors that compound habitat and host loss on breeding grounds in the USA (Brower et al. 2012; Flockhart et al. 2015). Despite apparent stressors and declines in monarchs at their overwintering grounds (Vidal and Rendon-Salinas 2014; Saenz-Romero et al. 2012; Brower et al. 2002), numbers have not declined at some of the fall stopover sites in the Eastern USA (e.g., Davis 2012) or summer breeding grounds (Ries et al. 2015). Also, weather has not been considered to have a significant effect on the eastern Monarch population during spring and summer (Zalucki et al. 2015). In contrast to the many detailed studies published on the eastern monarchs (e.g., Oberhauser and Peterson 2003; Batalden et al. 2007; Brindza et al. 2008; Davis and Dyer 2015; Oberhauser et al. 2015), the western migration has received less attention (Koenig 2006).

Here we utilize a single-observer dataset on monarch populations at ten locations throughout the breeding range across northern California (Fig. 1). To our knowledge, this is the longest and most temporally intensive dataset on western monarchs, and consists of biweekly observations during monarch flights for between 27 and 42 years, depending on the site. In addition to these biweekly data, we use publically available numbers characterizing adult densities at coastal overwintering locations, as well as data describing abundances of eastern monarchs to compare western and eastern population dynamics [Shapiro 2014; The Xerces Society 2015; North American Butterfly Association (NABA) 2015; Monarch Net 2015]. Through examination of these data we address the following questions: have monarch observations per year changed over time (between years and within years) at our ten focal sites? And, to what extent can fluctuations in observed monarchs per year at focal sites be predicted by local and regional weather variables, both at the summer sites and at the overwintering grounds? With respect to these questions, we predict monarch numbers to be declining, as previous studies have shown negative trends over time for most butterflies in the region, especially at low-elevation sites (Forister et al. 2011; Harrison et al. 2015). We also hypothesize that warming conditions will have had a negative influence on the population, as has been observed for other butterflies in northern California (Casner et al. 2014). We also ask, as an issue of secondary interest, if dynamics at our transect sites (on the western summer grounds) are similar to patterns observed at the California overwintering sites. This question is motivated in part by previous work by Stevens and Frey (2010) who suggested a positive association between breeding season precipitation in our study area and interannual variation in monarch counts at the coastal overwintering areas. Finally, in order to place the western populations in the larger, continental context for monitoring and management of this migratory species, we compare temporal dynamics among the following datasets: the western summer grounds (our ten focal sites), the western overwintering grounds, the eastern summer grounds, and the eastern (Mexican) overwintering grounds (Shapiro 2014; the Xerces Society 2015; NABA 2015; Monarch Net 2015).

Materials and methods

Data collection and sampling locations

Data were recorded from 1972 up to and including 2014 at ten locations in Northern California by A. M. S. (Shapiro 2014). These locations describe an elevational transect starting at sea level and extending up over the crest of the Sierra Nevada mountains at 2775 m, and down the eastern slope to Sierra Valley. Sites encompass an array of habitat types, from saltwater marsh to sub-alpine barrens. Each site was visited every 2 weeks and the presence or absence of monarchs was noted (henceforth presences are referred to as "day positives", as in other publications from these data, e.g., Forister et al. 2010). Surveys were conducted via the Pollard walk method (Pollard 1977) on days suitable for
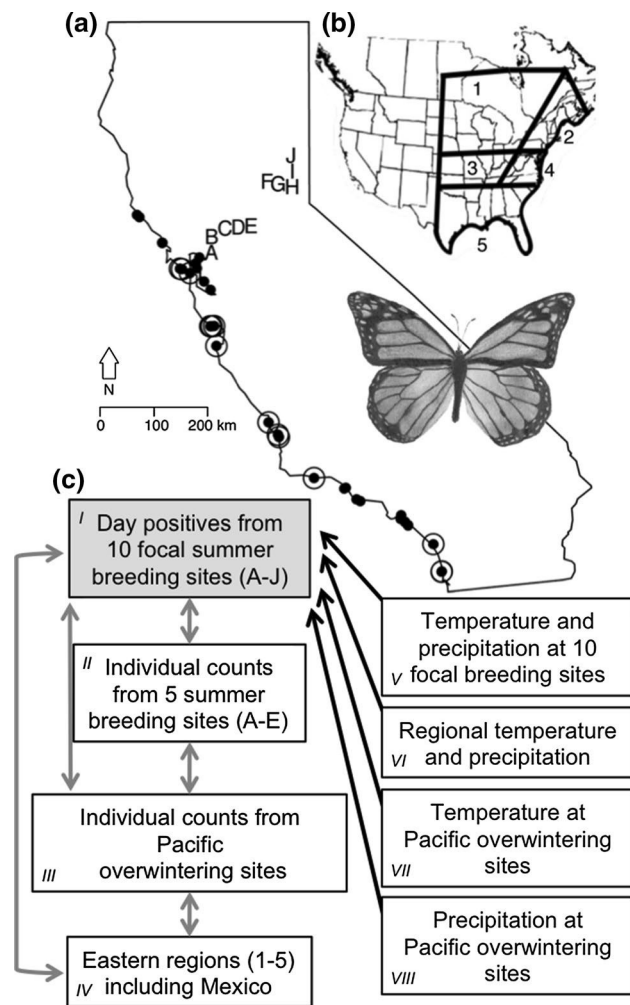
Fig. 1c a Map of California in the Western USA, including focal sites where observations of adults during the summer flight season were recorded [Suisun Marsh (*A*), Gates Canyon (*B*), West Sacramento (*C*), North Sacramento (*D*), Rancho Cordova (*E*), Washington (*F*), Lang Crossing (*G*), Castle Peak (*H*), Donner Pass (*I*), and Sierra Valley (*J*)]. *Large, open circles* along the coast are overwintering locations (see main text for details) from which abundance data were collated for use in analyses; *solid dots* are overwintering locations from which weather data were gathered for use in a subset of climatic analyses. **b** Map of North America showing eastern regions represented by count data from the summer flight season, as follows: North Central (*1*), (*2*) North East (*2*), Mid Central (*3*), Mid East (*4*), and South (*5*). **c** Diagram of datasets analyzed, as follows: "day positives" (*I*; counts of days on which adult monarchs were observed per year) at ten sites across the western breeding grounds; counts of adults at five of the low-elevation western breeding sites (*II*); counts of overwintering adults from a subset of western overwintering sites (*III*; *circled* on map; summary data from the eastern migration including summer population indices and hectares occupied by overwintering adults in Mexico (*IV*); climatic data from each of the ten focal western breeding sites (*V*); regional climatic conditions (*VI*; MEI 1 and MEI 2); climatic conditions at the Pacific overwintering sites (*VII*, *VIII*; treated separately, as explained in main text). Our focal dataset (day positives) is highlighted with a *gray background* and connected to climatic datasets (V–VIII) by *single-headed arrows* to represent multiple regressions. Relationships among monarch datasets (I–IV) were explored with correlations, indicated by *double-headed arrows* (for simplicity, not all connections are drawn). Illustration of adult monarch butterfly, *Danaus plexippus,* by Anne Espeset

Net 2015). These data consist of NABA Fourth of July counts from 1990 to 2009 (NABA 2015). Counts span five large geographical regions (north east, north central, mid east, mid central, and south; Fig. 1) and were collected by volunteers. Hectare overwintering data from Mexico were obtained from Monarch Butterfly Biosphere Reserve from 1994 to 2003 and World Wildlife Fund-Telcel Alliance from 2004 to 2015; the compiled data were accessed through The Xerces Society (2015).

Weather data

Weather specific to our ten transect sites was obtained from the PRISM working group (PRISM Climate Group 2015). **AQ1** These data are interpolated from neighboring weather stations incorporating local differences in topography, thus they potentially provide a more robust estimate of site-specific weather than raw data from the closest weather stations (Daly et al. 2008), which are subject to error and missing values. Data were grouped seasonally and reflect the water year, such that the 1980 water year, for example, starts with the fall of 1979. Specifically, "fall" is the previous year's September, October, and November; "winter" consists of the previous year's December and the focal year's January and February; "spring" is March up to and including May; and "summer" is June up to and including August. For each season, average daily temperature and

butterfly flight (sunny days with little wind). Abundance data (counts of adult monarchs) are available from five of our ten sites, and from a subset of years (1999–2012). The abundance data have been used previously to show that day positives are suitable proxies for monarch abundance (Casner et al. 2014), and we present limited analyses of the abundance data here [Electronic Supplementary Material (ESM) 1].

Count data from California overwintering locations were obtained from the Xerces Society Thanksgiving Count Database (The Xerces Society 2015). Data were collected from 1997 to 2014 by volunteers. Data from six overwintering counties were gathered for use in the present analyses: Marin, Monterey, San Luis Obispo, San Diego, Santa Barbara, and Santa Cruz. The overwintering data contains gaps (years without observations), but counties were chosen that had enough individual sites within them to provide coverage of the greatest number of years (1997–2014). All sightings within a county were averaged per year, giving a mean count/site per year. Data for the eastern monarch population were obtained from Monarch Net (Monarch

total precipitation were calculated (precipitation included snow for the high-elevation sites). Winter average temperature and precipitation data from PRISM were also obtained for each California overwintering location within the following eight counties: Alameda, Marin, Mendocino, Monterey, San Diego, San Luis Obispo, Sonoma, and Ventura. These counties were chosen to ensure that sampling encapsulated a wide range of overwintering conditions along the coast. In all cases (for focal and overwintering sites), PRISM data were taken from the latitude and longitude centroid of each site (using the default setting of 4-km^2 cells).

Because of the migratory nature of the monarch, we were interested in the possibility that regional weather variables could provide an informative contrast to the local data generated by PRISM. The multivariate El Niño Southern Oscillation index (MEI) was used to explore the impact of regional weather drivers (Wolter and Timlin 1993). The El Niño Southern Oscillation index (ENSO) is associated with unusual precipitation patterns throughout northern California (Schonher and Nicholson 1989), and MEI is the first principal component extracted from the analysis of six variables that together provide an index of the intensity of the ENSO for a given month. In order to reduce the complexity of the data to a manageable form, an additional principle components analysis on the MEI values across all 12 months was performed, and the first two components (MEI 1 and MEI 2) were extracted for analyses of monarch dynamics.

Overview of statistical methods

Analyses consisted of multiple, distinct models and combinations of data sources (Fig. 1c). The focus of analyses is data from our ten sites across the breeding grounds, because it is from those sites that we have the most reliable, temporally consistent data.

1. First, a hierarchical Bayesian model was used to study the effects of local and regional weather variables on monarch observations at focal sites across the summer breeding grounds ("local" weather for these models refers to PRISM data from the focal sites, while "regional" refers to MEI, as described above). This model included year as a predictor variable, and thus produced estimates of change in monarch observations across the breeding sites through time. As a complementary analysis, individual count data (available for a subset of years and sites) were used to ask if any changes across years have been localized to particular times of the year (more details below).

2. Next, a path analysis was used to place effects of weather and year effects (change over time in monarch observations) into a context that allows for the direct quantification of shifting climatic conditions on butterfly observations.

3. The approach in the first step (a hierarchical Bayesian model) was repeated, but investigated the effects of climate at the Pacific overwintering sites on monarch observations across the summer breeding grounds (in other words, investigating potential connections between conditions experienced during overwintering and observations made the following flight season).

4. Finally, simple correlations were used to investigate associations between all monarch datasets: our focal sites (observations during the breeding season), western overwintering sites, eastern regions, and Mexican overwintering sites. Because this step involved a large number of comparisons, we focus primarily on overall patterns rather than significance testing of individual correlations.

Hierarchical models

The impact of weather variables on monarch day positives was explored using a hierarchical Bayesian modeling approach. This analytical method is described in detail elsewhere (see Nice et al. 2014; Harrison et al. 2015). Briefly, the model estimates posterior probability distributions (PPDs) for partial regression coefficients associated with model terms at multiple hierarchical levels, in this case site and transect wide. Information from each site is used to inform transect-wide estimates and vice versa. A binomial response consisting of day positives and number of visits for a given year (i.e., the proportion of positive visits in a year) and site was modeled, thus accounting for variation in sampling effort among years. Model terms included site-specific seasonal average temperatures and total precipitation (summed over season) and our indices of MEI (as described above). Year was included in the model to quantify inter-annual population trends not directly associated with fluctuating climatic conditions. All predictor variables were converted to standardized z-scores prior to modeling. PPDs for each model term were estimated using the JAGS sampler [version 3.4.0 (Plummer 2013)], a Markov chain Monte Carlo (MCMC) algorithm, implemented in R (R Core Team 2014) using the rjags package [version 3-15 (Plummer 2015)]. The model was run using two search chains and uninformative priors and hyperpriors for 500,000 iterations of the sampling algorithm. To gauge model performance, effective sample sizes (ESS) were calculated for each parameter estimate, and trace plots of estimates against iterations were examined to evaluate mixing.

As described above, this modeling approach was used for different sets of weather variables (Fig. 1c). First, regional and local (associated with each focal site) weather

variables (MEI 1, MEI 2, temperature, and precipitation) were used to predict monarch observations at the focal sites across the breeding grounds. Second, the impact of overwintering weather conditions on subsequent-year observations was examined across the breeding grounds. Because of the large number of overwintering weather variables and the large number of relationships (associated with eight overwintering counties potentially affecting observations at ten breeding sites), two analyses were run with overwintering weather variables: first with all of the overwintering temperature data, and second with all of the overwintering precipitation data (analyses were also run with all weather data combined, which did not qualitatively alter results but did broaden credible intervals and lower precision as a result of reduced power). Year was included as a covariate in all models.

Climatic trends and path analyses

The analyses described in the previous section addressed the impact of climatic variables (local, regional and at the overwintering sites) on monarch observations at the focal breeding ground sites. To explicitly examine the impact of climate change on monarch day positives, a path analysis was used to compare the direct effect of year on monarchs with the indirect effect of year as mediated by weather. The path analysis was built using a suite of hierarchical Bayesian regression models that together characterized the path models. Specifically, we separately modeled the effect of year on each endogenous climate variable (assuming a normally distributed response variable, as opposed to the binomially distributed response variable described above). Path coefficient estimates describing the effect of climate variables on day positives were taken from the hierarchical multiple regression model described above which included all climate variables as predictors. PPDs of all models were characterized using two search chains each of 25,000 MCMC iterations. The mean and 95 % credible intervals from these distributions were used to characterize associated path coefficients. Indirect effects of year as mediated by a given climate variable were calculated by taking the product of the appropriate path coefficients. In order to incorporate uncertainty from parameter estimates, those products were generated from 50,000 samples from each of the PPDs for the two path coefficients involved in each comparison (means and 95 % credible intervals were then retained from the distribution of products).

Localization of temporal trends within years

The analyses described above included year as a predictor variable and thus estimated changes in monarch observations across the decades encompassed by our study. It is also of interest to ask if any demographic trends over the years were focused on any particular time during the breeding season, which could be informative with respect to causes of population trends (e.g., associated with the overwintering generation or with late-season immigrants from more distant breeding areas). To address this, counts of individuals were utilized from five of our focal sites (where such data are available), for 1999 to 2013, in a sliding window regression analysis. Specifically, counts of monarchs were calculated from 50-day windows organized by ordinal dates, counting from the first of the year. For each of those windows, the total count was regressed against years and the beta coefficient (slope of count vs. years) was saved and examined for intra-annual patterns in inter-annual trends.

Comparisons between western and eastern populations

To examine the relationship between eastern and western monarch populations, Spearman's rank correlation coefficients were calculated using data from 1997 to 2014 for eastern monarchs obtained from NABA through Monarch Net, overwintering data for eastern (at Mexican sites) and western monarchs (at California sites) obtained through the Xerces society, and day positives per year for each of our transect locations. Eastern regional count data were only available from 1997 onwards, therefore only those California overwintering locations with high abundances and complete records since 1997 were used for this analysis. California overwintering data were obtained from counts conducted in six counties spanning the mid to southern coast of California (Fig. 1). As with hierarchical Bayesian models, these analyses were performed using R (version 3.1.2, R Core Team 2014).

Results

Annual trends, climatic impacts, and the effect of a changing climate

The hierarchical Bayesian approach successfully characterized PPDs for partial regression coefficients for all models in which weather variables and year predicted monarch observations (day positives). Visual inspection of trace plots confirmed adequate mixing of model chains. ESS necessarily varied between parameter estimates, but were always greater than 1000. A decline in monarch observations is evident in both raw day positives (Fig. 2a), and in the year coefficient estimated across sites from the hierarchical model (Fig. 2b). The point estimate for the year coefficient as a log odds ratio across all sites was −0.6 (Fig. 2a). The exponential transformation of that coefficient (from log odds ratio to odds ratio) is 0.55, which means
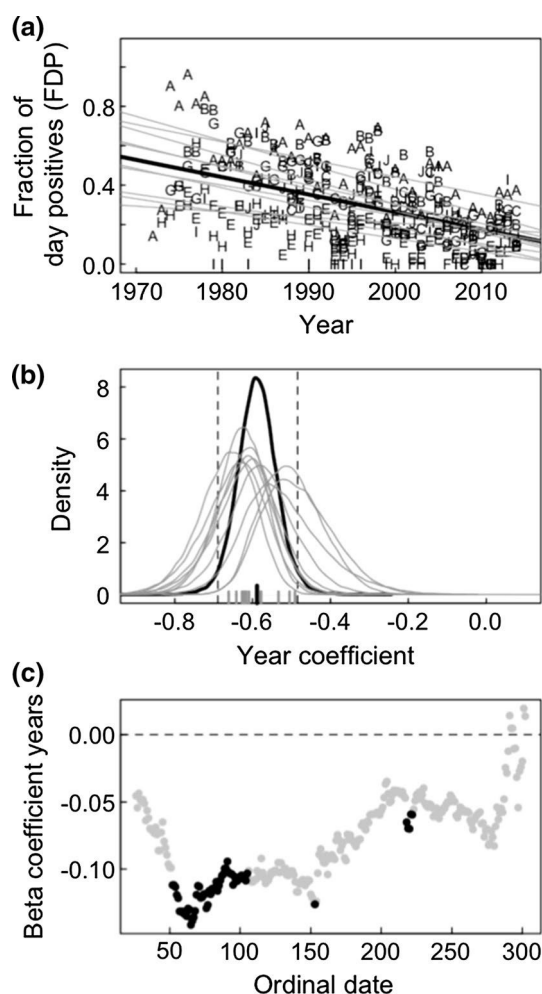
Fig. 2 **a** Temporal trends of monarch fractional day positives (*FDP*s) from 1972 to 2014. These values (*y*-axis) correspond to the fraction of days during the year in which a monarch adult was seen (out of the total number of visits in that year) at the focal sites. *Letters* (labeling the observations for each site) correspond to the site labels, as in Fig. 1. *Fitted lines* from simple linear regressions are shown for visualization (for each site separately as *gray lines*, and for all of the sites as the *darker line*). **b** Posterior probability distributions (PPDs) for the coefficient associated with year from a hierarchical Bayesian model predicting monarch observations across the ten focal sites. PPDs are shown in *light gray* for each site, and across sites in *black*; similarly, *tick marks* at the bottom of the graph show the mean estimate for each curve. *Dashed lines* indicate 95 % credible intervals for the PPD across sites. **c** Beta coefficients from moving window analysis of monarch abundance at five summer breeding sites where data on counts of individuals were available: *each point* indicates the relationship between abundance and year for monarch counts in 50-day windows (the *x*-axis is the midpoint of those windows in days from the start of the year). *Increasingly negative values* indicate more severe declines, with regressions significant at *P* < 0.05 shown in *black*. *Dotted horizontal line* at zero shown for reference

399   that the odds ratio of observing a monarch has decreased by
400   that factor (0.55) for every year. A decline can also be seen
401   in plots of adult counts from our focal sites for the subset
402   of recent years in which counts are available (ESM 1). The

403 declining observations of monarchs are not spread equally
404 across the breeding season, but appear to be localized ear-
405 lier in the season (Fig. 2c). It is important to note that local
406 breeding at the low-elevation sites (Fig. 1c, sites A–E) has
407 not been observed before May (A. M. S., personal observa-
408 tion), and in some years local breeding never happens. Thus
409 the reduced early spring numbers (Fig. 2c) likely involve a
410 reduction in immigration from coastal overwintering sites.
411 Reduced numbers of individuals observed at a particu-
412 lar time of the year could also be a result of phenological
413 shifts, but monarchs at the five low-elevation sites have not
414 been appearing earlier or later in the spring ($F_{1,13} = 0.06$;
415 $P = 0.81$) nor has phenology shifted at the end of the sea-
416 son ($F_{1,13} = 0.41$; $P = 0.53$).

417   Warmer temperatures in winter and spring (Fig. 3; for
418 results from all weather variables, see Table 1 and ESM **AQ2**
419 2–4) were positively and consistently associated with mon-
420 arch sightings at our ten focal sites. The standardized beta
421 coefficients for winter and spring temperatures estimated
422 across all breeding sites were 0.23 and 0.26, respectively.
423 Spring precipitation had a positive effect across sites, while
424 summer precipitation had a more heterogeneous effect
425 across sites (Fig. 3). The impact of overwintering condi-
426 tions on monarch observations at our focal sites the follow-
427 ing summer was also examined; complex and site-specific
428 relationships were revealed (ESM 5). In particular, both
429 temperature and precipitation have strong and significant
430 effects at a subset of the overwintering sites, but the direc-
431 tion of the effect (from positive to negative) varies (ESM
432 5). A path analysis allowed us to address the potential influ-
433 ence of climate change on monarch populations through
434 the examination of the indirect effect of year as mediated
435 by a given weather variable. The direct effect of year was
436 much greater than the indirect effect of year as mediated by
437 any one weather variable (Fig. 4).

Relationship between eastern and western monarch populations
438
439

440 In the west, overwintering population size and day positives
441 at the transect sites (in the subsequent year) were positively
442 correlated (Fig. 5). Monarch overwintering counts and day
443 positives along the transect were all negatively correlated
444 with year, consistent with the declining annual trend reported
445 from analyses above. Inspection of abundance data from the
446 western overwintering sites (ESM 6) confirms the downward
447 trajectories during the years studied. In contrast, observa-
448 tions of eastern breeding locations tended to be weakly or
449 positively related to year, although a decline is evident at the
450 Mexican overwintering grounds (negatively associated with
451 year). Eastern and western populations show no significant
452 correlations (neither positive or negative; all *P*-values were
453 > 0.05), with one anomalous exception (Gates Canyon and

Fig. 3 PPDs for a subset of weather variables predicting monarch observations from hierarchical Bayesian models [for results from all weather variables, see Table 1 and Electronic Supplementary Material (ESM) 2–4]. PPDs are shown in *light gray* for each site, and across sites in *black*; similarly, *tick marks* at the bottom of the graph show the mean estimate for each curve. *Insets* The probability that each site has a non-zero (either positive or negative) coefficient is shown (calculated as the proportion of the corresponding PPD greater than or less than zero). The *bars* indicating probability are labeled by site (*A–J*; see Fig. 1), and for the whole model. *Bars* above the *horizontal line* (at zero) are for coefficients with mean positive values, while *bars* below the *horizontal line* are for negative coefficients (the *top three panels* are dominated by positive coefficients, while the *bottom panel* includes a mix of positive and negative coefficients)

Winter temperature

Spring temperature

Spring precipitation

Summer precipitation
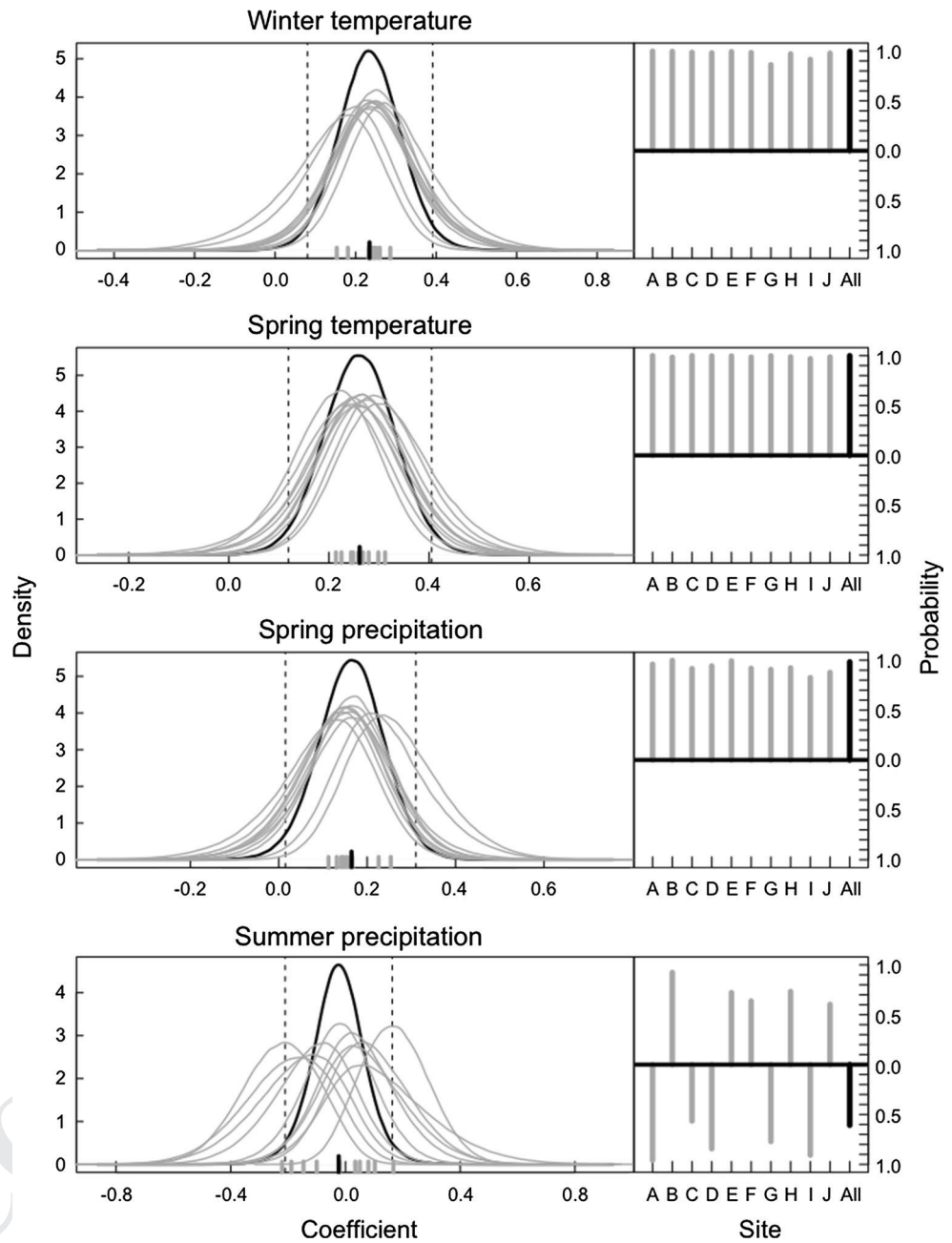
the mid-central eastern region), suggesting in general that an abundant year for one region is not necessarily an abundant year for the other (Fig. 5); for further details, see ESM 7 for a comparison of distributions of correlation coefficients within and among geographic regions.

Discussion

Monarch butterflies have received a great deal of attention as one of the most conspicuous migratory species in North America, but most research has focused on the larger, eastern migration. In this study, we found that the western migration of *Danaus plexippus* shows evidence of decline which is apparent in raw day positive data (Fig. 2a), abundance data from our focal sites (ESM 1), and abundance data from the Pacific coast overwintering sites (ESM 6). Moreover, the declines at the western breeding sites are concentrated early in the season, while abundances of adults have not been as reduced closer to the end of the breeding season (Fig. 2c). When considering this pattern in light of the associated decline in overwintering population size, it suggests that mortality could be increasing either during or immediately after overwintering. Alternatively,

Table 1 Standardized regression coefficients from hierarchical Bayesian models relating temperature, precipitation, and multivariate El Niño Southern Oscillation index (*MEI*) values (El Niño Southern Oscillation index indices) to monarch observations at the ten focal sites (coefficients are in log-linear units from binomial regressions)

	Temperature				Precipitation				MEI	
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	1	2
Suisun Marsh	0.26[a]	0.21[a]	−0.08	0.04	−0.14	0.26[a]	0.17	0.05	0.32	0.0029
Gates Canyon	0.30[a]	0.30[a]	−0.01	0.09	−0.05	0.17	−0.23	0.03	0.36	−0.052
West Sacramento	0.25[a]	0.32[a]	−0.01	0.09	−0.06	0.14	−0.02	0.12	0.37	−0.017
North Sacramento	0.24[a]	0.27[a]	−0.08	0.11	−0.05	0.16	−0.16	0.14	0.28	0.11
Rancho Cordova	0.27[a]	0.27[a]	−0.01	0.12	−0.03	0.23[a]	0.09	0.06	0.35	−0.034
Washington	0.25[a]	0.25[a]	−0.09	0.11	−0.07	0.15	0.06	0.06	0.33	0.0041
Lang Crossing	0.14	0.28[a]	−0.05	0.13†	−0.08	0.14	−0.11	0.07	0.37	0.023
Donner Pass	0.17	0.22	0.06	0.07	−0.09	0.1	−0.2	0.05	0.34	−0.17
Castle Peak	0.24	0.26[a]	0.05	0.12	−0.08	0.16	0.12	0.07	0.35	−0.027
Sierra Valley	0.23[a]	0.24[a]	0.05	0.06	−0.05	0.12	0.04	0.05	0.32	−0.13
Across sites[b]	0.23[a]	0.26[a]	−0.02	0.09	−0.07	0.16[a]	−0.02	0.07	0.34	−0.028

Numbers correspond to posterior probability distributions visualized in Fig. 3, and Electronic Supplementary Material (ESM) 2–4

[a] Coefficients with 95 % credible intervals that do not overlap zero

[b] Coefficients estimated across all sites

perhaps fewer butterflies are able to successfully migrate in the fall from their summer breeding grounds back to their overwintering colonies. Regardless, subsequent generations during the summer are able to at least partially rebound.

The climatic models we developed successfully predicted monarch observations. Warmer springs and winters, for example, have pronounced and positive effects on the frequency of monarch observations during the summer flight (Fig. 3). These effects of weather could be the result of positive associations with overwinter survival and reproduction of the first summer generation, although it is important to remember that these effects are of much smaller magnitude compared to the direct, negative association with years (Fig. 4). The positive effects of temperature could also be mediated through increased nectar and host plant growth, although we can only pose these possibilities as hypotheses at this time. The positive effect of precipitation is consistent with previous climatic modeling for the western monarch that suggested water as a limiting factor (Stevens and Frey 2010).

Although our analyses revealed effects of weather on monarch observations, it is clear that shifting climatic conditions are not the major factor in the observed linear population declines. This result can be seen both in the lack of directional change in most weather variables studied, and in the very small indirect effects of year as mediated through weather (Fig. 4). Summer temperatures are an exception as they are rising across our focal sites, but they do not appear to have an effect on monarch observations (Fig. 4; ESM 3).

The large, negative, direct effect of year suggests other (non-climatic) drivers of decline. In studies on eastern monarchs, it has been posited that dwindling host plant populations (Flockhart et al. 2015; Pleasants and Oberhauser 2012; Zalucki and Lammers 2010; Brower et al. 2006), the use of insecticides (Krischik et al. 2015; Pecenka and Lundgren 2015), and overwintering habitat destruction (Vidal and Rendon-Salinas 2014; Saenz-Romero et al. 2012; Brower et al. 2002) are primary drivers of decline. To our knowledge, a decline in milkweed abundance has not been reported within the range of the western monarch. The intra-annual pattern of declines (Fig. 2c) is relevant to this issue, as it suggests a reduced number of early spring immigrants over the years. If host plants throughout the breeding season were limiting, we might expect declines to be spread more evenly throughout the year or even concentrated towards the end of the season. Given the likely link between overwintering declines (ESM 6) and reduced immigration to the breeding grounds, habitat loss along the California coast is potentially important (Jepsen and Black 2015), and we can suggest that overwintering sites would be the logical next step for focused investigation. The need to better understand overwintering sites is also highlighted by the heterogeneous weather effects that we observed along the California coast, potentially mediated by variation in habitat and micro-climate. In general, a large number of butterflies are known to be declining in Northern California (Forister et al. 2010, 2011), for which causes are likely multifarious, though a combined effect of land use change and warming conditions has been implicated for many species (Casner et al. 2014). Finally, we compared population dynamics among western summer grounds, western overwintering sites, and the eastern migration, both breeding and overwintering sites (Fig. 5). The lack of correlation between western and eastern observations is consistent with previous studies (Frey and Schaffer 2004;
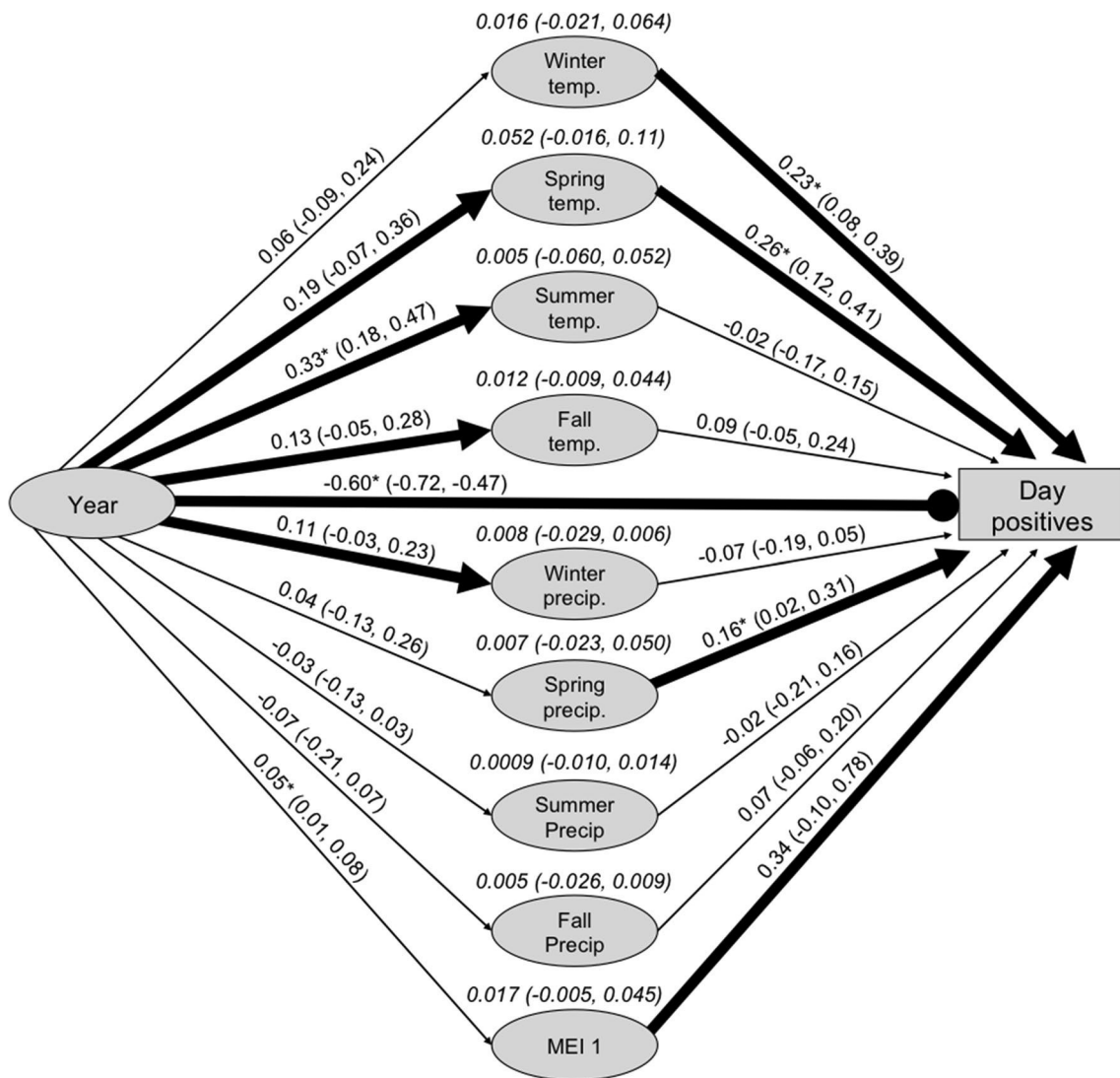
Fig. 4 Path diagram illustrating direct and indirect effects of year and weather variables on monarch sightings (day positives), as well as effects of year on weather variables. *Values next to each path* are means from Bayesian PPDs, and 95 % credible intervals (from the same analyses reported in Fig. 3: ESM 2–4). Indirect effects of year on day positives mediated through weather variables were all small in comparison to direct coefficients, and are shown as *italicized gray font* above the names of the weather coefficients. *Asterisks* indicate coefficients whose 95 % credible intervals do not overlap zero. Lines representing negative relationships end in *circles*. For abbreviations, see Figs. 2 and 3

Stevens and Frey 2010) and suggests that the two popula- tions are fluctuating independently.

In conclusion, we have successfully modeled effects of weather on monarch observations along an elevational transect encompassing a portion of the summer breeding ground of the western subpopulation of the monarch butter- fly. Although we were able to detect climatic effects, there is clearly more to be learned with respect to biotic-abiotic interactions playing out across the geographic extent of the range of the western monarch. This is particularly appar- ent in the variety of weather effects observed at the coastal overwintering grounds. In contrast to the complexity of weather, a negative, annual trend in monarch observa- tions was readily detected across all of the focal sites. The annual trend is not explained by shifting climatic condi- tions, which have been implicated in the declines of other butterflies in the region (Casner et al. 2014). Furthermore, the decline in observations is correlated with decreasing numbers at the overwintering sites that we studied along the Pacific coast.

An important caveat to these results is the fact that we have focused our analyses on observations of adults during the breeding season from ten sites that encompass a broad elevational transect, but a narrow portion of the breeding

Fig. 5 Correlations among our focal sites ("Transect sites" across the western breeding grounds), western overwintering sites averaged by county, summer observations from the eastern region, and areal extent of Mexican overwintering grounds (for all sets of data, years covered were 1997–2014). *Colors* indicate the magnitude of Spearman's rank correlation coefficients, and year was included (at the bottom of the figure) for quantification of temporal trends. Rank correlations were used because of the heterogeneous nature of the data (including fractional day positives for our focal sites, counts from the overwintering sites, and population indices from the eastern sites). *Black boxes* outline western transect sites vs. western overwintering sites (*upper left*), and western transect sites vs. eastern summer sites (*lower right*). To compare patterns among regions, histograms of correlations can be found in ESM 7
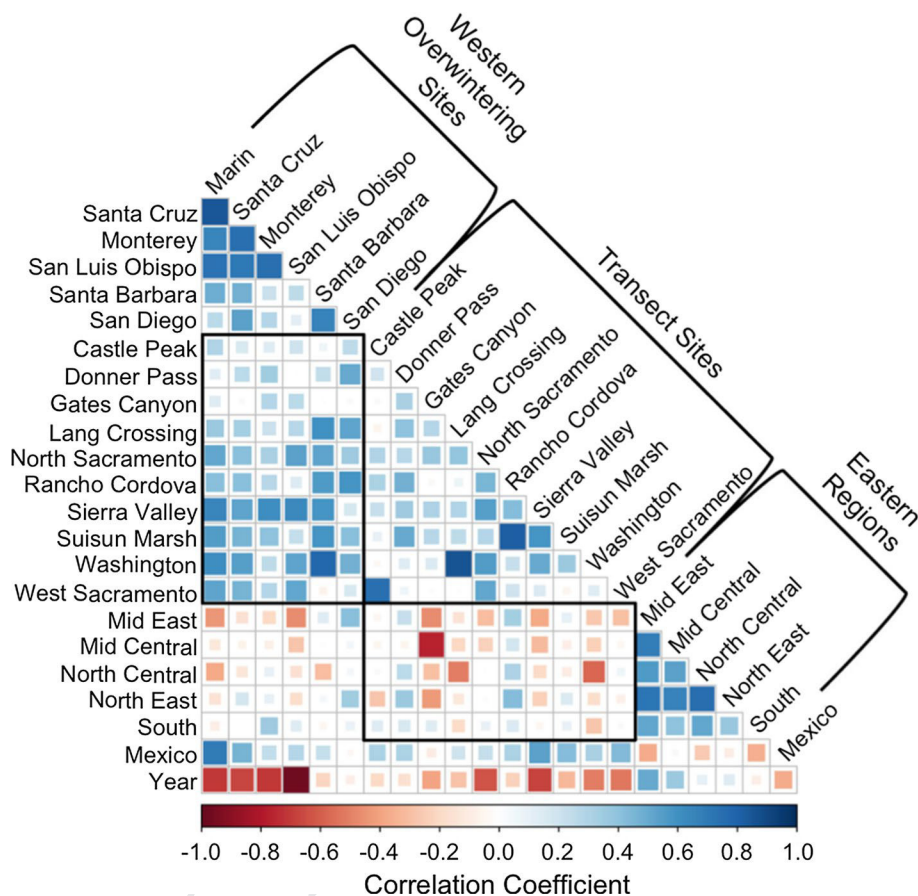
grounds. It is possible that the declines we have observed are the consequence of a shift in migration behavior rather than a demographic effect, although we have no particular reason (anecdotal or otherwise) to expect such a geographic shift, especially since our ten sites are not marginal to the breeding range. Indeed, analyses by Stevens and Frey (2010) place our transect within the geographical region best suited for monarch breeding, as determined by both thermal conditions, and host plant availability. The correlations observed between our focal sites and the western overwintering sites (Fig. 5) also suggest general declines rather than any localized shift in migration patterns. Finally, it is interesting to note that dynamics of the sites that we have studied (both the summer sites and overwintering sites) appear to be uncorrelated with dynamics in the eastern subpopulation. Thus, even though genetic differentiation between the western and eastern subpopulations has not been detected, from a conservation and management perspective they should be considered different entities.

Author contribution statement A. E. E. and M. L. F. conceived the idea. A. M. S. collected the data. C. C. N., A. E. E., J. G. H., M. L. F., and J. A. F. developed the statistical models; J. H. T. and D. P. W. managed and archived the data; A. E. E., J. G. H., and M. L. F. wrote the manuscript, while A. M. S., C. C. N., J. H. T., D. P. W., and J. A. F. reviewed the manuscript before submission.

AQ3

Compliance with ethical standards

References

AQ4

Batalden RV, Oberhauser K, Peterson AT (2007) Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: Danaidae): the ecology of migration and likely climate change implications. Environ Entomol 36:1365–1373

Brindza LJ, Brower LP, Davis AK, Van Hook T (2008) Comparative success of monarch butterfly migration to overwintering sites in

Journal : **Large 442**	Dispatch : **17-3-2016**	Pages : **12**
Article No : **3600**	☐ LE	☐ TYPESET
MS Code : **OECO-D-15-00964**	☑ CP	☑ DISK

Mexico from inland and coastal sites in Virginia. J Lepid Soc 62:189–200

Brower LP (1995) Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. J Lepid Soc 49:304–385

Brower AVZ, Boyce TM (1991) Mitochondrial-DNA variation in monarch butterflies. Evolution 45:1281–1286

Brower LP, Malcolm SB (1991) Animal migrations—endangered phenomena. Am Zool 31:265–276

Brower LP, Castilleja G, Peralta A, Lopez-Garcia J, Bojorquez-Tapia L, Diaz S, Melgarejo D, Missrie M (2002) Quantitative changes in forest quality in a principal overwintering area of the monarch butterfly in Mexico, 1971–1999. Conserv Biol 16:346–359

Brower LP, Fink LS, Walford P (2006) Fueling the fall migration of the monarch butterfly. Integr Comp Biol 46:1123–1142

Brower LP, Taylor OR, Williams EH, Slayback DA, Zubieta RR, Ramirez MI (2012) Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? Insect Conserv Diversity 5:95–100

Casner KL, Forister ML, O'Brien JM, Thorne J, Waetjen D, Shapiro AM (2014) Contribution of urban expansion and a changing climate to decline of a butterfly fauna. Conserv Biol 28:773–782

Chave J (2013) The problem of pattern and scale in ecology: what have we learned in 20 years? Ecol Lett 16:4–16

Congdon P (2014) Applied Bayesian modeling, vol. 595. Wiley

Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int J Climatol 28:2031–2064

Davis AK (2012) Are migratory monarchs really declining in eastern North America? Examining evidence from two fall census programs. Insect Conserv Divers 5:101–105

Davis, AK, Dyer LA (2015) Long-term trends in eastern North American monarch butterflies: a collection of studies focusing on spring, summer, and fall dynamics. Ann Entomol Soc Am 1–3

Dingle H, Zalucki MP, Rochester WA, Armijo-Prewitt T (2005) Distribution of the monarch butterfly, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), in western North America. Biol J Linn Soc Lond 85:491–500

Flockhart DTT, Pichancourt J-B, Norris DR, Martin TG (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

Forister ML, McCall AC, Sanders NJ, Fordyce JA, Thorne JH, O'Brien J, Waetjen DP, Shapiro AM (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. Proc Natl Acad Sci USA 107:2088–2092

Forister ML, Jahner JP, Casner KL, Wilson JS, Shapiro AM (2011) The race is not to the swift: long-term data reveal pervasive declines in California's low-elevation butterfly fauna. Ecology 92:2222–2235

Frey DF, Schaffer A (2004) Spatial and temporal patterns of monarch overwintering abundance in Western North America. Monarch butterfly biology and conservation. Cornell University Press, Ithaca, NY, pp 167–176

Harrison JG, Shapiro AM, Espeset AE, Nice CC, Jahner JP, Forister ML (2015) Species with more volatile population dynamics are differentially impacted by weather. Biol Lett 11:5

Hartzler RG (2010) Reduction in common milkweed (*Asclepias syriaca*) occurrence in Iowa cropland from 1999 to 2009. Crop Prot 29:1542–1544

Jepsen S, Black SH (2015) Understanding and conserving the Western North American monarch population. In: Oberhauser KR, Altizer NS (eds) Monarchs in a changing world. Biology and conservation of an iconic butterfly, chapter 11. Cornell University Press, Ithaca

Koenig WD (2006a) Spatial synchrony of monarch butterflies. Am Midl Nat 155:39–49

Krischik V, Rogers M, Gupta G, Varshney A (2015) Soil-applied imidacloprid translocates to ornamental flowers and reduces survival of adult *Coleomegilla maculata*, *Harmonia axyridis*, and *Hippodamia convergens* lady beetles, and larval *Danaus plexippus* and *Vanessa cardui* butterflies. PLoS One 10:22

Lyons JI, Pierce AA, Barribeau SM, Sternberg ED, Mongue AJ, de Roode JC (2012) Lack of genetic differentiation between monarch butterflies with divergent migration destinations. Mol Ecol 21:3433–3444

Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biol 18:1239–1252

McGill BJ (2010) Matters of scale. Science 328:575–576

Monarch Net (2015) Monarch abundance data. http://monarchnet.uga.edu/

Morisette JT, Richardson AD, Knapp AK, Fisher JI, Graham EA, Abatzoglou J, Wilson BE, Breshears DD, Henebry GM, Hanes JM, Liang L (2008) Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. Front Ecol Environ 7:253–260

Morris GM, Kline C, Morris SM (2015) Status of *Danaus plexippus* population in Arizona. J Lepid Soc 69:91–107

Nice CC, Forister ML, Gompert Z, Fordyce JA, Shapiro AM (2014) A hierarchical perspective on the diversity of butterfly. Species' responses to weather in the Sierra Nevada Mountains. Ecology 95:2155–2168

North American Butterfly Association (NABA) (2015) NABA butterfly counts from 1990 to 2009

Oberhauser K, Peterson AT (2003) Modeling current and future potential wintering distributions of eastern North American monarch butterflies. Proc Natl Acad Sci USA 100:14063–14068

Oberhauser KS, Nail KR, Altizer SM (2015) Monarchs in a changing world: biology and conservation of an iconic butterfly. Comstock, Ithaca

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Pecenka JR, Lundgren JG (2015) Non-target effects of clothianidin on monarch butterflies. Nat Sci 102:19

Pleasants JM, Oberhauser KS (2012) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. Insect Conserv Divers 6:135–144

Plummer M (2013) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Version 3:4

Plummer M (2015) Package rjags. Version 3-15

Pollard E (1977) Method for assessing changes in abundance of butterflies. Biol Conserv 12:115–134

Ponciano JM, Taper ML, Dennis B, Lele SR (2009) Hierarchical models in ecology: confidence intervals, hypothesis testing, and model selection using data cloning. Ecology 90:356–362

PRISM Climate Group (2015) Weather data. Oregon State University. http://prism.oregonstate.edu/

Ries L, Taron DJ, Rendón-Salinas E (2015) The disconnect between summer and winter monarch trends for the Eastern migratory population: possible links to differing drivers. Ann Entomol Soc Am 1–9

Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, Boston

R Core Team (2014) R: a language and environment for statistical computing. Version 3.1.2. R Foundation for Statistical computing, Vienna

Saenz-Romero C, Rehfeldt GE, Duval P, Lindig-Cisneros RA (2012) Abies religiosa habitat prediction in climatic change scenarios

and implications for monarch butterfly conservation in Mexico. For Ecol Manage 275:98–106

Schonher T, Nicholson SE (1989) The relationship between California rainfall and ENSO events. J Clim 2:1258–1269

Shapiro AM (2014) Species presence by site. Art Shapiro's butterfly site. http://butterfly.ucdavis.edu/

Stevens SR, Frey DF (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

The Xerces Society (2015)Western Monarch Thanksgiving Count from 1997 to 2014. http://www.xerces.org/wp-content/uploads/2011/04/WMTC-Data-1997-2014.pdf

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Urquhart FA, Urquhart NR (1977) Overwintering areas and migratory routes of monarch butterfly (*Danaus plexippus*, Lepidoptera Danaidae) in North America, with special reference to western population. Can Entomol 109:1583–1589

Vidal O, Rendon-Salinas E (2014) Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico. Biol Conserv 180:165–175

Weiss SB, Rich PM, Murphy DD, Calvert WH, Ehrlich PR (1991) Forest canopy structure at overwintering monarch butterfly sites: measurements with hemispherical photography. Conserv Biol 5:165–175

Wolter K, Timlin MS (1993) Monitoring ENSO in COADS with a seasonally adjusted principal component index. Proceedings of the 17th Climate Diagnostic,Norman, OK. pp 52–57

Wu Z, Dijkstra P, Koch GW, Penuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biol 17:927–942

Zalucki MP, Lammers JH (2010) Dispersal and egg shortfall in monarch butterflies: what happens when the matrix is cleaned up? Ecol Entomol 35:84–91

Zalucki MP, Brower LP, Malcolm SB, Slager BH (2015) Estimating the climate signal in monarch population decline. In: Oberhauser KR, Altizer NS (eds)Monarchs in a changing world. Biology and conservation of an iconic butterfly, chapter 11. Cornell University Press, Ithaca

Zhan S, Zhang W, Niitepold K, Hsu J, Haeger JF, Zalucki MP, Altizer S, de Roode JC, Reppert SM, Kronforst MR (2014) The genetics of monarch butterfly migration and warning colouration. Nature 514:317–321

Zipkin EF, Ries L, Reeves R, Regetz J, Oberhauser KS (2012) Tracking climate impacts on the migratory monarch butterfly. Global Change Biol 18:3039–3049

Springer

the language of science

Author Query Form

Please ensure you fill out your response to the queries raised below and return this form along with your corrections

Dear Author

During the process of typesetting your article, the following queries have arisen. Please check your typeset proof carefully against the queries listed below and mark the necessary changes either directly on the proof/online grid or in the 'Author's response' area provided below

Query	Details Required	Author's Response
AQ1	PRISM Climate Group 2013 has been changed to PRISM Climate Group 2015 so that this citation matches the list.	
AQ2	Please provide a definition for the significance of dagger symbol (†) in Table 1.	
AQ3	Koenig 2006b has been deleted as it is identical to Koenig 2006a.	
AQ4	The following references have not been cited: Brower and Boyce (1991), Pecenka and Lundgren (2015). Please cite these references or delete them from the list.	